La fatigue mentale : marqueurs électrophysiologiques et stratégies de compensation

Thomas Jacquet

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Par

Thomas JACQUET

La fatigue mentale : marqueurs électrophysiologiques et stratégies de compensation

Thèse présentée et soutenue à Dijon, le 11 Mars 2021

Composition du Jury :

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Ce travail a été présenté à plusieurs reprises dans le cadre de l'Experimentarium. Ce programme, proposé par l'Université de Bourgogne, permet de présenter ses travaux au grand public sous forme d'ateliers et de conférences.

MIEUX COMPRENDRE LE LIEN ENTRE FATIGUE MENTALE ET PERFORMANCES PHYSIQUES

→ SCIENCES DU SPORT

THOMAS JACQUET est jeune chercheur au laboratoire LEAD-CNRS* à Dijon. Son équipe s'intéresse à la fatigue mentale, sensation qui apparaît après avoir fait un effort mental prolongé. Il a été montré que la fatigue mentale pouvait avoir de nombreuses conséquences, comme une diminution de certaines performances physiques par exemple. Thomas cherche aujourd'hui à mieux identifier les interactions qu'il peut y avoir entre fatigue mentale et performance. En comprenant quels sont les mécanismes responsables de l'état de fatigue mentale, il pourra proposer des stratégies de compensation.

*Laboratoire d'Etudes de l'Apprentissage et du Développement, Centre National de la Recherche Scientifique

« *Lorsque j'ai commencé mes études, j'étais loin de m'imaginer que je ferai de la recherche un jour. C'est un milieu passionnant où la routine n'existe pas et dans lequel il y a toujours de nouvelles choses à tester, à expérimenter et à découvrir.* »

Thomas Jacquet

La fatigue est une sensation que chacun ressent au quotidien. Il existe deux types de fatigue : la fatigue physique, que l'on éprouve après une activité sportive, et la fatigue mentale que l'on ressent quand on doit se concentrer de façon intense et prolongée, après plusieurs heures sur ordinateur par exemple. Cette fatigue mentale peut entraîner de nombreux problèmes : accidents de la route, dépressions, baisse de productivité... Des chercheurs ont également montré que la fatigue mentale peut avoir des conséquences négatives sur les performances physiques. Par exemple, une personne étant en état de fatigue mentale courra moins vite et/ou moins longtemps lors d'un footing.

Thomas veut comprendre pourquoi et comment les performances physiques sont altérées en présence de fatigue mentale. Quelles sont les zones du cerveau impliquées ? Est-il possible de trouver des stratégies pour compenser cette fatigue mentale ?

Pour en savoir plus, Thomas recrute des personnes volontaires pour les faire participer à des expériences en deux étapes. Dans un premier temps, il leur fait faire des exercices sur ordinateur afin de les fatiguer mentalement. Après cela, il leur propose de réaliser différents exercices physiques. Pendant les deux étapes de ces expériences, il observe ce qui se passe au niveau de leur cerveau en enregistrant l'activité électrique de ce dernier grâce une technique appelée « électroencéphalographie ».

Une fois que Thomas aura identifié les zones du cerveau impliquées dans la fatigue mentale et la performance physique, il testera plusieurs stratégies pour tenter de réduire la fatigue mentale, comme écouter de la musique agréable par exemple.

LES OBJECTIFS

- Comprendre l'interaction entre fatigue mentale et fatigue physique
- Savoir ce qui se passe au niveau de notre cerveau lorsque l'on est mentalement fatigué
- Trouver des stratégies de compensation pour limiter les effets de la fatigue mentale

L'EXPÉ www.experimentarium.fr

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LISTE DES ABBREVIATIONS

AX-CPT : AX – *Continuous Performance Test*

BRUMS : *Brunel Mood Scale*

CCA : Cortex Cingulaire Antérieur

ECG : Électrocardiogramme

EEG : Électroencéphalographie

EMG : Électromyographie

VAS : Échelle Visuelle Analogique

IRMf : Imagerie fonctionnelle par Résonance Magnétique

NASA-TLX : *National Aeronautics and Space Administration – Task Load Index*

POMS : *Profile Of Mood States*

PVT : Tâche de Vigilance Psychomotrice

RPE : *Rate of Perceived Exertion* (Niveau de l'effort perçu)

TLDB : *Time Load Dual Back*

VFC : Variabilité de la Fréquence Cardiaque

I. INTRODUCTION GENERALE

Éprouver une sensation de manque d'énergie, avoir du mal à se concentrer, observer une diminution de son attention, de sa motivation ou encore être particulièrement irritable, tout le monde a déjà ressenti ces sensations, que ce soit après une journée de travail intense ou bien une journée d'école. Ces symptômes sont typiques de la fatigue. La fatigue est omniprésente dans notre société et impacte de façon non-négligeable les activités de notre vie quotidienne. Toutefois, sa prévalence reste difficile à estimer. En effet, il n'est pas toujours facile de détecter et d'identifier les signes de la fatigue, tant ils sont communs et courants. Une étude, menée sur plus de 28000 travailleurs américains âgés de 18 à 65 ans, démontre que la fatigue toucherait environ 37,9 % des employés (Ricci et al., 2007). Dans cette même étude, il a également été montré que cette fatigue pouvait amener à de nombreuses conséquences néfastes comme une baisse de la productivité, une augmentation du risque de dépression ou encore une augmentation des absences (Ricci et al., 2007). De plus, il a été montré que la fatigue était la principale cause d'accident du travail (McCormick et al., 2012).

La fatigue ne se retrouve pas seulement chez la population normale et dans la sphère professionnelle, on la retrouve également comme facteur associé dans de nombreuses pathologies. Ainsi, la sensation de fatigue est un symptôme rapporté chez les patients souffrant de fatigue chronique (Capuron et al., 2006; Walford et al., 1993), de sclérose en plaque, ayant fait un accident vasculaire cérébral (Colle et al., 2006; Duncan et al., 2012; Ingles et al., 1999), subit un traumatisme crânien (Belmont et al., 2006; Cantor et al., 2013; Ponsford et al., 1995) ou encore chez des personnes atteintes de la maladie de Parkinson (Friedman & Friedman, 1993; Friedman et al., 2007; Stocchi et al., 2014). Cependant, cette liste est loin d'être exhaustive, et la fatigue semble également présente ou à l'origine d'autres pathologies comme, la maladie de Lyme (Shadick et al., 1994), le cancer (Chang et al., 2000) ou la dépression (Fuhrer & Wessely, 1995).

Dans le contexte actuel lié à la pandémie de la COVID-19, la fatigue semble également être un symptôme communément rapporté qui semble persister même après la fin de l'infection (Del Rio & Malani, 2020). Mais la fatigue ne touche pas uniquement les patients atteints de la COVID-19. Du fait de la surcharge des services de santé partout à travers le monde, l'épidémie a également conduit les personnels soignants à souffrir d'une fatigue intense, parfois proche de l'épuisement (Adams & Walls, 2020). La population en générale ne semble pas épargnée par les problématiques liées à la fatigue au cours de cette crise sanitaire. Ainsi, même pour les personnes ayant « échappé » à la COVID-19, le développement du télétravail, l'augmentation du temps passé sur les écrans (e.g., smartphone, télévision, ordinateur, tablette) et le

changement du rythme de vie lors de la période de confinement, semblent être autant de facteurs ayant favorisés le développement de la fatigue et des comportements sédentaires lors de cette période (Gruet, 2020).

Bien que l'on parle souvent de fatigue dans son ensemble, son origine peut être variée. Ainsi la fatigue que nous pouvons ressentir après avoir couru un marathon n'est pas la même que la fatigue que nous ressentons après avoir passé une journée devant notre ordinateur ou après une journée de cours. Dans le premier cas, nous faisons plutôt référence à une fatigue que nous pouvons qualifier de fatigue physique. Ce type de fatigue, comme son nom l'indique, à pour cause un exercice physique, et a été définie comme étant « une altération de la performance induite par un exercice (physique) » (Enoka & Stuart, 1992). Dans le second cas, nous parlons de fatigue mentale, appelée également fatigue cognitive. Comme son nom l'indique, elle a pour cause à un exercice cognitif, et a été définie comme « un état psychobiologique causé par la réalisation prolongée d'une tâche cognitive et caractérisé par une sensation subjective d'épuisement et de manque d'énergie » (Boksem & Tops, 2008).

La fatigue mentale apparaît généralement lorsque nous devons maintenir notre attention et notre concentration de façon prolongée et/ou intense. Avec l'évolution de notre société, et une proportion de plus en plus importante de la population travaillant dans les secteurs tertiaires (e.g., secrétaire, comptabilité/finance, banque/assurance), la prévalence de la fatigue mentale ne cesse d'augmenter, surtout dans les pays les plus développés.

Cette thématique de la fatigue mentale suscite de ce fait un intérêt croissant de la communauté scientifique. Afin de pouvoir en étudier les effets, les chercheurs essayent de recréer cette sensation en laboratoire, avec l'utilisation de tâches plus au moins écologiques, allant de l'utilisation du smartphone (Fortes et al., 2020; Greco et al., 2018) à la conduite automobile, en passant par des tâches beaucoup plus standardisées comme la tâche de Stroop (e.g., Pageaux et al., 2014; Rozand et al., 2015) ou l'AX-CPT (e.g., Marcora et al., 2009; Pageaux et al., 2013). Les études menées jusqu'à présent ont montré que la fatigue mentale pouvait impacter de façon négative non seulement nos performances cognitives (e.g., Faber et al., 2012; Lorist et al., 2000) mais également nos performances physiques (e.g., Brown et al., 2020; Mosso, 1891; Pageaux & Lepers, 2018). Bien que ces effets semblent de mieux en mieux identifiés, les mécanismes neurophysiologiques sous-jacents à la fatigue mentale restent encore mal connus. Plusieurs modèles explicatifs ont été proposés afin d'expliquer l'origine et les causes de la fatigue mentale (Boksem & Tops, 2008; Hockey, 2011; Ishii et al., 2014) mettant

en avant l'implication de plusieurs structures corticales, dont le cortex cingulaire antérieur (Lorist et al., 2005).

Ainsi, plus d'un siècle et demi après la première étude connue sur la fatigue mentale (Davy, 1845), et bien que ses effets soient de plus en plus clairement identifiés, des parts d'ombres existent toujours sur ce phénomène. En 1917, le président de l'*American Psychological Association* de l'époque, Raymond Dodge, écrivait : « Je ne m'attends pas à ce que les lois de la fatigue mentale soient formulées dans un avenir immédiat » (Dodge, 1917). Le moins que l'on puisse dire est qu'il avait vu juste. Aujourd'hui encore, et malgré les progrès technologiques (développement des techniques d'imagerie notamment), il reste encore un certain nombre de questions à résoudre avant de pouvoir appréhender le phénomène de la fatigue mentale dans son intégralité.

Ce travail de thèse s'inscrit dans ce contexte. Son l'objectif est d'investiguer les conséquences de la fatigue mentale, d'en identifier les origines, mais aussi, si possible, d'essayer d'en limiter les effets négatifs. Ce manuscrit est composé de trois parties distinctes. Dans la première partie, une revue de la littérature sur la fatigue mentale sera présentée, mettant l'accent sur ses conséquences au niveau des performances (cognitives et/ou physiques), mais aussi sur ses origines et les théories explicatives proposées jusqu'à aujourd'hui. La seconde partie sera consacrée aux quatre études menées au cours de ce travail de thèse. Finalement, la troisième et dernière partie constituera la discussion générale et permettra de discuter les résultats obtenus lors de nos études et de proposer de nouvelles perspectives pour de futurs travaux.

II. CADRE THEORIQUE

1 La fatigue mentale

1.1 Définition et concept

Lorsque l'on parle de fatigue, on aborde une sensation commune que tout un chacun a déjà pu expérimenter au cours de sa vie. Tout le monde arrive alors à se représenter ce concept de fatigue sans forcément pouvoir en donner une définition claire et précise. La difficulté à définir le concept de fatigue provient notamment du caractère très varié de ces causes, pouvant être pathologiques ou non. Dans ce contexte, la fatigue est communément définie par le dictionnaire Larousse comme :

« Un état physiologique consécutif à un effort prolongé, à un travail physique ou intellectuel intense et se traduisant par une difficulté à continuer cet effort ou ce travail ».

Dans cette définition, nous retrouvons une dissociation entre deux types de fatigue : la fatigue dite « physique » qui résulte, comme son nom l'indique, d'un travail ou d'un effort physique, et la fatigue dite « mentale » (ou cognitive) qui résulte elle d'une activité ou d'un effort intellectuel. Cette multidimensionnalité dans le concept de fatigue, et notamment cette dissociation entre fatigue physique et fatigue mentale, n'est pas récente. Dès 1912, Arai explique que la fatigue est la résultante de trois composantes : la fatigue musculaire, la fatigue sensorielle et la fatigue mentale. Depuis, bien que la définition ait un peu évolué, la dissociation entre fatigue « physique » et « mentale » est toujours bien présente. À la toute fin du 20ème siècle, on note l'apparition d'une notion importante, la notion de « subjectivité », qui reste très présente dans les définitions actuelles de la fatigue. La fatigue a ainsi été définie comme :

« La perception consciente d'une diminution de la capacité à mener une activité physique et/ou mentale, due à un déséquilibre entre la disponibilité, l'utilisation et/ou le renouvellement des ressources nécessaires à cette activité » (Aaronson et al., 1999).

Outre la notion de subjectivité, Aaronson et al. (1999) indiquent que chaque individu dispose d'une certaine quantité de ressources disponibles. Lorsque ces ressources disponibles sont épuisées qu'apparaît la sensation de fatigue apparaît.

Dans ce travail de thèse, nous nous concentrerons plus spécifiquement sur la fatigue mentale. Cette notion de fatigue mentale apparait dans les écrits dès le 17ème siècle sous la plume du philosophe français René Descartes, avec le terme de « fatigue de l'esprit ». Lors d'une

correspondance de juin 1645 avec la princesse Elisabeth de Bohême, Descartes affirme que « l*es occupations trop sérieuses affaiblissent le corps en fatiguant l'esprit* » (Garnier, 1835). Cependant, il aura fallu attendre encore plusieurs années pour voir apparaître le terme de « fatigue mentale ». Une des premières publications à mentionner le terme de fatigue mentale fut l'œuvre de Thorndike (1899) intitulé « *Mental fatigue* ». Dans cet ouvrage cependant, le terme de fatigue mentale n'est jamais clairement défini. Thorndike (1899) indique simplement que cela fait référence un état qui suit une période passée à réaliser des multiplications mentales allant de 3 à 8 heures.

Bien que le concept de fatigue mentale soit très vite apparu dans la notion de fatigue, il aura fallu attendre de nombreuses années avant d'obtenir une définition spécifique de cette notion. Une des définitions la plus couramment utilisée aujourd'hui pour qualifier la notion de fatigue mentale est la définition proposée par Boksem et Tops (2008). Ils définissent la fatigue mentale comme :

« Un état psychobiologique causé par la réalisation prolongée d'une tâche cognitive et caractérisé par une sensation subjective d'épuisement et de manque d'énergie ».

À l'instar de la définition de la fatigue proposée par Aaronson et al. (1999), Boksem et Tops (2008) insistent également sur la caractère subjectif de la fatigue mentale qui implique qu'il s'agit d'une sensation propre à chacun. Dans cette définition, les auteurs évoquent également les causes de l'apparition de la fatigue mentale. Elle apparaîtrait à la suite d'un effort cognitif, réalisé de façon prolongé. Cependant à aucun moment la notion de difficulté de la tâche cognitive exécutée n'est abordée dans la définition. Pourtant cette notion semble essentielle et joue un rôle prépondérant dans l'instauration de la fatigue mentale. Si la tâche cognitive proposée est prolongée mais trop simple, elle induira une sensation d'ennui et non une sensation de fatigue mentale (Bartley & Chute, 1947). Une relation semble d'ailleurs exister entre la complexité de la tâche cognitive proposée et la durée nécessaire pour induire un état de fatigue mentale. Plus la tâche cognitive sera complexe, plus la fatigue mentale sera induite de façon rapide et inversement, plus la tâche cognitive sera simple, plus la durée nécessaire pour induire la fatigue mentale sera longue.

Ainsi, afin de tenir compte de la complexité de la tâche mentale réalisée et, compléter la définition de la fatigue mentale proposée par Boksem et Tops (2008), la fatigue mentale a été définie par Rozand et Lepers (2016) comme étant :

« Un état psychobiologique vécu par l'ensemble des individus après avoir réalisé une tâche cognitive intense et/ou prolongée, qui se caractérise par une sensation d'épuisement et de manque d'énergie ».

Pour résumer, le concept de fatigue a évolué au cours du temps, voyant apparaître notamment la notion de subjectivité. La fatigue est plus un état ressenti, propre à chacun. Ce concept est multidimensionnel et la communauté scientifique s'accorde à dire, depuis bien longtemps déjà, que l'on peut distinguer plusieurs « types » de fatigue, avec notamment une fatigue dite « physique » et une fatigue dite « mentale ». Si la notion de fatigue physique est bien ancrée et que sa définition est relativement stable depuis les années 90, la notion de fatigue mentale est, quant à elle, plus floue. Pour preuve, sa définition a continué à évoluer ces dernières années. La littérature semble quand même tendre vers un consensus selon lequel la fatigue mentale est une sensation subjective causée par la réalisation d'une tâche cognitive. Dans ce travail de thèse, nous nous appuierons sur la définition proposée par Rozand et Lepers (2016). Quand nous ferons référence à la fatigue mentale, nous parlerons « d'un état psychobiologique vécu par l'ensemble des individus après avoir réalisé une tâche cognitive intense et/ou prolongée, qui se caractérise par une sensation d'épuisement et de manque d'énergie ».

Afin de pouvoir étudier la fatigue mentale, le premier enjeu est de pouvoir créer ou recréer cette sensation en laboratoire. Nous verrons que les chercheurs, après avoir utilisé des tâches écologiques, ont construit et utilisé des tâches expérimentales afin de pouvoir induire une fatigue mentale aiguë. Ces tâches, bien que non-écologiques, permettent de limiter les facteurs confondants et de se focaliser sur les effets spécifiquement liés à la fatigue mentale.

1.2 Les principales tâches utilisées pour induire la fatigue mentale

La fatigue mentale est une sensation et un état que tout un chacun a déjà expérimenté dans la vie quotidienne. Pour en étudier les causes, en mesurer les effets et mieux comprendre quels sont les mécanismes impliqués, il est nécessaire de recréer la fatigue mentale en laboratoire. De manière générale, la méthode choisie pour induire la fatigue mentale en laboratoire est d'utiliser des tâches cognitives prolongées. Cependant, selon la définition proposée par Rozand et Lepers (2016), la durée de la tâche n'est pas la seule variable à prendre en compte dans l'instauration de la fatigue, il faut également prendre en considération la difficulté de la tâche mentale à réaliser. La durée de la tâche reste cependant la variable la plus communément manipulée. Les durées vont de quelques minutes (Borragan et al., 2017;

Borragan et al., 2016; O'Keeffe et al., 2020) à plusieurs heures (Boksem et al., 2005; Mizuno et al., 2010), voire même 8 heures de tâches cognitives dans la journée afin de récréer des conditions équivalentes à ce que pourrait être une journée de travail (Mizuno et al., 2011). Cependant, la durée des tâches cognitives utilisées pour induire la fatigue mentale est généralement comprise entre 30 et 90 minutes (e.g., Marcora et al., 2009; Pageaux et al., 2015; Van Cutsem, De Pauw, et al., 2017). La seconde variable, qui correspond à la complexité ou la difficulté de la tâche, est également très importante. Si la tâche cognitive proposée pour induire la fatigue mentale est trop simple, même si elle est prolongée, elle induira une sensation d'ennui et non de fatigue mentale (Bartley & Chute, 1947). Cameron (1973) indique qu'il existe une relation entre le temps nécessaire pour induire la fatigue mentale et la difficulté de la tâche réalisée. Ainsi la fatigue mentale induite par une tâche cognitivement très coûteuse mais réalisée sur une courte période de temps sera similaire à la fatigue induite par une tâche moins coûteuse réalisée pendant une période plus longue. Les tâches plus coûteuses, réalisée sur des périodes plus courtes, permettent cependant de limiter la probabilité d'induire une sensation d'ennui et/ou de somnolence, et ainsi de confondre fatigue mentale et ennui/somnolence.

1.2.1 Tâches écologiques

1.2.1.1 Les tâches de conduite automobile

Les premières études investiguant les effets de la fatigue mentale ont utilisé des tâches « écologiques » pour induire cette fatigue. Ainsi les effets de la fatigue mentale étaient observés après de longues conférences données par des professeurs ou bien après une journée d'étude. Avec l'évolution de nos modes de vie et l'essor qu'a connu l'automobile, la fatigue mentale a été étudiée au travers de tâches prolongées de conduite automobile. Aujourd'hui, par exemple, 3/4 des français utilisent leur voiture quotidiennement pour se rendre au travail (étude Ipsos réalisée pour Vinci Autoroutes) preuve s'il en ait que la conduite automobile fait partie de notre quotidien. Une des premières études investiguant les effets de la fatigue à la suite d'une tâche de conduite automobile date de 1936. Ryan et Warner (1936) se sont intéressés aux effets de la conduite automobile sur divers paramètres (e.g., coordination oculomotrice, tests visuels, posture), et ont montré des effets négatifs de la conduite automobile sur ces paramètres. Si cette étude, comme de nombreuses autres, a été réalisée dans des conditions réelles de conduite, les études plus récentes se réalisent pour la plupart en simulateur de conduite afin d'éviter tout risque d'accident lors des sessions de test.

La fatigue mentale a également été étudiée dans d'autres contextes écologiques comme dans le milieu scolaire que ce soit du côté des professeurs (Mosso, 1891) ou des élèves (Bellei, 1901; Li & Sullivan, 2016) ou dans des tâches « exceptionnelles » de conduite comme la conduite d'avion (Borghini et al., 2014). Des tâches moins attendues peuvent également générer de la fatigue mentale. L'une d'entre elles est l'imagerie motrice, qui est de pourtant plus en plus souvent proposée dans les programmes de réhabilitation physique.

1.2.1.2 L'imagerie motrice

L'imagerie motrice est définie comme étant la représentation mentale d'un mouvement sans production concomitante de ce dernier. Elle a pour particularité d'activer des zones cérébrales similaires à celles activées lors de mouvements réels, notamment l'activation du cortex moteur primaire. La pratique de l'imagerie motrice peut avoir de nombreux bénéfices sur les performances motrices (Feltz & Landers, 1983; Gentili et al., 2010), et sur la capacité de production de force maximale (Grosprêtre et al., 2018; Yue & Cole, 1992). De nos jours, l'imagerie motrice est recommandée dans de nombreux programmes de réhabilitation (Jackson et al., 2001) comme après un accident vasculaire cérébral (Cho et al., 2013; Kumar et al., 2016), ou une période d'immobilisation (Lebon et al., 2012; Zijdewind et al., 2006). Les effets positifs de l'imagerie motrice s'expliquent par le fait que les aires activées lors de l'imagination d'un mouvement sont similaires à celles activées lors de sa réalisation, ce qui permet de continuer de maintenir l'activité de ces aires motrices sans nécessité de réellement produire le mouvement (Decety et al., 1994; Lotze et al., 1999; Roland et al., 1980). Parmi les zones corticales activées à la fois lors de mouvements réels et imaginés, on retrouve l'aire motrice supplémentaire (Gerardin et al., 2000), l'aire pré-motrice (Decety et al., 1994), l'aire motrice primaire (Porro et al., 2000), ainsi que le cervelet et les noyaux gris centraux (Decety et al., 1994; Lotze et al., 1999). Cependant cette activation générée par l'imagerie motrice est plus faible que lors de mouvements réels. On note une baisse du niveau d'activation d'environ 30 % lors d'une tâche d'imagerie motrice en comparaison à la réalisation de mouvements réels (Porro et al., 1996).

Malgré ses effets bénéfiques, il semblerait que la pratique prolongée de l'imagerie motrice puisse avoir des effets délétères, notamment avec l'instauration de fatigue mentale. Dès 2010, on observe qu'après la réalisation de 60 mouvements imaginés d'une durée moyenne de 9 secondes, consistant à s'imaginer atteindre des cibles, on pouvait avoir une détérioration de la concentration (Gentili et al., 2010). Quelques années plus tard, une étude a mis en évidence que la réalisation d'une session d'imagerie motrice de 80 mouvements imaginés d'une durée

d'environ 20 minutes, était suffisante pour provoquer de la fatigue mentale (Rozand et al., 2014). Cette observation a par la suite été confirmée par plusieurs études (Graham et al., 2014; Rozand et al., 2016; Talukdar et al., 2019). Le fait qu'une session d'imagerie motrice puisse induire de la fatigue mentale est à prendre en considération dans la conception des séances et programmes d'entraînement et/ou de réhabilitation. On pourrait ainsi suggérer de pratiquer des sessions courtes d'imagerie motrice, 20 minutes maximum, pour éviter une diminution de la motivation et/ou l'apparition d'une sensation d'ennui ou de fatigue mentale (Driskell et al., 1994), et ainsi préservée une efficacité maximale de l'entraînement en imagerie motrice.

Toutes ces tâches écologiques ne semblent cependant pas être les plus appropriées pour isoler les effets de la fatigue mentale. Lors de ces tâches un grand nombre de facteurs confondants peuvent apparaître. Lors d'une tâche de conduite prolongée par exemple, une sensation de lassitude et/ou d'ennui peut s'instaurer et ainsi être confondue avec les effets de la fatigue mentale. Dans cette optique, les chercheurs ont tenté d'utiliser des tâches expérimentales pour induire la fatigue mentale. Outre le fait de limiter les facteurs confondants, l'utilisation de tâches expérimentales permet de rendre les passations plus standardisées (par exemple, dans le cas de la conduite automobile en condition écologique, de nombreux paramètres peuvent varier comme la circulation ou le nombre de stimuli) mais aussi de faciliter la mise en place des protocoles (avec des tâches expérimentales, une feuille et un stylo ou un ordinateur peuvent suffire). Nous nous intéresserons donc maintenant à quelques-unes des principales tâches expérimentales utilisées en laboratoire afin d'induire une fatigue mentale aiguë.

1.2.2 Tâches expérimentales

De nombreuses tâches expérimentales ont été utilisées afin d'induire la fatigue mentale. Parmi les tâches utilisées nous retrouvons les tâches de calcul mental, de Simon, de Flanker, ou encore la tâche de vigilance psychomotrice (PVT). Dans cette partie nous nous concentrerons cependant uniquement sur les deux tâches les plus couramment utilisées que sont la tâche de Stroop et la tâche d'AX-CPT, ainsi que sur une troisième tâche appelée « *Time Load Dual Task* », qui nous semble particulièrement intéressante pour induire la fatigue mentale dans une durée relativement courte.

1.2.2.1 La tâche de Stroop

La tâche de Stroop est une tâche développée en 1935 par le psychologue John Ridley Stroop. Il s'agit aujourd'hui d'une des tâches les plus connues dans le champ de la psychologie avec plus de 19000 citations sur Google Scholar. Initialement, le matériel expérimental était composé de trois planches avec chacune 100 items. Sur la première planche, il y avait des rectangles de couleur, et les participants devaient alors dénommer la couleur des rectangles. Sur la deuxième planche, des mots indiquant des noms de couleurs étaient écrits à l'encre noire et les participants devaient lire ces mots. Enfin, sur la dernière planche, des mots indiquant des noms de couleurs étaient écrits avec des encres de couleurs différentes du nom de couleur afin de créer un conflit entre la lecture du mot et la couleur de l'encre (e.g., le mot « bleu » écrit à l'encre verte ; **BLEU**). Dans une première expérience, Stroop (1935) a voulu voir si une tâche peu courante (la dénomination d'une couleur) pouvait avoir un impact sur une tâche courante (la lecture de mots). Pour cela, il a mesuré le temps que les participants mettaient pour lire les 100 noms de couleur écrits en noir et le temps mis pour lire les 100 noms de couleur écrits avec des encres différentes des noms de couleur. Il ne constata pas de différence significative entre les deux conditions et conclut que la couleur de l'encre utilisée (et par conséquent la dénomination d'une couleur) ne perturbait pas la lecture de mots. Dans une seconde expérience, il a évalué l'inverse, à savoir l'impact de la lecture de mots (i.e., tâche courante) sur une tâche de dénomination de couleur (i.e., tâche peu courante). Il a mesuré le temps que les participants mettaient pour dénommer la couleur des 100 rectangles colorés et le temps mis pour dénommer la couleur de l'encre des 100 noms de couleur écrits avec différentes couleurs d'encre. Stroop observa une différence significative entre les deux conditions et conclut que la lecture (tâche courante) perturbait la dénomination de la couleur (tâche peu courante), mettant ainsi en lumière un effet d'interférence de la lecture de mots sur la dénomination de couleurs.

Cette tâche de Stroop a depuis été largement reprise et modifiée. Aujourd'hui, lors de tâches de Stroop, on retrouve classiquement deux conditions (Figure 1) : une condition « congruente » dans laquelle le mot écrit et la couleur de l'encre correspondent (e.g., **BLEU**) et une condition « incongruente » dans laquelle le mot écrit et la couleur de l'encre ne correspondent pas (e.g., **BLEU**). Dans cette seconde condition, le participant doit inhiber la lecture du mot pour dénommer la couleur de l'encre dans laquelle est écrit le mot (dans l'exemple présenté, la réponse est « vert »).

Figure 1 : Visualisation d'une tâche de Stroop. Sur la première ligne uniquement des essais congruents sont présentés, sur la seconde uniquement des essais incongruents et sur les deux dernières ligne un mélange de ces deux types d'essais.

L'interférence créée par la tâche de Stroop est connue pour activer les aires corticales préfrontales (Schroeter et al., 2002; Zysset et al., 2001) dont le CCA (Salisbury et al.), plus précisément sa partie dorsale, mais aussi le cortex préfrontal dorsolatéral (Banich et al., 2001; MacDonald et al., 2000; Milham et al., 2001). Lors d'un conflit entre plusieurs informations, la partie dorsale du CCA permet l'intégration des différentes informations à traiter et les redirige vers les zones du contrôle cognitif afin que le conflit soit traité.

La tâche de Stroop, initialement développée pour mesurer l'interférence entre la lecture de mots et la dénomination d'une couleur, est aujourd'hui couramment utilisée pour induire la fatigue mentale. Le coût cognitif lié au traitement du conflit, lorsque la tâche de Stroop est effectuée de manière prolongée, permet de provoquer de façon expérimentale une sensation de fatigue mentale. Depuis 2010, on dénombre plus de 80 études ayant utilisé la tâche de Stroop dans le but d'induire la fatigue mentale.

Dans la cadre des études sur la fatigue mentale, une variante de la tâche de Stroop a récemment été proposée afin d'augmenter le coût cognitif lié à son exécution. Dans cette version modifiée, les participants doivent inhiber la lecture du mot pour dénommer la couleur de l'encre (e.g., si le stimulus est « BLEU », alors la réponse correcte est « vert »), sauf lorsque le mot est écrit à l'encre rouge. Dans ce cas, les participants doivent lire le mot qui est écrit tout en inhibant la couleur de l'encre (e.g., si le stimulus est « BLEU », alors la réponse correcte est « bleu »). Cette version modifiée a été créé afin d'éviter qu'une stratégie s'installe au cours du

temps et que les participants parviennent à constamment inhiber la lecture du mot en se focalisant uniquement sur la couleur de l'encre. Cette tâche de Stroop modifiée demande une flexibilité mentale plus importante et nécessite le maintien en mémoire de travail de deux objectifs, augmentant ainsi le coût cognitif de la tâche.

Finalement, on peut noter que la tâche de Stroop comprenant uniquement des items congruents, est parfois utilisée comme condition contrôle dans les études investiguant les effets de la fatigue mentale. Avec des essais uniquement congruents, il n'y a aucun conflit cognitif entre la couleur de l'encre et le nom de couleur et le un coût cognitif demandé pour réaliser la tâche est extrêmement faible, et par conséquent l'induction de la fatigue mentale est moindre.

1.2.2.2 La tâche d'AX-CPT

La tâche d'AX-CPT est en réalité une variante d'une tâche de CPT (C*ontinuous Performance Task* ou « tâche de performance continue ») initialement conçue pour mettre en évidence des troubles de l'attention soutenue chez des enfants ou des adultes ayant subi des lésions cérébrales (Rosvold et al., 1956). L'AX-CPT est une tâche qui sollicite plusieurs fonctions cognitives : l'attention (sélective), la mémoire (de travail) ainsi que les fonctions exécutives et plus spécifiquement le processus d'inhibition (Braver et al., 2001; Carter et al., 1998). Développée par Cohen et ses collaborateurs (Cohen et al., 1999; Servan-Schreiber et al., 1996), elle a souvent été utilisée pour mettre en évidence un déclin des fonctions cognitives lors du vieillissement (Braver et al., 2001).

D'autres études ont cependant utilisé cette tâche d'AX-CPT dans un but différent, celui d'induire la fatigue mentale (Marcora et al., 2009; Pageaux et al., 2013; van der Linden et al., 2006). Alors que la réalisation de la tâche d'AX-CPT ne dure habituellement que quelques minutes, les études souhaitant induire la fatigue mentale ont utilisé cette tâche pour des durée allant de 45 (Smith et al., 2019) à 90 min (van der Linden et al., 2006).

Dans cette tâche, des lettres sont présentées de manière continue sur un écran toutes les 1500 ms (cette durée inter-stimuli peut varier pour moduler la difficulté de la tâche). Les séquences commencent et se terminent avec une lettre écrite à l'encre rouge. Les lettres commençant la séquence sont soit un « A », soit un « B » et les lettres finissant la séquence sont soit un « X », soit un « Y ». Entre ces lettres, des lettres servant de distracteurs (toutes lettres de l'alphabet, excepté « A » et « Y ») sont écrites avec une encre blanche. Pour que la séquence

soit correcte, elle doit commencer par un « A » et se terminer par un « X » (Figure 2). Le participant doit identifier les séquences correctes et celles qui ne le sont pas.

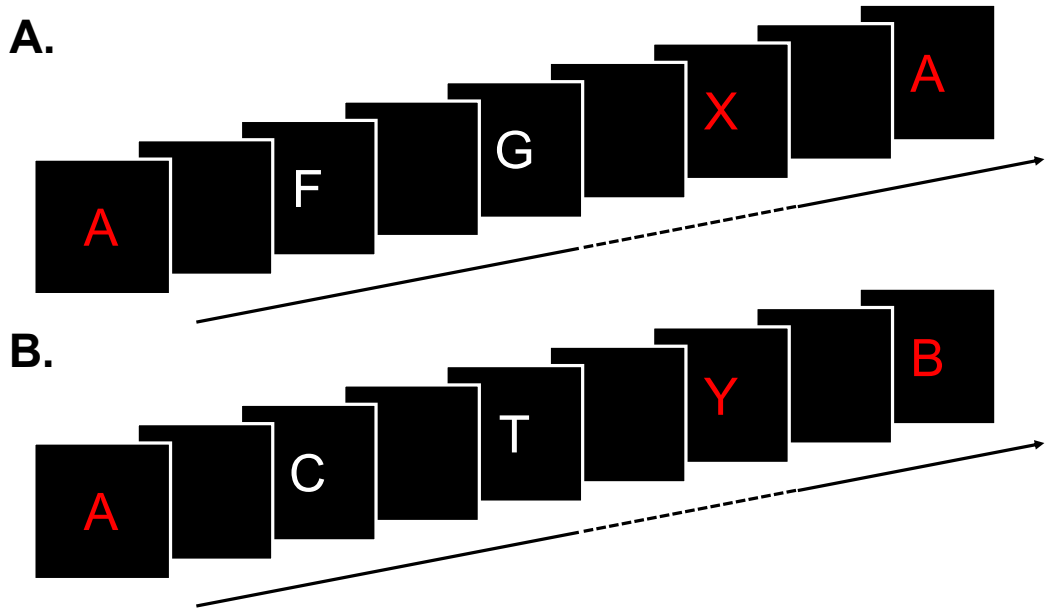


Figure 2 : Visualisation d'une tâche d'AX-*Continuous Performance Test* (AX-CPT). Les séquences commencent et se terminent par une lettre rouge. Entre elles, deux lettres blanches sont intercalées pour servir de distracteurs. Une séquence correcte commence par un A et se termine par un X (panel A), tout autre séquence est incorrecte (panel B).

La tâche d'AX-CPT est connue pour activer différentes régions corticales dont le cortex préfrontal dorsolatéral qui participe au maintien des objectifs (Paxton et al., 2008). De plus la tâche d'AX-CPT active également d'autres aires corticales comme le gyrus pariétal inférieur droit, le gyrus fusiforme bilatéral ou encore le CCA (Lopez-Garcia et al., 2016). Le CCA intervient dans divers aspects du contrôle attentionnel et de la résolution de conflit (Posner & DiGirolamo, 1998) et, nous le verrons par la suite, semble être une structure cérébrale particulièrement impliquée dans le processus de fatigue mentale.

1.2.2.3 La tâche de « *Time Load Dual Back* »

Comme indiqué précédemment, lors que l'on utilise des tâches cognitives relativement longues pour induire de la fatigue mentale, il est possible d'induire des effets non-désirés comme une sensation d'ennui ou de la somnolence. Il est extrêmement difficile de dissocier les effets liés à l'ennui des effets liés à la fatigue mentale. Afin de se focaliser sur les effets

réellement liés à la fatigue mentale, il est plus pertinent d'utiliser des tâches cognitives qui sont plus courtes mais également plus coûteuses sur le plan cognitif. La tâche de « *Time Load Dual Back* » (TLDB) est une tâche cognitive qui combine une tâche classique de mise à jour de la mémoire de travail, le *N*-back (Kirchner, 1958), avec une seconde tâche d'interférence (i.e., une décision sur la parité de chiffres). Dans cette tâche, des chiffres et des lettres sont présentés de façon alternée. Chaque stimulus est présenté pendant une durée de 1500 ms. Lorsque les participants voient les chiffres, ils doivent dire si le chiffre présenté est pair ou impair en appuyant avec la main droite respectivement sur la touche « 2 » ou « 1 » du pavé numérique. Lorsqu'ils voient les lettres, ils doivent presser la barre espace avec leur main gauche si la lettre présentée est identique à la lettre présentée immédiatement avant (avec l'apparition d'un chiffre entre les deux lettres à comparer, puisque la présentation des chiffres et des lettres est alternée ; Figure 3). L'avantage de cette tâche cognitive est que la charge de travail peut être ajustée individuellement en jouant sur la durée de présentation des stimuli. Lors d'une session de familiarisation effectuée afin d'accommoder les participants à la tâche, le seuil de présentation des stimuli est fixé au départ à 1500 ms. Afin de pousser les participants au maximum de leurs capacités, le seuil de présentation est abaissé par pas de 100 ms tant que le taux de réussite est supérieur ou égal à 85 %. Lorsque le taux de réussite à l'exercice passe sous la barre des 85 %, l'exercice est considéré comme étant trop difficile et on garde le dernier seuil de présentation auquel le participant était capable d'avoir un taux de réussite supérieur ou égal à 85 %. Le seuil de présentation est ainsi ajusté à chaque participant afin de lui demander un effort cognitif maximal. Des études ont révélé que 16 minutes de la tâche de TLDB étaient suffisantes pour induire une sensation subjective de fatigue mentale (Borragan et al., 2017; Borragan et al., 2016). On note enfin que cette tâche peut également être utilisée comme tâche contrôle en allongeant la durée de présentation des stimuli, ce qui diminue la difficulté de la tâche et n'engendre pas (ou peu) de fatigue mentale.

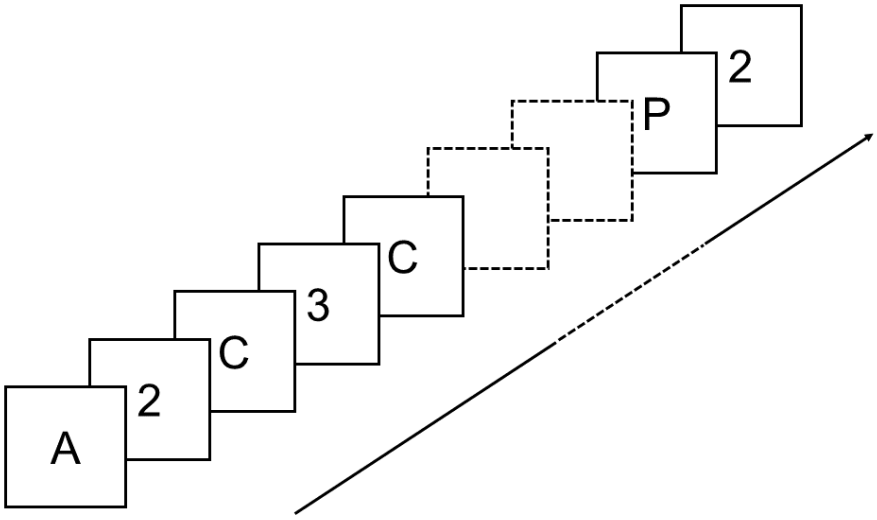


Figure 3 : Visualisation d'une tâche de « *Time Load Dual Back* ». Cette tâche consiste en une présentation alternée de lettres et de chiffres, avec une durée de présentation des stimuli fixe (inférieure à 1500 ms).

D'un point de vue neuroanatomique, la tâche de *N*-back entraîne l'activation de diverses aires corticales. Dans une méta-analyse regroupant 24 études réalisées en IRMf, Owen et al. (2005) ont identifié six régions corticales principalement activées : (1) le cortex pariétal postérieur bilatéral et médian incluant le précuneus et les lobules pariétaux inferieurs, (2) le cortex prémoteur bilatéral, le cortex cingulaire dorsal/cortex prémoteur médian incluant les aires motrices supplémentaires, (4) le cortex préfrontal rostral bilatéral, (5) le cortex préfrontal dorsolatéral bilatéral, et (6) le cortex préfrontal medio-ventrolatéral bilatéral. Parmi toutes les structures impliquées, on note une fois encore l'implication du CCA (Braver et al., 1997; Cohen et al., 1994), aire corticale également largement impliquée dans le processus de fatigue mentale et dans la tâche de Stroop (e.g., Cook et al., 2007; Lorist et al., 2005). La tâche de décision de parité ne sert, quant à elle, « que » de tâche distractrice, créant une situation de double tâche pour augmenter la difficulté de l'exercice.

1.2.3 Quel type de tâche privilégier pour induire la fatigue mentale ?

Nous avons présenté ici quelques tâches qui sont couramment utilisées pour induire la fatigue mentale en laboratoire. Cependant, et comme nous l'avons mentionné, cette liste n'est pas exhaustive. De nombreuses autres tâches comme les tâches écologiques ou expérimentales

de Flanker (Lorist et al., 2005), de Simon (Boksem et al., 2006), ou de calcul mental (Zhang & Yu, 2010) ont également été utilisées. Cependant, bien que les tâches pour induire la fatigue mentale soient nombreuses, on peut se demander quelle serait la tâche la plus efficace et la plus intéressante pour induire la fatigue mentale. Plusieurs études récentes ont utilisé plusieurs tâches cognitives afin d'induire la fatigue mentale et observer si les effets étaient similaires d'une tâche à l'autre (O'Keeffe et al., 2020; Smith et al., 2019). Dans l'étude de Smith et al. (2019), les trois tâches sélectionnées pour induire de la fatigue mentale étaient une tâche de Stroop, une tâche d'AX-CPT et une tâche de PVT. La durée des tâches cognitives était de 45 minutes. Une condition contrôle consistant à regarder un documentaire émotionnellement neutre était également proposée. Les résultats de l'étude montrent que les trois tâches cognitives induisaient la fatigue mentale même s'il semble que la tâche de Stroop induisait « plus » la fatigue mentale que la tâche de PVT (si l'on en croit les échelle subjectives utilisées dans l'étude pour quantifier la fatigue mentale). L'étude de O'Keeffe et al. (2020) compare l'utilisation de la tâche d'AX-CPT durant 90 minutes et celle de la tâche de TLDB durant 16 minutes. Les participants ont présenté un niveau d'excitation physiologique et psychologique significativement plus élevé après la tâche de TLDB alors que les deux tâches (AX-CPT et TLDB) ont induit une augmentation de la sensation de fatigue mentale. Ces résultats suggèrent de privilégier l'utilisation de tâches cognitives courtes avec des seuils individualisés pour induire de la fatigue mentale plutôt que des tâches cognitives longues et standardisées. Utiliser des tâches cognitives avec des seuils inter-stimuli individualisés pour induire la fatigue mentale plutôt que des tâches de Stroop ou AX-CPT pourrait permettre de dissocier les phénomènes de fatigue mentale et d'ennui. Cependant, cette barrière entre fatigue mentale et ennui/somnolence est mince, et ces deux facteurs peuvent être considérés comme des facteurs qui nuisent de manière synergique aux performances (Balkin & Wesensten, 2011).

La fatigue mentale est définie comme un état psychobiologique vécu par l'ensemble des individus après avoir réalisé une tâche cognitive intense et/ou prolongée, qui se caractérise par une sensation d'épuisement et de manque d'énergie. Bien qu'elle soit observable dans des situations de la vie quotidienne comme au travail ou lors de tâches de conduite automobile notamment, les chercheurs cherchent à recréer cette sensation de fatigue mentale en laboratoire afin de mieux pouvoir en comprendre les effets et les mécanismes. Les tâches les plus utilisées à cet effet sont la tâche de Stroop et la tâche d'AX-CPT, souvent réalisées durant 1 heure ou plus. Cependant, il semblerait qu'il faille privilégier l'utilisation de tâches plus coûteuses cognitivement, mais également moins longues, afin d'induire la fatigue mentale tout en limitant les facteurs confondants que peuvent être l'ennui et/ou la somnolence.

2 Effets de la fatigue mentale sur les performances cognitives et physiques

Les chercheurs ont commencé à s'intéresser à la fatigue mentale depuis le milieu du 19ème siècle. Le premier fût Davy (1845). Son étude avait pour but d'observer les effets de différentes variables (e.g., saison, heure de la journée, prise d'un repas) sur la température corporelle. Parmi les paramètres étudiés, il s'est intéressé à la variation de température liée à l'exécution d'un effort mental soutenu. Il montra ainsi que la réalisation d'un effort mental soutenu conduisait à une élévation de la température corporelle. Depuis cette étude princeps, les investigations concernant les effets de la fatigue mentale se sont multipliées. Dans cette partie, nous nous intéresserons dans un premier temps aux effets de la fatigue mentale sur les performances cognitives, puis sur les performances physiques. Enfin, nous verrons quelles peuvent être leurs répercussions sur notre vie quotidienne.

2.1 Effets de la fatigue mentale sur les performances cognitives

Dès les premières recherches investiguant les effets de la fatigue mentale, deux principales méthodes d'investigation ont été utilisées. La première méthode, que l'on peut nommer méthode « directe », consiste à observer l'évolution des performances au cours d'une tâche cognitivement coûteuse. Une courbe des performances au cours du temps est ainsi obtenue et permet d'évaluer les effets du temps passé à réaliser la tâche sur les performances. La seconde méthode, dite « indirecte », consiste à utiliser une tâche cognitivement coûteuse afin d'induire la fatigue mentale puis d'en observer les effets sur une autre tâche. Cette seconde méthode permet notamment de s'affranchir des soucis liés au désengagement qui peut intervenir au cours d'une tâche cognitive prolongée.

2.1.1 Méthode d'évaluation directe de la fatigue mentale : l'effet du « *Time on task* »

Lorsque l'on s'intéresse aux performances pendant la réalisation des tâches cognitives utilisées pour la fatigue mentale, on note que plusieurs patrons de résultats sont observables. Dans certains cas, avec le temps passé à réaliser la tâche, et donc avec une sensation de fatigue qui va en grandissant, on observe, comme on pourrait le pressentir, une diminution des performances avec généralement une augmentation des temps de réaction et/ou du nombre d'erreurs. Ainsi Boksem et al. (2005) ont montré pour une tâche d'attention visuelle durant 3

heures, qu'avec le temps il y avait une augmentation des temps de réaction, des fausses alarmes et des erreurs, reflétant ainsi une diminution des capacités attentionnelles avec l'instauration de fatigue mentale. Cette altération des capacités attentionnelles lors de tâches cognitives prolongées a largement été rapportée dans la littérature (e.g., Bonnefond et al., 2010; Csatho et al., 2012; Faber et al., 2012). De plus, d'autres capacités cognitives sont également altérées avec le temps passé à la réalisation d'une tâche comme, l'évaluation de l'information, la prise de décision (Guo et al., 2016) ou bien les processus de planification et de préparation (Lorist et al., 2000).

Cependant toutes les études ne retrouvent pas une diminution des performances au cours d'une tâche mentalement fatigante. Lors de certaines études, un maintien des performances cognitives au cours du temps est observé, voire même parfois une amélioration des performances lors de tâches cognitives prolongées. Si l'amélioration des performances est souvent due à des effets d'apprentissage liés à la tâche (reporté sous le terme de « *warm-up effect* » Thorndike (1921), la capacité à maintenir des performances au cours d'une tâche cognitivement coûteuse dépendrait de la motivation pour réaliser la tâche. Une motivation importante amènerait les participants à engager plus de ressources afin de continuer à maintenir un bon niveau de performances. Ainsi les performances seront maintenues tant que les participants voudront et/ou pourront augmenter les ressources investies pour l'exécution de la tâche. Cette théorie explicative reprend le modèle explicatif du « rapport coût/bénéfice » développé par Boksem et Tops (2008) et que nous verrons plus en détail dans la section 3.2.1. Pour illustrer l'importance de la motivation dans l'évolution des performances au cours d'une tâche cognitive prolongée nous prendrons l'exemple d'une étude menée par Boksem et al. (2006). Dans cette étude, les expérimentateurs ont manipulé la motivation par le biais d'une récompense financière. Une même tâche cognitive de 2 h 20 était proposée à deux groupes de participants : pour le premier groupe, la consigne était de répondre le plus rapidement possible, et pour le second groupe la consigne était de faire le moins d'erreurs possible. Alors que les performances se dégradaient lors des deux premières heures passées à réaliser la tâche cognitive, la récompense financière proposée lors des 20 dernières minutes a permis d'observer un rebond des performances. De façon intéressante, le rebond observé était spécifique à la consigne donnée. Dans le premier groupe, pour lequel la consigne était de répondre le plus rapidement possible, l'amélioration des performances a été observée sur les temps de réponse. Pour le second groupe, pour lequel la consigne était de faire le moins d'erreurs possible, l'amélioration des performances lors des 20 dernières minutes a été observée sur la précision

des réponses (Figure 4). La motivation et l'effort que l'on est prêt à investir lors d'une tâche cognitive prolongée jouent un rôle prépondérant dans nos performances (Boksem et al., 2006; Hopstaken et al., 2016). Ce facteur peut donc expliquer les différences de performances observées au cours d'une tâche cognitive prolongée.

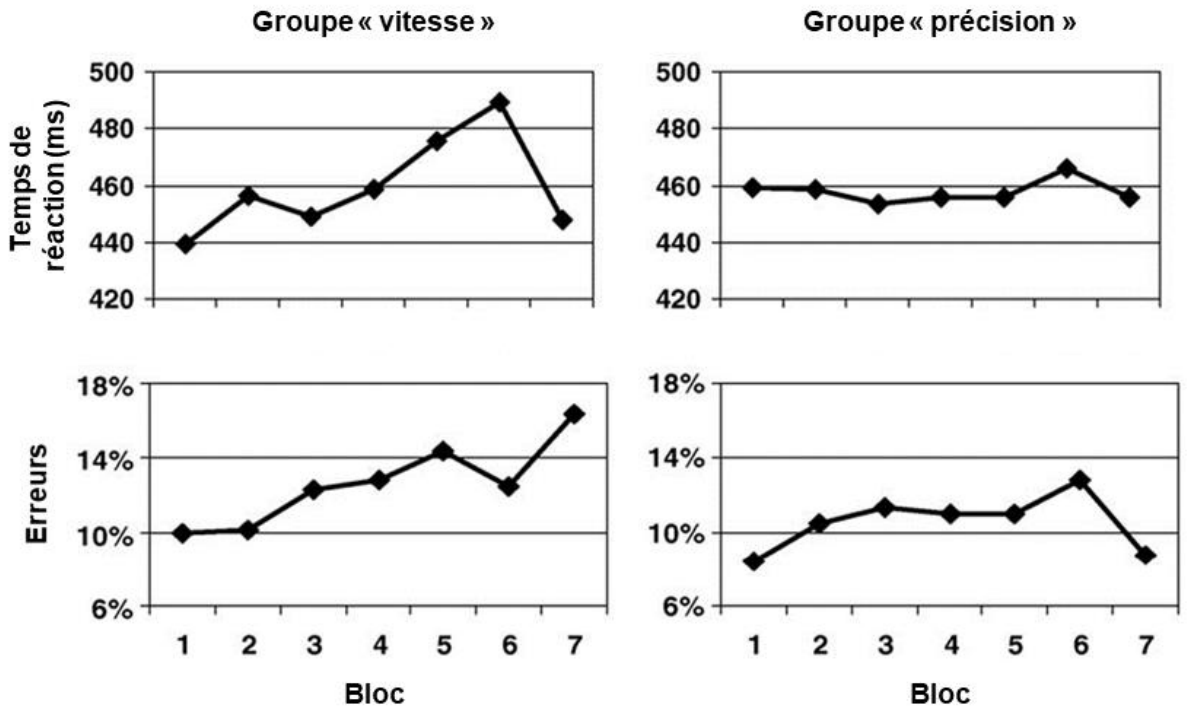


Figure 4 : Effet de la fatigue mentale lors d'une tâche cognitive prolongée. Les performances cognitives (temps de réaction et erreurs) sont altérées au cours d'une tâche cognitivement coûteuse de 2 h 20 (séparée en 7 blocs de 20 minutes). Cependant une augmentation de la motivation lors des 20 dernières minutes (i.e., un gain de 25€ si retour des performances au niveau initial) permet de compenser ces effets négatifs. Adapté de Boksem et al. (2006).

Des études ont cherché à mieux comprendre les mécanismes permettant de maintenir un niveau de performance stable malgré l'augmentation du temps passé à réaliser la tâche et l'apparition de fatigue mentale. Wang et al. (2016) ont étudié l'évolution des performances (temps de réaction et précision des réponses) au cours d'une tâche de Stroop de 160 minutes. Lors de cette tâche, les performances ont été maintenues durant 80 minutes avant de se détériorer. Ce maintien de performance a été relié à une augmentation de l'activité cérébrale au niveau antéro-frontal, et donc probablement à une augmentation des ressources engagées pour réaliser la tâche. Cependant l'origine exacte de ce mécanisme de compensation reste inconnue.

Les auteurs concluent que des études conduites en IRMf devraient permettre de mieux appréhender ce mécanisme.

Les effets différenciés sur les performances pendant une tâche cognitive prolongée ont été observés depuis bien longtemps. Dans une étude conduite par Martyn (1913), trois participants ont effectué des multiplications mentales pendant une période d'une heure. Le premier participant n'a présenté aucun changement dans ses performances, le second participant a montré une amélioration de ses performances, et le troisième participant a montré une détérioration de ses performances. Ces observations montrent qu'il existe une forte variabilité interindividuelle quant à l'évolution des performances au cours d'une tâche cognitive prolongée et que l'augmentation du temps passé sur la tâche n'est pas forcément synonyme de déclin des performances. Cette variabilité interindividuelle a été confirmée plus tard par d'autres études avec des échantillons beaucoup plus importants, allant jusqu'à 355 participants (Davis, 1946). Des différences entre études utilisant une tâche cognitive similaire ont également été observées. Ainsi, analyser seulement les performances en termes d'erreurs et/ou de temps de réaction lors d'une tâche cognitive prolongée ne semble pas être la méthode la plus pertinente pour identifier les effets de fatigue mentale.

L'étude d'un autre paramètre plus fin, et semble-t-il plus sensible à la fatigue mentale a été proposée. Il s'agit de l'étude de la variabilité des temps de réponse. Ainsi, certaines études montrent que, même si la fatigue mentale n'affecte pas directement les erreurs ou les temps de réponse, une augmentation de la variabilité des temps de réponse apparaît avec l'augmentation du temps passé à réaliser la tâche (Steinborn et al., 2010; Wang et al., 2014). Pour illustrer cela, Wang et al. (2014) ont proposé à des participants de réaliser une tâche de Stroop pendant 3 heures. Ils ont constaté que la variabilité des temps de réponse augmentait de façon linéaire avec le temps et ont observé des tailles d'effet statistique plus importantes que pour les mesures plus traditionnelles que sont les temps de réponse moyens et la précision des réponses. Cette augmentation de la variabilité des temps de réponse avec le temps passé à réaliser la tâche serait liée à l'instauration d'un « bruit neuronal ». Ces observations sont en accord avec les études sur les populations vieillissantes et les patients atteints de troubles neuropsychiatriques qui constatent également que la variabilité intra-individuelle identifie de manière plus sensible les populations ou les individus présentant des déficits de performance que le temps de réponse moyen (Bielak et al., 2010; Burton et al., 2002; de Frias et al., 2007). Ces données suggèrent que la variabilité intra-individuelle des temps de réponse (à ce jour peu employée dans les études portant sur la fatigue mentale) serait un marqueur plus sensible pour attester de la

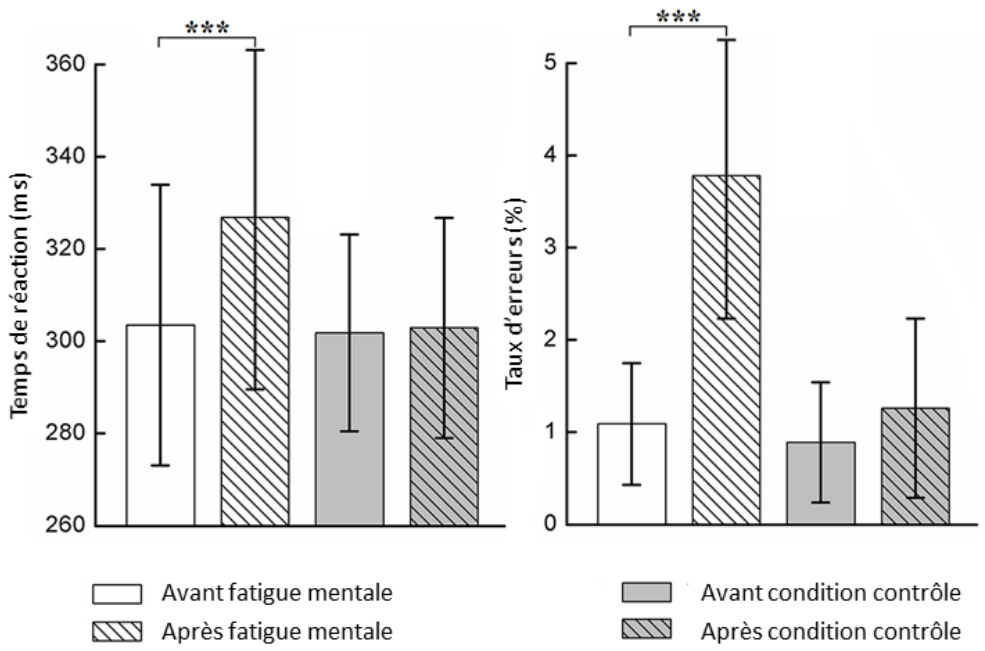
présence et de l'augmentation de la sensation de fatigue mentale avec l'augmentation du temps passé à réaliser la tâche.

Nous avons montré dans cette section qu'analyser les performances comportementales au cours d'une tâche cognitive prolongée peut aboutir à des résultats différents. Plusieurs profils semblent se dégager avec certaines personnes qui voient leurs performances se dégrader avec l'augmentation du temps passé à réaliser la tâche, d'autres qui sont capables de maintenir leurs performances et certaines qui sont même capables d'améliorer leurs performances (certainement lié à des processus d'apprentissage et/ou d'automatisation de la tâche). Nous verrons que mesurer les effets de la fatigue mentale sur des tâches cognitives différentes que celles qui ont été utilisées pour induire cette la fatigue mentale pourrait être protocole expérimental pertinent pour évaluer les effets de la fatigue mentale sur les performances cognitives. De plus, ce type d'études évaluant les effets de la fatigue mentale sur des tâches subséquentes à une tâche mentalement fatigante revêtent un aspect écologique important.

2.1.2 Méthode d'évaluation indirecte de la fatigue mentale : l'effet sur une tâche subséquente

La méthode d'évaluation indirecte de la fatigue mentale consiste à mesurer les performances cognitives sur une autre tâche que celle utilisée pour induire la fatigue mentale. Les résultats observés lors de ce type d'évaluation semblent beaucoup plus consistants que ceux observés à travers la méthode directe. En effet, lorsque les capacités cognitives sont étudiées via d'autres tâches cognitives que celles utilisées pour provoquer la fatigue mentale, on retrouve presque systématiquement une baisse des performances cognitives liée à l'instauration de fatigue mentale.

L'attention est une fonction cognitive particulièrement impactée par la fatigue mentale. Smith et al. (2019) ont mesuré les effets de la fatigue mentale sur les capacités attentionnelles en utilisant une tâche de vigilance psychomotrice (PVT ; Dinges & Powell, 1985), consistant à réagir le plus rapidement possible à une stimulation visuelle. Ils ont montré, qu'après une tâche mentalement fatigante (45 minutes d'une tâche d'AX-CPT, de tâche attentionnelle, ou de tâche Stroop), une augmentation des temps de réaction lors de la PVT était observée traduisant ainsi une détérioration des capacités attentionnelles en présence de fatigue mentale. L'altération des capacités attentionnelles en présence de fatigue est largement admise et également observée sur l'attention sélective (e.g., Guo et al., 2018; Slimani et al., 2018, Figure 5).



<u>Figure 5 :</u> Effet de la fatigue mentale sur une tâche cognitive subséquente. La fatigue mentale, induite par une tâche de recherche visuelle, altère les performanes (temps de réaction et précision des réponses) sur une tâche subséquente de Go/No-Go. *** : effet significatif du temps ($p < .001$). Adapté de Guo et al. (2018)

La fatigue mentale induit également un changement dans les processus de traitement de l'information. Le traitement de l'information serait effectué de façon moins analytique en présence de fatigue mentale. van der Linden et Eling (2006) ont montré que le traitement global des informations (e.g., un stimulus est identifié comme représentant une maison) était moins affecté que le traitement local (e.g., identifier les briques de la maison) par la fatigue mentale. Cela illustre bien le fait que toutes les fonctions attentionnelles ne sont pas altérées de la même façon par la fatigue mentale.

L'attention n'est cependant pas la seule fonction cognitive touchée par les effets de la fatigue mentale. van der Linden et al. (2003) ont réalisé une étude pour tester l'altération des fonctions exécutives en présence de fatigue mentale. La fatigue mentale a été induite par 2 heures de tâche cognitive (tâche sur ordinateur consistant à attribuer du travail à des employés fictifs), alors que les participants du groupe contrôle restaient 2 heures au le laboratoire à lire des magazines ou faire ce qu'ils souhaitaient à condition que cela ne représente pas une tâche cognitivement coûteuse. Les participants mentalement fatigués ont montré une altération significative de la flexibilité mentale (tendance à persévérer ou à s'accrocher à une stratégie inefficace, mesurée par le *Wisconsin Card Sorting task*) et des fonctions de planification (capacité à effectuer des actions dans un ordre planifié, mesuré par le *Tower London test*), et

donc de façon plus générale une altération des fonctions exécutives. D'autres capacités cognitives semblent également altérées, et des études ont rapporté des troubles dans la régulation des émotions (Grillon et al., 2015) et des déficits dans les prises de décisions (Smith, Zeuwts, et al., 2016).

La fatigue mentale n'a pas des répercussions uniquement sur les capacités cognitives. Il est largement reconnu que la fatigue mentale impacte également les capacités physiques. Cette relation entre fatigue mentale et capacités physiques, bien qu'elle puisse paraître surprenante, a été étudiée très tôt dans la littérature (Mosso, 1891) avant d'être quelque peu oubliée. Cependant, un regain d'intérêt concernant cette thématique est apparu depuis une dizaine d'années (Marcora et al., 2009), avec depuis de nombreuses publications.

2.2 Effets de la fatigue mentale sur les performances physiques

Le premier chercheur à investiguer les effets de la fatigue mentale sur des performances physiques fut le physiologiste italien Angelo Mosso (1891). Pour cela, il demanda à ses collègues, professeurs d'université de réaliser des contractions avant et après avoir donné des conférences. Il constata que ses collègues présentaient une diminution des leurs capacités en endurance après avoir donné des conférences. Suite à cette étude, il aura fallu attendre plus d'un siècle pour que l'on s'intéresse de nouveau à cette possible relation entre fatigue mentale et performances physiques.

2.2.1 Effets sur les performances en endurance

Les premières études « modernes », cherchant à étudier les effets de la fatigue mentale sur les performances physiques ont été menées sur des performances en endurance. Les exercices en endurance sont des exercices aérobies, sous maximaux, durant au minimum 75 secondes (Gastin, 2001). Ainsi, Marcora et al. (2009) ont mesuré l'impact d'une tâche mentalement fatigante sur un exercice de cyclisme. Les participants de cette étude ont réalisé le même exercice de cyclisme, consistant à pédaler à 80 % de leur puissance maximale aérobie le plus longtemps possible (i.e., jusqu'à épuisement), après avoir réalisé une tâche mentalement fatigante (90 minutes de la tâche d'AX-CPT) ou bien après 90 minutes passées à regarder un documentaire. Le temps avant épuisement était significativement plus court de 15 % après avoir effectué la tâche mentalement fatigante. Cet effet semble assez généralisé car une baisse du temps d'endurance a été observée chez 13 des 16 participants. La différence de performance

n'était ni associée à des changements cardiorespiratoires, ni à des changements musculoénergétiques (i.e., fréquence cardiaque, débit cardiaque, volume d'éjection systolique, pression artérielle, consommation d'oxygène, ventilation). L'unique différence observée au cours de cet exercice était le niveau de perception de l'effort durant l'exercice de cyclisme, qui était significativement plus élevé après la tâche mentalement fatigante qu'après la condition contrôle (Figure 6).

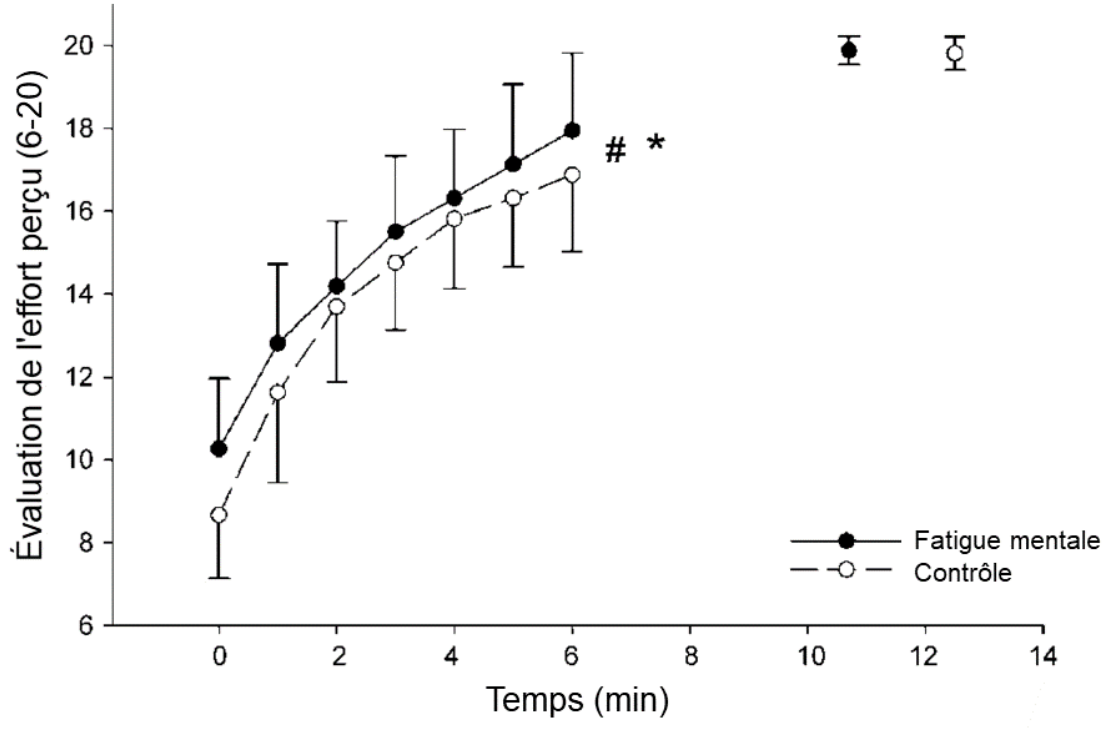


Figure 6 : Effet de la fatigue mentale sur la perception de l'effort lors d'un exercice de cyclisme à 80 % de la puissance maximale aérobie. # : effet significatif du temps ($p < .05$). * : effet significatif de la condition ($p < .05$). Adapté de Marcora et al. (2009).

Depuis cette étude, ces résultats ont été répliqués à de nombreuses reprises et sur différents exercices, comme la course à pied (MacMahon et al., 2014; Pageaux et al., 2014), le cyclisme (Pageaux et al., 2015; Salam et al., 2018), ou encore la natation (Penna et al., 2018). De plus, les effets négatifs de la fatigue mentale sur les performances en endurance ont été mis en évidence sur différents types d'exercices, comme le contre la montre (Filipas et al., 2019; Martin et al., 2016; Pires et al., 2018), le temps limite (Marcora et al., 2009; Pageaux et al., 2013), et les exercices incrémentaux (Smith, Coutts, et al., 2016; Veness et al., 2017) ou intermittents (Smith et al., 2015).

L'augmentation de la perception de l'effort semble à l'origine de la baisse des performances en endurance en présence de fatigue mentale. Cette perception de l'effort a été décrite par Noble et Robertson (1996) comme étant « l'intensité subjective de l'effort, de la tension, de l'inconfort et/ou de la fatigue qui sont ressentis pendant l'exercice physique ». Plusieurs échelles sont disponibles pour mesurer cette perception de l'effort : la « *Rating of perceived exertion* (RPE) *scale* » (Borg, 1982), la « CR10 *scale* » (Borg, 1998) ou la « CR100 *scale* » (Borg & Borg, 2001). Ces trois échelles peuvent être considérées comme fiables et valables pour mesurer la perception de l'effort dans la mesure où des procédures standardisées et normalisées sont suivies pour leur passation (Pageaux, 2016). Quand l'effort perçu devient trop important et/ou quand l'effort investi pour réaliser la tâche est trop important par rapport à la récompense attendue, on observe alors un arrêt de l'exercice ou une diminution de l'effort fourni (e.g., vitesse de course ou puissance développée), ce qui conduit à la diminution de la performance en endurance.

2.2.2 Effets sur la capacité de production de force

Bien que les études menées soient assez unanimes pour affirmer que la fatigue mentale impacte les performances en endurance, cela semble moins évident pour la capacité de production de force maximale. La première étude réalisée à ce sujet par Bray et al. (2012) montre qu'après 22 minutes de tâche de Stroop, la force de préhension étaient diminuée d'environ 10 %. Cependant, cette étude comporte quelques limites méthodologiques, comme par exemple l'absence de retour visuel sur la force produite, un facteur qui permet d'assurer une motivation maximale et une production de force maximale optimale (Gandevia, 2001). De plus, l'exercice de préhension réalisé sollicitait les muscles de l'avant-bras, muscles également potentiellement sollicités lors de la réponse manuelle à la tâche de Stroop. Ainsi la diminution de force observée pourrait être la résultante d'une fatigue physique induite par les réponses manuelles à la tâche de Stroop et non la résultante d'une fatigue mentale. Afin d'éliminer ces biais méthodologiques, cette étude a été reproduite par Rozand et al. (2014), avec un retour visuel de la force développée et une force maximale mesurée sur les extenseurs du genou. De plus, afin de compléter l'étude, trois conditions expérimentales étaient présentes : une condition « contrôle » (27 minutes à visionner un documentaire), une condition « effort mental faible » (27 minutes de Stroop congruent), et une condition « effort mental intense » (27 minutes de Stroop incongruent). Aucune diminution de la capacité de production de force n'a été observée dans aucune de ces trois conditions (Figure 7).

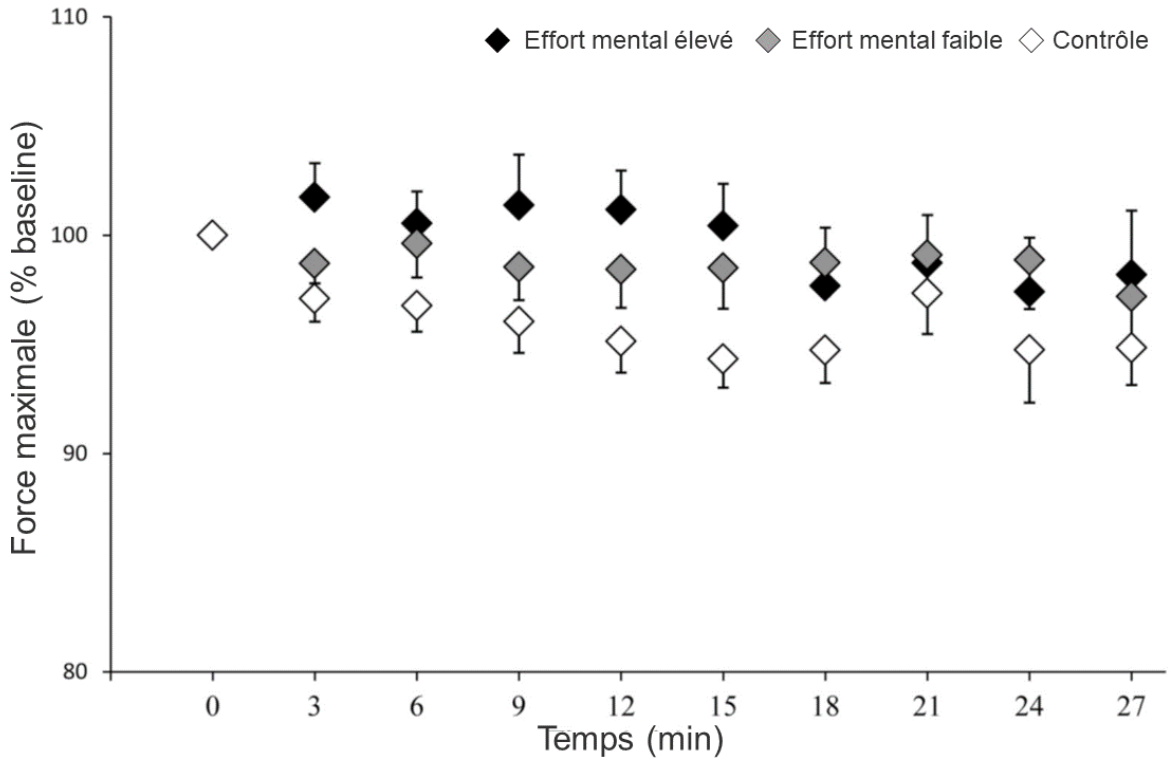


Figure 7 : Effet de la fatigue mentale sur la capacité de production de force maximale. Force maximale développée par les extenseurs du genou lors d'un effort mental élevé (noir), d'un effort mental faible (gris) et lors d'une tâche contrôle (blanc). Adapté de de Rozand et al. (2014)

Plusieurs autres études allant dans le sens de Rozand et al. (2014) ont confirmé que la fatigue mentale n'avait pas d'effet significatif sur la capacité de production de force maximale (Le Mansec et al., 2018; Pageaux et al., 2013; Smith et al., 2015).

2.2.3 Effets sur le contrôle moteur

Le terme « contrôle moteur » désigne le processus par lequel le système nerveux coordonne les muscles et les membres afin d'obtenir un mouvement ou un ensemble d'actions souhaité. Le contrôle moteur est particulièrement important dans nos activités de la vie quotidienne, il est impliqué dans la plupart de nos actions comme attraper un objet ou bien tenir en équilibre. De études ont montré que la fatigue mentale pouvait négativement impacter le contrôle moteur. Rozand et al. (2015) ont observé qu'à la suite de la réalisation d'une tâche de Stroop de 90 minutes, les performances sur une tâche de pointage étaient altérées (Figure 8). En moyenne, lors de cette étude, les mouvements étaient ralentis de 4,1 % lors de mouvements réels et de 9,6 % lors de mouvements imaginés. Ces résultats ont été répliqués à la suite d'une

tâche d'imagerie motrice prolongée avec une augmentation de la durée de mouvements de l'ordre de 18,6 % pour les mouvements réels et de 6,2 % pour les mouvements imaginés (Rozand et al., 2016). Les auteurs ont attribué l'altération de ces performances lors de tâches de pointage à une augmentation du bruit dans la commande motrice (Rozand et al., 2015). Comme en présence de fatigue physique, et afin de préserver la réussite du mouvement de pointage, ce dernier serait ralenti (Missenard et al., 2009).

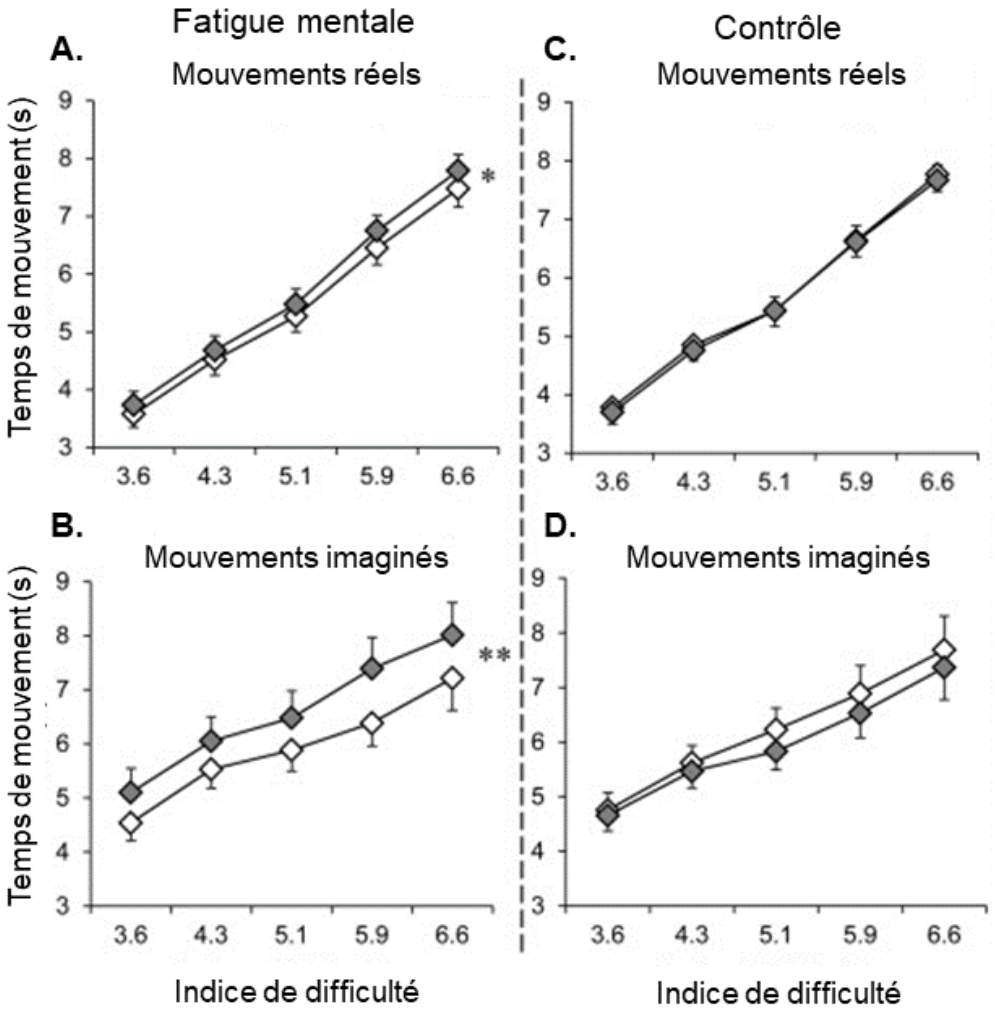


Figure 8 : Effet de la fatigue mentale sur une tâche de pointage. Durée des mouvements de pointage en prétest (blanc) et posttest (gris) pour la condition fatigue mentale (panel A : mouvements réels ; panel B : mouvements imaginés) et pour la condition contrôle (panel C : mouvements réels ; panel D : mouvements imaginés). La durée augmente avec l'indice de difficulté dans toutes les conditions ($p < .001$). * et ** : Différence significative entre les prétests et les posttests ($p < .05$ et $p <. 01$, respectivement). Adapté de Rozand et al. (2015).

Des études ont également été menées sur l'impact de la fatigue mentale sur le contrôle postural. Hachard et al. (2020) ont analysé le contrôle de l'équilibre après avoir réalisé une tâche d'AX-CPT de 90 minutes ou après avoir regardé un documentaire pendant une durée équivalente. Les résultats révèlent une altération du contrôle de l'équilibre après la tâche mentalement fatigante, mais également à la suite de la condition contrôle. Cependant les mécanismes pour expliquer l'altération du contrôle de l'équilibre dans les deux conditions diffèraient. Dans le cas de la fatigue mentale, l'altération du contrôle de l'équilibre serait due à une altération des processus attentionnels, alors que pour la condition contrôle cela s'expliquerait par un effet négatif d'une assise prolongée lors du visionnage du documentaire. Ces résultats en faveur d'une altération du contrôle de l'équilibre en présence de fatigue mentale ont également été retrouvés après 60 minutes de tâche mentalement fatigante chez des personnes âgées saines et des patients ayant subi un accident vasculaire cérébral (Varas-Diaz et al., 2020) ainsi qu'après une période de privation de sommeil de 12 heures (Ma et al., 2009).

2.2.4 Effets sur les performances sportives

Bien que la capacité de production de force semble préservée, la fatigue mentale semble impacter de façon négative les capacités d'endurance et altérer le contrôle moteur, il n'est donc pas étonnant que très rapidement, des études aient investigué les effets de la fatigue mentale sur les performances sportives. Parmi les sports les plus concernés par les investigations sur les effets de la fatigue mentale, on retrouve le football (Kunrath et al., 2020). Alors que les premières études se sont concentrées sur les effets de la fatigue mentale sur les performances physiques des footballeurs (Smith, Coutts, et al., 2016; Smith et al., 2015), très vite Smith, Coutts, et al. (2016) se sont intéressés aux compétences techniques. Pour évaluer les compétences techniques en football, des tests de passe et de tir pour le football de *Loughborough* ont été réalisés après la réalisation d'une tâche de Stroop de 30 minutes ou la lecture de magazines pendant une durée équivalente. Les résultats ont indiqué une diminution de la précision et de la vitesse des tirs. Ces résultats, indiquant une altération des performances techniques en football après une tâche mentalement fatigante, ont également été mis en lumière dans d'autres études avec une diminution de la précision des passes (Badin et al., 2016; Smith et al., 2017), de la précision des tacles (Badin et al., 2016) ou encore une altération dans les prises de décision (Gantois et al., 2020). Afin de rendre compte de ces différentes altérations, un modèle a été développé par Smith et al. (2018, Figure 9).

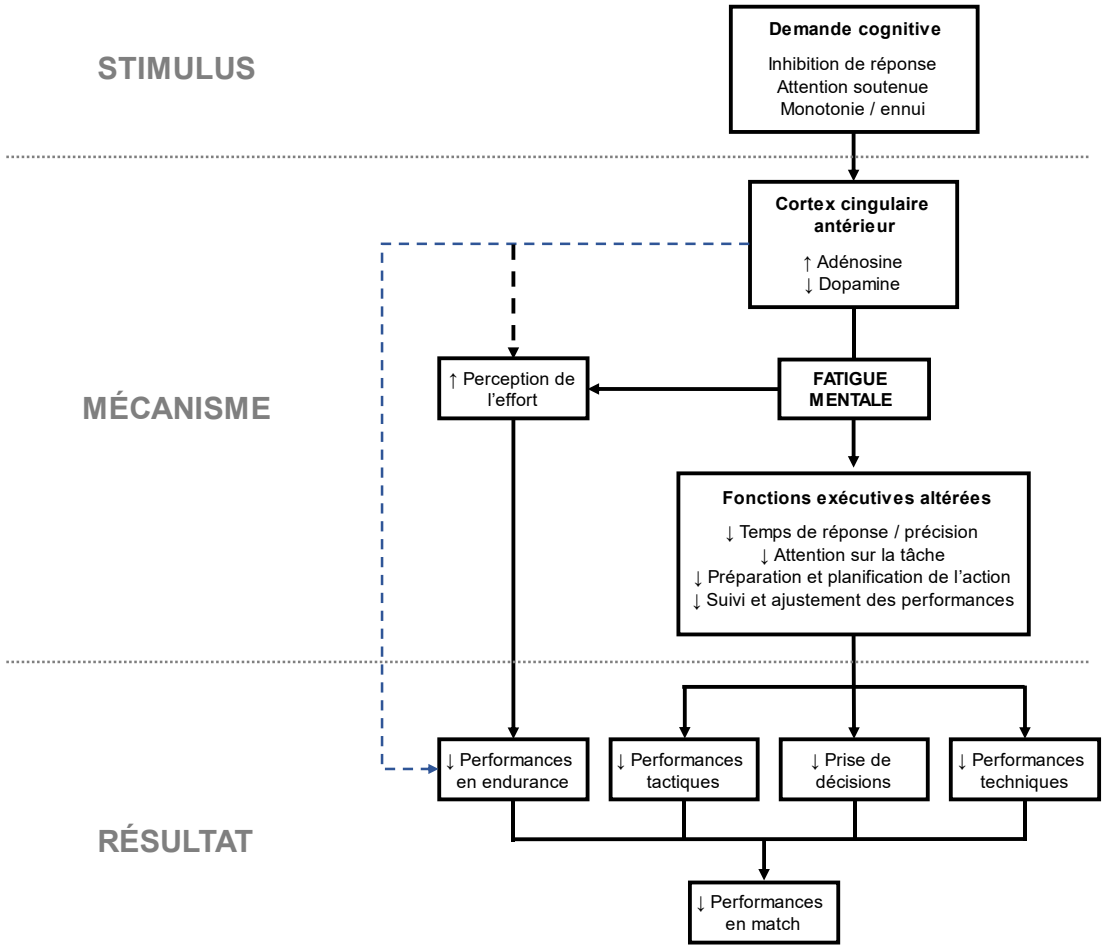


Figure 9 : Modèle conceptuel pour expliquer les effets délétères de la fatigue mentale sur les performances en football. La ligne bleue indique des preuves issues de la recherche animale, et la ligne pointillée indique un mécanisme proposé manquant de preuves empiriques. Adapté de Smith et al. (2018)

Le football n'est cependant pas la seule activité sportive impactée. Des études ont également montré un déclin des performances lors d'autres sports collectifs comme le basketball (Moreira et al., 2018) ou le handball (Macedo Penna et al., 2017) mais aussi dans d'autres activités comme le tennis de table (Le Mansec et al., 2018), le kayak (Staiano et al., 2019) ou le cricket (Veness et al., 2017). Ainsi la fatigue mentale semble être un facteur limitant dans de nombreuses activités sportives. Dans ce contexte, il peut être important de prendre ce facteur en compte dans la préparation et l'entraînement des sportifs afin d'améliorer et d'optimiser leurs performances lors de compétitions.

2.2.5 Conclusion

Bien que les études menées jusqu'à présent et les récentes revues de littérature (Brown et al., 2020; Pageaux & Lepers, 2018; Van Cutsem, Marcora, et al., 2017) semblent assez unanimement montrer des effets négatifs de la fatigue mentale sur les performances physiques, notamment en endurance, une récente méta-analyse montre que même si les effets d'une tâche cognitivement coûteuse réalisée pendant 90 minutes ou moins peut induire un déclin des performances physiques, cet effet resterait faible (McMorris et al., 2018).

2.3 Les effets de la fatigue mentale sur la vie quotidienne

Impactant à la fois nos performances cognitives et physiques, la fatigue mentale a naturellement des effets sur notre vie quotidienne. Ce sont d'ailleurs ces effets de la fatigue mentale sur notre vie quotidienne qui en ont fait un sujet de plus en plus étudié par la communauté scientifique. L'évolution des modes de vies, la sédentarisation (e.g., télévision, Internet, jeux vidéo), le développement des emplois dans le secteur tertiaire (notamment dû à la mécanisation) sont autant de facteurs pouvant favoriser l'omniprésence de la fatigue mentale dans la société moderne. Dans la population, on estime que 18 à 27 % des personnes se plaignent de fatigue (Dawson et al., 2012), ce qui coûte plus de 18 milliards de dollars par an aux États-Unis, par exemple. Alors même si la fatigue mentale n'est pas l'unique facteur de ces plaintes, elle y contribue largement. Les employés de bureau ne sont pas les seuls touchés, le corps médical est également impacté. Des études ont montré qu'en présence de fatigue mentale les erreurs médicales augmentaient que ce soit chez les infirmières (Nikpeyma & Gholamnejad, 2009) ou les médecins (Tawfik et al., 2018). D'autres corps de métier comme les militaires ou les pilotes d'avions (Karanikas & Nederend, 2019) sont également touchés, et ceci n'est que quelques exemples d'une longue liste.

Parmi les autres répercussions majeures de la fatigue mentale, comment ne pas évoquer son impact sur la conduite automobile. On suppose que 10 à 30 % des décès sur la route sont liés à une sensation de fatigue du conducteur (Karanikas & Nederend, 2019), la fatigue provoquant une baisse des capacités à maintenir la position du véhicule dans les voies de circulation (Du et al., 2014) ou une augmentation des temps de réaction (Ting et al., 2008).

Il est donc primordial de poursuivre les investigations et les études sur ce phénomène afin de mieux l'appréhender et d'essayer d'en limiter les effets. Depuis quelques années les

chercheurs ont essayé de trouver des stratégies, que nous détaillerons ci-après, afin de contrer ou au moins de limiter les effets de la fatigue mentale.

Bien que nous ayons vu que la fatigue mentale avait de nombreuses répercussions tant sur les performances physiques que cognitives pouvant impacter de façon négative nos activités quotidiennes, il n'est cependant pas toujours simple d'attester de la présence de fatigue mentale. Les marqueurs permettant d'attester de la présence de fatigue mentale restent encore discutés. Plusieurs méthodes, subjectives par le biais de questionnaires ou d'échelles, ou objectives à travers des mesures physiologiques, ont été utilisées pour attester de la présence de fatigue mentale.

La fatigue mentale détériore nos performances qu'elles soient cognitives ou physiques. Pour les performances cognitives, la fatigue mentale impacte principalement nos capacités d'attention, de planification et nos prises de décisions. Cependant, il semble que ces capacités soient d'avantages altérées lors de tâches subséquentes à une tâche cognitive prolongée. Lors des tâches cognitives prolongées, certaines personnes semblent capables de maintenir leur niveau de performance. Une motivation importante pourrait être à l'origine de ce phénomène. Concernant les performances physiques, toutes ne sont pas impactées de la même manière par la fatigue mentale. Alors que la capacité de production de force maximale semble préservée, les performances en endurance et les tâches relatives au contrôle moteur sont, elles à l'inverse, détériorées en présence de fatigue mentale. Ces altérations des fonctions cognitives et physiques en présence de fatigue mentale impactent négativement nos performances dans nos activités sportives, mais pas seulement. Elles engendrent également des répercussions négatives dans notre vie quotidienne, lors de nos déplacements (e.g., augmentation du risque d'accident), lors de notre travail (e.g., baisse de productivité, augmentation des risques d'accidents), ou sur notre psychisme (e.g., risque de dépression, de burnout).

2.4 Les marqueurs subjectifs de la fatigue mentale

Les méthodes subjectives d'évaluation de la fatigue ont été les premières à être utilisées pour attester la présence de fatigue mentale, bien avant l'utilisation de marqueurs plus objectifs comme l'enregistrement de l'activité cardiaque, oculaire ou cérébrale. Fait intéressant, la sensation subjective de fatigue apparaîtrait avant même que ses effets soient observables au niveau comportemental. Thorndike (1899) explique cela par le fait que la sensation de fatigue serait en fait un signal d'alarme donné par l'organisme indiquant à l'individu qu'il est temps de stopper ce qu'il est train de réaliser sans quoi il perdrait en efficacité. Grâce à leur facilité et leur rapidité de passation, plusieurs méthodes d'évaluation subjective de la fatigue ont été développées.

2.4.1 L'échelle visuelle analogique

L'échelle visuelle analogique (VAS) est généralement une ligne de 100 mm de longueur avec des descripteurs verbaux situés aux deux extrémités, en fonction de la variable observée. Une récente revue systématique de la littérature (Yeung & Wong, 2019) a montré que la première utilisation d'une VAS datait de 1921 (Hayes, 1921). Depuis, cette méthode a été couramment utilisée pour évaluer la douleur (Langley & Sheppeard, 1985; Woodforde & Merskey, 1972), l'anxiété (Hornblow & Kidson, 1976; van Duinen et al., 2008), ou encore la fatigue mentale (Lee et al., 1991). Dans le cadre de la fatigue mentale, les descripteurs verbaux utilisés comme bornes sont généralement « Pas du tout fatigué mentalement » et « Extrêmement fatigué mentalement » (voir Figure 10; Smith et al., 2019). Une critique qui peut être émise concernant ces descripteurs verbaux est qu'ils ne sont pas reportés dans la méthodologie de toutes les études ce qui peut rendre les résultats critiquables et impossibles à reproduire (Cook et al., 2007; Coutinho et al., 2018; Ishii, Tanaka, Iwamae, et al., 2013).

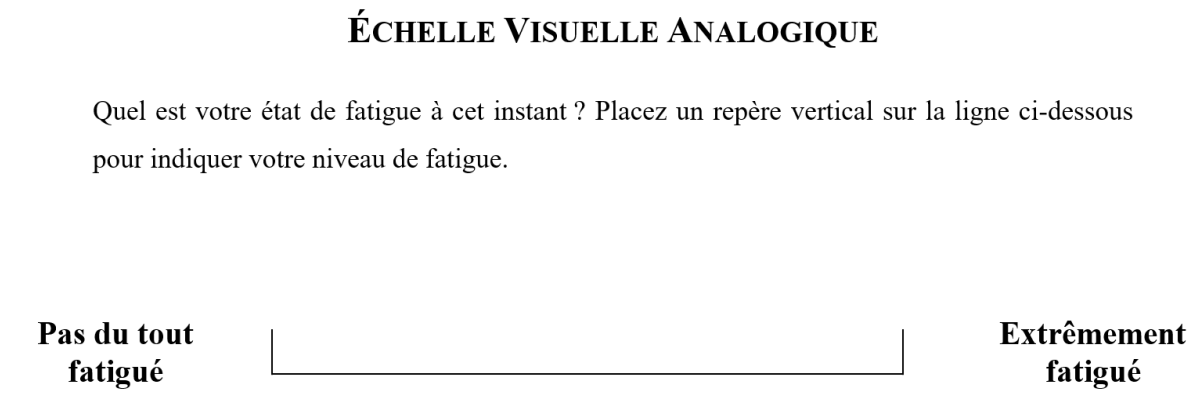


Figure 10 : Échelle visuelle analogique (VAS) permettant d'évaluer la fatigue mentale.

Aujourd'hui, cette échelle d'évaluation subjective a été reconnue comme étant la méthode la plus pratique pour attester de présence de fatigue mentale et est considérée comme un *Gold standard* (Smith et al., 2019), même s'il semblerait que cette échelle ne soit pas assez sensible pour dissocier fatigue mentale et somnolence (LaChapelle & Finlayson, 1998).

2.4.2 L'échelle d'humeur de Brunel

L'échelle d'humeur de Brunel a été développée par Terry et al. (1999) puis Terry et al. (2003). Dans la littérature, on la retrouve sous l'appellation BRUMS (*Brunel Mood Scale*). Cette échelle est composée de 24 items divisés en six sous-catégories : la colère, la confusion, la dépression, la fatigue, la tension et la vigueur. Pour chaque item (e.g., énervé, vif, désorienté, fatigué, hésitant), les participants doivent noter leur ressenti avec une note allant de 0 à 4 (0 = pas du tout, 1 = un peu, 2 = modérément, 3 = beaucoup, 4 = extrêmement). Cette échelle est en réalité une version raccourcie du questionnaire de POMS (*Profile Of Mood States*) constitué de 65 items (McNair et al., 1971).

L'échelle d'humeur de Brunel est couramment utilisée pour attester la présence de fatigue mentale. Tous les items ne sont cependant pas nécessaires, et en général seulement deux items sont conservés : la fatigue et la vigueur (Rozand et al., 2015). Une courte méta-analyse a été réalisée par Slimani et Bragazzi (2017) sur les effets de la fatigue mentale associés à l'item « Vigueur » de l'échelle de Brunel. Bien que cette mini méta-analyse ne comporte que six études, il a été constaté que la fatigue mentale n'avait pas d'impact sur le score de vigueur. Ceci peut être expliqué par le fait que les tâches contrôles peuvent également induire une diminution

de la vigueur (Marcora et al., 2009; Pageaux et al., 2013). Cependant, le résultat de cette mini méta-analyse reste contestable du fait du faible nombre d'études incluses. On note d'ailleurs que des études, non-incluses, ont reporté une diminution significative du score de vigueur avec l'instauration de la fatigue mentale (Rozand et al., 2015). Concernant l'item « Fatigue », les effets de la fatigue mentale semblent beaucoup plus consistants. Toutes les études reportent en effet une augmentation significative sur l'item « Fatigue ».

Si l'utilisation de l'échelle de Brunel pour attester la présence de fatigue mentale a été largement acceptée, la passation de l'ensemble du questionnaire ne semble pas nécessaire et seul l'item « Fatigue » peut être conservé. Une limite existe cependant concernant l'utilisation de ce questionnaire, aucune distinction n'est faite entre la fatigue d'origine mentale et la fatigue d'origine physique. Ainsi si l'on utilise des tâches cognitives standardisées devant un ordinateur (e.g., tâche de Stroop ou tâche de TLDB), l'utilisation de ce questionnaire peut être appropriée, en revanche si l'on s'intéresse à la fatigue mentale induite lors de conditions écologiques, travail en usine ou lors d'un match de football par exemple, l'utilisation de ce questionnaire ne semble pas des plus opportunes, car elle ne permettra pas de différencier la fatigue mentale de la fatigue physique.

2.4.3 Le National Aeronautics and Space Administration Task Load Index

Le NASA-TLX (*National Aeronautics and Space Administration Task Load Index*) est un questionnaire développé par Hart et Staveland (1988), principalement utilisé pour évaluer, de manière subjective, la charge de travail et l'exigence d'une tâche. Ce questionnaire est composé de six sous-échelles permettant de mesurer (1) la charge mentale (« Quelle était la difficulté mentale de la tâche ? »), (2) la charge physique (« Quelle était la difficulté physique de la tâche ? »), la contrainte temporelle (« Comment avez-vous ressenti la pression temporelle lors de la réalisation de la tâche? »), la performance (« Avez-vous réussi à accomplir la tâche demandée »), l'effort (« À quel point l'exercice fut-il difficile à accomplir ? »), et la frustration (« Étiez-vous stressé, découragé, agacé, inconfortable ? »). Les participants doivent noter chacun des éléments sur une échelle divisée en 20 intervalles égaux ancrés par un descripteur bipolaire (e.g., haut/bas). Ce score est ensuite multiplié par 5, pour donner un score final compris entre 0 et 100 pour chacune des sous-échelles.

Dans le cadre des études concernant la fatigue mentale on observe que les tâches mentalement fatigantes ont pour principal effet d'augmenter la charge mentale et/ou l'effort

demandé. Cependant il n'existe pas de « valeur seuil », pour attester qu'une tâche cognitive est exigeante. L'utilisation de ce questionnaire permet de comparer plusieurs tâches cognitives entre elles, et/ou de la/les comparer avec une tâche contrôle. Les études concernant la fatigue mentale présentent souvent un plan expérimental avec deux conditions : une condition mentalement fatigante (e.g., tâche de Stroop, *Time Load Dual Back*) et une condition contrôle (e.g., visionnage d'un documentaire, tâche cognitive simple). En définitif, ce questionnaire permet d'évaluer l'exigence d'une tâche et non pas d'attester de la présence de fatigue mentale. Le caractère multidimensionnel de ce questionnaire permet cependant de différencier les origines de la fatigue et permet notamment de distinguer et de différencier la fatigue mentale et la fatigue physique, ce qui n'est pas réalisable avec l'échelle d'humeur de Brunel.

Pour conclure, les différents questionnaires présentent chacun leurs avantages et leurs inconvénients pour attester et identifier la présence de fatigue mentale. Le principal avantage qui ressort de l'utilisation de ces différents questionnaires est qu'ils sont très simples à mettre en place, peu coûteux, rapides et efficaces pour repérer, de façon subjective, la présence de fatigue mentale. Comme indiqué précédemment, des auteurs ont même considéré que l'évaluation de la présence de fatigue mentale grâce à une VAS pouvait être considérée comme un *Gold standard* et comme étant la manière la plus efficace pour mettre en évidence la présence de fatigue mentale.

2.5 Les marqueurs physiologiques objectifs de la fatigue mentale

Outre les marqueurs subjectifs présentés précédemment, des marqueurs objectifs peuvent également être utilisés pour mettre en évidence la présence de fatigue mentale. Plusieurs techniques enregistrant des mesures physiologiques ont été utilisées comme l'électrocardiographie (Mascord & Heath, 1992), l'oculométrie (Martins & Carvalho, 2015) ou l'électroencéphalographie (Tran et al., 2020). Nous commencerons cette partie par la dernière méthode citée car elle a été reconnue comme étant la plus prometteuse pour attester de la présence de fatigue mentale (Lal & Craig, 2001) et ce sera utilisée dans toutes les études conduites dans ce travail de thèse.

2.5.1 L'électroencéphalographie

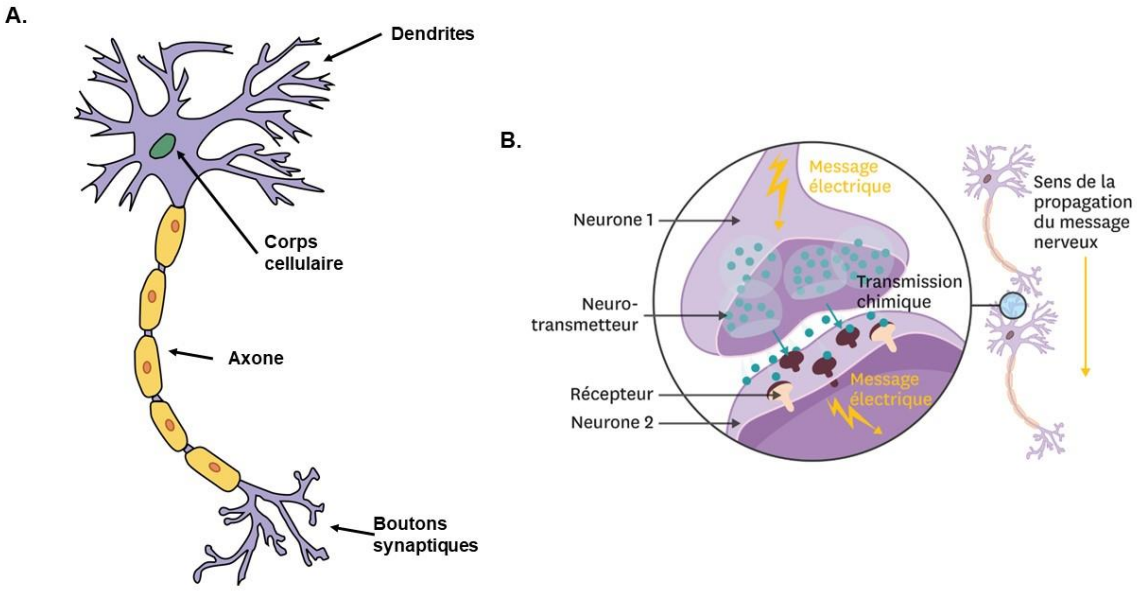
2.5.1.1 Définition et historique de l'EEG

L'EEG est une technique d'exploration cérébrale permettant d'enregistrer l'activité électrique émanant du cerveau via des électrodes. Si les électrodes sont placées à la surface du scalp, on appelle alors l'enregistrement obtenu un électroencéphalogramme (méthode la plus couramment utilisée), si les électrodes sont placées sur le cortex cérébral on appelle alors le tracé un électrocorticogramme, et si les électrodes sont implantées directement dans les structures cérébrales on parle alors de stéréoélectroencéphalographie. Richard Caton fut le premier à découvrir qu'il y avait une activité électrique dans le cerveau grâce à une étude réalisée sur le singe et sur le lapin en 1875 (Caton, 1875). Il fallut attendre plus de 50 ans, et 1929 pour être précis, avant que Hans Berger n'enregistre une activité électrique issue d'un cerveau humain (Berger, 1929). Cette activité électrique, qui provient des neurones, est un indicateur de l'activité corticale et donc plus précisément de l'activité neuronale du cerveau. Si au début les variations de l'activité corticale étaient observées via les mouvements de l'aiguille d'un galvanomètre, l'inscription à jet d'encre (ancêtre de notre imprimante moderne) introduite par Grass en 1935 a permis de visualiser les tracés de l'activité cérébrale sur papier. Depuis les techniques ont grandement évolué, notamment grâce à l'avènement de l'aire de l'informatique et des ordinateurs, il est possible d'enregistrer et de visualiser presque instantanément l'activité cérébrale enregistrée par des systèmes comprenant plusieurs centaines d'électrodes.

2.5.1.2 Bases électrophysiologiques

Le cerveau, aussi appelé encéphale, appartient au système central et a de nombreuses fonctions, allant des plus inconscientes comme la gestion du rythme cardiaque ou la sécrétion d'hormones jusqu'aux plus élaborées comme le raisonnement ou le contrôle de la motricité. Le cerveau est divisé en quatre lobes : les lobes frontal, pariétal, temporal et occipital. Chaque lobe est associé à de grandes fonctions : le lobe frontal est responsable notamment de la parole, du raisonnement, de la mémoire, de la prise de décision, ou encore de la motricité ; le lobe pariétal de la lecture, du repérage dans l'espace ou de la sensibilité ; le lobe temporal du langage, de la mémoire ou des émotions ; et le lobe occipital de la vision. Un physiologiste allemand, Brodmann a subdivisé le cerveau de façon plus fine, en 52 zones selon la fonctionnalité de ces zones.

Le cortex cérébral est constitué de neurones situés dans la matière grise. On estime leur nombre entre 10 et 100 milliards. Le rôle des neurones est de recevoir, traiter et transmettre les informations. Un neurone est composé de trois parties bien distinctes (Figure 11, panel A) : le noyau (ou péricaryon), les dendrites et l'axone. La communication neuronale est possible grâce à deux modes de transmission de l'influx nerveux, la transmission par le potentiel d'action (PA) et la transmission par les potentiels post-synaptiques (PPS). Les PA se propagent le long de l'axone à vitesse constante et sans atténuation en fonction de plusieurs paramètres dont l'épaisseur de la gaine de myéline et du diamètre de l'axone. Ces PA sont très transitoires et ont une durée de 1 à 3 ms, en revanche leur amplitude est importante, environ 100 mV. Le PA a toujours la même amplitude une fois généré, ce n'est donc pas son amplitude mais sa fréquence qui code sa valeur informative. Les PPS sont quant à eux générés au niveau de la synapse (zone de contact entre deux neurones, Figure 11, panel B). Lorsqu'il arrive au bout de l'axone, au niveau des boutons terminaux, le PA permet la libération de neurotransmetteurs au niveau de la fente post-synaptique. Ces neurotransmetteurs se fixent sur des récepteurs du neurone post-synaptique et permettent ainsi la transmission de l'influx nerveux, ou message nerveux. Les PPS peuvent être de deux natures : excitateurs ou inhibiteurs. Les PPS excitateurs favorisent le déclenchement d'un PA dans le neurone post-synaptique alors que les PPS inhibiteurs empêchent de ce déclenchement. Les PPS se propagent le long des dendrites jusqu'au corps cellulaire du neurone. Au niveau de ce corps cellulaire, le rapport entre PPS excitateur et inhibiteur est réalisé, si le rapport en est en faveur des PPS excitateurs, alors un nouveau PA est généré, si à l'inverse le rapport est en faveur des PPS inhibiteurs, alors la propagation du PA s'arrête.



<u>Figure 11 :</u> Représentation schématique d'un neurone (A), et d'une synapse chimique (B). Interface chimique entre deux neurones permettant la propagation d'un potentiel d'action.

L'activité recueillie à la surface du scalp dépend en fait beaucoup plus des PPS, qui sont plus persistants, que des PA, trop éphémères (Elul, 1972). Par ailleurs, ce n'est pas l'activité d'un seul neurone qui est enregistrée mais l'activité d'un groupe de neurones, estimés entre 10^7 et 10^9 neurones (Nunez, 1981). Une activité ne peut être enregistrée que si de nombreux signaux ont lieu de façon synchrone (i.e., un signal similaire émis en même temps).

Grâce à des électrodes placées sur le scalp de façon normalisée selon le Système International 10-20 (Figure 12), nous sommes en mesure d'enregistrer via ces électrodes l'activité électrique des neurones. Ce placement standardisé des électrodes selon le Système International 10-20 a été initié lors du premier congrès EEG qui s'est tenu à Londres en 1947. Il permet ainsi de s'accorder sur le placement de chaque électrode. Les électrodes sont localisées sur l'axe antéro-postérieur grâce à des lettres (e.g., « F » : Frontal, « C » : Central, « P » : Pariétal, « O » : Occipital), tandis qu'elles sont repérées sur l'axe médio-latéral grâce à des nombres. Les électrodes avec un nombre pair (e.g., C2) sont situées au niveau de l'hémisphère droit, les électrodes avec un nombre impair (e.g., C1) au niveau de l'hémisphère gauche, et les électrodes se situant en position médiane, sur la ligne allant du nasion à l'inion se terminent par la lettre « z » (e.g., Cz).

2.5.1.3 Méthodologie d'enregistrement

L'activité EEG est donc le plus communément recueillie à la surface du scalp grâce à des électrodes positionnées de manière standardisée. Ce n'est pas une activité électrique qui est directement enregistrée mais une différence de potentiel par rapport à une ou des électrodes de référence. Pour le placement de ces électrodes de référence il faut choisir un site le plus « neutre » possible, non-affecté par l'activité électrique. Il est conseillé de prendre en compte trois facteurs dans le choix du positionnement de la ou des électrode(s) de référence. Le premier est de choisir un endroit aussi confortable que possible afin de ne pas gêner le participant, le second de choisir des sites déjà utilisés dans des études précédentes pour permettre des comparaisons et, enfin, troisièmement, le point le plus important est d'éviter un site qui est biaisé vers un hémisphère en sélectionnant un site à distance égale de toutes les électrodes. Généralement, les sites les plus utilisée sont les lobes des oreilles ou bien les mastoïdes (petits os situés derrière les oreilles). Luck (2005) conseille tout de même de positionner les électrodes de référence sur les mastoïdes car il est plus facile d'y obtenir une bonne connexion. Enfin l'utilisation d'une électrode de masse (généralement en position frontale) est conseillée pour prévenir l'accumulation de charges statiques (Picton et al., 2000) et prévenir le bruit dans le signal EEG (Butler, 1993). Certains systèmes, comme le système BIOSEMI utilisé au cours de ce travail de thèse, ont choisi de remplacer cette électrode de masse par deux électrodes distinctes situées sur le scalp : CMS (*Common Mode Sense* ; électrode active idéalement placée au centre des électrodes de mesure) et DRL (*Driven Right Leg* ; électrode passive idéalement placée loin des électrodes de mesure).

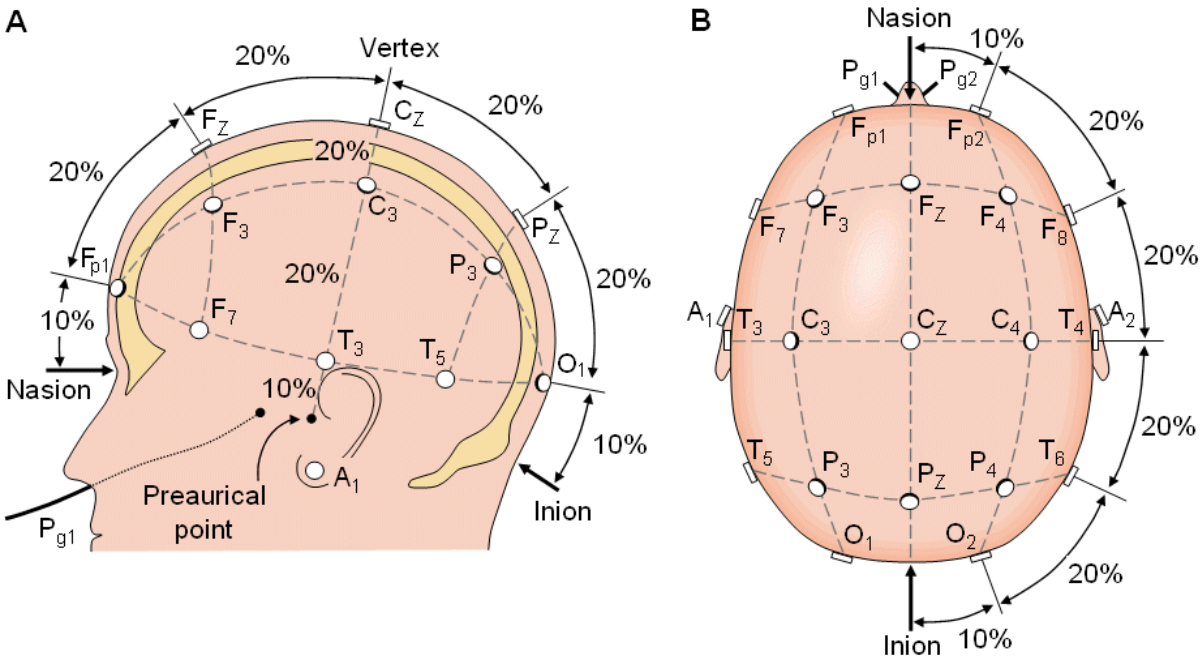


Figure 12 : Placement des électrodes EEG selon le Système International 10-20 (Malmivuo & Plonsey, 1995).

Cette activité électrique permet de déterminer l'activation des différentes aires cérébrales. Cette technique non-invasive peut être utilisée aussi bien chez l'adulte que chez l'enfant, ainsi que sur la personne saine ou pathologique. Grâce à cette technique, on dispose d'une très bonne résolution temporelle mais d'une résolution spatiale plus faible que celle de l'IRMf.

2.5.1.4 Les modalités de l'analyse électroencéphalographique

Une fois que le signal EEG est enregistré, nous disposons de plusieurs méthodes afin d'analyser ce qui se passe au niveau cérébral. Nous pouvons réaliser principalement deux grands types d'analyses, des analyses fréquentielles et des analyses temporelles. Enfin, il faut savoir que même si la résolution spatiale est faible en EEG, il est possible d'effectuer des analyses spatiales en effectuant de la localisation de source, notamment grâce à la méthode LORETA (*Low Resolution Electrical Tomography* ; Pascual-Marqui et al., 1994), nous permettant ainsi de connaître la source de l'activation liée à un événement.

- **Les analyses fréquentielles**

De façon spontanée, une activité électrique de base est toujours présente au sein du cerveau, une absence d'activité électrique au niveau cérébral signifiant un état de mort

cérébrale. Cette activité spontanée, de nature périodique, peut être séparée en différentes bandes de fréquence en fonction de sa fréquence d'oscillation (Figure 13). La fréquence d'oscillation est exprimée en Hertz (Hz) et est définie par le nombre de cycles observés en 1 seconde. Classiquement le spectre de fréquence est divisé en cinq bandes de fréquence :

- Bande delta : < 4 Hz
- Bande thêta : 4-7 Hz
- Bande alpha : 8-12 Hz
- Bande bêta : 12-30 Hz
- Bande gamma : > 30 Hz

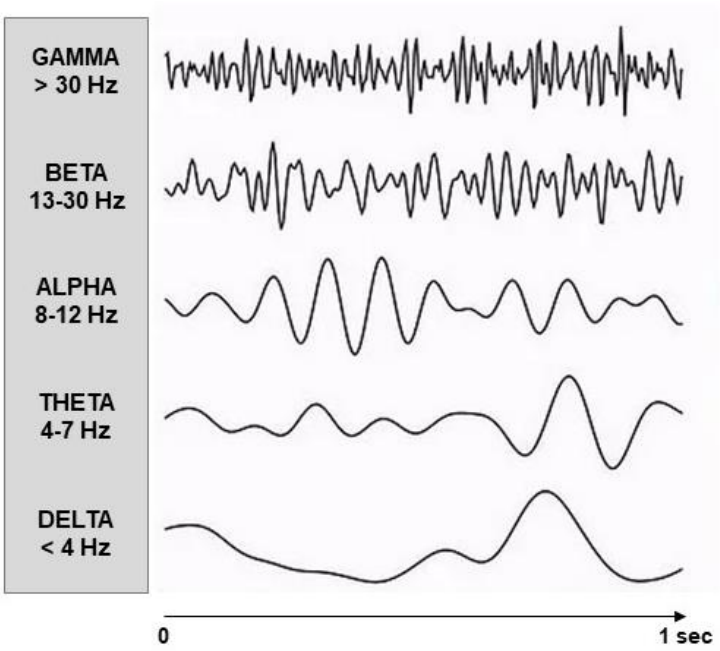


Figure 13 : Illustration des oscillations cérébrales. On distingue classiquement cinq bandes de fréquences pour les oscillations cérébrales : delta (< 4 Hz), thêta (4-8 Hz), alpha (8-12 Hz), bêta (12-30 Hz) et gamma (> 30 Hz).

Cette décomposition du signal EEG complexe en plusieurs bandes de fréquence repose sur la théorie de Fourier qui dit que tout signal périodique peut être décomposé en une somme d'ondes sinusoïdales. Ainsi nous pouvons passer d'un signal complexe non-exploitable à des signaux sinusoïdaux, plus simples, nous permettant de nous renseigner sur l'état cérébral.

C'est à cette activité fréquentielle que se sont intéressées les premières études EEG sur l'homme. Hans Berger (1929) observa une augmentation des ondes alpha lorsque les

participants de son expérience avaient les yeux fermés. Depuis les ondes alpha ont largement été rattachées à un état de relaxation et à l'état de sommeil.

- **Les analyses temporelles ou analyses de potentiels évoqués**

Une seconde manière de procéder est d'observer la réaction d'une population de neurones à la suite d'un événement qui peut être externe (e.g., la présentation d'une image, une stimulation auditive) ou interne (e.g., activité cognitive, réalisation d'un mouvement). La réaction de ce groupe de neurones crée un courant électrique avec une polarité positive ou négative (selon le placement des électrodes de référence) qui est caractérisée non seulement par sa polarité mais également par son amplitude, sa latence ainsi que sa localisation topographique. On parle de potentiel évoqué, composante ou onde. La composante N100, par exemple, est une onde négative qui apparaît environ 100 ms après l'apparition de la stimulation, et la composante P300 est une onde positive qui apparaît environ 300 ms après le début de la stimulation (Figure 14). Les ondes sont toujours relatives à un niveau de base, appelé *baseline*, qui est souvent mesuré avant l'apparition de la stimulation, ce qui permet d'atténuer le bruit contenu dans le signal. Afin d'obtenir des résultats interprétables, il est nécessaire de moyenner un grand nombre d'essais pour extraire le signal du bruit de fond. Le nombre d'essais à moyenner dépend du ratio signal/bruit. Plus le bruit sera élevé et/ou plus l'onde observée sera de faible amplitude, plus il faudra moyenner d'essais.

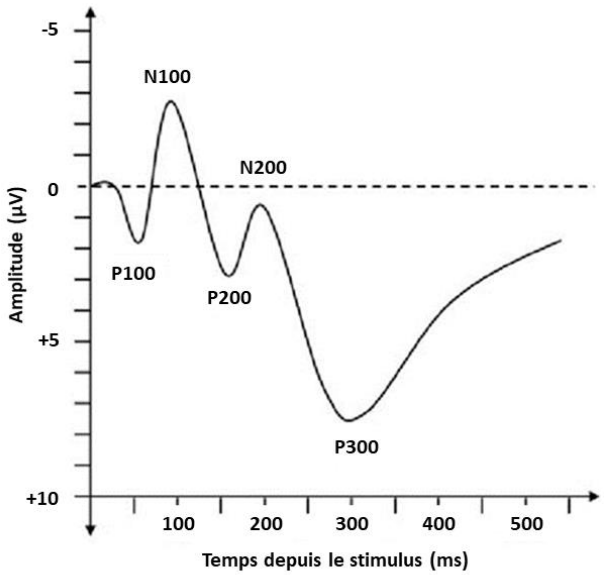


Figure 14 : Représentation de potentiels évoqués.

2.5.1.5 Marqueurs électroencéphalographiques de la fatigue mentale

- **Principaux effets sur les oscillations cérébrales**

Dès 1946, une étude s'est intéressée aux variations induites par une tâche mentalement fatigante sur les ondes alpha en région occipitale (Barnes & Brieger, 1946). Les résultats ne furent cependant que peu probants. Sur 27 participants, quatre participants n'avaient pas d'ondes alpha, quatre présentaient une augmentation de l'alpha, sept présentaient une diminution de l'alpha et enfin chez 12 participants il n'y avait aucune modification de l'onde alpha au cours du temps. De nombreuses études ont été réalisées depuis, et elles semblent assez unanimes pour indiquer qu'une augmentation des ondes alpha est observée avec l'instauration de la fatigue mentale (Arnau et al., 2017; Zhao et al., 2012), même si quelques études révèlent parfois une diminution (Ishii, Tanaka, Shigihara, et al., 2013; Tanaka, Shigihara, et al., 2012). Malgré ces quelques études divergentes, la majorité des études s'accorde pour dire qu'en présence de fatigue mentale une augmentation des ondes alpha est observée (pour revue : Lal & Craig, 2001; Tran et al., 2020). Une étude portant sur la conduite automobile a montré que les ondes alpha étaient significativement plus présentes lors des cinq dernières minutes de la tâche de conduite que lors des cinq premières au niveau des régions centrale, pariétale, occipitale et temporale (Figure 15). Cette augmentation des ondes alpha au cours d'une tâche de conduite automobile a été reportée dans d'autres études (Borghini et al., 2014; Lal & Craig, 2002), notamment lors de tâches prolongées d'attention visuelle classiquement utilisées pour induire la fatigue mentale (Boksem et al., 2005; Fan et al., 2015; Wascher et al., 2014). Il a été montré dans la littérature que les ondes alpha diminuaient avec l'allocation de l'attention (Herrmann & Knight, 2001) et avec l'augmentation des exigences en matière de mémoire de travail (Klimesch, 2012). Ainsi une augmentation de l'alpha en condition de fatigue mentale pourrait refléter un retrait attentionnel ou un désengagement de la tâche (Wascher et al., 2016; Wascher et al., 2014).

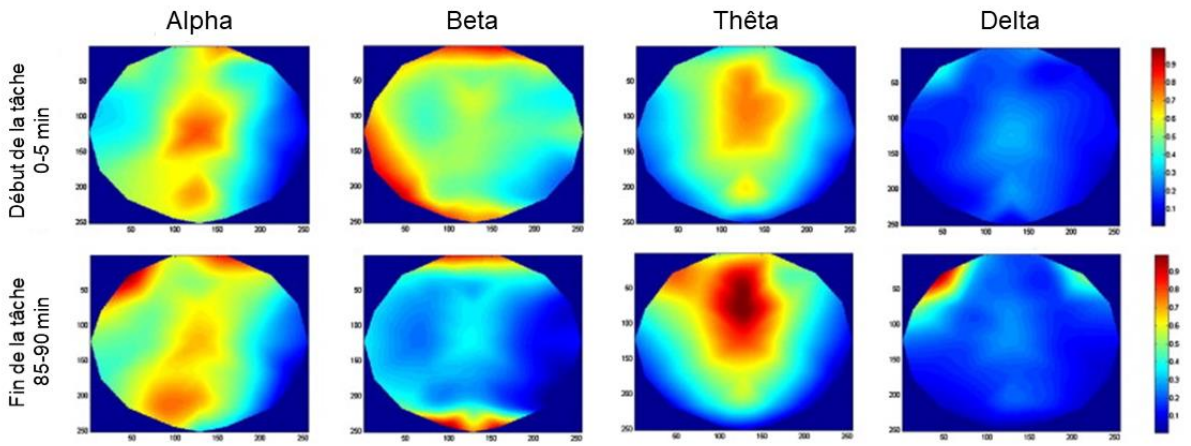


Figure 15 : Évolution des oscillations cérébrales lors d'une tâche mentalement fatigante. On observe ici l'évolution des ondes Alpha, Bêta, Thêta et Delta au cours d'une tâche de conduite automobile (5 premières versus 5 dernières minutes). Adapté de Zhao et al. (2012).

Cependant bien que très courante, l'augmentation de l'alpha au cours d'une tâche cognitive n'est pas toujours rapportée. Lorsque les tâches cognitives sont très exigeantes, un maintien de l'alpha est observé pour rester impliqué dans la tâche (Fairclough & Venables, 2006). L'augmentation des ondes alpha serait la transition entre la charge de travail mental et la fatigue mentale (Borghini et al., 2014). Une récente revue systématique avec méta-analyse (Tran et al., 2020) a indiqué que l'augmentation des ondes alpha était un marqueur robuste de la fatigue mentale et quelle était localisée notamment au niveau des régions centrale et postérieure (pariétale et occipitale). Dans cette même méta-analyse, les auteurs ont suggéré que les ondes thêta serait un marqueur encore plus fiable de la fatigue mentale (Figure 16).

Les ondes thêta sont souvent étudiées lorsque l'on se place dans le contexte de la fatigue mentale et il couramment rapporté qu'en présence de fatigue mentale une augmentation des ondes thêta est observée (Arnau et al., 2017; Craig, Tran, Wijesuriya & Nguyen, 2012; Lal & Craig, 2002; Tanaka, Shigihara, et al., 2012; Wascher et al., 2014). Ces ondes thêta ont été reliées à la demande cognitive liée à la tâche, plus la tâche est difficile plus la présence des ondes thêta est marquée (Onton et al., 2005). Ainsi, lors de tâche de maintien en mémoire par exemple, une augmentation significative des ondes thêta est observée au niveau central (Jensen & Tesche, 2002).

Les autres bandes de fréquences sont quant à elles moins étudiées dans le contexte de la fatigue mentale, même si l'on tend à avoir de plus en plus d'études qui s'intéressent aux ondes bêta. Cependant les effets de la fatigue mentale sur cette onde sont contradictoires. Certaines

études trouvent une augmentation des ondes bêta avec l'instauration de fatigue mentale (Boksem et al., 2005; Tanaka et al., 2014) alors qu'au contraire certaines montrent une diminution des ondes bêta (Fan et al., 2015; Zhao et al., 2012). L'activité bêta se produit avec une augmentation de l'excitation corticale qui est associée à une augmentation de l'activité ou de l'effort mental. Ainsi une augmentation des ondes bêta en présence de fatigue mentale pourrait être liée à une augmentation de l'effort mental pour rester vigilant (Craig, Tran, Wijesuriya & Middleton, 2012), alors que la diminution des ondes bêta pourrait traduire à l'inverse une diminution de l'effort mental investi.

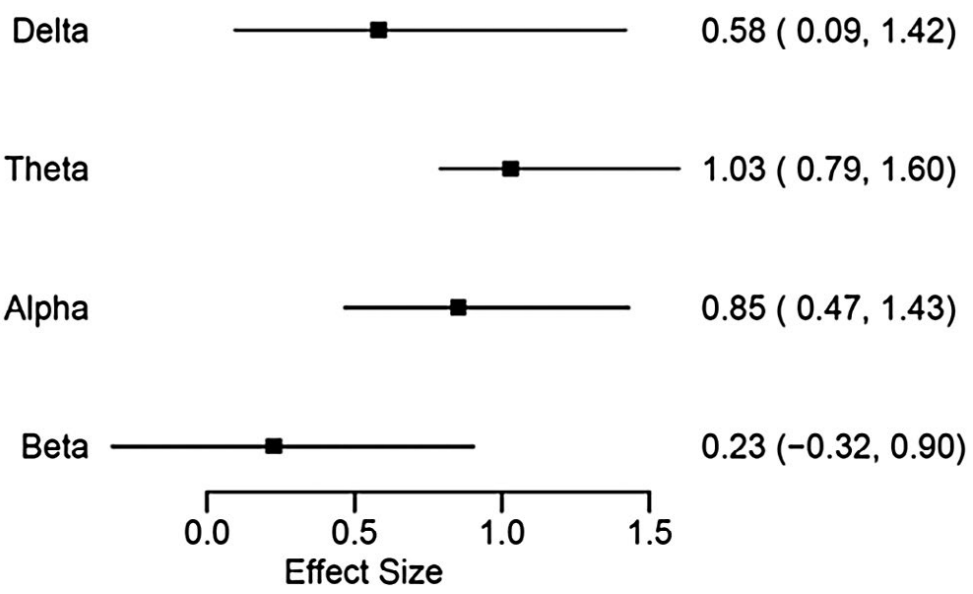


Figure 16 : Effet de la fatigue mentale sur les oscillations cérébrales. Résultats d'une méta-analyse réalisée par Tran et al. (2020) indiquant que la fatigue mentale influence surtout la présence des ondes Thêta et Alpha. Les intervalles de confiance à 95% sont entre parenthèses.

- **Principaux effets sur les potentiels évoqués**

Bien que des études semblent s'être intéressées aux oscillations cérébrales afin d'attester de la présence de fatigue mentale, l'analyse des potentiels évoqués peut également fournir des preuves robustes de la présence de fatigue mentale. L'analyse des potentiels évoqués engendrés à la suite d'un stimulus a été utilisée pour attester de façon objective de la présence de fatigue mentale. En effet avec l'instauration de la fatigue mentale, nous pouvons observer des modulations spécifiques de potentiels évoqués selon la tâche utilisée. La P300 semble particulièrement touchée par les effets de la fatigue mentale. Généralement, une diminution de

l'amplitude de la P300 est observée avec l'instauration de la fatigue mentale (Möckel et al., 2015; Murata et al., 2005; Uetake & Murata, 2000; Zhao et al., 2012). Cette diminution a été interprétée comme étant le reflet d'une baisse de la vigilance au cours de la tâche (Koelega et al., 1992; Schmidt et al., 2009). En effet l'amplitude de la P300 a été reliée à des processus attentionnels. Son amplitude dépendrait de l'attention allouée à la tâche et de son implication dans la tâche (Lammers & Badia, 1989). Ainsi lorsque la tâche que l'on réalise nécessite plus d'attention ou bien lorsque l'on se rend compte qu'une erreur a été commise, on augmente l'attention allouée à la tâche pour éviter de se tromper de nouveau (Falkenstein et al., 1995; Galbraith et al., 1988).

Outre l'amplitude de la composante P300, un autre paramètre semble particulièrement intéressant à observer, sa latence. La latence d'un potentiel évoqué reflète la rapidité avec laquelle l'information est traitée. Celle de la P300 semble augmenter avec l'instauration de fatigue mentale (Guo et al., 2018; Uetake & Murata, 2000). La latence de la P300 représentant la vitesse de traitement à haut niveau (Kok, 1997), il semblerait que la fatigue mentale retarde le traitement de l'information lors de l'évaluation des stimuli et de la décision d'inhibition (Kato et al., 2009).

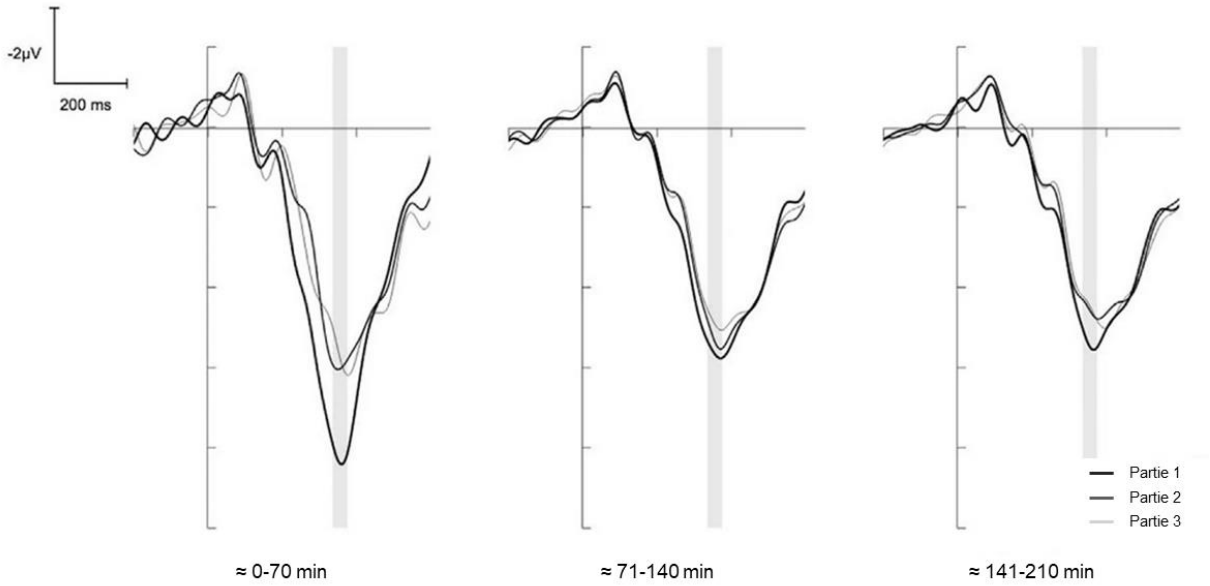


Figure 17 : Illustration des effets de la fatigue mentale sur la P300. On observe une diminution de l'amplitude au niveau de l'électrode Pz de la P300 (zone grisée) avec l'augmentation du temps passé sur une tâche de Simon d'une durée de 3 heures et donc avec l'instauration de fatigue mentale. Adapté de (Möckel et al., 2015).

D'autres potentiels évoqués ont également été étudiés dans le cadre de la fatigue mentale comme par exemple la N100 et la N200. La N100, une composante très précoce liée plus spécifiquement à l'attention visuelle. Des études ont montré une décroissance de cette N100, au niveau pariétal, avec l'augmentation du temps passé sur une tâche cognitive et donc avec l'instauration de fatigue mentale (Boksem et al., 2005; Faber et al., 2012). Les études ayant montré ces résultats utilisaient des tâches d'attention sélective comme tâches cognitives afin d'induire la fatigue mentale. La décroissance de l'amplitude de la N100 a été interprétée comme reflétant une baisse de la capacité de discrimination visuelle. D'ailleurs en parallèle de cette décroissance de la N100 au cours du temps, un déclin des performances de discrimination (erreurs) était observé. Une autre étude portant elle sur les effets de la fatigue mentale sur une tâche auditive a également montré une diminution de l'amplitude de la N100 avec l'augmentation du temps passé sur la tâche, qui était corrélée avec une réduction de la motivation (Moore et al., 2017). Les études précédemment citées ont étudié la N100 au cours d'une tâche mentalement fatigante. Key et al. (2017), qui ont, eux, investigué les effets de la fatigue mentale grâce à la méthode indirecte (pré/post tâche mentalement fatigante), n'ont pas trouvé d'effet de la fatigue mentale sur la N100 lors d'une tâche auditive réalisée avant et après fatigue mentale chez des enfants (6-13 ans). Cela montre bien l'importance de préciser les conditions de mesure des potentiels évoqués car les effets peuvent varier d'une condition à une autre. La diminution de la N100 au cours d'une tâche mentalement fatigante est assez cohérente avec les études qui ont mis en évidence une diminution de la N100 avec l'augmentation de la charge mentale (Kramer et al., 1995; Miller et al., 2011).

Le dernier potentiel évoqué auquel nous nous intéresserons dans cette partie est la N200. La latence de cette N200 reflète la rapidité du suivi des conflits, alors que son amplitude représente la quantité de ressources allouée à la résolution du conflit. Il a été montré que son amplitude augmentait lorsque la résolution de conflit devenait plus difficile (Bekker et al., 2004; Yeung & Cohen, 2006). Cependant en présence de fatigue il a été montré que son amplitude diminuait au cours de la tâche (Boksem et al., 2005; Guo et al., 2018). Cette diminution pourrait refléter une diminution des ressources allouées à la résolution du conflit, expliquant ainsi la baisse de la précision des réponses lors de ce type de tâche en présence de fatigue mentale. Cependant ces effets de fatigue mentale sur l'amplitude de la N200 n'ont pas été rapportés dans toutes les études (Faber et al., 2012).

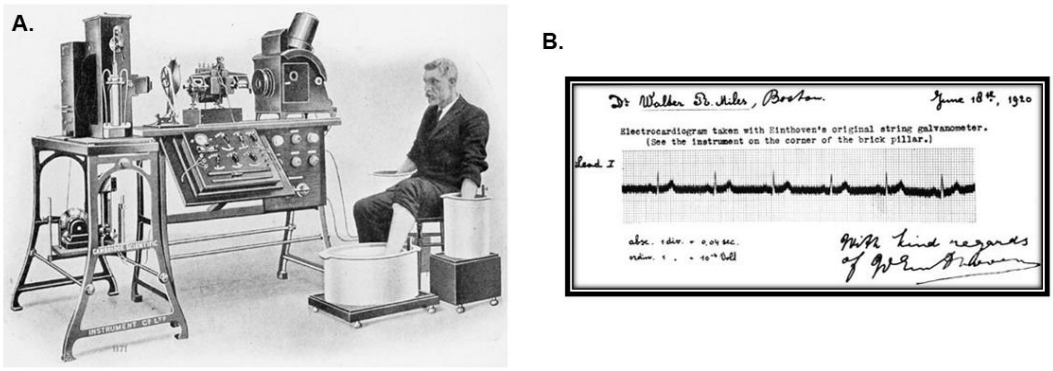
L'analyse des potentiels évoqués peut donc s'avérer intéressante pour attester de la présence de fatigue mentale, en complément de analyses spectrales. Même si l'EEG a été considérée comme étant la méthode la plus prometteuse pour identifier des marqueurs électrophysiologiques objectifs de la fatigue mentale (Lal & Craig, 2001), d'autres mesures complémentaires peuvent également être utilisées. Ainsi, certaines études ont utilisé la fréquence cardiaque comme marqueur électrophysiologique objectif de la fatigue mentale.

2.5.2 L'électrocardiographie

2.5.2.1 Définition et historique

L'électrocardiographie est l'enregistrement de l'activité électrique du muscle cardiaque. Le premier enregistrement date de 1903 et fut réalisé par Einthoven. Bien loin de nos techniques actuelles, il fallait à l'époque plonger les extrémités du corps (deux bras et une jambe) dans une solution saline (Figure 18, panel A). Ensuite, grâce à un galvanomètre à cordes, Einthoven pouvait mesurer la tension entre le bras droit et le bras gauche (dérivation I), le bras droit et la jambe gauche (dérivation II) et le bras gauche et la jambe gauche (dérivation III ; Pour une revue complète sur l'historique de l'électrocardiogramme : Fisch, 2000).

Aujourd'hui, le principe de dérivation est toujours utilisé mais il suffit de poser des électrodes adhésives sur le torse pour enregistrer l'activité cardiaque, et grâce aux progrès de la science et à l'invention de nouvelles technologies, il est beaucoup plus aisé de mesurer la fréquence cardiaque. Une montre ou une caméra peuvent suffire. Le principe est d'envoyer de la lumière verte dans les capillaires (vaisseaux sanguins les plus fins) et, selon le niveau de lumière reflété, le capteur sera capable de déterminer l'afflux de sang dans ces capillaires et par conséquent la fréquence cardiaque.



<u>Figure 18 :</u> Illustration de la première machine commercialisée pour enregistrer l'activité cardiaque selon la méthode découverte par Einthoven (A) et illustration d'un des premiers tracés ECG obtenu (B).

Les principales mesures que l'on peut obtenir grâce à l'enregistrement de l'activité électrique du cœur sont la fréquence cardiaque (nombre de battements de cœur par minute) et la variabilité de la fréquence cardiaque (VFC ; temps qui s'écoule entre deux battements de cœur). Une baisse de la fréquence cardiaque et une augmentation la VFC reflètent une activation du système parasympathique, alors qu'une augmentation de la fréquence cardiaque et une diminution de la VFC reflètent une activation du système sympathique.

La mesure de la variabilité cardiaque consiste à mesurer le temps séparant deux battements cardiaques (intervalle R-R), plus le temps entre deux battements est constant, plus la variabilité cardiaque est faible, et inversement. À partir de cet intervalle R-R, plusieurs variables peuvent être calculées, notamment :

- le « SDNN » : écart-type de tous les intervalles R-R normaux pendant une période de 24 heures, exprimé en msec ;
- le « SDANN » : écart-type des intervalles R-R moyennés sur des périodes de cinq minutes, exprimé en msec;
- le « NN50 » : nombre absolu de différences de plus de 50 msec, entre les intervalles R-R successifs ;
- Le pNN50 : pourcentage de différences de plus de 50 msec, entre les intervalles R-R successifs ;
- La RMSSD (msec) : racine carrée de la moyenne des différences au carré entre les intervalles R-R successifs.

Une autre manière d'aborder la variabilité cardiaque est d'effectuer des analyses spectrales, grâce à la transformée de Fourier. La première étude à réaliser ce type d'analyse fut menée par Akselrod et al. (1981). Cela permet d'identifier différentes oscillations périodiques et de les séparer en plusieurs composantes :

- Les hautes fréquences (HF, entre 0,15 Hz et 0,45 Hz)
- Les basses fréquences (BF, entre 0,04 Hz et 0,15 Hz)
- Les très basses fréquences (TBF, entre 0,003 Hz et 0,04 Hz)
- Les ultra basses fréquences (UBF < 0,003 Hz)

Il a été montré depuis bien longtemps que certains neurotransmetteurs impliqués dans le phénomène de fatigue mentale, comme la dopamine (voir section 3.1.2), pouvaient influencer le rythme cardiaque (Holmes & Fowler, 1962). On a donc cherché à utiliser le rythme cardiaque comme possible marqueur de la fatigue mentale.

2.5.2.2 Marqueurs ECG de la fatigue mentale

Plusieurs études se sont intéressées aux effets de la fatigue mentale sur le rythme cardiaque et sur sa variabilité. Aucune étude n'a montré d'effet significatif de la fatigue mentale sur le rythme cardiaque. En revanche, lors de tâches qui sont cognitivement coûteuse on peut observer une fréquence cardiaque plus élevée que lors d'une de tâches contrôles (e.g., Marcora et al., 2009; Pageaux et al., 2014) indiquant que la tâche qui est en train d'être réalisée est difficile (Richter et al., 2008).

D'autres études se sont intéressées aux changements spectraux dans la variabilité du rythme cardiaque induit par la fatigue mentale. Il a été montré que le pourcentage de BF et le ratio BF/HF étaient positivement corrélés au niveau de fatigue évalué sur une échelle subjective, alors que la corrélation était négative entre le pourcentage de HF et le score de fatigue (Tanaka et al., 2011). Cependant, il semblerait que le ratio BF/HF soit un indicateur plus fiable que les mesures « brutes ». Ainsi d'autres études ont montré qu'une augmentation du ratio BF/HF était un indicateur de fatigue mentale (Mizuno et al., 2011), montrant notamment une corrélation entre le ratio BF/HF et le niveau subjectif de fatigue mentale reporté sur une VAS (Figure 19).

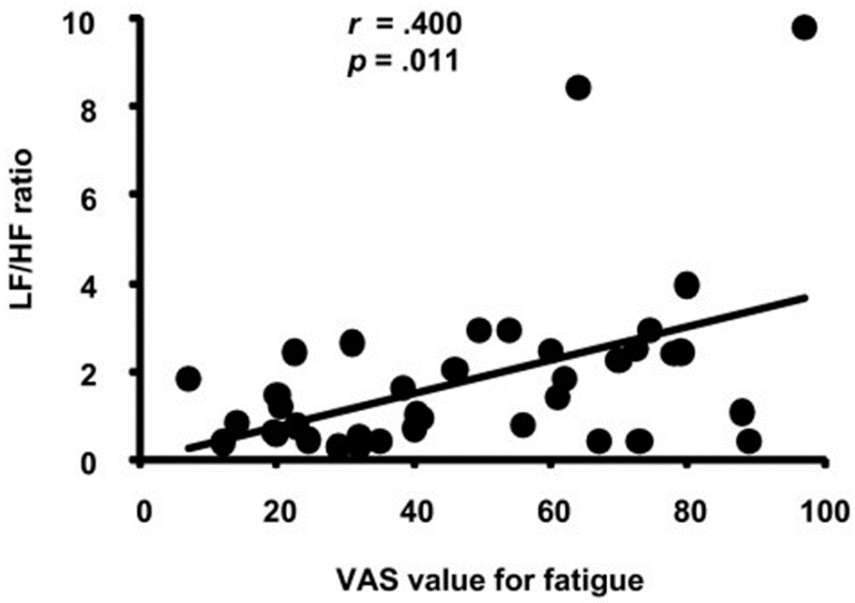


Figure 19 : Relation entre fatigue mentale subjective et fréquence cardiaque. Il existe une corrélation entre le score de fatigue obtenu sur une échelle visuelle analogique (VAS) et le ratio basse fréquence/haute fréquence (BF/HF). Valeur *p* obtenue avec une corrélation de Spearman. D'après Mizuno et al. (2011).

Une étude récente qui avait pour but de détecter les signes de fatigue à partir de données ECG a conclu que les indicateurs les plus fiables pour attester de la présence de fatigue mentale étaient l'intervalle R-R moyen, le pNN50, la puissance spectrale totale (mesure de l'activité autonome globale), et LF (Huang et al., 2018). Dans une récente étude, O'Keeffe et al. (2020) ont étudié la variabilité cardiaque, plus spécifiquement la RMSSD et le PNN50 après avoir induite de la fatigue mentale grâce à une tâche d'AX-CPT de 90 minutes ou bien 16 minutes d'une tâche cognitivement plus coûteuse, ta la tâche de TLDB. Bien que les deux tâches aient induit une augmentation de la sensation subjective de fatigue mentale, la RMSSD et le PNN50 ont été réduits seulement après la tâche de TLDB. Ainsi l'étude de ces paramètres pourrait être intéressante pour mettre en évidence la fatigue mentale et différencier la fatigue induite par des tâches cognitives longues mais peu coûteuses (i.e., Stroop, AX-CPT : pouvant générer de l'ennui et ou de la somnolence) et la fatigue induite par des tâches présentant une charge cognitive plus importante.

2.5.3 Oculométrie : Diamètre pupillaire et mouvements oculaires

2.5.3.1 Définition et historique

Bien que l'analyse du diamètre pupillaire date de la fin du 19ème siècle, elle reste cependant assez compliquée d'un point de vue méthodologique car elle est sensible à de nombreux facteurs environnementaux comme le niveau de luminosité (entre 2 et 8 mm selon si l'illumination est forte ou faible ; Crawford, 1936) ou bien endogènes comme l'âge (Birren et al., 1950), le niveau de fatigue visuelle (Smith, 1979) ou la consommation d'opioïdes (Barvais et al., 2003).

Les premières études sur les mouvements oculaires datent également de la fin du 19ème siècle. Javal (1878) a observé les mouvements oculaires de personnes qui étaient en train de lire à l'aide d'un miroir. Il s'est aperçu que, lors de la lecture, l'œil effectuait des mouvements discontinus composés de saccades (mouvements rapides de l'œil) et de fixations (regards fixes sur un point). Depuis les méthodes ont grandement évolué et nous disposons de nombreux moyens pour analyser les mouvements des yeux lors de différentes tâches (pour revue : Holmqvist et al., 2011). Ainsi parmi les variables les plus étudiées nous retrouvons la durée des fixations, le nombre de fixations, l'amplitude des saccades, la durée des saccades ou encore leur vitesse. En parallèle des mouvements oculaires, nous pouvons également étudier le clignement de yeux. Bien qu'à la base le clignement de l'œil soit un réflexe nous permettant d'humidifier la cornée, son étude peut être une porte d'entrée pour étudier le fonctionnement de notre cerveau.

2.5.3.2 Diamètre pupillaire et mouvements oculaires : marqueurs de la fatigue mentale

Dès les années 60, il a été montré que le diamètre pupillaire pouvait être considéré comme une mesure directe de l'activité mentale. Hess et Polt (1964) ont observé que lors d'une tâche de calcul (e.g., multiplication), la taille de la pupille était corrélée avec la difficulté du calcul effectué. Beatty (1982) a confirmé, avec l'utilisation d'autres types de tâches, que le diamètre pupillaire était corrélé à la charge mentale. Cette augmentation du diamètre pupillaire semble flagrante selon Kahneman (1973) : « Face à un miroir, regardez vos yeux et inventez un problème mathématique, tel que 81 fois 17. Essayez de résoudre le problème et observez votre élève en même temps, un exercice assez difficile en cas de division de l'attention. Après

quelques tentatives, presque tout le monde est capable d'observer la dilatation pupillaire qui accompagne l'effort mental ». En lien avec ces observations, le diamètre pupillaire a été étudié dans le cadre de la fatigue mentale. Herlambang et al. (2019) ont mesuré l'évolution du diamètre pupillaire au cours d'une tâche cognitive de 2 h 30. Alors que le diamètre pupillaire décroit au début de l'expérience, certainement lié à des effets d'apprentissage et donc à une diminution de la charge cognitive nécessaire pour effectuer la tâche, une augmentation est ensuite observée avec le temps passé à réaliser la tâche.

Le diamètre pupillaire ne semble pas être la seule variable intéressante à regarder. L'étude du clignement des yeux semble particulièrement intéressante. Il a été montré qu'avec le temps passé à réaliser une tâche cognitive le nombre de clignements des yeux augmentait (Fukuda et al., 2005; Stern et al., 1994). Benedetto et al. (2011) ont toutefois proposé que la durée de la fermeture des yeux lors d'un clignement d'œil serait une mesure plus sensible de la charge de travail et pourrait ainsi être un meilleur marqueur de fatigue mentale.

L'évaluation de la fatigue mentale est une problématique importante, qui reste encore aujourd'hui discutée. Plusieurs stratégies ont été proposées afin d'obtenir des marqueurs fiables et robustes de la fatigue mentale. L'utilisation de divers échelles et questionnaires, bien que pratique et relativement robuste, pose toujours le problème de la subjectivité dans l'évaluation de la fatigue mentale. Plusieurs méthodes objectives via l'utilisation de l'électroencéphalographie, l'électrocardiographie ou encore l'oculométrie ont alors été évaluées. Même s'il semble que ces mesures objectives soient toujours perfectibles, des progrès ont été effectués ces dernières années. La méthode choisie pour évaluer la fatigue mentalement dépendra majoritairement des contraintes présentes (e.g., environnementales, logistiques, financières). Plutôt que d'utiliser une seule méthode d'évaluation de la fatigue mentale, combiner l'utilisation de plusieurs marqueurs subjectifs et/ou physiologiques est à recommander afin d'obtenir des évidences plus fiables de la présence de fatigue mentale.

3 Origine des effets de la fatigue mentale

Bien que les effets de la fatigue mentale soient de mieux en mieux connus et que plusieurs marqueurs sont utilisés pour tenter d'identifier les signes et la présence de fatigue mentale, ses corrélats neurophysiologiques restent encore assez mal connus. Pour tenter de mieux comprendre les origines de la fatigue mentale, nous nous intéresserons aux effets de la fatigue mentale sur plusieurs catécholamines présentes au sein du système nerveux. Leur fonction principale est de transmettre l'influx nerveux. Une modulation du taux de ces catécholamines en présence de fatigue pourrait donc être à l'origine des effets délétères de la fatigue mentale. Nous verrons également que plusieurs modèles ont été développés pour tenter d'expliquer les effets de la fatigue mentale. Mais avant de parler des modèles explicatifs globaux, dans un premier temps nous nous placerons à un niveau moléculaire et relaterons les effets de la fatigue mentale sur plusieurs neurotransmetteurs.

3.1 Implications des différents neurotransmetteurs dans la fatigue mentale

3.1.1 L'adénosine

L'adénosine est un neurotransmetteur participant à l'inhibition de l'activité des neurones qui est notamment produite par dégradation de nucléotides comme l'adénosine triphosphate (ATP). Une activité mentale prolongée induisant de la fatigue mentale augmenterait les concentrations en adénosine (Lovatt et al., 2012). Cette augmentation de la concentration en adénosine serait responsable de l'augmentation de la perception de l'effort, notamment lors d'un effort physique, en présence de fatigue mentale (Martin et al., 2018; Pageaux et al., 2014). La modulation du niveau d'adénosine a également des effets sur d'autres neurotransmetteurs comme par exemple la dopamine (Myers & Pugsley, 1986). Le récepteur A_{2A} de l'adénosine joue un rôle important dans la régulation de la dopamine. Du fait de sa colocalisation avec les récepteurs D_2 de la dopamine dans les neurones GABAergiques post-synaptiques, l'adénosine bloque le signal dopaminergique. L'augmentation du taux d'adénosine pourrait ainsi conduire à une diminution du taux de dopamine. C'est d'ailleurs pour cela, au moins en partie, que la caféine est efficace pour lutter contre la fatigue mentale. La caféine est connue pour bloquer les récepteurs A_{2A} (Huang et al., 2005) empêchant ainsi l'adénosine de se fixer sur les récepteurs A_{2A} et maintenant le signal dopaminergique.

3.1.2 La dopamine

La dopamine, autre catécholamine, est synthétisée à partir de la tyrosine et, plus en amont de la phénylalanine, un acide aminé essentiel. Elle joue un rôle primordial dans la prédiction de la récompense (Schultz, 2010), le conditionnement (Hazy et al., 2010), l'éveil (Horvitz, 2000), la réalisation et le maintien d'un effort (Niv et al., 2007; Salamone et al., 2009), ou encore la motivation (Berridge & Robinson, 1998). L'apparition de la fatigue mentale serait due à une diminution du taux de dopamine provenant des effets de l'adénosine sur les récepteurs D_2 de la dopamine (Schiffmann et al., 2007).

Preuve de l'implication de la dopamine dans le phénomène de fatigue mentale, Caldwell et Caldwell (1997) ont montré que l'administration de dextroamphétamine (un agoniste dopaminergique indirect) permettait d'améliorer les performances de pilotes d'hélicoptère lors des 23 dernières heures d'un vol qui en durait 40 sans interruption. De plus, l'administration de dextroamphétamine permettait également de réduire l'instauration d'une sensation de fatigue au cours de 40 heures de vol. La consommation de café (Volkow et al., 2015) ou une motivation financière (Arias-Carrión et al., 2010) semblent agir de la même façon en augmentant le taux de dopamine (Figure 20).

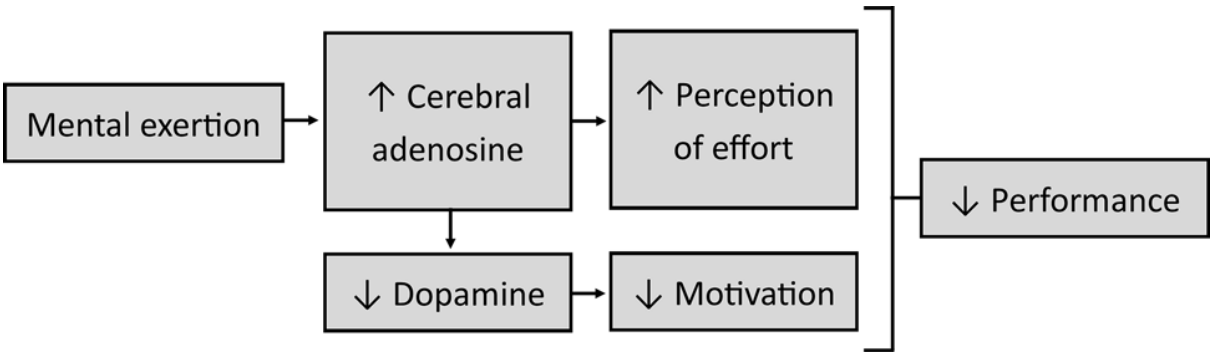


Figure 20 : Représentation schématique des effets du couple adénosine/dopamine sur les performances. D'après Martin et al. (2018).

Une autre possibilité pouvant expliquer la baisse de la dopamine en présence de fatigue est une réduction de l'activité des systèmes de projections dopaminergiques, comprenant les ganglions de la base et les structures frontales médianes comme le CCA (Boksem et al., 2006). Plusieurs études en neuroimagerie ont confirmé cette théorie en montrant une diminution de l'activité du CCA en présence de fatigue mentale (e.g., Lorist et al., 2005).

3.1.3 Le rôle de la norépinephrine (ou noradrénaline)

La norépinephrine, appelée également noradrénaline, est une catécholamine qui joue un rôle de neurotransmetteur au niveau du système nerveux central et qui est impliquée, entre autres, dans les processus d'attention sélective, de vigilance et de régulation des émotions (Berridge & Waterhouse, 2003; Moret & Briley, 2011). La norépinephrine est synthétisée au niveau du locus cœuruleus (Benarroch, 2009). Des études ont montré que la dilatation de la pupille ainsi que l'amplitude de la P300 au niveau pariétal étaient reliées à l'activité du locus cœuruleus et donc au niveau cortical de norépinéphrine (Gilzenrat et al., 2010; Murphy et al., 2014; Murphy et al., 2011; Nieuwenhuis et al., 2005), faisant ainsi de ces deux paramètres une porte d'entrée accessible pour étudier les effets de la fatigue mentale sur ce neurotransmetteur. Lors de la réalisation d'une tâche de 2*N-back* de 2 heures, Hopstaken et al. (2015b) ont observé une augmentation de la sensation de fatigue mentale au cours de la tâche en parallèle d'une diminution du diamètre pupillaire, reflétant ainsi une diminution du taux de norépinephrine. De plus, dans une autre étude, utilisant 2 heures de *N-back*, Hopstaken et al. (2015a) ont montré qu'avec l'augmentation de la fatigue et du temps passé à réaliser une tâche cognitive, l'amplitude de la P300 (en pariétal) et le diamètre de la pupille diminuaient, confirmant ainsi une diminution de l'activité du locus cœuruleus et donc une diminution du taux de norépinephrine.

3.1.4 Le rôle de la sérotonine

La sérotonine (également appelée 5-hydroxytryptamine ; 5-HT) est un neurotransmetteur présent notamment dans le système nerveux central. Un faible taux de sérotonine est associé à l'extraversion, l'impulsivité, l'irritabilité, l'agressivité ou à la dépression (Meltzer, 1990). Concernant son implication dans la fatigue, son rôle a surtout été étudié dans le cadre de la fatigue centrale (Davis et al., 2000; Meeusen et al., 2006). La fatigue centrale s'instaure dans le cas de contraction musculaire en amont de la jonction neuromusculaire et reflète l'incapacité du système nerveux central à générer et/ou maintenir l'activation centrale du muscle (Gandevia, 2001). Il a été proposé que l'augmentation de la sérotonine au niveau cérébral serait à l'origine d'un déclin des performances à cause d'une léthargie accrue et d'une perception plus élevée de l'effort, modifiant ainsi la tolérance à la douleur ou à l'inconfort (Davis & Bailey, 1997; Meeusen et al., 2006). Malgré sa possible implication dans le phénomène de fatigue, et son interaction connue avec la dopamine, très peu d'études se sont pour l'instant penchées sur la relation entre sérotonine et fatigue mentale.

Les seules études réalisées à ce jour ont été conduites auprès de personnes souffrant de fatigue mentale pathologique. Une étude menée sur des patients atteints de fatigue chronique a montré que l'utilisation de « duloxétine », un inhibiteur de la recapture de la sérotonine qui a pour fonction d'augmenter le taux de sérotonine, permettait de réduire la fatigue mentale (Arnold et al., 2015). Cependant malgré ces preuves montrant qu'un taux de sérotonine élevé augmenterait la fatigue mentale, une étude menée sur des patients atteints de la maladie de Parkinson a montré que le taux de sérotonine mesuré dans le liquide céphalorachidien était négativement corrélé au niveau de fatigue mentale (Zuo et al., 2016). Ce résultat contredit l'hypothèse selon laquelle l'élévation du taux de sérotonine permettrait de réduire la fatigue mentale. Une possible explication pourrait être une relation en « U » entre la concentration en sérotonine et la présence de fatigue mentale, expliquant ainsi pourquoi à la fois une faible et une importante concentration en sérotonine sont liées à une augmentation de la fatigue mentale. Cette hypothèse n'étant que purement spéculative, elle demande à être vérifiée. Ainsi, des investigations supplémentaires sont nécessaires afin de mieux comprendre la place et le rôle de la sérotonine dans la sensation de fatigue mentale.

3.2 Les modèles explicatifs de la fatigue mentale

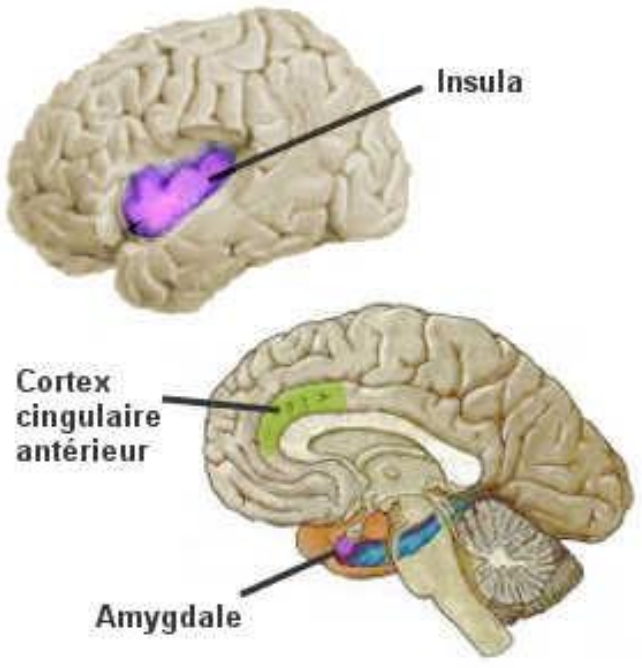
En parallèle de ces études portant sur les principaux neurotransmetteurs impliqués dans la sensation de fatigue, différents modèles ont été proposés afin de mieux appréhender les causes et les conséquences de la fatigue mentale.

3.2.1 Le modèle du « coût/bénéfice »

En 2008, Boksem et Tops ont proposé un modèle explicatif de la fatigue mentale basé à la fois sur les bénéfices attendus et sur les dépenses énergétiques nécessaires pour réaliser une tâche prolongée et/ou intense (Boksem & Tops, 2008). Ainsi lorsque le bénéfice attendu devient moins important que la dépense énergétique nécessaire pour la poursuite de la tâche, il y a une diminution de l'effort investi dans la tâche conduisant ainsi à un déclin de la performance.

Dans l'environnement, il y a en général de multiples récompenses possibles possédant chacune des valeurs de récompense différentes. Plusieurs structures corticales sont impliquées dans le codage des récompenses et dans leur valeurs appétives ou aversives (Figure 21) :

- le cortex orbitofrontal
- l'amygdale basolatérale
- l'insula
- le CCA
- les noyaux accumbens.



<u>Figure 21 :</u> Localisation de certaines zones cérébrales particulièrement impliquées dans le phénomène de fatigue mentale.

Bien que chacune de ces structures cérébrales soient impliquées dans le codage des récompenses, elles possèdent chacune des spécificités et des particularités. Ainsi, ce n'est que grâce à l'action combinée de toutes ces structures que la valeur d'une récompense peut être déterminée.

<u>Le cortex orbitofrontal</u> code la valeur de la récompense comparé aux autres récompenses disponibles (Tremblay & Schultz, 1999) avec une dissociation entre le cortex orbitofrontal médial qui intervient plutôt dans le suivi, la mémorisation et l'apprentissage de la valeur des

récompenses, et le cortex orbitofrontal latéral qui lui est plutôt impliqué dans l'évaluation des punitions et des événements aversifs (Kringelbach & Rolls, 2004; O'Doherty et al., 2001; Seymour et al., 2007). Il signale également la valeur attendue des stimuli et des événements attendus (Gottfried et al., 2003; Nobre et al., 1999), et s'il y a des changements dans ces derniers, il modifie l'association stimulus/récompense (Walton et al., 2004).

L'amygdale basolatérale, qui possède des connexions réciproques avec le cortex orbitofrontal (Ongur & Price, 2000) et reçoit des projections du cortex sensoriel (Mcdonald, 1998), est impliquée dans les processus de renforcement négatif (e.g., douleurs, peur, anxiété) mais aussi de renforcement positif (e.g., nourriture, affection, compliments). Elle donne des informations complémentaires à celles du cortex orbitofrontal en codant la valeur des récompenses (Killcross et al., 1997), signalant les changements dans le ratio stimulus/récompense (Corbit & Balleine, 2005), et donnant des informations sur la valeur des récompenses différées (Winstanley et al., 2004).

L'insula, qui est réciproquement liée au cortex orbitofrontal latéral (Carmichael & Price, 1995) et à l'amygdale basolatérale (Reynolds & Zahm, 2005), est impliquée dans le codage des valeurs aversives (Nitschke et al., 2006; Small et al., 2001), mais aussi, comme les deux structures précédemment citées, dans l'évaluation des coûts et des punitions lors de la prise de décision. Une fois que le codage de la valeur appétive ou aversive des différents événements possibles est réalisé, ces informations sont envoyées au CCA (Salisbury et al., 2001).

Le cortex cingulaire antérieur (Salisbury et al.) est impliqué dans la discrimination des valeurs attribuées aux récompenses lorsque plusieurs sont disponibles (Cardinal et al., 2002; Parkinson et al., 2000). Il choisit ensuite le comportement à adopter de façon à obtenir la plus grande récompense possible (Bush et al., 2002; Shima & Tanji, 1998; Williams et al., 2004). Le CCA semble aussi construire un « historique » des récompenses et/ou punitions reçues en fonction des choix réalisés afin de guider les comportement futurs (Kennerley et al., 2006). La transformation de l'analyse de ces résultats est transmise aux noyaux accumbens pour donner lieu à un comportement ou à une action.

Les noyaux accumbens reçoivent des projections glutaminergiques de nombreuses structures donc le CCA, le cortex orbitofrontal, l'insula et semblent être sous contrôle de l'amygdale basolatérale. Le niveau de dopamine au niveau des noyaux accumbens peut moduler le comportement. Les valeurs de récompense arrivant au niveau des noyaux accumbens peuvent

être amplifiées grâce à la dopamine (Everitt et al., 1989) et ainsi favoriser la poursuite ou l'engagement dans une activité.

Toutes ces structures sont interconnectées et, avec l'intervention de certains neurotransmetteurs, leurs activités respectives aboutissent au comportement adopté : ajustement du niveau de performance (amélioration, maintien ou déclin), maintien ou arrêt de l'activité (Figure 22).

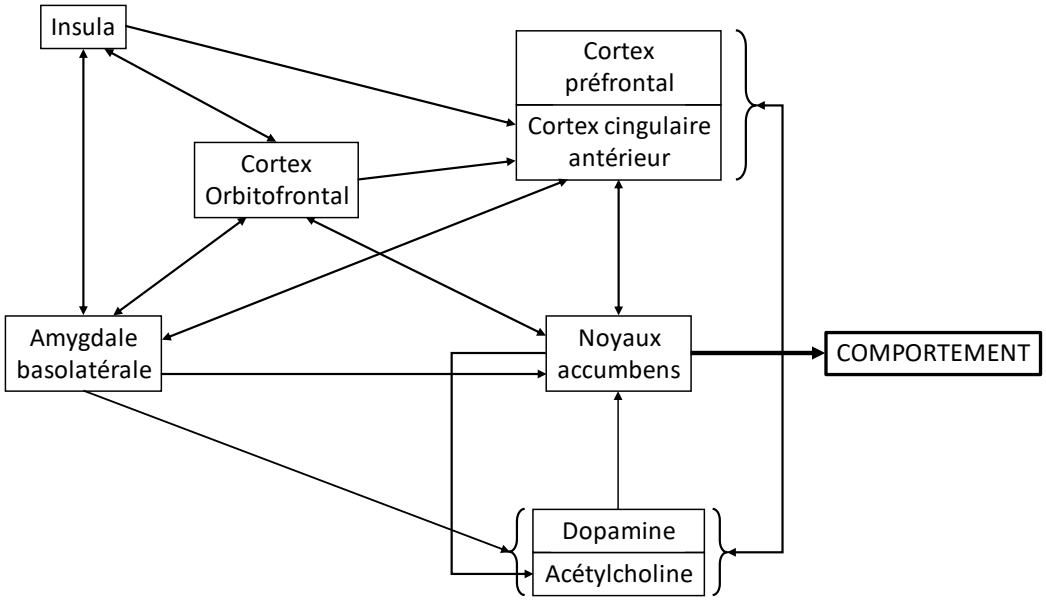


Figure 22 : Interconnections entre les principales structures cérébrales et neurotransmetteurs impliqués dans la régulation du comportement avec l'instauration de fatigue mentale. D'après le modèle du coût/bénéfice de Boksem et Tops (2008).

Pour qu'une tâche soit effectuée ou continuée dans le temps, il faut donc que son bénéfice soit supérieur au coût engagé. Lorsque l'on s'engage dans une tâche, le coût énergétique de cette dernière augmente progressivement avec le temps. Lorsque ce coût devient trop important, on peut observer un désengagement de la tâche et une diminution des performances. Le temps passé à réaliser la tâche induit une modulation de l'activité des zones cérébrales précitées. Avec l'apparition de la fatigue mentale, une diminution de l'activité cérébrale dans le cortex préfrontal, notamment le CCA (Lorist et al., 2005; Tanaka et al., 2014), est observée (Suda et al., 2009; Terentjeviene et al., 2018). Ainsi la diminution de l'activité dans ces zones cérébrales, en lien avec l'apparition de la fatigue mentale, induirait une réévaluation des bénéfices attendus avec la poursuite de la tâche. Lorsque le bénéfice ne serait

plus assez important par rapport au coût de la tâche, une baisse des performances ou un désengagement pour poursuivre la tâche seraient alors observés.

Cependant, comme déjà mentionné un facteur important est à prendre en compte dans le phénomène de fatigue mentale : la motivation. La motivation permet d'augmenter l'activité du cortex préfrontal (Luethi et al., 2016) et pourrait expliquer que, même avec l'instauration de fatigue mentale, des personnes particulièrement motivées puissent maintenir leurs performances. Pour valider cette importance de la motivation dans les performances, Boksem et al. (2006) ont montré que si des performances au cours d'une tâche cognitive de 2 heures avaient baissé, une récompense financière pour les 20 dernières minutes de l'expérience permettait de retrouver le niveau de performance initial. Cette expérience montre donc l'importance de la motivation dans le phénomène de fatigue mentale. Un autre modèle a d'ailleurs placé la motivation au cœur de son modèle explicatif.

3.2.2 La théorie du « contrôle motivationnel »

La théorie du « contrôle motivationnel » a été développée par Hockey (1997, 2011) pour expliquer et comprendre les effets de la fatigue mentale. Comme son nom l'indique, cette théorie accorde une place très importante à la motivation dans la régulation de la fatigue mentale. Si la motivation pour réaliser la tâche est suffisamment importante, alors elle mobilisera les ressources cognitives nécessaires afin d'atteindre l'objectif, même si cela se fait au prix d'un inconfort. Ainsi, si la motivation est forte et que l'objectif à atteindre revêt une relativement grande importance pour la personne en train de réaliser la tâche, elle engagera les ressources mentales nécessaires afin de mener la tâche à bien et garder ainsi un niveau de performance stable. Des études ont montré que la motivation pouvait être modulée par plusieurs facteurs comme la perception individuelle des exigences, la valeur des objectifs ou des compétences perçue dans la tâche (Brehm & Self, 1989 ; Meyer & Hallerman, 1977). Plus que la diminution des ressources au cours du temps, la fatigue mentale nous pousserait à changer nos objectifs au cours du temps. La fatigue serait en fait un dispositif nous poussant à nous tourner vers une meilleure alternative présente dans l'environnement (Evans et al., 2016). Ainsi si l'objectif que l'on est en train de poursuivre nécessite trop de ressources ou si l'on se rend compte que l'on n'est plus capable de maintenir cet objectif (e.g., réaliser la meilleure performance possible), alors nous nous tournerons vers un objectif réalisable (e.g., économiser ses ressources quitte à commettre des erreurs). En fonction de plusieurs paramètres, dont la

motivation qui déterminera quelle quantité de ressources nous sommes prêts à allouer à une tâche, nos objectifs lors d'une tâche pourront changer, modulant ainsi nos comportements (Figure 23).

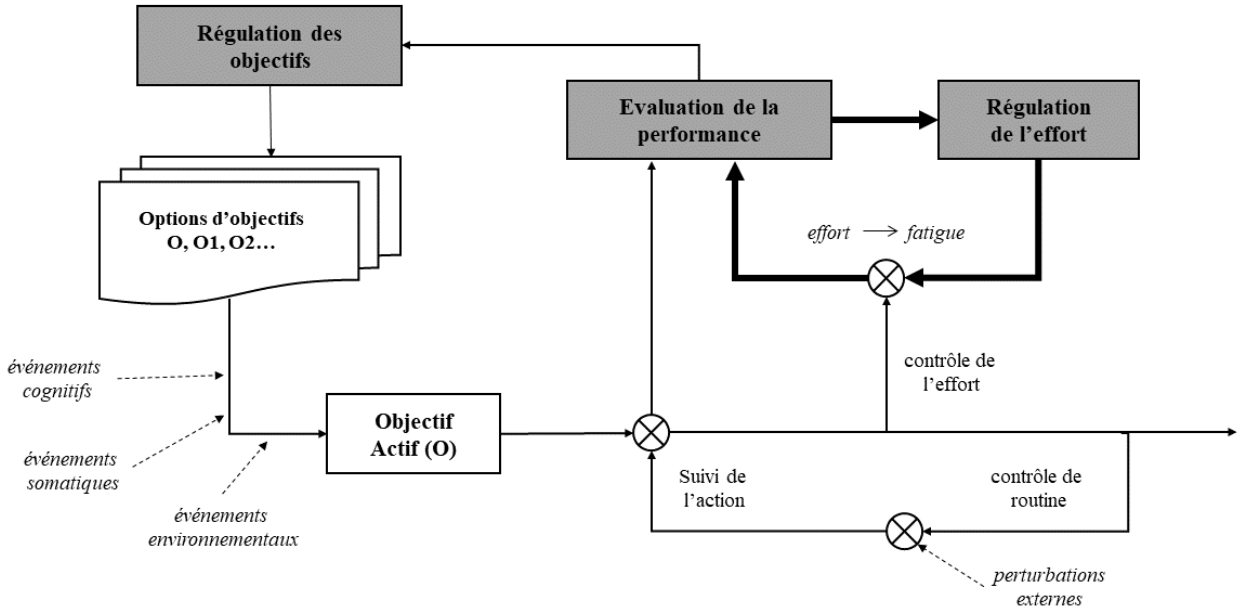


Figure 23 : Modèle du contrôle motivationnel. Adapté de Hockey (1997, 2011).

3.2.3 Le modèle de la double régulation de la fatigue mentale

Ce modèle de la double régulation de la fatigue mentale a été développé par Ishii et al., (2014) et se base sur le fait que les mécanismes neuronaux de la fatigue mentale liés aux performances lors de tâches cognitive sont plus complexes que précédemment expliqués et ne sont pas causés seulement par une diminution de l'activité dans la zone cérébrale liée à la tâche réalisée. Deux mécanismes seraient impliqués lors du maintien ou non des performances en présence de fatigue mentale : un mécanisme de facilitation et un mécanisme d'inhibition.

Le système de facilitation a pour but de maintenir les performances (e.g., temps de réaction, précision) lors de tâches cognitives servant à induire la fatigue mentale. Ainsi, par exemple, on peut voir que lors de tâches cognitives durant plusieurs heures, les performances peuvent être maintenues malgré une sensation subjective de fatigue mentale reportée sur une échelle subjective. Lors d'une tâche subséquente, on observe en revanche un déclin des performances, marqué par une augmentation des erreurs. Tanaka et al. (2009) ont montré que le système nerveux sympathique était actif lors d'une tâche cognitive induisant la fatigue mentale. De plus, il a été montré que l'activité du système nerveux sympathique était positivement liée à une

augmentation de la motivation et de l'effort mental. On peut ainsi penser que l'augmentation de l'activité du système nerveux sympathique durant une tâche de fatigue mentale reflète une augmentation de la motivation et de l'effort mental lors de la tâche, expliquant ainsi le maintien du niveau de performances.

L'activation de ce système de facilitation permet le maintien des performances malgré la présence de fatigue mentale et peut donc être jugé comme favorable. Cependant, une activation excessive de ce système de facilitation peut induire un dysfonctionnement de ce dernier et induire une fatigue mentale encore plus grande. Ainsi, si on sollicite de façon trop importante et/ou trop régulière ce système, cela peut causer une fatigue mentale chronique.

Le système d'inhibition est lui à l'origine de la détérioration des performances au cours d'une tâche cognitive. Alors qu'il faudrait engager d'avantage d'efforts et de ressources pour continuer à être performant au cours de la tâche cognitive, le système inhibe cet engagement supplémentaire, estimant que celui-ci deviendrait trop coûteux et/ou pas assez bénéfique, et une dégradation des performances est observée. Deux structures semblent particulièrement impliquées dans ce système d'inhibition, le cortex insulaire (insula) et le cortex cingulaire postérieur.

L'insula est impliquée dans l'évaluation des valeurs aversives (Nitschke et al., 2006; Small et al., 2001). Dans une étude d'IRMf, il a été montré que le niveau d'activation de l'insula était lié à la probabilité de sélectionner une réponse "sûre" après avoir choisi une réponse entraînant une sanction (Krain et al., 2006). De plus, son activité a aussi été liée à la perception de l'effort lors d'un exercice physique (de Graaf et al., 2004; Williamson et al., 1999).

Le cortex cingulaire postérieur est impliqué dans l'auto-évaluation de la sensation de fatigue aussi bien physique que mentale. Une étude en IRMf a montré que, lors de tâches mentalement fatigantes, son activité est positivement corrélée au niveau de fatigue reporté sur une VAS ou évaluée via le POMS (Cook et al., 2007).

Selon cette même étude, le niveau de fatigue serait également positivement corrélé à l'activité du cervelet, de l'hippocampe, du vermis du cervelet et du cortex frontal inférieur. Il semblerait donc que la fatigue mentale implique un large réseau d'aires corticales et ne se limite pas à une zone spécifique.

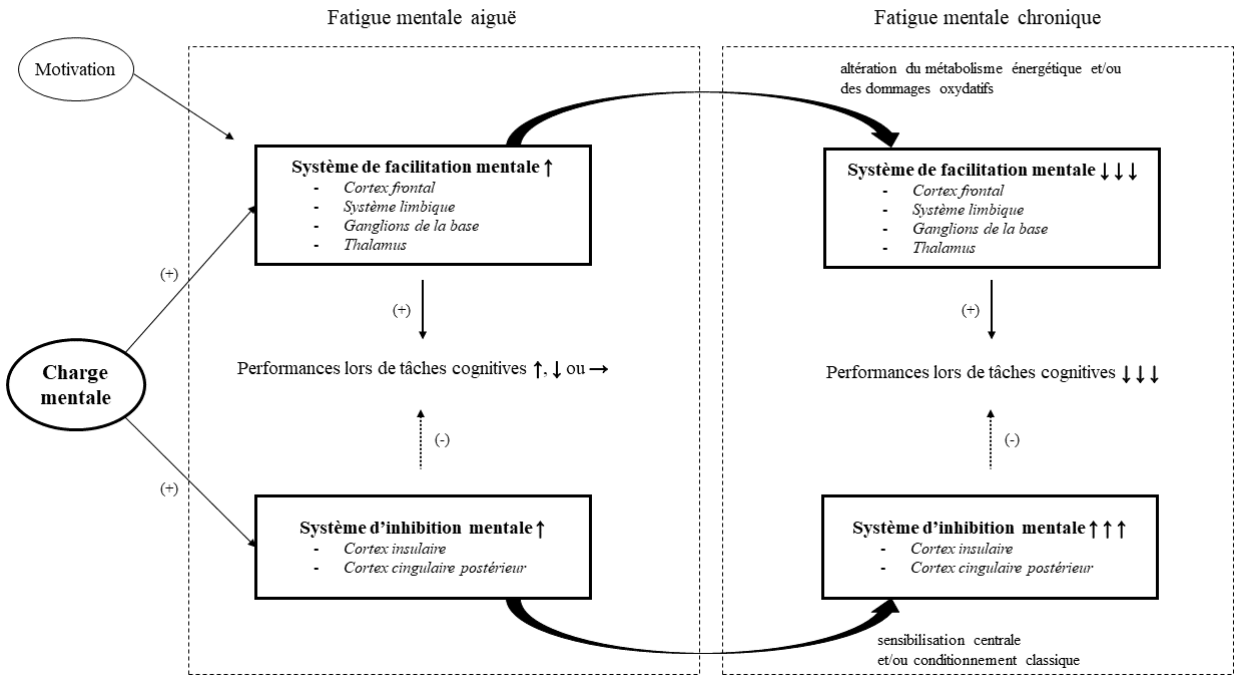


Figure 24 : Modèle de la double régulation de la fatigue mentale. Adapté de Ishii et al., (2014).

3.2.4 Conclusion sur les modèles théoriques de la fatigue mentale

Dans ce travail, nous avons présenté trois principaux modèles explicatifs de la fatigue mentale mais cette liste n'est pas exhaustive, et il existe d'autre modèles explicatifs parmi lesquels, par exemple, le modèle de « *l'ego déplétion* » (ou de l'épuisement de soi). Cette théorie de l'épuisement de soi développée par Baumeister et al. (1998), émet l'hypothèse que nous disposons d'une quantité limitée d'énergie. Une fois ce « réservoir » d'énergie épuisé, nous ne sommes plus en mesure de poursuivre l'activité en cours. Cependant, l'expérience de Boksem et al. (2006), qui montre qu'en proposant une récompense (financière) les performances étaient améliorées, n'est pas en accord avec cette théorie de l'épuisement du soi dans le processus de fatigue mentale.

Dans les trois modèles que nous avons présentés, même si chacun possède ses spécificités, ils s'accordent à montrer que la sensation de fatigue mentale, et la modulation des performances qui en découle, sont dues à l'activité d'aires préfrontales, notamment le CCA et l'insula. L'importance de la motivation quant aux performances en présence de fatigue mentale est aussi un point central dans les modèles proposés. Tous montrent qu'une motivation importante serait capable de contrer l'effet négatif de la fatigue mentale induite au cours d'une

tâche cognitive. Les modèles restent cependant plus vagues sur les effets de la fatigue mentale sur une tâche subséquente à son instauration. Des études sont encore nécessaires pour comprendre le phénomène complexe qu'est la fatigue mentale. Malgré plus d'un siècle de recherche sur cette thématique de nombreuses questions restent en suspens mais l'évolution des techniques d'investigation, en neuroimagerie notamment, nous permettent d'aller de plus en plus loin et nous permettrons, un jour peut-être, d'avoir une vision plus complète de ce qu'est la fatigue mentale et ses causes.

De nombreuses études se sont intéressées aux origines de la fatigue mentale. Dans un premier temps les recherches se sont focalisées sur les modulations de concentrations de certains neurotransmetteurs comme l'adénosine, la dopamine, la norépinephrine ou encore la sérotonine. En présence de fatigue mentale, une élévation du taux de sérotonine et d'adénosine serait à l'origine d'une augmentation de la perception de l'effort au cours d'une tâche. De leur côté, les taux de dopamine et de norépinephrine diminuent, reflétant respectivement une baisse de la motivation et une baisse de l'attention. L'impact de la fatigue mentale sur ces différents neurotransmetteurs serait donc à l'origine de l'altération des performances observée. Dans un second temps, plusieurs études se sont intéressées aux structures cérébrales impliquées dans le phénomène de fatigue mentale. Ainsi, plusieurs modèles ont été proposés afin d'essayer de mieux comprendre le phénomène de fatigue mentale. Bien que différents, tous les modèles semblent s'accorder sur l'implication de certaines structures cérébrales dans le phénomène de fatigue mentale, notamment le cortex cingulaire antérieur et l'insula. Cependant, à l'heure actuelle, les mécanismes sous-jacents à la fatigue mentale restent encore mal connus et des études complémentaires sont nécessaires pour mieux comprendre ce phénomène.

4 Les stratégies de compensation de la fatigue mentale

Avec tous les effets négatifs de la fatigue mentale, que ce soit sur les performances cognitives et/ou physiques, se répercutant ensuite sur les activités de la vie quotidienne, l'étude de possibles stratégies de compensation de la fatigue mentale est un champ d'investigation particulièrement porteur. Différentes approches sont possibles, que ce soit le moment où l'on souhaite intervenir pour réduire la fatigue mentale (avant une tâche cognitive, pendant ou après), concernant la ou les stratégie(s) employée(s) à cet effet (substances bioactives ou stratégies non-bioactives), ou encore son administration (aiguë ou chronique). Dans ce travail, nous aborderons dans un premier temps la question du moment de l'intervention puis, nous verrons les différentes stratégies pouvant être utilisées. La question du mode d'administration ne sera, quant à lui, pas développé car à l'heure actuelle trop peu d'études ont été menées sur ce sujet.

4.1 Prévenir, limiter ou compenser les effets de la fatigue mentale

Comme nous l'avons évoqué précédemment, la première question à se poser si l'on veut contrecarrer les effets de la fatigue mentale est de savoir à quel moment on peut intervenir. Dans ce cadre, trois stratégies distinctes semblent possibles.

- La prévention : que peut-on faire, **avant** de réaliser une tâche mentalement fatigante pour éviter que cette dernière n'instaure trop de fatigue mentale ?
- La limitation : que peut-on faire **pendant** une tâche mentalement fatigante pour éviter qu'elle n'instaure trop de fatigue mentale ?
- La compensation : que peut-on faire **après** une tâche mentalement fatigante pour éviter qu'elle n'ait trop de conséquences négatives ?

Ainsi, plusieurs options sont envisageables pour lutter contre les effets délétères de la fatigue mentale. Si nous avons présenté ces trois différentes stratégies de façon séparée, elles ne sont pas incompatibles et il pourrait aussi être intéressant de les combiner. Cependant, comme nous le verrons, les études investiguant ces stratégies sur la fatigue restent encore peu nombreuses.

4.2 Stratégies utilisant des substances bioactives

Afin de contrer et/ou limiter les effets de la fatigue mentale, des études se sont penchées sur les effets de l'utilisation de substances bioactives. Une substance bioactive est définie comme une substance ayant un effet, provoquant une réaction ou déclenchant une réponse dans un tissu vivant (Abdelkarim et al., 2014).

Parmi les substances utilisées pour lutter contre la fatigue mentale, on en retrouve une très commune et consommée quotidiennement par une grande partie de la population : la caféine. Azevedo et al. (2016) ont observé que l'ingestion de caféine (dose = 5 mg/kg) à la suite d'une tâche mentalement fatigante de 90 minutes (tâche d'AX-CPT), permettait d'augmenter les performances en endurance d'environ 14 % par rapport à l'ingestion d'un placebo ou à l'absence d'ingestion. Les performances étaient même meilleures qu'en absence de fatigue mentale. D'autres études semblent montrer que l'ingestion combinée de caféine et de glucides (i.e., glucose) aurait de meilleurs effets sur les fonctions cognitives et pourrait ainsi contrecarrer de façon encore plus efficace les effets de fatigue mentale (pour revue : Childs, 2014). Cependant, comme rapporté par Van Cutsem et al. (2018), l'ingestion de caféine peut entraîner des effets secondaires comme des troubles du sommeil, du rythme cardiaque, l'apparition d'anxiété ou des troubles gastro-intestinaux (McLellan et al., 2016). Afin de limiter ces effets négatifs, Van Cutsem et al. (2018) ont cherché à évaluer les effets de bains de bouche fréquents avec une solution de caféine-maltodextrine (caféine + glucose) au cours d'une tâche cognitive prolongée et exigeante (90 minutes de Stroop). Dix participants ont réalisé deux sessions expérimentales consistant à réaliser une tâche de Flanker avant et après 90 minutes d'une tâche de Stroop, avec lors de la tâche de Stroop un rinçage de bouche, approximativement toutes les 11 minutes, avec une solution de caféine-maltodextrine (condition expérimentale) ou avec une solution de salive artificielle (condition contrôle). Un effet bénéfique de la solution de caféine-maltodextrine a été observé sur la sensation de fatigue subjective, et cette substance a permis d'améliorer la précision des réponses lors de la tâche de Stroop prolongée. De plus, avec l'utilisation de cette solution, la précision des réponses lors de la tâche de Flanker étaient globalement meilleures, indiquant un effet bénéfique de la solution de caféine-maltodextrine sur les performances cognitives.

D'autres substances bioactives plus « originales » ont également été utilisées afin de contrecarrer les effets négatifs de la fatigue, par exemple l'essence de poulet. La consommation d'essence de poulet, le matin pendant une période de sept jours, a été montrée comme étant

efficace pour diminuer la sensation de fatigue lors de la réalisation de tâches cognitives et conduisait à une amélioration des performances lors d'une tâche de calcul mental et lors d'un test de mémoire à court terme (Nagai et al., 1996). Yamano et al. (2013) indiquent que la consommation quotidienne d'essence de poulet pourrait être efficace pour prévenir les effets de la fatigue mentale. Nous pouvons également citer le Guarana (plante originaire d'Amazonie et dont la principale substance active est la caféine) parmi les substances bioactives efficaces pour lutter contre la fatigue mentale. Cette substance permet non seulement de diminuer la sensation subjective de fatigue induite par une tâche cognitivement coûteuse mais aussi des limiter ses effets au niveau des performances comportementales (Kennedy et al., 2008). Cependant comme la principale substance active de cette plante est la caféine, des effets secondaires analogues à ceux observés avec la consommation de caféine sont reportés, notamment l'apparition d'anxiété et/ou de troubles gastro-intestinaux. Un récapitulatif des principales études ayant utilisé des stratégies bioactives pour lutter contre la fatigue mentale et contrer ces effets est proposé dans la Table 1.

L'utilisation de certaines substances bioactives semble donc efficace pour lutter contre la fatigue mentale et ses effets. Des effets bénéfiques sont observés sur les marqueurs subjectifs comme sur les marqueurs objectifs de fatigue mentale, avec à la clef un maintien, voire parfois même une amélioration des performances comportementales. Cependant, l'utilisation de ces substances peut entraîner des effets secondaires néfastes pour les individus et leur santé. Dans ce contexte, il semble intéressant de voir si des stratégies non-bioactives, comme l'activité physique ou l'écoute de musique, pourraient également se montrer efficaces pour lutter contre la fatigue mentale et ses effets.

Références	Participants	Stratégie de compensation	Protocole de fatigue mentale	Marqueurs de fatigue mentale	Résultats
Ataka et al. (2008)	9 femmes et 8 hommes	**Caféine** (200 mg) ou **D-ribose** (un sucre simple ; 2000 mg) : prise pendant une semaine	30 min de tâche de calcul + 30 min de Trail Making Test	VAS fatigue, motivation et ennui Performances cognitives	Aucun effet du D-ribose. Caféine : ↑ performances cognitives
Azevedo et al. (2016)	8 hommes actifs	**Caféine** : prise avant tâche cognitive (dose = 5 mg/kg)	90 min de tâche d'AX-CPT	POMS Temps limite en cyclisme à 80 % de la puissance maximale	↑ du score de vigueur sur le POMS ↑ du temps limite
Brietzke et al. (2020)	20 cyclistes bien entraînés	Rinçage buccal (25 ml) à la **maltodextrine** (glucide)	40 min de tâche de RVIP (détecter une cible dans une séquence de chiffres)	VAS fatigue EEG Test incrémental maximal de cyclisme	Pas d'effet la fatigue (VAS) Pas d'effet sur l'activité EEG ↑ des performances au test incrémental
Franco-Alvarenga et al. (2019)	12 cyclistes non professionnels entrainés	**Caféine** : prise avant tâche cognitive (dose = 5 mg/kg)	40 min de tâche de RVIP	VAS fatigue EEG Contre la montre de 20km	↓ de la fatigue (VAS) Pas d'effet significatif de la caféine sur l'activité EEG ↑ performance au contre la montre
Kennedy et Scholey (2004)	30 participants	**Caféine et glucose** : prise avant tâche cognitive et toutes les 10min durant la tâche (doses : variables)	60 min de tâches cognitives (alternance entre soustractions mentales et RVIP)	VAS fatigue Performances cognitives	↓ de la fatigue (VAS) ↑ performances cognitives

Kennedy et al. (2008)	70 femmes et 60 hommes	**Guarana/vitamines/minéraux** : prise avant la tâche cognitive	60 min de tâches cognitives (alternance entre soustractions mentales et RVIP)	VAS fatigue Performances cognitives	↓ de la fatigue (VAS) ↑ performances cognitives
Nagai et al. (1996)	20 hommes	**Essence de poulet** : 1/jour pendant 7 jours (70ml, Cerebos Pacific Ldt., Singapour)	1600 essais d'une tâche de calcul + tâche de mémoire à court terme	POMS (vigueur) Performances cognitives Cortisol sanguin	↑ du score de vigueur ↑ performances pour la tâche de calcul et de mémoire à court terme ↑ récupération cortisol
Van Cutsem et al. (2018)	10 hommes actifs	Rinçage buccal (25ml) à la **caféine et** à la **maltodextrine** au début de la tâche et toutes les 11min15sec durant la tâche	90 min de tâche de Stroop	POMS VAS fatigue EEG Performances cognitives	↓ de la fatigue (VAS) ↑ précision lors du Stroop → amplitude de la P200 lors du Stroop
Van Cutsem et al. (2020)	4 femmes et 10 hommes	**Créatine** : 4×/jour pendant 7 jours avant tâche de fatigue mentale (dose = 1g créatine monohydrate par prise)	90 min de tâche de Stroop	VAS fatigue Tâche endurance sur « *handgrip* » Performances cognitives	Pas d'effet sur la fatigue (VAS) Pas d'effet sur la tâche d'endurance ↑ précision lors du Stroop
Watanabe et al. (2002)	5 femmes et 19 hommes	**Créatine :** 8g/jour pendant 5 jours	40 min de tâche de calcul mental	Performance au calcul mental Oxygénation cérébrale	↑ performances à la tâche de calcul ↑ oxygénation cérébrale
Yamano et al. (2013)	20 hommes	**Essence de poulet** : 1×/jour pendant 4 semaines (70ml, Cerebos Pacific Ldt., Singapour)	40 min de tâche de n 2-back	VAS fatigue Performances cognitives	↓ de la fatigue (VAS) ↑ performances cognitives

Table 1 : Liste des études ayant utilisé des stratégies bioactives pour compenser les effets de la fatigue mentale. VAS = Échelle Visuelle Analogique. POMS = « *Profile Of Mood States* ». RVIP = « *Rapid Visual Information Processing* » (attention soutenue).

4.3 Stratégies non-bioactives

L'utilisation de substances bioactives, bien que pouvant être efficaces, pour lutter contre la fatigue mentale peut entraîner des effets négatifs. Nous verrons dans cette partie si d'autres méthodes moins invasives, plus « naturelles » et « douces » peuvent également s'avérer efficaces pour lutter contre la fatigue mentale. Parmi ces méthodes nous pensons notamment à l'utilisation de la musique ou de la méditation, mais nous verrons que d'autres méthodes plus originales voir même insolites ont été utilisées dans l'optique de lutter contre les effets de la fatigue mentale.

La première stratégie non-bioactive, à priori évidente pour lutter contre les effets de la fatigue mentale, est l'utilisation de la musique. La musique est connue pour améliorer les performances cognitives (Cockerton et al., 1997; Hallam et al., 2002). Elle a également des effets positifs sur les performances physiques (Karageorghis & Terry, 1997) notamment en réduisant la perception de l'effort (Potteiger et al., 2000; Yamashita et al., 2006), particulièrement impactée par la fatigue mentale (Pageaux & Lepers, 2018; Van Cutsem, Marcora, et al., 2017). Pour induire de la fatigue mentale, Guo et al. (2015) ont proposé à leurs participants de réaliser une tâche d'AX-CPT pendant 1 heure dans le silence (groupe contrôle) ou en écoutant de la musique relaxante (groupe musique). Les résultats ont montré qu'au terme de la tâche mentalement fatigante, même si la sensation subjective de fatigue mentale avait augmenté pour le groupe musique, elle était significativement moins importante que pour le groupe contrôle. De plus, alors qu'une dégradation des performances pour les participants du groupe contrôle était observée (i.e., augmentation du temps de réaction), les participants du groupe musique étaient capables de maintenir leur niveau de performance tout au long de la tâche mentalement fatigante. Une étude récente semble confirmer les bienfaits de la musique en situation de fatigue mentale. L'écoute de sons binauraux, où deux fréquences sonores légèrement différentes sont jouées dans chaque oreille, pendant 12 minutes après une tâche mentalement fatigue (90 minutes d'AX-CPT) a pu compenser les effets de la fatigue mentale (Axelsen et al., 2020). Par ailleurs, dans cette même étude, les auteurs se sont intéressés à une autre stratégie de compensation : la méditation de pleine conscience. Les résultats ont montré que la réalisation de 12 minutes de méditation de pleine conscience après une tâche mentalement fatigante permettait de rendre les performances sur une tâche d'attention soutenue

meilleures qu'avant l'instauration de la fatigue mentale. La méditation de pleine de conscience semblerait d'autant plus efficace chez des personnes expérimentées à cette pratique.

D'autres études ont également mis en évidence l'efficacité d'autres stratégies comme la présence d'odeurs intermittentes (e.g., odeur citral, verte ou menthol) durant la tâche mentalement fatigante (Kato et al., 2012) ou bien se plonger dans un bain de vapeur après cette dernière (Mizuno et al., 2010). Cependant ces études méritent plus d'investigations afin d'être validées et permettre une meilleure compréhension des mécanismes impliqués pour contrecarrer les effets négatifs de la fatigue mentale. Les incitations financières semblent également efficaces pour contrecarrer les effets de la fatigue mentale (Brown & Bray, 2017). Dans cette étude, les performances en endurance lors d'un exercice de serrage de la main étaient mesurées avant et après une tâche mentalement fatigante (2 heures de Stroop incongruent). Alors que, comme attendu, les performances étaient altérées en condition contrôle (pas de rémunération), elles étaient maintenues en donnant une récompense financière (10 $) aux participants qui parvenaient à maintenir voire même à améliorer leurs performances en présence de fatigue mentale. Cette étude a ainsi confirmé les résultats de Boksem et al. (2006) indiquant qu'une incitation financière donnée lors d'une tâche cognitive prolongée pouvait contrer les effets de la fatigue mentale et restaurer les performances. Un récapitulatif des principales études ayant utilisé des stratégies non-bioactives pour lutter et contrer la fatigue mentale et ces effets est présenté dans la Table 2.

Références	Participants	Stratégie de compensation	Protocole de fatigue mentale	Marqueurs de fatigue mentale	Résultats
Axelsen et al. (2020)	47 femmes et 42 hommes	Méditation ou écoute de sons binomiaux durant 12 min après fatigue mentale	90 min de tâche d'AX-CPT	BRUMS fatigue Fréquence cardiaque Performances cognitives (Go/No-Go)	Pour les deux stratégies : ↑ des performances cognitives
Boksem et al. (2006)	9 femmes et 9 hommes	Incitation financière de 25€ à 20 min de la fin de la tâche cognitive prolongée	140 min exigeant attention visuelle et suivi de l'action	EEG Performances cognitives	↑ de l'amplitude de la négativité liée aux erreurs (latence 50-200ms). ↑ des performance cognitives
Guo et al. (2015)	18 femmes et 18 hommes	Écoute de musique relaxante lors de la tâche de fatigue mentale	60 min de tâche d'AX-CPT	VAS fatigue EEG Performances cognitives (Go/no-Go)	↓ de la fatigue (VAS) ↑ de l'amplitude de la P300 ↑ des performances cognitives subséquentes
Smolders et de Kort (2014)	16 femmes et 12 hommes	Changement de condition lumineuse (1000 lux vs. 200 lux)	29 min de tâches cognitives (9 min tâche surveillance, de gestion de ressources et de suivi + 20 min Stroop)	Échelle somnolence de Karolinska Attention Fréquence cardiaque	↓ de la somnolence avec lumière élevée (1000 lux) ↓ de l'attention plus faible avec lumière élevée Pas d'effet sur la fréquence cardiaque
Kato et al. (2012)	18 femmes et 18 hommes	Présentation d'odeurs intermittentes (odeurs citral, verte et menthol) durant la tâche de fatigue mentale	60 min tâche Go/No-Go	VAS fatigue EEG Performances cognitives (Go/No-Go)	Pas d'effet sur la fatigue (VAS) ↑ de l'amplitude de la P300 ↑ des performance cognitives

Mizuno et al. (2010)	14 hommes	Bain à courant léger après fatigue mentale	4 h de tâches cognitives (alternance *Trail Making test* ; 30 min, et *N2-back* ; 30 min)	VAS fatigue Fréquence cardiaque Raideur musculaire Analyse sanguine	Pas d'effet sur la fatigue (VAS) ↑ de la fréquence cardiaque ↓ de la raideur musculaire pour la hanche Pas d'effet sur l'analyse sanguine
Tanaka, Yamada, et al. (2012)	7 femmes et 9 hommes	Récupération dans une salle avec un poêle à granulé, durant 30 min après la fatigue mentale	30 min de tâche de *N2-back*	VAS fatigue Performances cognitives (Go/No-Go)	↓ de la fatigue (VAS) ↑ des performance cognitives
Yang et al. (2017)	14 participants	Stimulation magnétique aux points d'acupuncture (sur la main)	4 h de lecture de papiers en anglais (langue maternelle : chinois)	Échelle somnolence de Karolinska EEG	↓ de la somnolence ↑ de l'amplitude P300b

Table 2 : Liste des études ayant utilisé des stratégies non-bioactives pour compenser les effets de la fatigue mentale. VAS = Échelle Visuelle Analogique.

Diverses méthodes utilisant des stratégies non-bioactives, plus ou moins communes, semblent efficaces pour lutter contre les effets de la fatigue mentale. Cependant plusieurs pistes, pourtant prometteuses n'ont pas encore été étudiées. En effet, des études semblent indiquer que le niveau d'activité physique (notamment dans les activités physiques d'endurance) pourrait avoir des effets bénéfiques pour prévenir et augmenter la résistance à la fatigue mentale. Une étude a montré que les performances sur un temps d'endurance chez des cyclistes amateurs étaient négativement impactées par la fatigue mentale (30 minutes de Stroop incongruent) alors que ce n'était pas chez des cyclistes professionnels (Martin et al., 2016). Il semble ainsi que plus la pratique en endurance est élevée plus la résistance à la fatigue mentale est importante. Une autre étude a également mis en avant le fait que des personnes ne pratiquant pas aucune activité physique étaient davantage impactées par une tâche mentalement fatigante que des personnes non-athlètes pratiquant une activité sportive (Jaydari Fard et al., 2019). De plus, on sait depuis maintenant quelques années que l'exercice physique qu'il soit aigu ou chronique a des bienfaits sur les fonctions cognitives (Audiffren et al., 2011; McMorris et al., 2009). Les effets bénéfiques de la pratique d'une activité physique aiguë sur les performances cognitives sont principalement dus à l'état d'excitation physiologique induit par l'exercice (Brisswalter et al., 2002), tandis que les effets de la pratique régulière d'activité physique serait dus à la libération de certaines neurotrophines comme par exemple le BDNF (Brain Derived Neurotrophic Factor ; Coelho et al., 2012; Yarrow et al., 2010), qui joue un rôle important dans l'apprentissage, l'attention ou encore la mémoire (Tyler et al., 2002). Ces effets bénéfiques de l'activité physique sur la concentration de BDNF ont également été rapportés après des exercices aigus (Griffin et al., 2011; Rasmussen et al., 2009).

Dans ce contexte, bien que l'activité physique n'ait encore jamais été utilisée comme stratégie de compensation pour limiter et/ou contrer les effets de la fatigue mentale, cette stratégie pourrait être efficace. Ainsi, il semble intéressant de tester les effets d'une pratique chronique ou aiguë de l'activité physique sur la prévention et/ou la compensation de la fatigue mentale.

Dans la mesure où nous avons vu précédemment que la fatigue mentale pouvait détériorer nos performances (cognitive et/ou physique) entraînant une altération dans nos activités de la vie quotidienne, sportives et/ou professionnelles, des études ont cherché à contrer ces effets négatifs. Plusieurs types d'interventions se dégagent. Certaines visent à limiter l'instauration de la fatigue mentale avant de réaliser une tâche cognitivement coûteuse, d'autres lors de la tâche cognitivement coûteuse et enfin certaines stratégies sont appliquées après la tâche cognitivement coûteuse pour essayer d'en limiter ses effets. À ce stade, nous n'avons pas assez de données pour savoir si une intervention est plus efficace qu'une autre et, si, combiner les interventions (e.g., intervenir avant et après une tâche cognitivement coûteuse) pourrait augmenter leur efficacité. Des substances bioactives comme la caféine ou l'ingestion de glucides semblent efficaces pour contrer les effets de la fatigue mentale (qu'elles soient ingérées avant, pendant ou après la tâche cognitive), cependant ces substances bioactives ont des effets secondaires néfastes. Certaines études se sont alors penchées sur l'utilisation de stratégies non-bioactives, qui semblent également efficaces comme la musique ou la méditation. Il serait intéressant de continuer dans cette voie car peu d'études ont à ce jour, été menées quant à l'utilisation de stratégies non-bioactives. D'autres pistes, comme, par exemple la pratique d'une activité physique (aiguë ou chronique), sembleraient intéressantes à explorer.

III. PROBLEMATIQUE

La fatigue mentale fatigue est une sensation omniprésente dans la société actuelle et peut altérer nos performances cognitives comme physiques. Bien que la fatigue mentale soit une thématique particulièrement étudiée, notamment au niveau de ses effets comportementaux, de nombreuses questions restent en suspens.

Ce travail de thèse s'articule autour de deux axes de recherche principaux (Figure 25). Premièrement, nous voulons mettre en évidence les corrélats électrophysiologiques liés aux effets de la fatigue mentale que ce soit au cours d'une tâche mentalement fatigante (Étude 1) ou lors d'un exercice subséquent en endurance (i.e., une capacité largement altérée par la fatigue mentale ; Étude 2). Le second axe de ce travail s'articule autour des effets de la fatigue mentale dans le temps. Bien que de nombreuses études se soient intéressées aux effets immédiats de la fatigue mentale, la question des effets de persistance n'a que très rarement été abordée. Nous verrons ainsi si les effets de la fatigue mentale durent dans le temps (Étude 3) et s'il est possible de proposer de nouvelles stratégies non-bioactives pour les contrecarrer (Étude 4).

L'objectif de la première étude est d'observer les changements électrophysiologiques engendrés par une tâche prolongée de Stroop modifiée. Bien que l'utilisation de la tâche de Stroop soit une des méthodes les plus utilisées en laboratoire pour induire la fatigue mentale, aucune étude n'a, à ce jour, spécifier les changements EEG lors de la réalisation de cette tâche. Nous émettons l'hypothèse que lors de la tâche Stroop prolongée nous devrions observer des modulations au niveau des oscillations cérébrales, avec notamment une augmentation des ondes thêta et alpha, synonyme de fatigue mentale. Nous nous attendons également à observer des modulations spécifiques au niveau des potentiels évoqués avec une diminution de l'amplitude des composantes N100, N200 et P300, synonyme également d'induction de fatigue mentale.

Lors de la seconde étude, nous avons focalisé notre attention sur les effets de la fatigue mentale sur un exercice d'endurance musculaire consistant à réaliser des contractions isométriques intermittentes des extenseurs du genou. Il est admis que la fatigue mentale altère les performances en endurance à cause d'une augmentation de la perception de l'effort. L'objectif de cette étude est de déterminer l'origine de cette augmentation de perception de l'effort en présence de fatigue mentale. Des études récentes semblent montrer que la perception de l'effort serait liée à l'activité de nos aires motrices et prémotrices. Nous émettons donc l'hypothèse qu'en présence de fatigue mentale, l'activation des aires motrices et prémotrices serait plus importante, ce qui induirait une perception de l'effort plus importante.

La troisième étude a pour objectif de mesurer les effets de la fatigue mentale dans le temps. Nous savons que la fatigue mentale impacte nos performances, mais nous ne savons pas comment ces effets évoluent dans le temps. Les effets de fatigue mentale sont-ils toujours présents 10 min, 20 min après avoir réalisé une tâche mentalement fatigante ? Nous avons choisi d'étudier ces effets de persistance de la fatigue mentale sur une tâche de contrôle moteur. Ce choix a été fait d'une part, car des études précédentes avaient mis en évidence un effet négatif de la fatigue sur le contrôle moteur avec un ralentissement de la vitesse des mouvements, et d'autre part car le contrôle moteur est impliqué dans de nombreuses activités de la vie quotidienne comme par exemple attraper un objet. Nous avons fait l'hypothèse qu'avec le temps qui passe un effet de récupération se mettrait en place, la vitesse des mouvements devrait être de moins en moins ralentie par les effets de la fatigue mentale, montrant ainsi les bénéfices d'une période d'inactivité sur la récupération des effets de la fatigue mentale.

Enfin la quatrième et dernière étude vise à tester des stratégies pour contrecarrer les effets de la fatigue mentale. Nous verrons avec l'Étude 3 que 20 min d'inactivité ne permettaient pas de récupérer des effets de la fatigue mentale, et qu'à l'inverse, plus le temps passait plus le contrôle moteur semblait altéré. L'objectif de l'Étude 4 est donc de tester différentes stratégies de compensation afin de récupérer plus efficacement et plus rapidement des effets délétères de la fatigue mentale. Pour les mêmes raisons que lors de l'Étude 3, nous avons de nouveau choisi d'évaluer les effets de la fatigue mentale et des stratégies de compensation sur le contrôle moteur. Nous avons choisi deux stratégies de compensation qui seront réalisées après la réalisation de la tâche cognitivement fatigante : l'écoute de musique agréable et la pratique d'une activité physique à intensité modérée. Ces stratégies ont été choisies pour leurs effets positifs sur les fonctions cognitives. Nous avons émis l'hypothèse que les deux stratégies de compensation proposées pourraient avoir des effets bénéfiques et limiter les altérations induites par une tâche mentalement fatigante sur le contrôle moteur. La pratique d'une activité physique ou l'écoute de musique serait ainsi plus bénéfique qu'une simple pause pour récupérer des effets de la fatigue mentale.

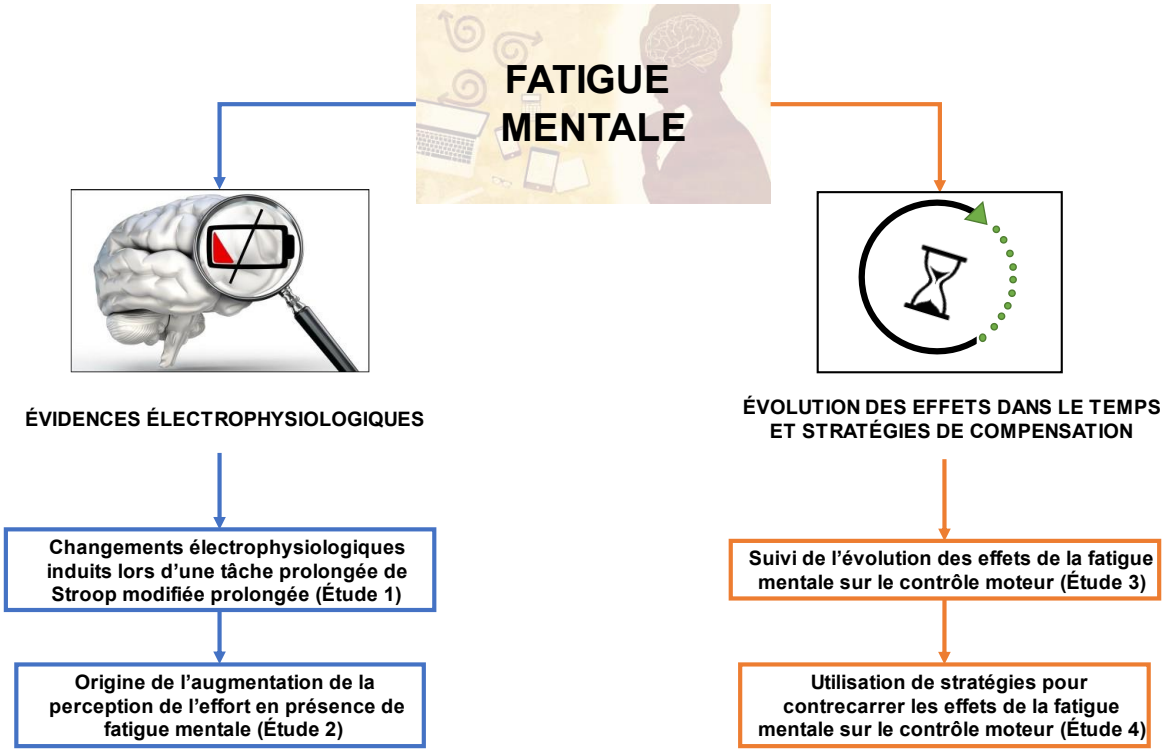


Figure 25 : Schéma récapitulatif des études de la thèse. La thèse s'articule autour de deux axes : la mise en évidence des corrélats électrophysiologiques liés aux effets de la fatigue mentale (bleu), et l'investigation de l'évolution des effets de la fatigue mentale dans le temps (orange).

IV. PARTIE EXPERIMENTALE

1 Étude 1

Les marqueurs électrophysiologiques de fatigue mentale lors d'une tâche de Stroop prolongée

The electrophysiological markers of mental fatigue during a prolonged Stroop task

Thomas Jacquet, Romuald Lepers, Patrick Bard, Benjamin Pageaux, and Bénédicte Poulin-Charronnat

À soumettre dans Psycholphysiology

1.1 Résumé

Bien que la fatigue mentale soit un réel problème dans la société moderne, c'est aussi un phénomène très complexe, dont les mécanismes sous-jacents restent méconnus. Dans cette étude, afin d'améliorer les connaissances sur ce phénomène complexe de fatigue mentale, nous avons examiné les effets de la fatigue mentale sur 90 minutes d'une tâche de Stroop modifiée, à la fois avec des mesures subjectives (i.e., la sensation subjective de fatigue mentale) mais aussi avec des mesures objectives (i.e., performances comportementales et enregistrements électroencéphalographiques). Concernant les marqueurs électrophysiologiques de la fatigue mentale, nous avons observé une augmentation dans le temps de la puissance alpha et thêta (bien que l'augmentation de la puissance thêta n'était pas été significative). Une diminution globale de l'amplitude dans le temps a été notée pour trois potentiels évoqués connus pour être liés aux processus attentionnels (i.e., les composantes N100, P200 et P300). Ces résultats répliquent des effets déjà observés dans la littérature et suggèrent que, indépendamment de la tâche cognitive exigeante utilisée pour induire la fatigue mentale, des mécanismes neuronaux similaires pourraient être identifiés. En outre, bien qu'une augmentation de la sensation subjective de fatigue mentale ait été signalée après l'achèvement de la tâche de Stroop prolongée, ainsi que les changements cérébraux mentionnés précédemment, aucun effet de la fatigue mentale n'a été observé sur la performance (c'est-à-dire aucune baisse de performance). Il est suggéré d'utiliser plus systématiquement une combinaison de plusieurs mesures afin de mieux comprendre les mécanismes cognitifs et physiologiques impliqués dans le phénomène de la fatigue mentale.

The electrophysiological markers of mental fatigue during a prolonged stroop task

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Abstract

Although mental fatigue is a real problem in modern society, it is also a very complex phenomenon, whose the underlying mechanisms remain insufficiently understood. In this study, in order to improve knowledge on that complex phenomenon of mental fatigue, we examined the effects of mental fatigue on 90 min of a modified Stroop task on both subjective measures (i.e., subjective feeling of mental fatigue) and objective measures (performance and electroencephalographical recordings). Concerning the electrophysiological markers of mental fatigue we observed an increase over time in alpha and theta power (although the increase in theta power did not reach significance), and an overall decrease in amplitude over time was reported for three ERP components known to be related to attentional processes (i.e., N100, P200, and P300 components. These findings replicate previous findings reported in the literature and suggest that irrespective of the cognitively demanding task used to induce mental fatigue, similar neuronal mechanisms could be identified. In addition, while an increase in the subjective feeling of mental fatigue was reported after the completion of the prolonged Stroop task, as well as the previously mentioned brain changes, no effect of mental fatigue was observed on performance (i.e., no performance decline). It is suggested that a more systematic use of a combination of several measures is recommended to better understand the cognitive and physiological mechanisms involved in the phenomenon of mental fatigue.

1 INTRODUCTION

Mental fatigue is a pervasive phenomenon, which can have adverse effects in both professional and personal life, resulting in an overall diminished quality of life. In professional life, mental fatigue can lead to a decline in productivity in industry or, worse still, can increase work accidents (Dinges, 1995) and burnout (Gavelin et al., 2020). Mental fatigue also plays a large role in road accidents (Brown, 1994; Lal & Craig, 2001) and medical errors (Stec et al., 2018; Taylor-Phillips & Stinton, 2019), while in personal life mental fatigue can result in depression (Lavidor et al., 2002). It is worth noting that mental fatigue is also one of the symptoms the most present in clinical pathologies (Chaudhuri & Behan, 2004). Although mental fatigue is a real problem in modern society, it is also a very complex phenomenon, whose the underlying mechanisms remain insufficiently understood. A better understanding of the mechanisms involved in mental fatigue is needed to prevent and overcome it.

In psychological terms, mental fatigue is defined as the subjective feeling of "tiredness" and lack of "energy" that one may experience after or during prolonged and/or intense periods of cognitively demanding activity (Boksem & Tops, 2008; Rozand & Lepers, 2016). In laboratory settings, mental fatigue has been shown to have negative effects on both cognitive and physical performances. Cognitive processes, such as attentional processes (e.g., Boksem et al., 2005; van der Linden & Eling, 2006) or cognitive control processes (e.g., Boksem et al., 2006; Lorist, 2008; Lorist et al., 2000, 2005; van der Linden et al., 2003) have been shown to be highly susceptible to mental fatigue effects. Regarding physical performances, although the maximum force production capacity does not seem to be affected by mental fatigue (e.g., Martin et al., 2015; Pageaux et al., 2013), most physical performances such as endurance performance (e.g., Marcora et al., 2009; Pageaux et al., 2014), decision making (e.g., Harris & Bray, 2019; Smith et al., 2016), as well as motor skills (e.g., Le Mansec et al., 2018; Rozand et al., 2015), have been shown to be impacted by mental fatigue (see Brown et al., 2020; Pageaux & Lepers, 2018, for reviews).

In order to study mental fatigue in the laboratory, it is usual to generate acute mental fatigue by asking the participants to perform prolonged and/or intense cognitive demanding tasks, such as the AX-CPT (e.g., Marcora et al., 2009; Pageaux et al., 2013; Smith et al., 2015), mental arithmetic (e.g., Mehta & Agnew, 2012; Noteboom et al., 2001; Yoon et al., 2009), the n-back task (e.g., Hopstaken et al. 2015; Tanaka et al., 2012; Yamano et al., 2013), the Time Load Dual Back task (e.g., Borragan et al., 2016, 2017; Jacquet et al., 2021), the Eriksen flanker task (e.g., Csatho et al., 2012, Faber et al., 2012; Lorist, 2008) or the Stroop task (e.g., Pageaux

et al., 2015; Rozand et al., 2015; Van Cutsem et al., 2018). During the last decade, at least 80 studies used the Stroop task and its variants (e.g., modified Stroop task) as cognitively demanding tasks to induce mental fatigue.

In the Stroop task, color words are presented printed with different ink colors (Stroop, 1935). In a congruent condition, color and word refer to the same color (e.g., the word BLUE printed in blue ink), while in an incongruent condition color and word refer to different colors (e.g., the word BLUE printed in red ink). Usually, it is required to name the color of the ink in which the color word is written, while ignoring the word itself (i.e., inhibiting word reading). Prolonged Stroop tasks are widely used in mental fatigue studies because the Stroop task involves several cognitive processes, such as inhibitory processes and cognitive control processes, which are thought to be highly vulnerable to mental fatigue. Although the Stroop task was widely used to induce mental fatigue, the psychophysiological mechanisms underlying mental fatigue when performing a prolonged Stroop task have never been studied per se. The present study aimed at examining the psychophysiological mechanisms involved when inducing mental fatigue with a prolonged Stroop task, by combining subjective (i.e., visual analog scale) and objective measures (i.e., performance and electroencephalography – EEG).

Subjective measures (e.g., visual analog scale, Profile of Mood States questionnaire) is an easy way to characterize mental fatigue and thus are frequently used. An increase in the subjective feeling of mental fatigue is usually reported, either in pretest/posttest designs or in time-on-task designs. The participants perceive themselves as being more mentally fatigued after having performed a cognitively demanding task than before, and subjective feeling of mental fatigue has been shown to increase over time during prolonged cognitively demanding tasks. Although the evaluation of the subjective feeling of mental fatigue on a visual analog scale (VAS) has been recently suggested as "the most practical method" to attest to the presence of mental fatigue (Smith et al., 2019), it remained a subjective measure and the use of more objective measures is required.

Performance is one of the objective measures the most used to assess the effects of mental fatigue. Although in pretest/posttest designs a decrement in performance is usually observed after mental fatigue induction, a decrement in performance is not always observed during the cognitively demanding task itself, even though performance decrement has been considered by some authors as the gold standard measure of mental fatigue (Hockey, 2011). It is likely that some learning effects occur during a prolonged cognitively demanding task, and limit the effects of mental fatigue on performance, even though a subjective increase in the level

of mental fatigue is reported (e.g., Filipas et al., 2019; Smith et al., 2019; Verschueren et al., 2020).

Recently, it has been proposed that EEG is a promising technique to access objective measure of the effects of mental fatigue (Lal & Craig, 2001). Regarding brain oscillations, an increase in theta and alpha power has been consistently observed in the presence of mental fatigue (see Tran et al., 2020, for a meta-analysis). Concerning event-related potentials (ERPs), consistent effects of mental fatigue have been observed on the N100, N200, and P300 components. For these three components, a decrease in amplitude over time has been observed and interpreted as reflecting a top-down modulation of sensory processing for the N100 (Boksem et al., 2005; Faber et al., 2012), a decrease in cognitive control for the N200 (Boksem et al., 2006; Möckel et al., 2015), and a decrease in attention for the P300 (Murata et al., 2005; Schmidt et al., 2009).

Although electrophysiological changes associated with the effects of mental fatigue have been assessed with other tasks than the Stroop task, to our knowledge and although the Stroop task is widely used as a cognitively demanding task to induce mental fatigue, onlt very few studies have previously investigated the electrophysiological changes during the realization of a prolonged Stroop task. We found two studies on fatigue mental reporting EEG recordings during a prolonged Stroop task (Van Cutsem et al., 2017, 2018). However, these studies investigated the effects of mental fatigue on physical performances under very special circumstances. The first study evaluated the use of frequent mouth rinses during a 90-min prolonged Stroop task on mental fatigue, and the second one was conducted under a temperature of 30°C.

It is worth noting that the different cognitively demanding tasks used to induce mental fatigue might involve specific cognitive processes that could result in specific brain changes in the presence of mental fatigue. For a given task, it would be relevant to know precisely the electrophysiological changes related to the presence of mental fatigue. More importantly, comparing the electrophysiological changes observed during different cognitively demanding tasks could evidence some brain changes common to all the cognitively demanding tasks, and as a consequence might help to highlight markers of mental fatigue that would be independent of the cognitively demanding tasks used.

The main aim of the present study was to characterize mental fatigue with subjective, behavioral, and electrophysiological measures to provide new data in order to improve knowledge on that complex phenomenon of mental fatigue. A 90-min modified Stroop task

(i.e., depending on the color of ink the participants are required to either name the color of the ink or read the color word) was used as a cognitively demanding task to induce mental fatigue, while combining three types of measures, the evaluation of the subjective feeling of mental fatigue, behavioral measures (performance), and electroencephalographical recordings (brain oscillations and ERPs). According to the findings of previous studies (e.g., Rozand et al., 2015; Smith et al., 2016), and with the assumption that the effects of mental fatigue should present some similarities independently of the cognitively demanding task used, it is expected that mental fatigue should increase the subjective feeling of fatigue after 90 min of the modified Stroop task. Although performance impairment is not always observed during the cognitively demanding task, it is expected a decrement in performance over time (more errors and slower response times) due to the long duration of the cognitively demanding task. Concerning brain activity, we firstly hypothesized for brain oscillations that theta and alpha power should increase over time (see Tran et al., 2020, for a meta-analysis). Secondly, we expected that ERP components more directly linked to cognitive processes vulnerable to the effects of mental fatigue should be modified over time. More precisely, a decrease in amplitude should be observed for the N100, the N200, and the P300 components, as observed in previous studies on mental fatigue using other tasks than the Stroop task.

2 METHODS

2.1 PARTICIPANTS

Eight volunteer participants took part in this study (*M* ± *SD*; age: 25.5 ± 4.6 years; 4 males and 4 females). All participants reported normal or corrected-to-normal vision and none of them had a history of neurological disorders. Each participant provided written informed consent to participate in the experiment. All participants were given instructions to sleep for at least 7 h and not to consume alcohol the day before each visit. Participants were also instructed not to consume caffeine and nicotine at least 3 h before testing and were asked to declare if they had taken any medication or had any acute illness, injury, or infection. The experiment was conducted in conformity with the latest version of the Declaration of Helsinki (1964).

2.2 APPARATUS AND MATERIALS

The Experiment Builder software (SR Research) was used to present the stimuli. French color words (*JAUNE*, *VERT*, *BLEU*, and *ROUGE*) printed in standard uppercase 43-point Arial-font and in different ink color were presented at the center of a black screen. The computer screen had a resolution of 1024 × 768, a 60-Hz refresh rate, and was placed 1 m in front of the

participant. Responses were recorded on a button box with four buttons (yellow, green, blue, and red), going from left to right.

The participants were also required to complete a Visual Analogue Scale (VAS) to estimate their feeling of mental fatigue before and after performing the prolonged modified Stroop task. The VAS consisted of a line measuring 100 mm in length, with bipolar end anchors (0 mm = ‘‘No mentally tired at all”; 100 mm = ‘‘Extremely mentally tired”). Participants were asked to place a mark along the line to indicate their level of mental fatigue. VAS score corresponded to the distance between the first anchor (0 mm = ‘‘No mentally tired at all”) and the mark placed by the participant.

2.3 PROCEDURE

Participants visited the laboratory on two different occasions. The first visit was for a familiarization session. During this session, participants discovered the VAS used in the experiment and practiced the modified Stroop task for 15 min to reduce learning effects in the following experimental session. The design of the modified Stroop task is shown in Figure 1. In this modified version of the Stroop task, participants are required to perform two intermixed tasks, the usual color-naming task and the (less used) word-reading task.

French color words (i.e., *JAUNE*, *VERT*, *BLEU*, or *ROUGE*) were presented with different color inks (i.e., yellow, green, blue, or red). In the color-naming task, participants have to name the color of the ink, while ignoring the written word. In the word-reading task, they have to read the word, while ignoring the color of the ink. The two tasks (i.e., color naming and word reading) were mixed and are dependent on the color of the ink of the presented words. When the color words were printed in blue, yellow, and green, participants had to name the color of the ink and to inhibit word reading (i.e., color-naming task). When the color words were printed in red, participants were asked to read the word while ignoring the color of the ink (i.e., word-reading task). The color-naming trials represented approximately 75% of all stimuli, with approximately 50% of congruent trials (e.g., the word *red* printed in red ink) and approximately 50% of incongruent trials (e.g., the word *red* printed in blue ink). The word-reading trials represented approximately 25% of all stimuli, with approximately 50% of congruent trials and approximately 50% of incongruent trials.

This modified Stroop task prevents the development of strategies with time on task (e.g., concentrating the attention on the ink color only), and is more challenging because two goals have to be maintained in mind as a function of the color of the ink. This modified Stroop task is thus particularly appropriate to generate and evaluate mental fatigue, because it implies high

cognitive control processes, such as switching, selective attention, and inhibition, which have been shown to be particularly vulnerable to mental fatigue.

Each trial began with a white fixation cross, which was displayed for 500 ms at the center of the screen before the occurrence of the color word, which stayed on the screen during 500 ms. Participants could respond as soon as the color word appeared and until 2000 ms after the stimulus apparition (i.e., timeout). The interval between the response and the next trial was 1000 ms. The trials were randomly ordered for each participant.

Participants responded on a four-button response box by pressing buttons with the middle and index fingers of each hand (left middle finger on the yellow button, left index finger on the green button, right index finger on the blue button, and right middle finger on the red button). Participants responded by pressing the button corresponding to their response, and were instructed to respond as fast and as accurately as possible.

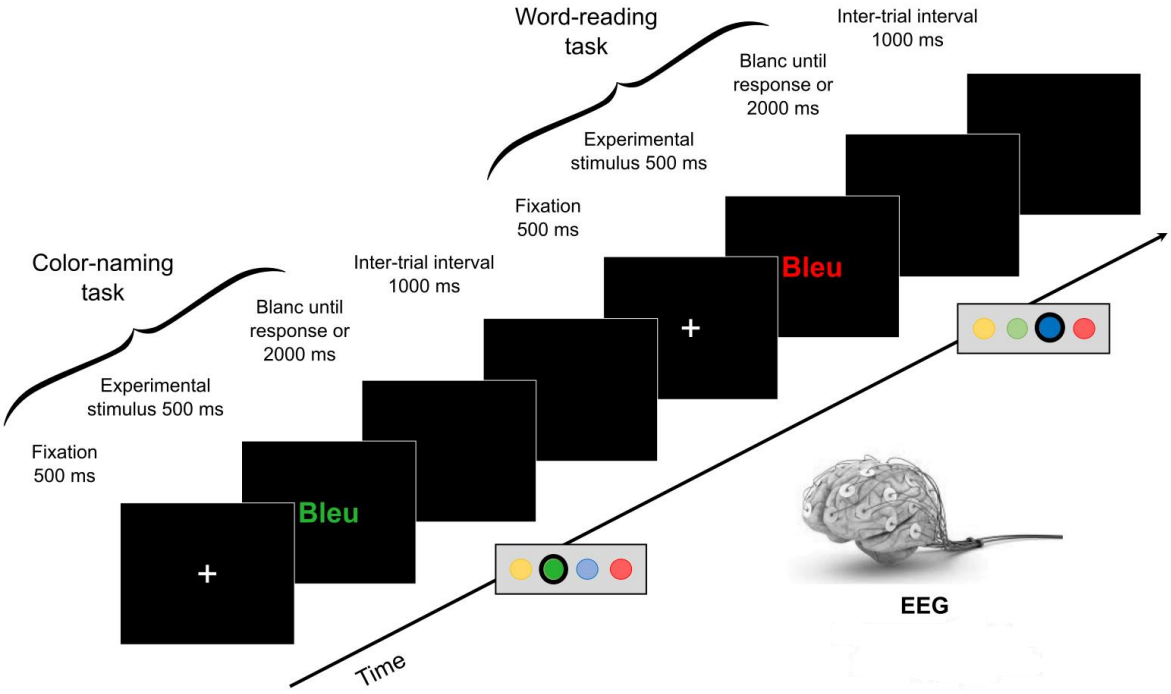

Figure 1. An example of a sequence of events in the modified Stroop task. Each trial began with a fixation cross of 500 ms, followed by an experimental stimulus. The stimulus stayed on the screen for 500 ms and participants had until 2000 ms after the apparition of the stimulus to respond. The next trial started 1000 ms after the participant's response or after a timeout of 2000 ms. Trials were randomly ordered for each participant.

The second visit to the laboratory was the experimental session, during which the participants had to perform the same modified Stroop task, but for 90 min. At the beginning of the experimental session, participants had to report their mental fatigue level on a VAS, while the electrodes for the EEG recording were positioned on her/his scalp. Mental fatigue level was also evaluated on a VAS immediately after the achievement of the prolonged modified Stroop task. The familiarization and experimental sessions were completed over a period of one week with a minimum of 48 h between visits.

2.4 EEG RECORDING AND PREPROCESSING

The electroencephalogram was recorded continuously through the Active Two BioSemi system from 64 electrodes according to the 10-20 International system. Horizontal eye movements were monitored with electrodes placed on the outer left and right canthi, while eye blinks were monitored with an electrode placed under the left eye. Two additional electrodes were placed on the left and right mastoids (A1, A2). During recording, the BioSemi system's common mode sense electrode served as the reference electrode. Electrophysiological signals were digitized at 2048 Hz sampling rate and acquired with ActiView software. Offline data analyses were performed using MATLAB (MathWorks, Natick, MA, USA) and the EEGLAB toolbox (Delorme & Makeig, 2004). Continuous data were downsampled to 512 Hz, band-pass filtered at 0.1–100 Hz, and re-referenced to the average of A1 and A2. Noisy electrodes were identified with the *probability* and *spectrum* methods proposed in EEGLAB (threshold, Z = 5) and interpolated when necessary with a spherical method. To remove eye-movement artifacts, EEGLAB's Runica routine was used to perform independent component analyses, and components reflecting eye artifacts were identified by visual inspection and removed. Continuous data were segmented into epochs of 1200 ms from 200 ms before to 1000 ms after the appearance of the color word, and were baseline corrected using the pre-trial period from -200 ms to 0 ms. Contaminated epochs were rejected by visual inspection before averaging and excluded from further analysis.

2.5 DATA ANALYSIS

Performance. Response times faster than 200 ms were excluded from the analysis. Response times beyond three standard deviations of the mean were also excluded from the analysis, with standard deviations calculated for each congruence condition (congruent, incongruent). Using this method, 1.7% (±0.4%) of trials were removed for congruent trials and 1.2% (±0.6%) for incongruent trials.

EEG data. For ERP analyses, only trials with correct responses were considered. Epochs were averaged separately for each condition and each participant. ERPs were obtained by computing the mean amplitude in the time window for each ERP component, and by grand-averaging data across participants. For the sake of simplicity, only the results directly linked to the main issue of the present study are presented, that is the behavioral results and the brain activity (oscillations and ERPs) affected by time on task for the usual color-naming task. All the other analyses (i.e., congruence effect for the color-naming task and the analyses for the word-reading task) are provided in the supplementary data. To anticipate it is worth noting that all the classical effects observed in both performance (i.e., Stroop interference) and ERP analyses (N450 and Late Negativity [LN]) have been replicated (e.g., Hanslmayr et al., 2008).

Based on visual inspection of peak amplitude, the following time windows were used for ERP components: N100 (25-130 ms), P200 (130-260 ms), and P300 (340-400 ms). For spectral analysis, Fast Fourier Transform (FFT) was performed, using the *spectopo* function of the EEGLAB toolbox. EEG power was divided into five frequency bands: delta, 1–4 Hz; theta, 4–7 Hz; alpha, 8–12 Hz; beta 13–30 Hz; and gamma, 30–40 Hz. Nine regions of interest (ROIs) were constituted to perform analyses on both ERPs and spectral data (e.g., Arendsen et al., 2020; Jacquet et al., 2021): Frontal Left (FL; mean of FP1, AF3, AF7, F3, F5, F7), Frontal Median (FM; mean of FPz, AFz, F1, Fz, F2), Frontal Right (FR: mean of FP2, AF4, AF8, F4, F6, F8), Central Left (CL: mean of FC3, FC5, FT7, C3, C5, T7, CP3, CP5, TP7), Central Median (CM: mean of FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2), Central Right (CR: mean of FC4, FC6, FT8, C4, C6, T8, CP4, CP6, TP8), Posterior Left (PL: mean of P3, P5, P7, PO3, PO7, O1), Posterior Median (PM: mean of P1, Pz, P2, POz, Oz), and Posterior Right (PR: mean of P4, P6, P8, PO4, PO8, O2).

2.6 STATISTICS

Greenhouse-Geisser's correction to the degrees of freedom was applied when violations of sphericity were present (corrected *p*-values are reported). Only significant effects are reported, except when nonsignificance is relevant for the hypotheses being tested.

Response times, accuracy, ERPs, and power density were analyzed using two-way repeated-measures ANOVAs with congruence (congruent, incongruent) and time on task (Part 1: 0-30 min, Part 2: 30-60 min, Part 3: 60-90 min) as within-subject factors. For the VAS, paired *t*-tests were used to evaluate mental fatigue. All analyses were performed using the Statistical Package for the Social Sciences, version 24 for Windows (SPSS Inc., Chicago, IL, USA). For each ANOVA, partial eta squared was calculated. Thresholds for small, moderate, and large

effects were set at 0.01, 0.07, and 0.14, respectively (Cohen, 1988). Cohen's *d* was calculated for each *t*-test using JASP (Version 0.13.1.0) [Windows software]. Thresholds for small, moderate, and large effects were set at 0.2, 0.5, and 0.8 respectively (Cohen, 1988).

3 RESULTS

3.1 VISUAL ANALOG SCALE

The VAS scores are shown in Figure 2, Panel A. An analysis performed on the VAS scores showed a significant increase of subjective mental fatigue feeling after the prolonged modified Stroop task compared to before [$t_{(7)}$ = -3.391, p = .012, d = -1.199].

3.2 PERFORMANCE

For the error rates, neither the effect of time on task nor the Congruence × Time-on-task interaction was significant [*ps* > .05], suggesting that the performance was maintained for the 90 min of the modified Stroop task.

Correct response times are shown in Figure 1, Panel B. A significant main effect of time on task was observed [$F_{(1, 7)}$ = 9.628, p < .014, η_p^2 = .579], with a significant linear trend [$F_{(1, 7)}$ = 9.896, p = .016, η_p^2 = .586], reflecting a linear decrease in response times over time. This main effect was qualified by a Congruence × Time-on-task interaction [$F_{(2, 14)}$ = 23.794, p = .001 , η_p^2 = .773], with a significant quadratic trend [$F_{(2, 14)}$ = 31.309, p = .001 , η_p^2 = .817], indicating that the decrease over time was more pronounced for the incongruent trials, especially for the second part (i.e., 30-60 min) of the prolonged modified Stroop task (averaged decrease between Part 2 and Part 1: $M_{\text{congruent}}$ = 24.403, $M_{\text{incongruent}}$ = 61.252; averaged decrease between Part 3 and Part 2: $M_{\text{congruent}}$ = 12.995, $M_{\text{incongruent}}$ = 23.396).

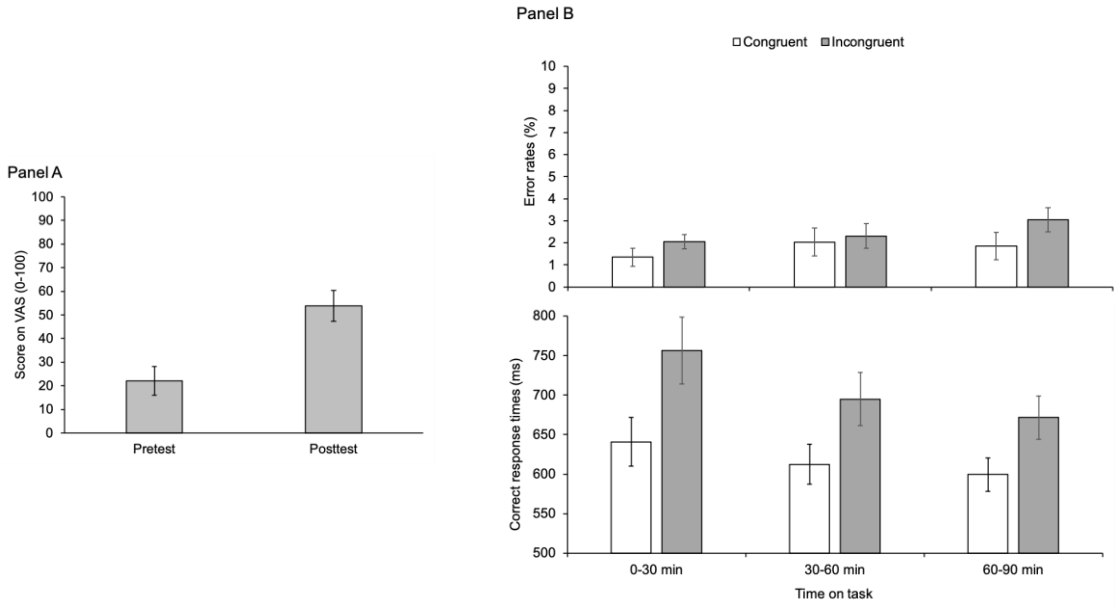

Figure 2. Panel A: Subjective feeling of mental fatigue before (Pretest) and after (Posttest) performing the prolonged modified Strop task. Panel B: Error rates and correct response times as a function of congruence and time on task. A significant effect of time on task was observed for the response times, with a decrease in response times over time. Error bars indicate standard errors.

3.2 EEG ANALYSES

3.2.1. POWER SPECTRA ANALYSIS

Figure 3 shows the results of the power spectra analysis. Only results about theta and alpha power, which are the power of main interest in mental fatigue studies, are reported in the Results section, the other brain oscillations (i.e., delta, beta, and gamma power) being reported in supplementary data.

Theta (4-7 Hz). Although the results did not reach significance, theta power tended to be modulated by time on task for all frontal regions [FL: $F_{(2, 14)} = 3.874$, $p = .055$, $\eta_p^2 = .356$; FM: $F_{(2, 14)} = 3.637$, $p = .058$, $\eta_p^2 = .342$; FR: $F_{(2, 14)} = 3.943$, $p = .059$, $\eta_p^2 = .360$], with tendantial linear increases over time [FL: $F_{(1, 7)} = 4.870$, $p = .063$, $\eta_p^2 = .410$; FM: $F_{(1, 7)} = 5.621$, $p = .050$, $\eta_p^2 = .445$; FR, $F_{(1, 7)} = 4.330$, $p = .076$, $\eta_p^2 = .382$].

Alpha (8-12 Hz). Significant main effects of time on task were observed on FM [$F_{(2, 14)} = 4.350$, $p = .049$, $\eta_p^2 = .383$], CM [$F_{(2, 14)} = 4.370$, $p = .049$, $\eta_p^2 = .384$], and CR regions [$F_{(2, 14)} = 4.703$, $p = .039$, $\eta_p^2 = .402$], with a significant linear increase of alpha power on CR region [$F_{(1, 7)} = 5.998$, $p = .044$, $\eta_p^2 = .461$] and a tendential linear increase in FM [$F_{(1, 7)} = 5.316$, $p = .055$, $\eta_p^2 = .432$] and CM regions [$F_{(1, 7)} = 4.795$, $p = .065$, $\eta_p^2 = .407$].

Tendential effects of time on task were observed for FR [$F_{(2, 14)}$ = 3.684, p = .073, η_p^2 = .345] and PR regions [$F_{(2, 14)}$ = 3.408, p = .079, η_p^2 = .327], with and a tendential linear increase of alpha power over time [FR: $F_{(1, 7)}$ = 4.683, p = .067, η_p^2 = .401; PR: $F_{(1, 7)}$ = 4.440, p = .073, η_p^2 = .388].

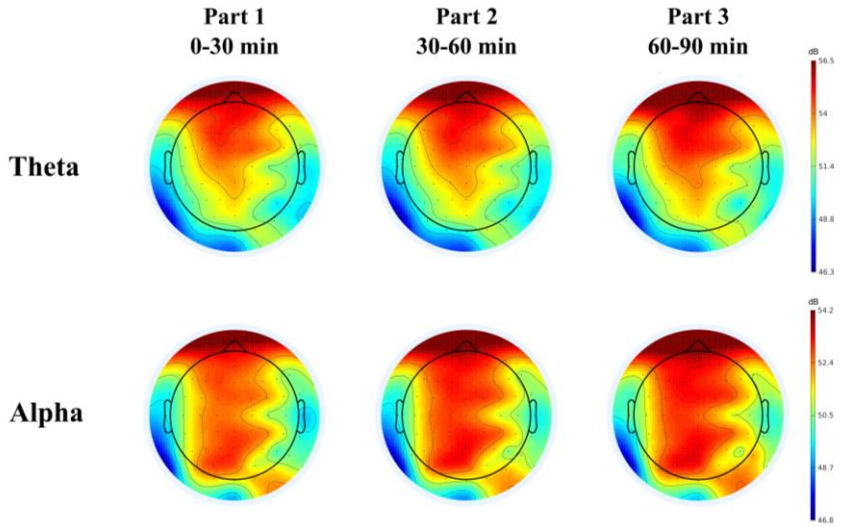

Figure 3: Scalp topography of power density activity for the theta power (4-7 Hz), and the alpha power (8-12 Hz) over time.

3.2.2. Event-Related Potential Analysis

Figure 4 shows the results of the ERP analysis for the effect of time on task.

N100: A significant Time-on-task × Congruence interaction was observed in fronto-central regions [FL: $F_{(2, 14)}$ = 5.703, p = .016, η_p^2 = .449; FM: $F_{(2, 14)}$ = 7.661, p = .012, η_p^2 = .523; CM: $F_{(2, 14)}$ = 4.144, p = .048, η_p^2 = .372; and CR: $F_{(2, 14)}$ = 5.409, p = .023, η_p^2 = .436], with a significant quadratic trend [FL: $F_{(1, 7)}$ = 13.001, p = .009, η_p^2 = .650; FM: $F_{(1, 7)}$ = 26.207, p = .001, η_p^2 = .789; CM: $F_{(1, 7)}$ = 13.662, p = .008, η_p^2 = .661; and CR: $F_{(1, 7)}$ = 12.279, p = .01, η_p^2 = .637]. The quadratic trend indicated a decrease in the N100 amplitude over time. This decrease began earlier for the incongruent trials (30-60 min) and later for the congruent trial (60-90 min).

P200: A significant Time-on-task × Congruence interaction was observed for the FM [$F_{(2, 14)}$ = 5.703, p = .016, η_p^2 = .449] and the CM regions [$F_{(2, 14)}$ = 4.417, p = .035, η_p^2 = .387], with a significant quadratic trend [FM: $F_{(1, 7)}$ = 13.001, p = .009, η_p^2 = .650; CM: $F_{(1, 7)}$ = 10.335, p = .015, η_p^2 = .596]. The quadratic trend indicated a decrease in the P200 amplitude over time.

This decrease began earlier for the incongruent trials (30-60 min) than for the congruent trials (60-90 min)

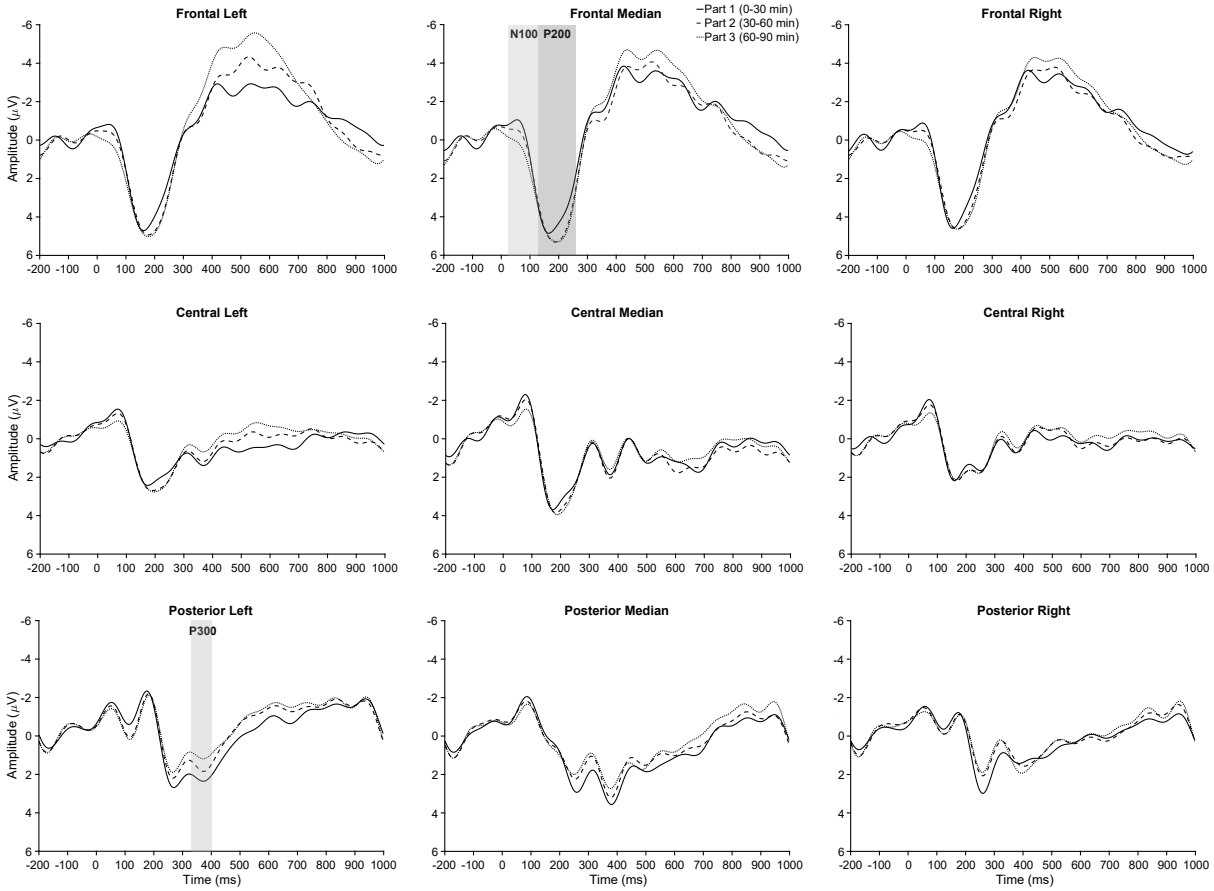

Figure 4: Grand average of the EEG signal for the effect of time on task for the color-naming task as a function of the regions of interest. The rectangles show the time window used for the analyses of the N100, P200, and P300 components in the regions of interest for which the statistical effect was the strongest.

P300: A significant effect of time was observed in the PL region [$F_{(2, 14)} = 4.910$, $p = .046$, $\eta_p^2 = .412$], with a significant linear trend [$F_{(1, 7)} = 5.727$, $p = .048$, $\eta_p^2 = .450$], indicating a decrease in the P300 amplitude over time.

4. DISCUSSION

The present study investigated the effects of mental fatigue on a prolonged modified Stroop task on both subjective measures (VAS) and objective measures (performance and brain activity analyzed with ERPs and power spectra). The main contributions of the present study

are 1) to identify the electrophysiological markers of mental fatigue during the performance of a prolonged Stroop task, in order to better understand the cognitive and neural mechanisms underlying mental fatigue and to highlight (dis)similarities in brain changes between the different cognitively demanding tasks used to induce mental fatigue; and 2) to show that subjective and objective measures did not always result in convergent findings.

Regarding the first contribution, we replicated the previously observed increase over time in alpha and theta power (although the increase in theta power did not reach significance). We also replicated the effects of mental fatigue observed with other cognitively demanding tasks than the Stroop task on the N100, P200, and P300 components, which showed an overall decrease in amplitude over time. We also observed some discrepancies with previous data. While some studies observed a significant effect of mental fatigue on the N200 component, in the present study we did not observe a decrease in the N200 amplitude.

Concerning the second contribution, while an increase in the subjective feeling of mental fatigue was reported after the completion of the prolonged Stroop task and brain activity changes were observed during its realization, no effect of mental fatigue was observed on performance (i.e., no decrement in performance).

4.1. PERFORMANCE DURING THE PROLONGED STROOP TASK

In the present study, no detrimental effect of mental fatigue was observed on Stroop performance, and response times even decreased over time. This decrease in response times very likely reflected learning effects due to the numerous repetitions of the stimuli performed during the 90 min of the modified Stroop task. Although the participants performed a 15-min training on the modified Stroop task during the familiarization phase in order to reduce learning effects during the experimental session, learning effects still occurred over the 90-min of the modified Stroop task. These learning effects could be linked to the learning of the key/color/finger associations, and also to an improvement in the triggering of task switching over time (color-naming versus word-reading task as a function of the ink color). Wang et al. (2016) have evaluated the evolution of performance during the realization of a Stroop task for 160 min, and they reported that the performance was maintained for 80 min, before deteriorating. It is likely that 90 min of the Stroop task was not long enough to see performance decrement. Nevertheless, the present result indicated that the participants were able to maintain and even improve their level of performance during a prolonged cognitively demanding task, even though they reported an increase in their subjective feeling of mental fatigue. Previous

data in the literature regarding the maintenance or the decrease in performance during a mentally fatiguing task are disparate. Some studies reported a decrease in performance (i.e. slower response time and/or a decrease in accuracy) over time (e.g., Head et al., 2016; Marcora et al., 2009; Martin et al., 2015), while others reported no performance alteration (e.g., Pageaux et al., 2015). A possible explanation for the absence of performance alteration despite the long duration of the task may be related to the motivation and the commitment of the participant to perform the cognitively demanding task. In a recent study, Herlambang et al. (2019) showed that during a prolonged cognitive task, participants have seen their response accuracy decline in non-reward blocks (low motivation), whereas their response accuracy remained stable over time in reward blocks (high motivation). Motivation seems therefore be an important factor that could counteract the effects of mental fatigue on performance, and that it would have been relevant to take motivation into account in the present study.

4.2. VIGILANCE AND MENTAL WORKLOAD DURING PROLONGED COGNITIVE TASKS

In the present study, we observed an overall decrease over time in alpha and theta power, although non-significant for the theta power. Such decrease has been interpreting as reflecting a decrease in arousal and vigilance (Tran et al., 2020). The absence of a significant decrease in theta power in the present study could be due to the fact that the EEG was recorded during the Stroop task and not at rest. Jacquet et al. (2021) reported an increase in theta power over time when the EEG was recorded during rest periods, whereas they observed a decrease in theta power over time during the cognitively demanding task. Recently, Li et al. (2020) suggested that in mental fatigue studies, brain oscillations should be recorded during rest periods before and after the cognitively demanding task.

Regarding ERP components, in previous studies, the N100 was linked to attentional engagement and attention orienting (Luck et al., 2000; Rugg et al., 1987). A large amplitude of N100 may reflect a greater attentional allocation to the information to process, whereas a small N100 amplitude could reflect a lower attentional allocation. In addition, it has been previously shown that the N100 amplitude decreased with an increase of mental workload (Kramer et al., 1995) and a decrease in vigilance (Boksem et al., 2005; Faber et al., 2012). In the present study, we observed a decrease in the amplitude for both N100 and P200 over the prolonged modified Stroop task. These decreases in both N100 and P200 amplitude started to occur for the incongruent trials (i.e., the more attentionally demanding trials) and then in the last part of the

prolonged modified Stroop task, the congruent trials showed also a decrease in N100 and P200 amplitude. The decrease observed in N100 and P200 amplitude over time during the prolonged modified Stroop task could reflect a decrease in attentional allocation due to the presence of mental fatigue. Lorist and Tops (2003) in a review paper on caffeine, fatigue and cognition, reported several studies that showed a decrease in N100 and P200 amplitude with the presence of mental fatigue. This decrease could be counteracted by the intake of caffeine, which is known to affect the attention system. Van Cutsem et al. (2017), which used a prolonged Stroop task to induce mental fatigue and recorded EEG, also observed a decrease in the amplitude of a P200 over time in their placebo group (which served as a comparison to a caffeine-maltodextrin mouth rinsing group).

Another ERP component, which has attracted a lot of attention in studies interested in brain changes during mental fatigue is the P300 component. In the present study, as previously reported (Murata et al., 2005; Schmidt et al., 2009), a decrease in P300 amplitude was observed. This decrease in P300 amplitude could be explained by an increase of mental workload over time as reported in previous studies (Horat et al., 2016; Käthner et al., 2014) or by a decrease in vigilance or attentional resources (Lammers & Badia, 1989; Schmidt et al., 2009).

4.3. CONCLUSION

The present study reported, with a 90-min Stroop task, similar brain changes due to mental fatigue as those previously observed with other cognitively demanding tasks. These findings suggest that irrespective of the cognitively demanding task used to induce mental fatigue, similar neuronal mechanisms are involved such as an increase in theta and alpha power and a decrease in amplitude over time for attentional ERPs (e.g., N100, P200 and P300). On the contrary, a decline in behavioral performances did not always occur during a cognitively demanding task inducing mental fatigue, suggesting that the interpretation of changes in performance should be make with caution. A more systematic use of a combination of several measures (i.e., subjective feeling, performance, and physiological recordings) is recommended to better understand the cognitive and physiological mechanisms involved in the phenomenon of mental fatigue.

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SUPPLEMENTARY DATA

Power spectra analyses

Figure 1 shows the results of the power spectra analysis.

Delta (1-4 Hz). No significant effects of time on task were observed (all *ps* > .10).

Beta (13-30 Hz). A significant main effect of time on task were observed on CL region [$F_{(2, 14)}$ = 4.721, p = .042, η_p^2 = .403], with a tendential linear increase in beta power over time [$F_{(1, 7)}$ = 4.801, p = .065, η_p^2 = .407].

Gamma (30-40 Hz). The analyses revealed significant main effects of time on task for the FM [$F_{(2, 14)}$ = 4.153, p = .042, η_p^2 = .372], FR [$F_{(2, 14)}$ = 4.740, p = .028, η_p^2 = .404], CL [$F_{(2, 14)}$ = 8.906, p = .003, η_p^2 = .560], and CR regions [$F_{(2, 14)}$ = 4.935, p = .024, η_p^2 = .414], with significant linear increases of gamma power over time for all these regions of interest [FM: $F_{(1, 7)}$ = 6.443, p = .039, η_p^2 = .479; FR: $F_{(1, 7)}$ = 8.747, p = .021, η_p^2 = .555; CL: $F_{(1, 7)}$ = 13.584, p = .008, η_p^2 = .660; and CR: $F_{(1, 7)}$ = 8.052, p = .025, η_p^2 = .535].

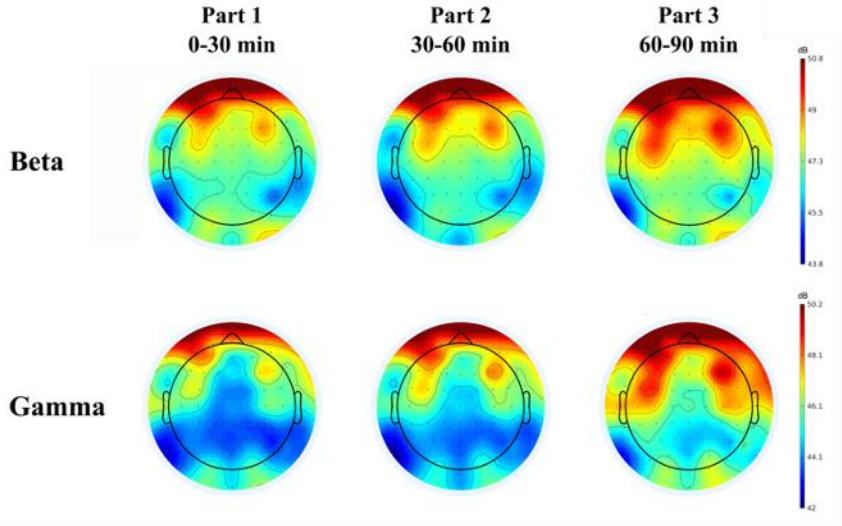

Figure 1: Scalp topography of power density activity for the beta power (13-30 Hz), and the gamma power (30-40 Hz) over time.

Color-naming task

Performance

The ANOVA performed on the rate of errors showed a significant main effect of congruence [$F_{(1, 7)}$ = 8.955, p = .020, η_p^2 = .561]. The rate of errors was higher for the incongruent trials (M = 2.478, SD = 1.353) than for the congruent trials (M = 1.748, SD = 1.563), reflecting the presence of a Stroop effect.

As for the rate of errors, the ANOVA performed on response times showed a significant main effect of congruence [$F_{(1, 7)}$ = 45.395, p < .001, η_p^2 = .866], with shorter response times for congruent than incongruent trials reflecting, the presence of a Stroop effect.

Event-Related Potential Analyses

Based on visual inspection of peak amplitude, the following time windows were used for ERP components: N450 (400-700 ms) and Late Negativity (LN; 700-900 ms). Figure 2 shows the grand-average ERP for the effect of congruence.

N450: A significant effect of congruence was observed for median-right regions [FM: $F_{(1, 7)}$ = 10.402, p = .015, η_p^2 = .605; FR: $F_{(1, 7)}$ = 10.714, p = .014, η_p^2 = .598; CM: $F_{(1, 7)}$ = 17.146, p = .004, η_p^2 = .710; CR: $F_{(1, 7)}$ = 27.850, p = .001, η_p^2 = .799; PM: $F_{(1, 7)}$ = 6.217, p = .019, η_p^2 = .569; and in PR: $F_{(1, 7)}$ = 7.472, p = .029, η_p^2 = .516], indicating that the amplitude of the N450 was larger for the incongruent trials that for the congruent trials.

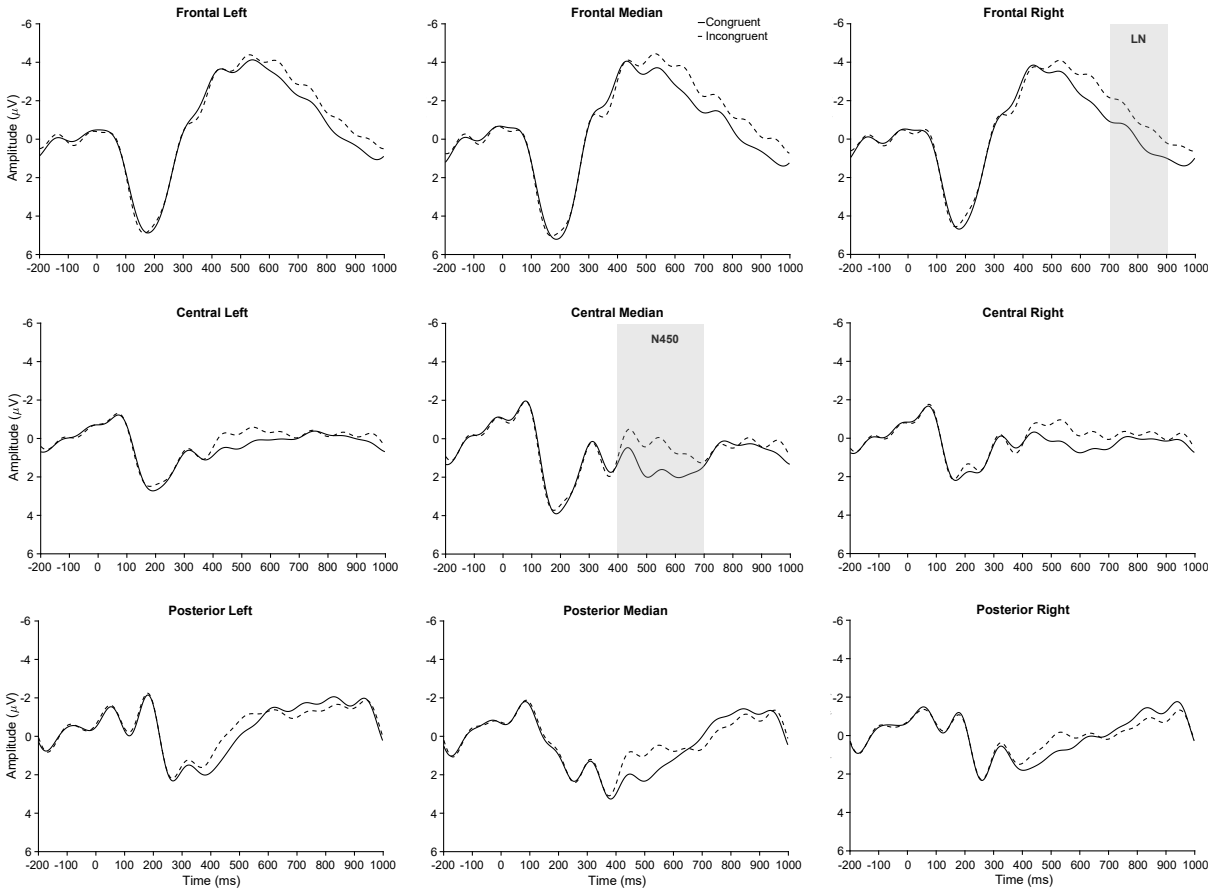

Figure 2: Grand average of the EEG signal for the effect of congruence for the color-naming task as a function of the regions of interest. The rectangles show the time window used for the analyses of the N450 and LN components in the regions of interest for which the statistical effect was the strongest.

Late Negativity: A significant effect of congruence was observed for the FR region of interest [$F_{(1, 7)} = 6.264$, $p = .041$, $\eta_p^2 = .472$], indication a larger amplitude of the LN for the incongruent trials than for the congruent trials.

Word-reading task

Performance

Figure 3 shows the error rates and correct response times obtained for the word-reading task. The ANOVA performed on the rate of errors showed a tendantial main effect of congruence [$F_{(1, 7)}$ = 4.987, p = .061, η_p^2 = .416], which was qualified by a significant Time-on-task × Congruence interaction [$F_{(2, 14)}$ = 5.537, p = .035, η_p^2 = .442], with a significant linear trend [$F_{(1, 7)}$ = 5.585, p = .05, η_p^2 = .444], which indicated that the rate of errors was higher for the incongruent trials than for the congruent trials, reflecting the presence of a reverse Stroop effect, which linearly decreased over time.

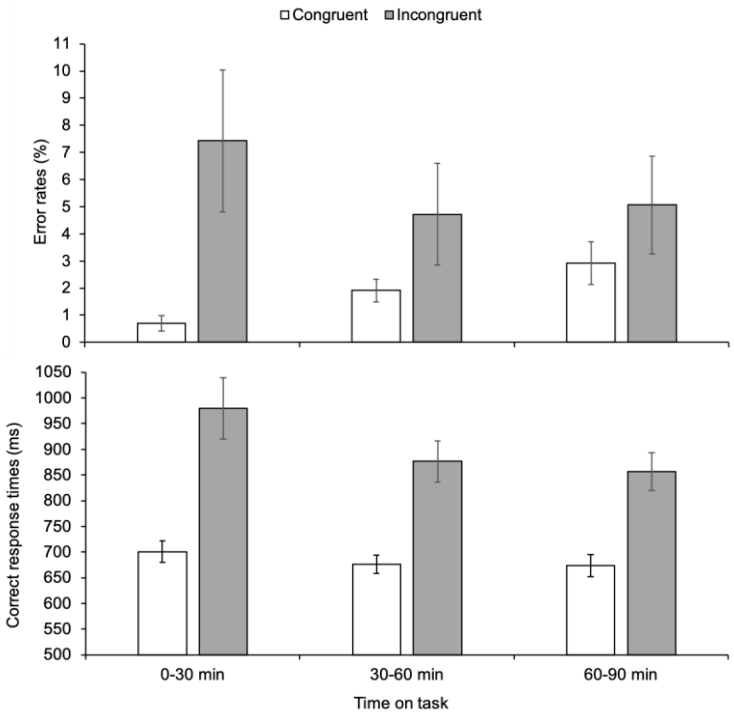

Figure 3: Error rates and correct response times as a function of congruence and time on task. Error bars indicate standard errors.

The ANOVA performed on response times showed a significant main effect of congruence [$F_{(1, 7)}$ = 41.494, p < .001, η_p^2 = .856], with shorter response times for congruent than incongruent trials reflecting, the presence of a reverse Stroop effect. In addition, a significant main effect of time on task was revealed [$F_{(1, 7)}$ = 8.420, p < .015, η_p^2 = .546], with a significant linear trend [$F_{(1, 7)}$ = 8.422, p = .023, η_p^2 = .546], indicating shorter response times with time on task. These main effects were qualified by a significant Time-on-task ×

Congruence interaction [$F_{(2, 14)}$ = 14.177, p = .004, η_p^2 = .669], with a significant linear trend [$F_{(1, 7)}$ = 16.577, p = .005, η_p^2 = .703], which indicated that the reverse Stroop effect decreased over time.

Event-Related Potential Analyses

Based on visual inspection of peak amplitude, the following time windows were used for ERP components: N100 (40-110 ms), P200 (200-320 ms), N450 (550-700 ms) and LN (700-900ms). Figure 4 shows the results of the ERP analysis for the Time effect, while Figure 5 shows the results of the ERP analysis for the Congruence effect.

N100: A significant effect of time on task was observed in CL region [$F_{(2, 14)}$ = 5.325, p = .024, η_p^2 = .432], with a significant linear trend [$F_{(1, 7)}$ = 16.26, p = .005, η_p^2 = .699], indicating a decrease in the N100 amplitude over time. This effect of time on task was qualified by a significant Time-on-task × Congruence interaction [$F_{(2, 14)}$ = 5.144, p = .04, η_p^2 = .424], with a significant quadratic trend [$F_{(1, 7)}$ = 13.996, p = .007, η_p^2 = .667], which indicated that the N100 amplitude decreased for both the congruent and the incongruent trials from the first part to the second part of the experiment, and that it continued to decrease during the last part of the experiment for the incongruent trials only.

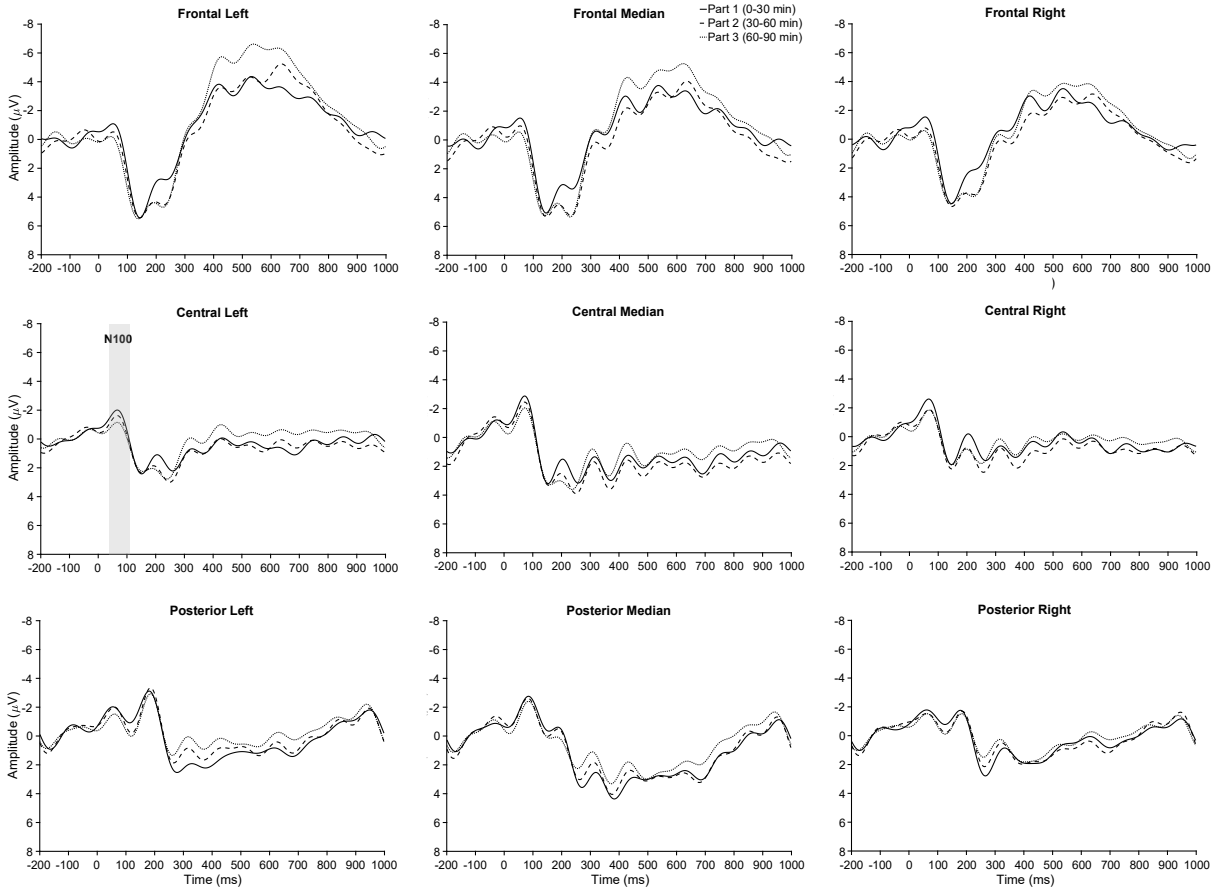

Figure 4: Grand average of the EEG signal for the effect of time on task for the word-reading task as a function of the regions of interest. The rectangles show time window used for the analyses of the N100 component in the region of interest for which the statistical effect was the strongest.

P200: A significant effect of congruence was observed in fronto-central regions [FL: $F_{(1, 7)}$ = 5.765, p = .047, η_p^2 = .452; FM: $F_{(1, 7)}$ = 10.790, p = .013, η_p^2 = .607; FR: $F_{(1, 7)}$ = 9.903, p = .016, η_p^2 = .586; CM: $F_{(1, 7)}$ = 11.874, p = .011, η_p^2 = .629; and CR: $F_{(1, 7)}$ = 8.709, p = .021, η_p^2 = .554], indicating that the amplitude of the P200 was larger for the incongruent trials that for the congruent trials.

N450: A significant effect of congruence was observed only in the FR regions [$F_{(1, 7)}$ = 6.292, p = .040, η_p^2 = .473], indicating that the amplitude of the N450 was larger for the incongruent trials than for the congruent trials.

LN: A significant effect of congruence was observed for [FM: $F_{(1, 7)}$ = 5.906, p = .045, η_p^2 = .458; FR: $F_{(1, 7)}$ = 10.976, p = .013, η_p^2 = .611; PL: $F_{(1, 7)}$ = 12.052, p = .010, η_p^2 = .633; and PM:

$F_{(1, 7)}$ = 10.194, p = .015, η_p^2 = .593], indicating that the amplitude of the LN was larger for the incongruent trials than for the congruent trials in frontal regions, and a reverse effect in posterior regions.

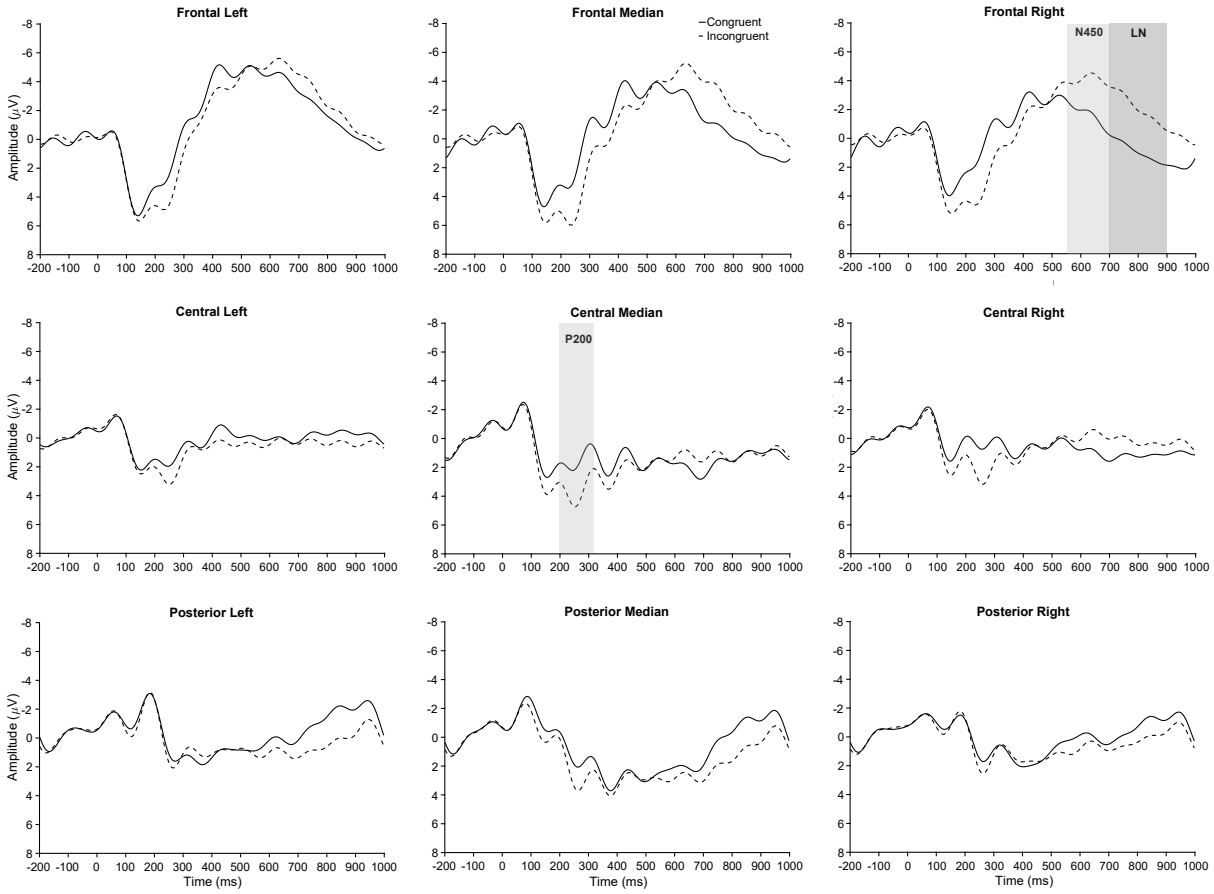

Figure 5: Grand average of the EEG signal for the effect of congruence for the word-reading task as a function of the regions of interest. The rectangles show the time window used for the analyses of the P200, N450 and LN components in the regions of interest for which the statistical effect was the strongest.

1.2 Synthèse

Dans cette première étude, nous avons induit une augmentation significative de fatigue mentale avec 90 minutes d'une tâche de Stroop modifiée, cependant aucune dégradation des performances n'a été observée au cours des 90 minutes, une amélioration des performances a même été rapportée. Or il a été proposé que la baisse des performances lors d'une tâche cognitive prolongée pourrait être considéré comme un « *Gold standard* » pour attester de la présence de fatigue mentale. L'amélioration des performances observée lors de notre étude pourrait s'expliquer par des effets bénéfiques liés à l'apprentissage, et ce malgré la réalisation d'une session de familiarisation. Ainsi l'analyse des performances au cours d'une tâche cognitive ne semble pas être un bon indicateur pour évaluer la fatigue mentale.

L'activité cérébrale recueillie via EEG, nous a permis de mettre en évidence la présence de marqueurs objectifs de fatigue mentale. Au niveau des oscillations cérébrales, nous avons observé une augmentation significative des ondes alpha et tendancielle des ondes thêta, ces deux ondes étant deux déjà connues comme reflétant des indicateurs robustes de présence de fatigue mentale. L'augmentation seulement tendancielle des ondes thêta pourrait cependant être soit lié à la faible taille de notre échantillon (n = 8), soit au fait que l'enregistrement des ondes cérébrales était effectué pendant la réalisation de la tâche de Stroop et non lors de courtes phases de repos. Il aurait fallu effectuer cet enregistrement au repos pour éviter que les ondes cérébrales propres à la fatigue mentale ne soient potentiellement contaminées par les processus cognitifs impliquées dans la tâche de Stroop. Concernant les potentiels évoqués, nous avons mis en évidence une diminution de l'amplitudes des composantes N100, P200 et P300 au cours du temps. Ces trois composantes ont été précédemment reliées à des processus attentionnels, et leur diminution pourrait refléter une baisse des ressources attentionnelles allouées à la réalisation de la tâche de Stroop au cours du temps.

Bien que la tâche de Stroop soit une tâche couramment utilisée pour induire de la fatigue mentale, cette étude est une des premières à montrer des modulations d'activité cérébrale lorsque cette tâche est réalisée de façon prolongée. Les principaux résultats semblent montrer une diminution des ressources attentionnelles allouées à la tâche avec une augmentation de la sensation subjective de fatigue mentale. Malgré tout, les performances lors de la tâche de Stroop prolongée s'améliorent au cours du temps. Ainsi, il serait préférable d'utiliser la combinaison de plusieurs mesures (échelle subjective, performance et mesures physiologiques) afin d'attester de la présence de fatigue mentale.

2 Étude 2

La fatigue mentale induite par une tâche d'imagerie motrice prolongée augmente la perception de l'effort et l'activité des aires motrices

Mental fatigue induced by prolonged motor imagery increases perception of effort and the activity of motor areas

Thomas Jacquet, Romuald Lepers, Bénédicte Poulin-Charronnat, Patrick Bard, Philippe Pfister, et Benjamin Pageaux

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2.1 Résumé

La littérature récente suggère que lorsqu'elle est prolongée, l'imagerie motrice (IM) induit une fatigue mentale et a un impact négatif sur l'exercice physique ultérieur. L'objectif de cette étude était de confirmer cette possibilité par des mesures neurophysiologiques et psychologiques. Treize participants ont effectué 200 contractions isométriques imaginées des extenseurs du genou (condition IM prolongée) ou ont regardé un documentaire (condition témoin), puis ont effectué 150 extensions isométriques réelles du genou. L'électroencéphalographie a été enregistrée en continu pour obtenir l'amplitude du potentiel cortical lié à la motricité à l'électrode Cz (appelé MRCP, index de l'activité de l'aire motrice) pour chaque contraction imaginée et réelle. L'électromyographie du muscle vaste latéral ainsi que l'effort perçu nécessaire ont été mesurés lors des contractions imaginées, du visionnage du documentaire et lors de l'exercice physique. Lors de l'IM prolongée, le niveau de fatigue mentale, l'effort requis pour imaginer les contractions, et l'amplitude des MRCPs ont augmenté avec le temps. En présence de fatigue mentale, une interaction significative entre la condition et le temps a indiqué que, par rapport à la condition contrôle, l'exercice physique réalisé en présence de fatigue mentale était perçu comme plus exigeant et, était associé à une augmentation spécifique de l'EMG RMS du muscle vaste externe. Ces altérations observées en présence de fatigue mentale pendant la contraction réelle, combinées à celles observées pendant l'IM prolongée, suggèrent que l'IM prolongé peut altérer la commande motrice nécessaire pour effectuer des contractions imaginées ou réelles. Bien que l'effet de la fatigue mentale sur l'amplitude des MRCPs ait été clair pendant l'IM, des études futures devraient menées en adaptant l'exercice physique réalisé, afin de minimiser la diminution de la capacité de production de force induite par l'exercice et contrôler ainsi les effets confondants sur l'amplitude des MRCPs en présence de fatigue mentale.

Mental fatigue induced by prolonged motor imagery increases perception of effort and the activity of motor areas

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Abstract

Recent literature suggests that when prolonged, motor imagery (MI) induces mental fatigue and negatively impacts subsequent physical exercise. The aim of this study was to confirm this possibility with neurophysiological and self-reported measures. Thirteen participants performed 200 imagined isometric knee extension contractions (Prolonged MI condition) or watched a documentary (Control condition), and then performed 150 actual isometric knee extensions. Electroencephalography was continuously recorded to obtain motor-related cortical potential amplitude at Cz electrode (MRCP, index of motor area activity) for each imagined and actual contractions. Electromyography of the vastus lateralis muscle as well as the perceived effort required to perform prolonged MI, watch the documentary, and perform the actual contractions were measured. During prolonged MI, mental fatigue level, the effort required to imagine the contractions and MRCP amplitude increased over time. The increase in the effort required to imagine the contractions was significantly correlated with the MRCP amplitude. During the physical exercise, a significant condition × time interaction revealed a greater increase over time in perceived effort in the prolonged MI condition compared to the control condition, as well as a specific alteration in EMG RMS of the vastus lateralis muscle. These alterations observed in the presence of mental fatigue during actual contractions, combined with those observed during prolonged MI, suggest that prolonged MI may impair the motor command required to perform imagined or actual contractions. While the observed effect of mental fatigue on MRCP amplitude was clear during MI, future studies should tailor the physical exercise to minimize the exercise-induced decrease in force production capacity and control for its confounding effects on MRCP amplitude in the presence of mental fatigue.

Keywords: Electroencephalography (EEG), Mental fatigue, Cognitive fatigue, Perception of effort, Perceived exertion, Motor related cortical potential (MRCP)

Acronyms: EEG = Electroencephalography; EMG = Electromyography; MI = Motor Imagery; MRCP = Motor Related Cortical Potential; MVC = Maximal Voluntary Contraction; NASA-TLX = National Aeronautics and Space Administration Task Load Index; RFD = Rate of Force Development; RMS = Root Mean Square; RPE = Rating of Perceived Effort; VAS = Visual Analogue Scale

1. INTRODUCTION

Mental fatigue is defined as a psychobiological state caused by prolonged periods of demanding cognitive activity and characterized by subjective feelings of "tiredness" and "lack of energy" (Boksem and Tops, 2008). Since the pioneer study of Marcora et al. (2009) demonstrating an impairment in cycling endurance performance following prolonged engagement in a demanding cognitive task, numerous studies confirmed the negative impact of mental fatigue on physical performances (for reviews see: Pageaux and Lepers, 2018; Brown et al., 2020). Mental fatigue impairs sport-related decision making (Head et al., 2017; e.g., Smith et al., 2016b), technical skills (Le Mansec et al., 2018; e.g., Smith et al., 2016a), motor control (e.g., Duncan et al., 2015; Rozand et al., 2015) and endurance (MacMahon et al., 2014; e.g., Pageaux et al., 2013) performances. Decrease in physical performances is generally associated with alteration in cardiorespiratory or metabolic responses and/or an inability of the brain to maximally recruit the working muscles (Taylor et al., 2016). However, mental fatigue does not induce such alterations (Marcora et al., 2009; Pageaux et al., 2013). The only variable consistently associated with the decrease in physical performance was a greater perception of effort in the presence of mental fatigue (Brown et al., 2020; Le Mansec et al., 2018; Pageaux and Lepers, 2018, 2016).

Mental fatigue is traditionally induced by prolonged engagement in cognitive tasks involving the response inhibition process, such as the AX-CPT (Marcora et al., 2009; Pageaux et al., 2013; Smith et al., 2015) or the Stroop task (Rozand et al., 2015; Smith et al., 2016a). Interestingly, recent studies using motor imagery demonstrated that such cognitive exertion may also induce mental fatigue (Graham et al., 2014; Rozand et al., 2016, 2014). Motor imagery is defined as the internal simulation of movement without corresponding motor output (Decety, 1996a). Briefly, two main categories of motor imagery exist: visual motor imagery and kinesthetic motor imagery. Visual motor imagery consists of imagining seeing yourself performing the task and activates predominantly the occipital network (Chholak et al., 2019; Guillot et al., 2009). Kinesthetic motor imagery consists of imagining the sensations produced by the actual task and activates to a lesser extent similar brain areas than those activated during actual movements such as the premotor cortex, the parietal cortex and the cerebellum (e.g., Batula et al., 2017; Decety, 1996b; Ruffino et al., 2017; Solodkin et al., 2004; Stinear et al., 2006). In a meta-analysis, Schuster et al. (2011) reported that ~17 minutes of motor imagery is optimal to observe positive effects on physical performance (e.g., Yue and Cole, 1992;

Grosprêtre et al., 2018; Ranganathan et al., 2004), thus reinforcing the potential for its use in rehabilitation programs (e.g., Jackson et al., 2001; Lebon et al., 2012; Cho et al., 2013; Kumar, 2016). However, the positive effects of motor imagery seem to disappear when motor imagery is performed longer than the optimal duration proposed by Schuster et al. (2011). Indeed, Rozand et al. (2016) recently demonstrated that 100 imagined contractions (i.e., ~30 min) induced mental fatigue and increased movement duration during a pointing task. The involvement of the sustained attention and the inhibitory processes during a motor imagery task (Bart et al., 2020; O'Shea and Moran, 2017), as in cognitive tasks classically used to induce mental fatigue (e.g., AX-CPT, Stroop), could be one of the underlying mechanisms explaining the occurrence of mental fatigue. As mental fatigue could counteract the positive effects of motor imagery on subsequent performance, and therefore impair rehabilitation programs, it is important to investigate the occurrence of mental fatigue induced by prolonged motor imagery.

While the underlying mechanisms causing the decrease in physical performance in the presence of mental fatigue remain unclear, analysis of brain oscillations via electroencephalography (EEG) has been an efficient tool to identify mental fatigue-induced cerebral alterations during the completion of cognitive tasks (for review: Craig et al., 2012; Tran et al., 2020). Analyses of brain oscillations reveal a consistent increase in the theta power (e.g., Barwick et al., 2012) and alpha power (e.g., Shou and Ding, 2013) in the presence of mental fatigue. These changes were not only reported after cognitive tasks requiring predominantly the response inhibition process but also after cognitive tasks requiring concentration and attention (Lal and Craig, 2002; van der Linden et al., 2003). As these studies did not use prolonged motor imagery to induce mental fatigue, it remains unknown whether these alterations are transferable to mental fatigue induced by prolonged motor imagery.

When measuring cerebral activity with EEG, it is possible to monitor for each contraction (actual or imagined) a specific event-related potential called motor-related cortical potential (MRCP; e.g., Jankelowitz and Colebatch, 2002; do Nascimento et al., 2006). This potential was discovered during hand movements by Bates (1951) and recorded from the scalp overlying motor and premotor areas. MRCP amplitude is directly linked to the intensity of muscle contraction and has been extensively used in the literature as an index of the motor command (de Morree et al., 2014, 2012; Siemionow et al., 2000). In the presence of decreased maximal force production capacity, also known as muscle fatigue (Gandevia, 2001), previous studies observed an increased MRCP while the level of muscle force during each contraction remained constant (de Morree et al., 2014, 2012). As previous studies observed i) alterations in

electromyographic signal of the working muscles during submaximal physical exercise following engagement in demanding cognitive tasks (Bray et al., 2008; Graham et al., 2014; Pageaux et al., 2015), and ii) longer duration of actual and imagined movement in the presence of mental fatigue (Rozand et al., 2015), it is plausible that mental fatigue may impact the regulation of the motor command and consequently alter MRCPs. This hypothesis is also supported by recent studies demonstrating an association between changes in MRCPs and perception of effort (de Morree et al., 2014, 2012). While an ongoing debate is still existing in the literature on the sensory signal generating perception of effort (peripheral vs central origin; e.g., Amann and Light, 2014; Broxterman et al., 2018; Marcora, 2009; Pageaux, 2016; Smirmaul, 2014; Steele and Fisher, 2018), this perception has been classically used as a marker of the motor command for decades (Kjær et al., 1999; McCloskey et al., 1974; Mitchell et al., 1989), and its consistent increase in the presence of mental fatigue (Brown et al., 2020; Pageaux and Lepers, 2018, 2016) reinforces the possible interaction between mental fatigue and the motor command.

In this context, the primary aim of the present study was to induce mental fatigue using prolonged motor imagery. EEG was recorded during four blocks of fifty imagined contractions, and subjective feelings of fatigue, as well as the effort required to imagine the contractions were reported. We hypothesized that prolonged motor imagery will successfully induce mental fatigue evidenced by an increase in feelings of fatigue as well as in the effort required to imagine the contractions, and an increase in both alpha and theta power. Due to the known negative impact of mental fatigue on subsequent physical performance (for review see: Pageaux and Lepers, 2018; Brown et al., 2020), the secondary aim of our study was to identify, during a subsequent physical exercise, neurophysiological alterations caused by mental fatigue. Finally, as i) mental fatigue is known to increase the perception of effort during physical exercises (Pageaux and Lepers, 2018), and ii), previous studies demonstrated an association between changes in perceived effort and changes in MRCP (de Morree et al., 2014, 2012) we expect that prolonged motor imagery will increase the amplitude of MRCPs during both imagined and actual contractions.

2. EXPERIMENTAL PROCEDURES

2.1. PARTICIPANTS

Thirteen physically active right-handed adults (7 males and 6 females) volunteered in this study (mean ± SD; age: 25 ± 4 years, height: 182 ± 5 cm, weight: 77 ± 11 kg). This sample size was determined based on a previous study using a similar physical exercise with the knee extensors and investigating the relation between MRCP and physical fatigue in the presence and absence of caffeine (de Morree et al., 2014). All participants were involved in physical activity and declared to practice a physical activity at least one time per week. None of the participants had any known mental or somatic disorders or any injuries of the right leg during the last six months. All participants were given written instructions describing all procedures related to the study but were naive of its aims and hypotheses. The participants have never been informed prior to the experiment that motor imagery (MI) was used to generate mental fatigue. They were instructed that the aim of the study was to investigate the possible positive effects of motor imagery on a subsequent physical exercise. Each participant provided written informed consent. At the end of the last visit, participants were fully debriefed and asked not to discuss the real aims of the study with other participants. The study conformed to the standards set by the World Medical Association Declaration of Helsinki "Ethical Principles for Medical Research Involving Human Subjects" (2008). The experimental design of the study was approved by the regional ethics committee (CPP EST: approval no. A00064-49).

2.2. PROCEDURE

Participants visited the laboratory on three different occasions. Each participant completed all three visits over three weeks with a minimum of six days of recovery period between visits. All visits started between 8:30 a.m. and 10:00 a.m. All participants were given instructions to sleep for at least seven hours, refrain from the consumption of alcohol, and not to practice vigorous physical activity the day before each visit. Participants were also instructed not to consume caffeine and nicotine for at least three hours before testing and were asked to declare if they had taken any medication or had any acute illness, injury, or infection. At the beginning of each session, the participants attested that they had complied with all instructions. For all the sessions, participants sat on the same isometric ergometer chair (Multi-form, la Roque d'Anthéron, France).

During the first visit, participants were familiarized with the laboratory and all the procedures. For all different questionnaires, oral and written instructions were provided during this familiarization (and recalled at the beginning of each visit). About the physical exercise, after a warm-up, participants performed 150 submaximal isometric knee extensions at 50% of their maximal voluntary contraction (MVC). If the physical exercise was too difficult during the familiarization session (i.e., excessive head movements and sweating) the target force was fixed at 45% of their MVC. On the contrary, if the physical exercise was too easy (i.e., low perceived effort at the end of the exercise and no muscular fatigue), the target force was fixed at 55% of their MVC. At the end of the familiarization, participants performed maximal imagined isometric contractions of the right knee extensors to get used to MI. After the familiarization, all participants reported that they successfully imagined the 50 contractions, felt associated sensations, and reported a score of at least 5 on the Likert scale used to record the MI vividness (see section 2.4.4 Motor imagery vividness).

The second and third visits were randomized and counterbalanced. An overview of each visit is presented in Fig. 1. Each visit consisted of performing either prolonged MI or a control task (i.e., watching a documentary) for approximately 50 min, followed by a physical exercise (150 isometric knee extensions). In each visit, participants reported their level of mental fatigue and performed MVC with their right knee extensors to assess force production capacity before and after (Post 1, before the subsequent physical exercise) the prolonged MI or documentary watching, as well as after the physical exercise (Post 2). Motivation to perform prolonged MI or watch the documentary, and perform the subsequent physical exercise was measured before completion of each task. Participants reported their perceived workload of the prolonged MI session, documentary watching and physical exercise after completion of each task. Electromyographical (EMG) and electroencephalographic (EEG) signals were continuously recorded during all tasks; and the participants reported their perceived effort to perform MI, watch the documentary or perform the physical exercise.

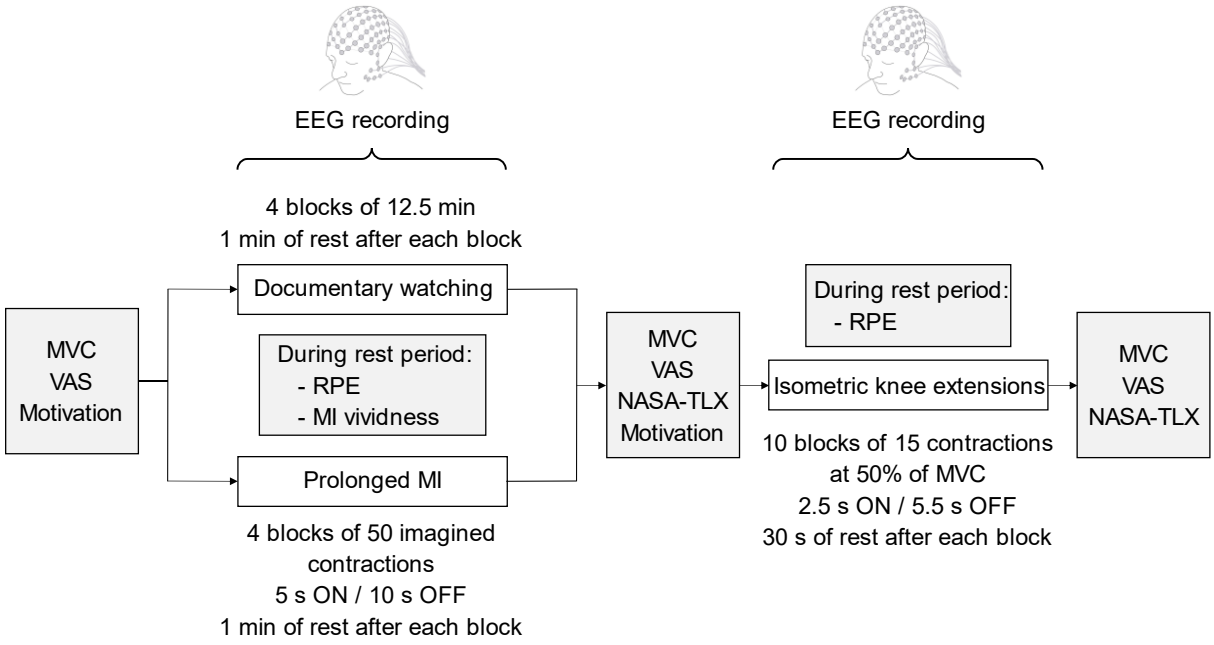

Figure 1. Overview of the experimental protocol.

Order and timing were the same for each participant and each session. VAS = fatigue visual analogue scale, RPE = rating of perceived effort, MI = motor imagery, MVC = maximal voluntary contraction, NASA-TLX = National Aeronautics and Space Administration Task Load Index.

2.3. EXPERIMENTAL TASKS

2.3.1. PROLONGED MOTOR IMAGERY

Prolonged MI consisted of four blocks of 12.5 min of kinesthetic MI for a total of approximately 50 min. During imagined maximal isometric knee extensions, participants were instructed to perform kinesthetic MI and to perceive muscle contractions and joint tension with the same sensations they experienced during the completion of the previous MVC. Each participant was instructed to not contract her/his quadricep muscles during MI. An experimenter was seated behind the participant to check the EMG signal of the vastus lateralis muscle in order to control that the participant did not contract her/his muscle during imagined contractions. Participants performed MI, with their eyes closed, seated on the same isometric ergometer chair than the one used for the MVCs and intermittent isometric extensions of the knee extensors.

Participants performed four blocks of 50 imagined contractions of 5 s, with a 10-s rest period between each imagined contraction and 1-min rest period between blocks (total duration

of one block = 12.5 min, total duration of prolonged MI = 53 min). Three instructions were given during prolonged MI. Two seconds before starting the imagined contraction participants heard "Get ready", then "Push" to start the imagined contraction, and "Relax" to stop the imagined contraction. The Experiment Builder software was used to time the instructions for each imagined contraction (SR Research). At the end of each block, perceived effort to accomplish prolonged MI and MI vividness were assessed.

2.3.2. CONTROL CONDITION

The control condition consisted of watching an emotionally neutral documentary, "Home" by Y. Arthus-Bertrand, which was used as control condition in previous studies on mental fatigue (Le Mansec et al., 2018; Rozand et al., 2015). In these previous studies, it has been shown that this documentary did not induce any increase in subjective feeling of mental fatigue. Participants were sitting in a dark room on the same isometric ergometer chair than the one used for the intermittent MVCs of the knee extensors. The movie was projected on a screen placed 2 m in front of the participant. It was divided into four blocks of 12.5 min with 1 min of rest between each block to match with prolonged MI and to assess the perceived effort to watch the documentary.

2.3.3. PHYSICAL EXERCISE

Following prolonged MI or watching the documentary, participants performed the physical exercise, which consisted in performing 150 submaximal isometric contractions of the right knee extensor muscles.

Beeps were presented as follows, a first beep to start the contractions and a second beep to stop the contractions. The contractions lasted 2.5 s with 5.5 s rest in between. Contractions were performed by blocks of 15 contractions interspaced by 25 s during which perception of effort was assessed.

Isometric contractions were performed at 50% of MVC (± 5%). Visual feedback of the target strength was presented on a screen placed 2 m in front of the participant.

The Experiment Builder software was used to time the submaximal isometric contractions of the knee extensor muscles.

2.4. PSYCHOLOGICAL MEASURES

2.4.1 MOTIVATION

Motivation is defined as "the attribute that moves us to do or not to do something" (Gredler, 2001). Motivation has been proposed to influence performance (Richter et al., 2016) and interact with fatigue (Müller and Apps, 2019). Motivation to watch the documentary (control task), perform both motor imagery and physical exercise was measured with the motivation scale developed by Matthews et al., (2001). This questionnaire has seven questions on intrinsic motivation (e.g., "I wish to do my best") and seven questions on extrinsic motivation (e.g., "I performed this exercise only because of an outside reward"). For each question, there are five possible answers (0 = not at all, 1 = a little bit, 2 = somewhat, 3 = very much, 4 = extremely). The score of each motivation ranges between 0 and 28.

2.4.2. SUBJECTIVE WORKLOAD

The National Aeronautics and Space Administration Task Load Index (NASA-TLX) was used to evaluate subjective workload (Hart and Staveland, 1988). The NASA-TLX is composed of six subscales: mental demand (how much mental and perceptual activity was required?), physical demand (how much physical activity was required?), temporal demand (how much time pressure did you feel due to the rate or pace at which the task occurred?), performance (how much successful do you think you were in accomplishing the goals of the task set by the experimenter?), effort (how hard did you have to work to accomplish your level of performance?), and frustration (how much irritating, annoying did you perceive the task?). The participants had to score each of the items on a scale divided into 20 equal intervals anchored by a bipolar descriptor (e.g. high/low). This score was multiplied by 5, resulting in a final score between 0 and 100 for each of the subscales.

2.4.3. MENTAL FATIGUE LEVEL

A visual analogue scale (VAS) was used to measure feelings of mental fatigue before and after prolonged MI and documentary watching. The VAS consisted of a line measuring 100 mm in length, with bipolar end anchors (0 mm = ''No tired at all"; 100 mm = ''Extremely tired"). The following question was asked to access the level of mental fatigue: "What is your feeling of mental fatigue right now?". Participants were asked to place a mark along the line to indicate how they currently felt. VAS score is defined by the distance between the first anchor (0 mm: "No tired at all") and the mark placed by the participant.

2.4.4. MOTOR IMAGERY VIVIDNESS

MI vividness is defined as the clarity of the kinesthetic sensations elicited by MI (Saimpont et al., 2012). Participant had to evaluate their MI vividness on a Likert scale (1 = ‘‘Not clear at all’’, 1 = ‘‘Very unclear’’, 3 = ‘‘Unclear”, 4 = ‘‘Moderately clear”, 5 = ‘‘Quite clear’’, 6 = ‘‘Clear’’ 7 =‘‘Very clear”). This measure, performed each 50 imagined contractions, allows monitoring the evolution of MI vividness.

2.4.5. PERCEPTION OF EFFORT

Perception of effort is defined as the conscious sensation of “how hard, heavy and strenuous a physical task is” (Marcora, 2010, 2009; Pageaux, 2016). During each task, participants reported the intensity of the effort invested. The intensity of perceived effort was reported with a modified version of the CR100 scale (Borg and Kaijser, 2006). This scale ranges from 0 (Nothing at all) to 100 (Maximal) and includes verbal anchors such as Weak/Light (13), Moderate (25), Strong/Heavy (50) or Very Strong (70). Modifications on the scale were made on the anchoring 0 and 100 to include the word effort in the description as follow: 0 = No effort at all ;100 = Maximal effort.

During prolonged MI and documentary watching, participants were asked each 12.5 min to answer the following question: “How hard and intense is it for you to imagine the contractions (or watch the documentary)?”. During the physical task, participants were asked at the end of each block to answer the following question: “How hard and intense is it for you to drive your leg?”.

The scale allows values above 100 to be specified if the participant perceives an effort higher than the “Maximal exertion” (i.e., rating 100). Each participant was provided verbal examples of “No exertion” (e.g., not doing any cognitive work or sitting on the couch relaxing) and “Maximal exertion” (e.g., the most intense effort experienced in their life during prior cognitive activities or the sensations perceived during an MVC).

2.5. PHYSIOLOGICAL MEASUREMENT

2.5.1. FORCE RECORDING

Right knee extension force was recorded using a homemade isometric ergometer that comprised a machine typically used for strength training connected to two strain gauges (STC 250 kg; sensitivity: 2.9997 mV/V; Celtron Technologies Inc., Santa Clara, CA, USA)

(Matkowski et al., 2011). The signal force was recorded with a commercially available software (AcqKnowledge 4.1 for MP Systems, Biopac Systems Inc., Goleta, CA, USA). Knee angle was fixed at 100° to perform isometric knee extensions (0° = full knee extension).

Force data were analyzed offline using Matlab (The Mathworks, Natick, MA). The onset and offset of the muscle contractions were determined automatically based on the positive and negative peaks in the second differential of the force signal (5^{th}-order Bessel low-pass filter). For each contraction (i.e., from the onset to the offset of muscle force signal), a time window of 500 ms was used to calculate the mean force. This 500 ms was defined as 250 ms around the middle of the contraction. Rate of Force Development (RFD) was calculated for each submaximal contraction as the average slope of the force-time curve (force/time) over the time interval 0-200 ms (Aagaard et al., 2002). The onset of force production was defined as the time point where the force exceeded the baseline by 2 SD. The baseline is calculated on a 1-second sliding window during the rest period previous each contraction. The offset of force production was defined as the point time where the force became lower than the baseline +2 SD Mean force and RFD during the submaximal trials were averaged over the first (contractions 1 to 75) and the second half (contractions 76 to 150) of the trials.

Force tremor, which represents the variability in force production during intermittent contractions, was calculated as the force coefficient of variation (CV). For each contraction (i.e., from the onset to the offset of muscle force signal), a time window of 1.5 s was used to calculate the force tremor. This 1.5 s was defined as 750 ms around the middle of the contraction.

2.5.2. EMG RECORDING

Electromyography (EMG) activity of the vastus lateralis was recorded with a pair of bipolar silver chloride circular (recording diameter of 10 mm) surface electrodes (Swaromed, Nessler Medizintechnik, ref 1066, Innsbruck, Austria) with an interelectrode (center-to-center) distance of 20 mm. The vastus lateralis muscle was chosen as representative of quadriceps muscle activity (Place et al., 2007). Low resistance between the two electrodes was obtained by shaving the skin and the skin was cleaned with alcohol. The electrodes were placed as close as possible to the patella for the vastus lateralis. The position of the electrodes followed the direction of the muscle fibers, according to the SENIAM recommendations (Hermens et al., 2000), and was aligned in the longitudinal direction of the muscle fibers. The reference electrode was placed on the ipsilateral patella. Myoelectrical signal was amplified with a

bandwidth frequency ranging from 10 to 500 Hz (gain = 1000), digitized on-line at a sampling frequency of 2 kHz, and recorded with commercially available software (AcqKnowledge 4.1 for MP Systems, Biopac Systems Inc., Goleta, CA, USA).

The Root Mean Square (RMS) of the vastus lateralis EMG signal was calculated for each contraction from the onset to the offset of the EMG burst. The onset of muscle activity was considered to occur when the amplitude of the RMS-processed EMG exceeded +3 SD above the baseline EMG activity (mean activity calculated during a 400-ms time period immediately before impact). Thus, the contraction duration was defined as the time elapsed between the onset and the offset of EMG activation. The resulting values were averaged over the first half (contractions 1 to 75) and the second half (contractions 76 to 150) of the contractions.

2.5.3. EEG DATA

The electroencephalogram was recorded at 64-scalp sites using a 10-20 system (BioSemi ActiveTwo). Horizontal eye movements were monitored with electrodes placed on the outer left and right canthi. Vertical eye movements were monitored with an electrode placed under the left eye. Two additional electrodes were placed on the left and right mastoids (A1, A2). During recording, the BioSemi ActiveTwo system's common-mode sense electrode served as the reference electrode. Each electrode was filled with Signa gel for improving signal transduction. Electrophysiological signals were digitized at a 2,048 Hz sampling rate and acquired with ActiView software. From the instructions given for imagined contractions and from the two beeps used for actual contractions, triggers were automatically reported on the EEG recording to signal the beginning and the end of each actual and imagined contraction. A trigger was also reported on the EEG recording when the participant had to prepare to imagine a movement. The EEG signals were analyzed using the EEGLAB (version 14.1) toolbox for Matlab (https://sccn.ucsd.edu/wiki/EEGLAB) (Delorme and Makeig, 2004).

Offline, data were re-referenced against the mean of electrodes A1 and A2 and downsampled to 512 Hz. EEG data were filtered with a 0.01 to 5 Hz band-pass filter for MRCP analysis, while a 1 to 40 Hz band-pass filter was performed for spectral analyses. To correct for eye movement artifacts, EEGLAB's runica routine was used to perform independent component analyses. Noisy electrodes were identified with the probability method in EEGLAB (Z = 5) and interpolated when necessary with a spherical method. EEG signals were segmented into 150 epochs of 8,000 ms each (from 2,500 ms before to 5,500 ms after beep tone) for actual

contractions, and into 200 epochs of 15,000 ms each (from 2,500 ms before to 12,500 ms after contraction onset) for imagined contractions. All trials were baseline corrected with -2,500 ms to -2,000 ms. These epochs were used for MRCP analyses. During MI, MRCP amplitudes were averaged for each block (Block 1: imagined contractions 1 to 50, Block 2: imagined contractions 51 to 100, Block 3: imagined contractions 101 to 150, Block 4: imagined contractions 151 to 200). During actual contractions, MRCP amplitudes were averaged over the first half (contractions 1 to 75) and the second half (contractions 76 to 150) of the physical exercise. During the physical exercise, the MRCPs obtained during contractions producing a force above ± 5% of the target force were excluded from the analysis. A visual inspection was also performed on all epochs, including actuals and imagined contractions, to remove contractions associated with movement artefacts (e.g., head movements).

EEG power was divided into five frequency bands: delta, 1–4 Hz; theta, 4–7 Hz; alpha, 8–12 Hz; beta 13–30 Hz; and gamma, 30–40 Hz. Spectral data were analyzed during the first 5 min and the last 5 min of the prolonged MI and documentary watching. To observe changes in brain activation all over the scalp, we used nine regions of interests (ROIs) as previously suggested by Arendsen et al., (2020): Anterior Left (mean of FP1, AF3, AF7, F3, F5, F7, FC3, FC5, FT7), Anterior Median (mean of FPz, AFz, F1, Fz, F2, FC1, FCz, FC2), Anterior Right (mean of FP2, AF4, AF8, F4, F6, F8, FC4, FC6, FT8), Central Left (mean of C3, C5, T7, CP3, CP5, TP7), Central Median (mean of C1, Cz, C2, CP1, CPz, CP2), Central Right (mean of C4, C6, T8, CP4, CP6, TP8), Posterior Left (mean of P9, P7, P5, P3, PO7, PO3, O1), Posterior Median (mean of P1, Pz, P2, Poz, Oz), and Posterior Right (mean of P4, P6, P8, PO4, PO8, O2).

2.6. STATISTICS

All data are presented as means ± SE.

Paired *t*-tests were used to assess the effect of condition (Prolonged MI, Control) on motivation and NASA-TLX scores.

One-way repeated measures ANOVAs were used to test the effect of time (4 blocks of 12.5 min) on imagery vividness and MRCP amplitude during prolonged MI. Two-way repeated-measures 2 × 4 ANOVAs were used to test the effects of condition (Prolonged MI, Control) and time (4 blocks of 12.5 min) on perceived effort. Two-way repeated-measures 2 × 2 ANOVAs were used to test the effects of condition (Prolonged MI, Control) and time (First 5 min, Last 5 min) on delta, theta, alpha, beta, and gamma power during prolonged MI and

documentary watching. To test the effects of prolonged MI on force production capacity, a two-way repeated-measures 2 × 2 ANOVA was used to test the effects of condition (Prolonged MI, Control) and time (Pre, Post 1) on MVC.

Two-way repeated-measures 2 × 2 ANOVAs were used to test the effects of condition (MI, Control) and time (First part: contractions 1 to 75, Second part: contractions 76 to 150) on the numbers of MRCPs analyzed, the MRCP amplitude, rating of perceived effort, force, RFD, tremor, and contraction duration during physical exercise. To test the effect of the physical exercise on force production capacity, a two-way repeated-measures 2 × 2 ANOVA was used to test the effects of condition (Prolonged MI, Control) and time (Post 1, Post 2) on MVC.

Greenhouse-Geisser correction to the degrees of freedom was applied when violations of sphericity were present (corrected degree of freedom and *p*-values are reported). For ANOVAs, when significant, main effects and condition × time interaction were followed up with Bonferroni tests as appropriate.

Partial eta squared are reported, and thresholds for small, moderate, and large effects were set at 0.01, 0.07, and 0.14, respectively (Cohen, 1988). Analyses were conducted using JASP (version 0.10.2.0 for Windows). For paired t-tests, Cohen's dz were calculated using G*Power software (version 3.1.6, Universität Düsseldorf, Germany) and thresholds for small, moderate and large effects were set at 0.2, 0.5, and 0.8 respectively (Cohen, 1988). Correlations were performed between perception of effort and MRCP amplitude for both the imagined and actual contractions, with the R package 'rmcorr' assessing repeated measures correlation (Bakdash and Marusich, 2017; Bland and Altman, 1995). Level of significance was set at $p < .05$ (two-tailed).

3. RESULTS

Due to excessive head movements, one participant was excluded from the analyses related to the physical exercise. Therefore, the sample size was $N = 13$ for analyses related to the prolonged MI or the control condition (watching a documentary), and $n = 12$ for analyses related to the physical exercise.

3.1. MENTAL FATIGUE ASSESSMENT

3.1.1. EFFECTS OF PROLONGED MOTOR IMAGERY ON PSYCHOLOGICAL MEASUREMENTS

Motivation to perform prolonged MI or watch the documentary did not differ for extrinsic ($t_{(12)}$ = -0.267, p =.794, dz = .077; Prolonged MI: 15.9 ± 1.3, Control condition: 16.1 ± 1.2) and intrinsic ($t_{(12)}$ = -1.945, p = .076, dz = .538; Prolonged MI: 17.6 ± 1.0, Control condition: 19.0 ± 0.9) motivation.

The effects of prolonged MI and the documentary watching on feelings of fatigue, perception of effort, subjective workload and MI vividness are displayed in Figure 2. Feelings of fatigue (Figure 2.A) increased over time ($F_{(1, 12)}$ = 18.306, p = .001, η_p^2 = .604), with no significant main effect of condition ($F_{(1, 12)}$ = 1.563, p = .235, η_p^2 = .115) or condition × time interaction ($F_{(1, 12)}$ = 3.464, p = .087, η_p^2 = .224). Perception of effort (Figure 2.B), was greater in the Prolonged MI condition compared to the Control condition ($F_{(1, 12)}$ = 10.518, p = .007, η_p^2 = .467) and increased over time ($F_{(1.311, 15.732)}$ = 16.637, p < .001, η_p^2 = .581). A condition × time interaction ($F_{(1.443, 17.319)}$ =8.256, p = .006, η_p^2 = .408) revealed that the effort required to imagine the contractions increased over time and was significantly higher at Block 3 ($t_{(12)}$ = -5.448, p < .001, dz = -1.248) and Block 4 ($t_{(12)}$ = -8.141, p < .001, d = -1.117) compared to Block 1. The effort reported to watch the documentary did not change over time (all ps > .20, all dz < .95). The effort reported to imagine contractions compared to watch the documentary was reported as significantly greater solely at Block 4 ($t_{(12)}$ = -8.141, p = .008, dz = -1.226).

Analyses on the reported subjective workload (Figure 2.C) revealed a greater mental demand ($t_{(12)}$ = 5.556, p < .001, dz = 1.541), physical demand ($t_{(12)}$ = 2.456, p = .030, dz = 0.681), temporal demand ($t_{(12)}$ = 2.379, p = .035, dz = .660) and performance ($t_{(12)}$ = 4.573, p < .001, dz = 1.268) following completion of prolonged MI compared to the documentary watching. However, the subscales frustration ($t_{(12)}$ = -.623, p = .545, dz = -.171) and effort ($t_{(12)}$ = 2.060, p = .062, dz = .571) did not change significantly.

MI vividness (Figure 2.D) decreased over time ($F_{(1.490, 17.877)}$ =8.163, p = .024, η_p^2 = .301). As shown with the comparison with Block 1 (vs. Block 2: $t_{(12)}$ = 0.617, p = 1.000, dz = 0.171; vs. Block 3: $t_{(12)}$ = 1.339, p = 1.000, dz = 0.385; vs. Block 4: $t_{(12)}$ = 2.449, p = 0.184, dz = 0.679), and Block 2 vs. Block 4 ($t_{(12)}$ = 3.395, p < .032, d = 0.942), the decrease in MI vividness occurred towards the end of second half of the prolonged MI.

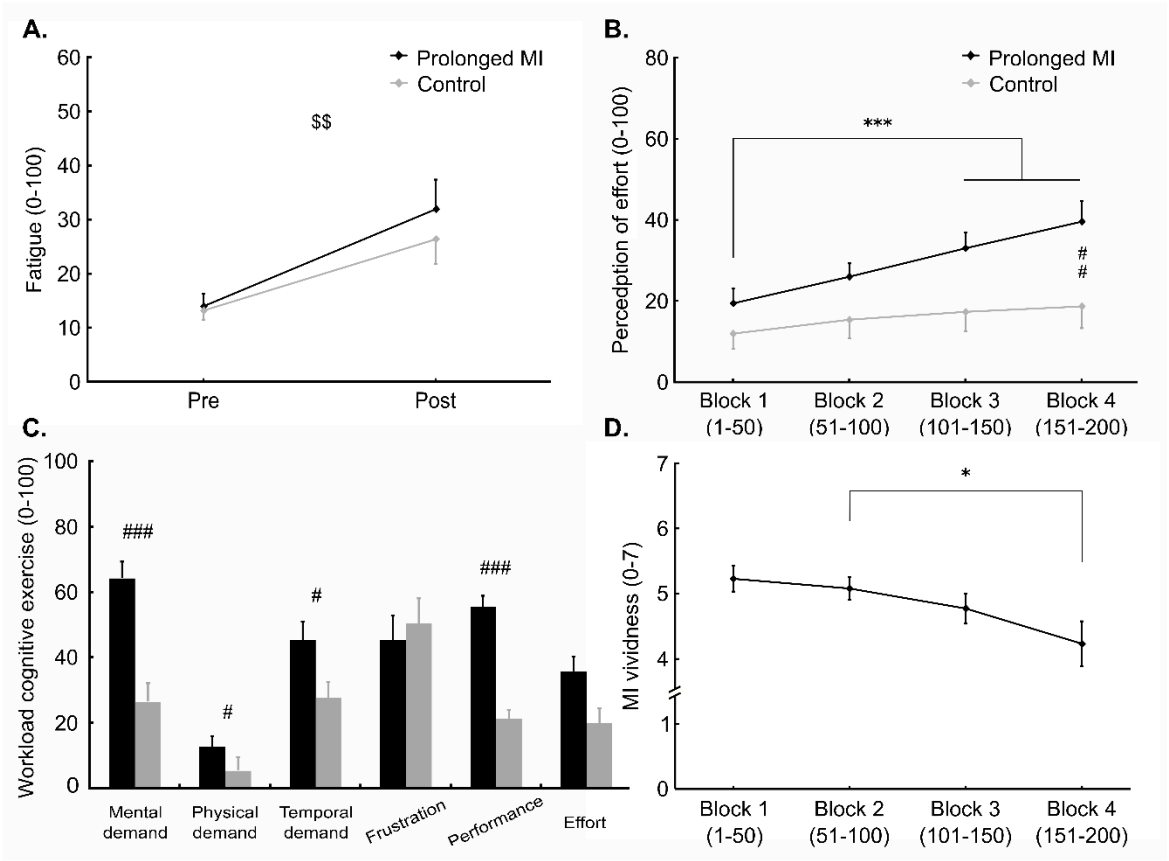

Figure 2. Feelings of fatigue (panel A), rating of perceived effort to perform prolonged motor imagery (MI) and to watch the documentary (Control condition) (panel B), subjective workload of the prolonged MI and control task , and rating of MI vividness during prolonged MI evaluated with a Likert scale (panel D). $$: Significant main effect of time ($p < .01$). * and, ***: Significant difference between two time points within the same condition ($p < .05$ and, $p < .001$). #, ## and, ###: Significant difference between conditions at the same time of measurement ($p < .05$, $p < .01$ and, $p < .001$). Data are presented as means ± SE ($N = 13$).

3.1.2. EFFECTS OF PROLONGED MOTOR IMAGERY ON NEUROPHYSIOLOGICAL MEASUREMENTS

➢ Force production capacity

The force production capacity of the knee extensors decreased over time ($F_{(1, 12)}$ = 11.050, p =.006, η_p^2 = .479) with no main effect of condition ($F_{(1, 12)}$ < .001, p =.992, η_p^2 < .001) or condition × time interaction ($F_{(1, 12)}$ = 1.141, p =.306, η_p^2 = .086; Prolonged MI condition: 206.9 ± 15.9 N to 195.6 ± 14.3 N, Control condition: 204.2 ± 16.6 N to 198.1 ± 16.9 N).

➢ Brain oscillations analysis

All the results on brain oscillations are presented in the Supplementary data (Table S1). Significant differences related to alpha power and theta power are presented below.

Theta (4-7 Hz). Theta power at the Parietal Left region decreased over time ($F_{(1, 11)}$ = 6.250, p =.030, η_p^2 = .362). For all ROIs, no significant interaction was observed (all *ps* > .25, all η_p^2 < .119).

Alpha (8-12 Hz). A greater alpha power was observed in the Prolonged MI condition compared to the Control condition at the Frontal Median ($F_{(1, 11)}$ = 9.057, p = .012, η_p^2 = .452), Central Median ($F_{(1, 11)}$ = 7.876, p = .017, η_p^2 = .417), and Central Right ($F_{(1, 11)}$ = 11.477, p = .006, η_p^2 = .511), Parietal Left ($F_{(1, 11)}$ = 11.423, p = .006, η_p^2 = .509), Parietal Median ($F_{(1, 11)}$ = 15.867, p = .002, η_p^2 = .591), and Parietal Right ($F_{(1, 11)}$ = 13.700, p = .003, η_p^2 = .555) regions. However, for all ROIs, no significant interaction was reported (all *ps* > .30, all η_p^2 < .098).

- **Motor and premotor area activity**

99.8 ± 0.1% of imagined contractions were analysed. During prolonged MI, MRCP amplitude at Cz electrode (Figure 3.) increased over time ($F_{(3, 36)}$ = 4.259, p = .011, η_p^2 = .262). As shown with the comparison with Block 1 (vs. Block 2: $t_{(12)}$ = -0.569, p = 1.000, dz = -0.158; vs. Block 3: $t_{(12)}$ = -3.050, p = .060, dz = -0.846) , MRCP amplitude at Cz progressively increased up to significance at Block 4 ($t_{(12)}$ = -4.358, p = .006, dz = -1.242). The repeated measures correlation analysis revealed a significant correlation between MRCP amplitude and perception of effort during imagined contractions (r(38)= .369, p = .019).

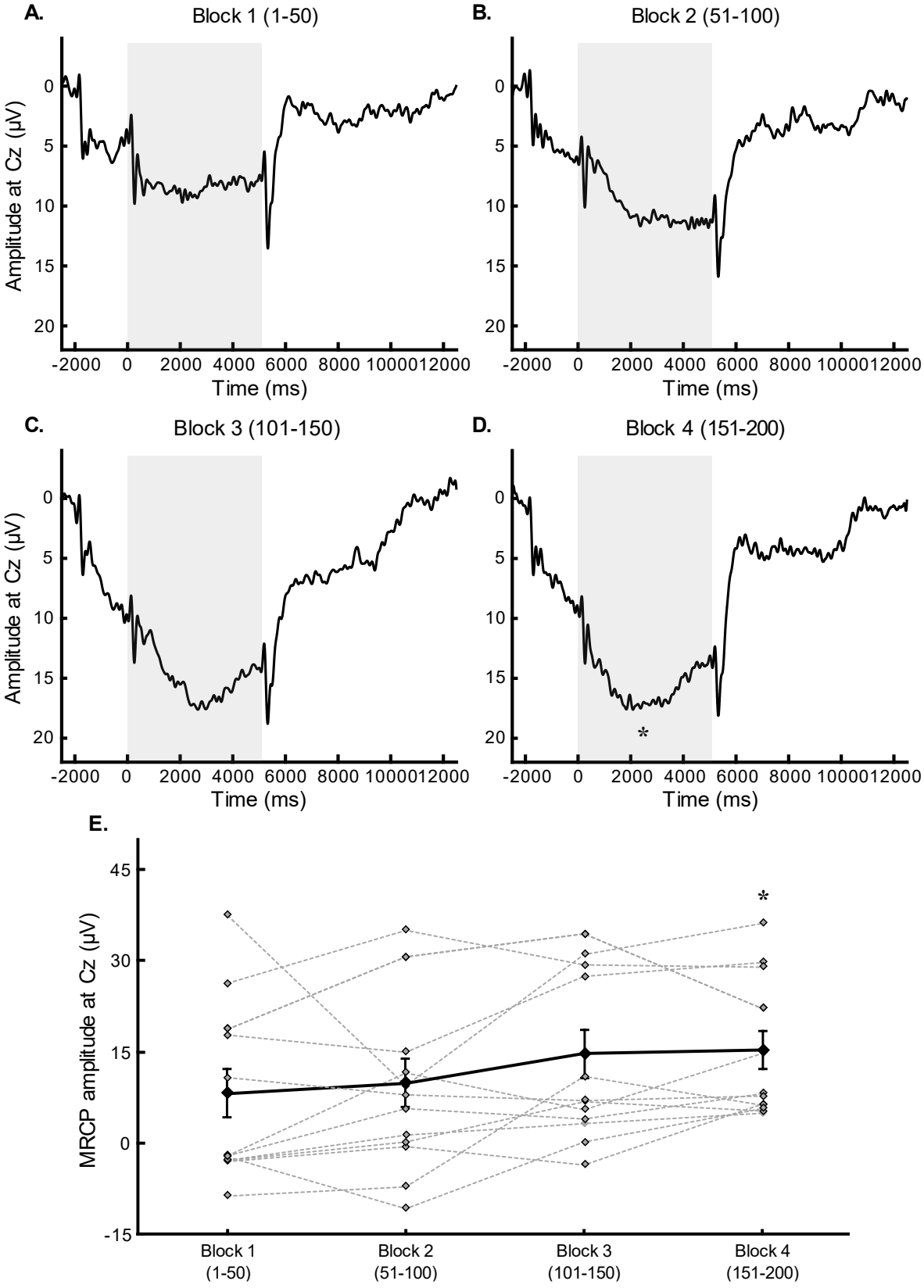

Figure 3. Grand averages (N = 13) of the EEG signal amplitude at Cz electrode for the first block (panel A; imagined contraction 1 to 50), the second block (panel B; imagined contraction 51 to 100), the third block

(panel C; imagined contractions 101 to 150), and the fourth block (panel D; imagined contractions 151 to 200) of the imagined isometric right knee extensions. Time 0 corresponds to the audio signal to start the contraction (panels A, B, C, and D), and the shaded area on the panels A, B, C and D represents the time window used for the analysis of the MRCP amplitude. Individual values of MRCP for each participants (panel E; grey bars indicate individual values and dark bars indicate averaged values). *: Significantly different from Block 1 ($p < .05$).

3.2. EFFECTS OF MENTAL FATIGUE INDUCED BY PROLONGED MOTOR IMAGERY ON PHYSICAL EXERCISE

Motivation to perform physical exercise did not differ between conditions for intrinsic ($t_{(12)} = 0.217$, $p = .832$, $dz = .026$; Prolonged MI: 18.8 ± 1.3, Control condition: 18.7 ± 1.2) or extrinsic motivation ($t_{(12)} = -0.378$, $p = .713$, $dz = -.111$; Prolonged MI: 16.9 ± 1.2, Control condition: 16.8 ± 1.5).

3.2.1. PSYGHOLOGICAL CHANGES

The NASA TLX scale (Figure 4.A) revealed that in the Prolonged MI condition, participants reported a greater physical demand compared to the Control condition ($t_{(11)} = 2.185$, $p = .049$, $dz = .639$). No difference was reported for mental demand, temporal demand, performance, effort and frustration subscales (all ps > .70, all $|dz| < .45$).

Perception of effort (Figure 4.B) increased over time ($F_{(1, 11)} = 65.466$, $p < .001$, $\eta_p^2 = .856$), and was higher in the Prolonged MI condition compared to the Control condition ($F_{(1, 11)} = 5.320$, $p = .042$, $\eta_p^2 = .326$). The condition × time interaction ($F_{(1, 11)} = 6.922$, $p = .023$, $\eta_p^2 = .386$) revealed a greater increase in perceived effort over time following prolonged MI ($t_{(11)} = -8.432$, $p < .001$, $dz = -2.458$) compared to watching a documentary ($t_{(11)} = -6.151$, $p < .001$, $dz = -1.758$). No significant difference between conditions ($t_{(11)} = -.906$, $p = 1.000$, $dz = -.262$) was observed during the first part of the physical exercise. During the second part of the physical exercise, perception of effort was higher in the Prolonged MI condition compared to Control condition ($t_{(11)} = -3.232$, $p = .031$, $dz = -.933$).

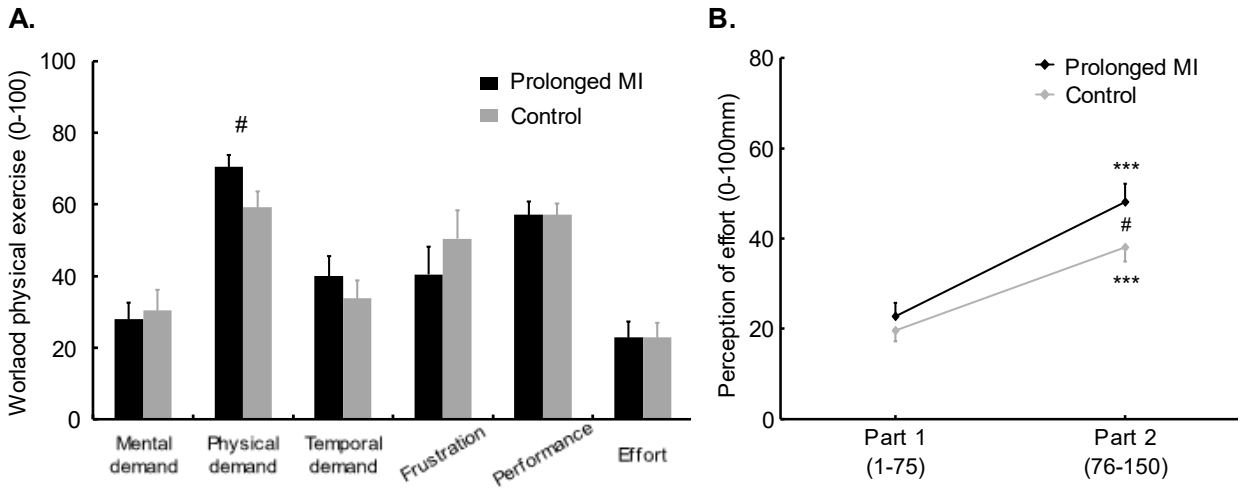

Figure 4. Results for the subjective workload (NASA-TLX) (panel A) and the rating of perceived effort to perform the physical exercise following prolonged MI (black) and documentary watching (grey). #: Significant difference between conditions at the same time of measurement ($p < .05$). ***: Significant difference between two time points within the same condition ($p < .001$). Data are presented as means ± SE ($n = 12$).

3.2.2. PHYSIOLOGICAL CHANGES

➢ Neuromuscular changes

The 150 right knee isometric contractions induced a decrease in force production capacity ($F_{(1, 11)} = 22.323$, $p < .001$, $\eta_p^2 = .670$) with no difference between conditions ($F_{(1, 11)} = 1.068$, $p = .324$, $\eta_p^2 = .088$) and no significant condition × time interaction ($F_{(1, 11)} = 3.522$, $p = .087$, $\eta_p^2 = .243$; Prolonged MI condition: 195.6 N ± 15.5 to 167.0 N ± 12.4, Control condition: 196.1 N ± 18.2 to 175.8 N ± 14.0).

Neuromuscular responses to the physical exercise, results of the ANOVAs, and the relevant follow-up tests are presented in Table 1. Neuromuscular responses did not differ between conditions, except for the VL EMG RMS. The condition × time interaction ($F_{(1, 11)} = 8.711$, $p = .013$, $\eta_p^2 = .442$) revealed an increase solely in the Prolonged MI condition ($t_{(11)} = -2.976$, $p = .054$, $dz = -0.859$) and not in the Control condition ($t_{(11)} = -0.377$, $p = .713$, $dz = -0.109$).

Variables	**Prolonged MI**		**Control**		**Condition**	**Time**	**Interaction**
	Part 1 (0-75)	Part 2 (76-150)	Part 1 (0-75)	Part 2 (76-150)	p (η_p^2)	p (η_p^2)	p (η_p^2)
Force (N)	105.7 ± 8.1	104.9 ± 7.9	104.4 ± 7.9	104.1 ± 7.8	.473 (.048)	.297 (.098)	.405 (.064)
RFD mean (N/s)	271.8 ± 40.7	272.8 ±45.3	286.2 ±30.2	273.9 ± 39.1	.798 (.006)	.721 (.012)	.576 (.029)
Tremor (%)	2.23 ± 0.40	2.33 ± 0.31	2.15 ± 0.29	2.17 ± 0.23	.736 (.011)	.802 (.006)	.905 (.001)
Contraction duration (s)	2.88 ± 0.04	2.85 ± 0.03	2.91 ± 0.05	2.93 ± 0.05	.405 (.064)	.844 (.004)	.110 (.215)
VL EMG RMS (% RMS max)	30.3 ± 2.2	32.7 ± 2.6	30.9 ± 2.7	31.2 ± 2.9	.827 (.005)	.089 (.241)	.013 (.442)

Table 1. Mean force, rate of force development (RFD), tremor, contraction duration, and vastus lateralis (VL) EMG RMS during the isometric knee extensions, during the first part (contractions 1 to 75) and the second part (contractions 76 to 150) of the physical exercise in Prolonged MI and Control conditions. Data are presented as means ± SE (n = 12).

➢ Motor and premotor area activity

For the MRCP amplitude analysis, 18.3 ± 0.9 contractions per part of the exercise were excluded due to an incorrect force development and 2.4 ± 0.9 due to the presence of movement artefacts. In total, 72.4 ± 1.3% of the total number of contractions were included in the statistical analysis. The numbers of contractions analyzed did not differ between the experimental conditions ($F_{(1,11)}$ = 4.009, p = .071, η_p^2 = .267) and did not change over time ($F_{(1,11)}$ = 0.920, p = .358, η_p^2 = .077). The condition × time interaction was also not significant ($F_{(1,11)}$ = 0.044, p = .838, η_p^2 = .004).

MRCP amplitude at Cz during the physical exercise (Figure 5) increased over time ($F_{(1,11)}$ = 10.325, p = .008, η_p^2 = .484) with no main effect of condition ($F_{(1,11)}$ = 2.222, p = .164, η_p^2 = .168) or condition × time interaction ($F_{(1,11)}$ = 3.832, p = .076 , η_p^2 = .258). As shown in Figure 5B and 5C, MRCP amplitude responses to the actual contractions presented a notable variability. The repeated measures correlation analysis failed to reveal a significant correlation between MRCP amplitude and perception of effort for actual contractions (r(35)= .311, p = .060).

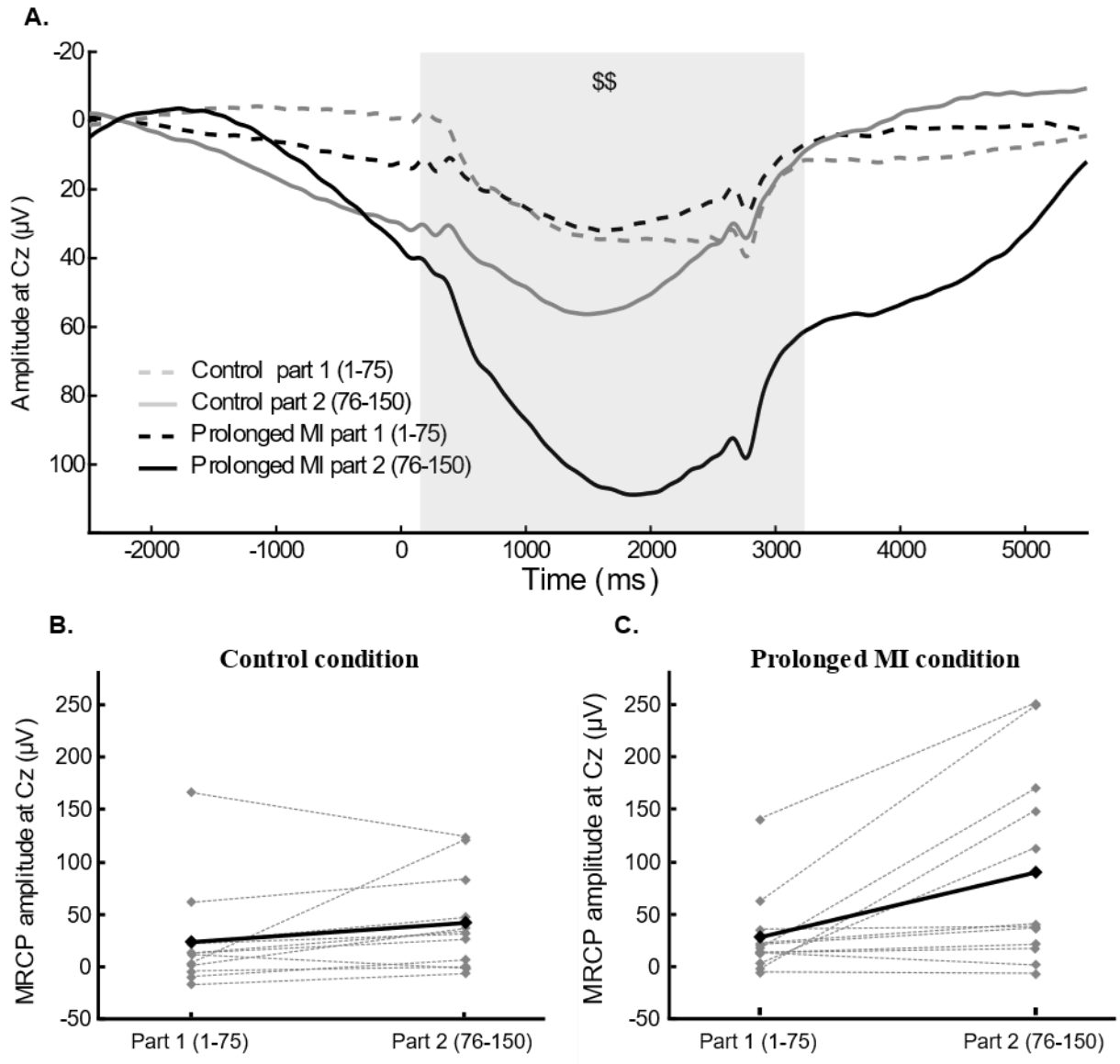

Figure 5. Grand average (n = 12) of the EEG signal amplitude at Cz electrode for the first part (contractions 1 to 75) and the second part (contractions 76 to 150) of the submaximal isometric right knee extensions in both Prolonged MI and Control conditions. Time 0 corresponds to the audio signal to start the contraction (panel A), and the shaded area on the panel A represents the time window used for the analyse of the MRCP amplitude as presented in panels B and C. Individual mean amplitude of MRCP for the first and the second part of isometric knee extensions in the Control condition (panel B) and in the Prolonged MI condition (panel C). $$: Significant main effect of time on MRCP amplitude (p < .01).

4. DISCUSSION

The main aim of the present study was to confirm that, when prolonged, motor imagery could induce a state of mental fatigue. The progressive increase in motor and premotor area activity required to imagine the contractions, in combination with the decreased quality of motor imagery and the increased feelings of fatigue, confirms that prolonged motor imagery induces mental fatigue. The secondary aim of the study was to identify during a subsequent physical exercise neurophysiological alterations caused by mental fatigue. While this study confirms previous observations that perception of effort during a physical exercise is increased in the presence of mental fatigue (for review see: Pageaux and Lepers, 2018; Brown et al., 2020), the results of the analysis of the MRCP amplitude cannot firmly confirm that this higher perceived effort is related to greater activation of the motor and premotor areas required to perform the isometric knee extensions. As discussed thereafter, this study needs to be replicated with specific adjustments on the physical exercise protocol to limit the exercise-induced decrease in force production capacity. Such adjustments will facilitate the possibility to observe clearer specific alterations in MRCP amplitude related to mental fatigue during an actual physical exercise.

4.1. EVIDENCE OF MOTOR IMAGERY

When requiring participants to engage in motor imagery, it is difficult to assess whether they actually imagine and execute the task. The greater alpha power during the prolonged motor imagery condition compared to the control condition, as well as the higher effort and mental demand experienced during the prolonged motor imagery condition, suggest the involvement of different cognitive processes during both prolonged motor imagery and documentary watching (Beyer et al., 1990). As previously observed, the imagination of maximal voluntary contractions was associated with the presence of MRCPs, confirming a specific activation of motor and premotor areas (do Nascimento et al., 2006; Jankelowitz and Colebatch, 2002). The MRCP amplitudes at Cz electrode during the imagined contractions were smaller than during the actual contractions (M = 12.00 µV vs. M = 45.56 µV). This result is in line with neuroimaging studies reporting lower activation of motor and premotor areas during imagined contractions compared to actual contractions (Batula et al., 2017; Porro et al., 1996). Furthermore, it is important to note that the absence of EMG activity during the imagination of contractions confirms that the participants imagined without activating their knee extensors.

The integration of these results altogether confirms that the participants accurately performed motor imagery.

4.2. EVIDENCE OF MENTAL FATIGUE INDUCED BY PROLONGED MOTOR IMAGERY

Mental fatigue is characterized by subjective feelings of "tiredness" and "lack of energy", associated or not with a decrease in cognitive performance (Boksem and Tops, 2008; Brown et al., 2020; Pageaux and Lepers, 2018). Mental fatigue is also known to increase the effort required to perform cognitive or physical activities (Nolte et al., 2008; Pageaux and Lepers, 2016). In the present study, feelings of fatigue increased over time, and the quality of motor imagery measured with the report of motor imagery vividness decreased during the prolonged motor imagery session, suggesting that prolonged motor imagery induces mental fatigue. The induction of mental fatigue by engagement in prolonged motor imagery is also confirmed by the progressive increase in the effort required to imagine the contractions over time.

In the present study, both the prolonged motor imagery and documentary watching increased feelings of fatigue. While the lack of significant condition × time interaction on the reported feelings of fatigue refrains the firm conclusion that the prolonged motor imagery condition induced a greater level of mental fatigue than the control condition, it is important to note that the participants experienced more effort to perform the subsequent physical exercise in the prolonged motor imagery condition compared to the control condition. A higher than normal perception of effort during a physical exercise is a well-reported alteration induced by the presence of mental fatigue (for review see: Pageaux and Lepers, 2018; Brown et al., 2020). Therefore, by considering that i) the effort required to perform motor imagery or watching a documentary increased solely in the prolonged motor imagery condition, and ii) the effort required to perform the subsequent physical exercise increased solely in the prolonged motor imagery condition, we are confident that the level of mental fatigue was greater following prolonged motor imagery compared to watching a documentary for the same duration. As boredom and sleepiness are proposed to interact with mental fatigue, it cannot be excluded that the observed increase in feelings of fatigue in the control condition confounds with changes in boredom and/or sleepiness, as recently suggested (O'Keeffe et al., 2020). As feelings of fatigue and boredom (Pattyn et al., 2008), as well as feelings of fatigue and sleepiness (Shen et al., 2006), can be dissociated from each other, future studies inducing mental fatigue should

monitor the changes in these three constructs during prolonged engagement in demanding cognitive tasks. Such approach is likely to open new opportunities for researchers interested in better understanding the neurophenomenological differences between the experience of fatigue, boredom and sleepiness.

4.3. ARE BRAIN OSCILLATIONS A GOOD MARKER OF MENTAL FATIGUE INDUCED BY PROLONGED MOTOR IMAGERY?

The analysis of brain oscillations recorded with electroencephalography is a well-used marker of mental fatigue induced by prolonged engagement in demanding cognitive tasks. A recent meta-analysis reported that changes in brain oscillations on the theta and alpha power are consistently observed in the presence of mental fatigue (Tran et al., 2020). Prolonged engagement in demanding cognitive tasks has been shown to increase the oscillations on both alpha (e.g., Craig et al., 2012) and theta (e.g., Wascher et al., 2014) power. In the present study, no significant main effect of time or condition × time interaction was reported for the oscillations of the alpha power, suggesting that the completion of prolonged motor imagery did not induce a specific change over time in this parameter. Also, contrary to the hypothesis expecting an increased theta power in the presence of mental fatigue, the oscillations of the theta power decreased over time in the left parietal region. The observed changes in the oscillations of the theta power and the lack of changes in the oscillations of the alpha power do not support the possibility to use changes in brain oscillations as a marker of mental fatigue induced by prolonged motor imagery. These results are in line with a recent study showing that the engagement in different cognitive tasks leading to mental fatigue (psychomotor vigilance task, AX-CPT and Stroop task) does not elicit clear effects on EEG responses (Smith et al., 2019). The integration of our results with those of Smith et al (2019) suggests that future studies should aim at identifying EEG-markers of mental fatigue that could provide coherent responses between different tasks known to induce a state of mental fatigue.

4.4. PROLONGED MOTOR IMAGERY INCREASES THE MOTOR AND PREMOTOR AREA ACTIVITY REQUIRED TO IMAGINE MUSCLE CONTRACTIONS

While the analysis of brain oscillations was not successful to identify the presence of mental fatigue, this study is to the best of our knowledge, the first to identify a neurophysiological alteration caused by mental fatigue induced by prolonged motor imagery. The progressive increase in MRCP amplitude suggests that a greater motor and premotor area activity is required to imagine muscle contractions in the presence of mental fatigue. It is

therefore plausible that mental fatigue induces alterations in the motor command required to accurately perform imagined or actual muscle contractions. The hypothesis of an altered motor command in the presence of mental fatigue has been originally reported in a previous study demonstrating alterations in the speed-accuracy trade-off in the presence of mental fatigue (Rozand et al., 2015). In this study, the authors observed a longer duration of actual and imagined movements during a pointing task performed following 90 min of an incongruent Stroop task, compared to watching an emotionally neutral documentary for the same duration. In the present study, the observed increase in MRCP amplitude in the presence of mental fatigue, as well as the correlation between MRCP amplitude and perception of effort, provides neurophysiological evidence that mental fatigue could increase the magnitude of the motor command required to imagine a movement, and supports the hypothesis of an altered motor command in the presence of mental fatigue proposed by Rozand et al. (2015).

While the present study confirms that prolonged motor imagery induces mental fatigue, it is crucial to acknowledge that motor imagery is an efficient tool in rehabilitation when its use is not prolonged. By integrating the results of the objective (increase in MRCP amplitude over time) and subjective (increase in the effort required to imagine the contractions over time and decreased motor imagery vividness) markers of mental fatigue, our results reconcile with the recent meta-analysis of Schuster et al. (2011) suggesting that ~17 minutes of motor imagery is optimal to observe positive effects on physical performance. Indeed, in the present study, significant alterations in the effort required to perform imagined contractions was apparent after 25 min of motor imagery (i.e., from Block 3). By integrating the results of the meta-analysis of Schuster et al. (2011) with the results of the present study, future studies willing to use motor imagery and control for mental fatigue induction should use motor imagery sessions lasting no longer than 20 min.

4.5. EFFECTS OF MENTAL FATIGUE INDUCED BY PROLONGED MOTOR IMAGERY ON A SUBSEQUENT PHYSICAL EXERCISE

As observed in previous studies, performing repeated muscle contractions for a prolonged duration induces a decrease in force production capacity that in turn increases the effort required to perform the physical exercise (Gandevia, 2001). This decrease in force production capacity highlights the presence of neuromuscular fatigue (Gandevia, 2001) and explains the increase in perception of effort and MRCP amplitude during the second half of the physical exercise in both prolonged motor imagery and control conditions (de Morree et al.,

2014, 2012). Indeed, as perception of effort during physical exercise reflects the neuronal process of the motor command (de Morree et al., 2014, 2012; Pageaux, 2016; Pageaux and Gaveau, 2016), producing the same absolute level of force in the presence of neuromuscular fatigue requires an increased motor command to counteract the negative effects of neuromuscular fatigue on the corticospinal pathway and recruit additional muscle fibers (de Morree et al., 2012; Pageaux, 2016).

Contrary to previous studies demonstrating a higher perceived effort at the onset of the physical exercise performed in the presence of mental fatigue (Pageaux et al., 2015, 2014, 2013), in the present study the effort reported by the participants during the first half of the physical exercise did not differ between the prolonged motor imagery and the control conditions. Perception of effort was greater in the presence of mental fatigue solely in the second half of the physical exercise. As the studies observing a higher effort at the onset of the physical exercise used cognitive tasks predominantly involving the response inhibition process and not prolonged motor imagery, the discrepancy in these results suggests that mental fatigue may have different effects on a physical exercise depending on the method used to induce it. It can be speculated that, the absence of difference in perceived effort in the first half of the physical exercice could be due to the positive immediate effects of an acute motor imagery session on corticospinal plasticity (Ruffino et al., 2019). It cannot be excluded that the positive effects of motor imagery on the corticospinal pathway could counteract at the onset of the physical exercise the negative effects of mental fatigue on subsequent physical performance. Further studies should investigate a duration-response relationship on the effects of a single session of motor imagery on subsequent physical performance.

4.6. EFFECT OF MENTAL FATIGUE ON MOTOR AND PREMOTOR AREA ACTIVITY

Perception of effort is proposed to be generated by the neuronal process of a corollary discharge of the motor command (de Morree et al., 2014, 2012; Pageaux, 2016; Pageaux and Gaveau, 2016), and is traditionally used in the neurophysiology literature as a marker of the central motor command (e.g., Kjær et al., 1999; McCloskey et al., 1974; Mitchell et al., 1989; Seed et al., 2019). Muscle activation measured with EMG is traditionally used as a marker of the motor command sent to the working muscles in studies interested in the regulation of muscle contractions and movements (e.g., Carrier et al., 2011; Thoroughman and Shadmehr, 1999). The vastus lateralis EMG RMS increased solely in the prolonged motor imagery condition and not in the control condition. The specific alterations in objective (EMG) and subjective

(perception of effort) indices of the motor command suggest that prolonged motor imagery alters the motor command in a subsequent physical exercise, and that underlying neurophysiological alterations progressively develop over time. However, both the nonsignificant condition × time interaction on the analysis of the MRCP amplitude and the nonsignificant correlation between MRCP amplitude and perception of effort do not allow to clearly conclude on that point. The observed variability in changes in MRCP amplitude during the physical exercise performed following prolonged motor imagery (Figure 5.C) also suggests between-participant differences in response to mental fatigue. Although all participants declared to engage in a physical activity at least one time per week, their exact training status and sport expertise was not collected. As expertise in endurance sports seems to be associated with greater resistance to mental fatigue (Martin et al., 2016), the variability observed in changes in MRCP amplitude could be due to differences between participant in training status, sport expertise or physical activity level. In this context, studies interested in investigating mental fatigue should carefully record at least the physical activity level of their participants, and if possible their sport expertise and associated performance level (Decroix et al., 2016; Pauw et al., 2013).

As previous studies also observed alterations in EMG signal of the working muscles during submaximal physical exercices following engagement in demanding cognitive tasks (Bray et al., 2008; Graham et al., 2014; Pageaux et al., 2015), we believe that the absence of significance in the condition × time interaction is likely due to the confounding effects of neuromuscular fatigue on MRCP amplitude (de Morree et al., 2014, 2012) rather than the absence of a true effects of mental fatigue on this parameter. Indeed, as a reduction in force production capacity is known to increase MRCP amplitude (de Morree et al., 2012), and our physical exercise induced a decrease in force production capacity, future studies should be conducted by tailoring the physical exercise to limit as much as possible the presence of exercise-induced neuromuscular fatigue. As the magnitude of neuromuscular fatigue is known to be intensity and contraction duration dependent (Burnley et al., 2012; Mendez-Villanueva et al., 2009), such tailoring could be done by decreasing the level of the relative force target to reach during each contraction or the duration of the contractions, as well as by increasing the recovery period between the contractions. Such changes in the physical exercise protocol are also likely to reduce the number of excluded MRCPs due to head or body movement during the muscle contractions. Even if knee extensions were investigated for their relevance to locomotion and other activities of the daily life in this study, these contractions involve a large

muscle group and generate large artifacts on the EEG signal. Therefore, we also suggest that future studies should consider involving a smaller muscle group and perform movements such as elbow flexions, wrist flexions or handgrip contractions. Involving a smaller muscle group compared to the knee extensors, or decreasing the intensity of the physical exercise, will also reduce cardiorespiratory responses to the physical exercise (Mitchell et al., 1980) and render the physical exercise more accessible to various populations and not only physically active and healthy young adults. Finally, we acknowledge that the limit of our sample size does not allow to clearly conclude on the condition × time interaction on the MRCP amplitude during the physical exercise (p = .076 , η_p^2 = .258) performed following the prolonged motor imagery. An increased sample size in future studies is i) likely to overcome this limitation and ii) of great importance for studies interested in gender and sex differences in the effect of mental fatigue on subsequent physical performance.

4.7. CONCLUSION AND PERSPECTIVES

The present study confirms that, when prolonged, motor imagery induces a state of mental fatigue. The presence of mental fatigue was evidenced by the progressive increase in motor and premotor area activity required to imagine the contractions (i.e., increase in MRCP amplitude over time), in combination with the decreased quality of motor imagery and the increased feelings of fatigue. In the presence of mental fatigue induced by prolonged motor imagery, the subsequent physical exercise was perceived as being more effortful in the second part of the exercise and was associated with a specific increase in EMG RMS of the vastus lateralis muscle. These alterations suggest that mental fatigue induced by prolonged motor imagery may alter the motor command required to perform imagined and actual contractions. However, due to the marked decrease in knee extensors force production capacity induced by the physical exercise and consequently its confounding effects on the observed increase in MRCP amplitude (de Morree et al., 2012), future studies will be necessary to replicate and reinforce the results of the present study, notably by tailoring the physical exercise to avoid, or at least minimize, neuromuscular fatigue.

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SUPPLEMENTARY DATA

	Condition p (η_p^2)	**Time** p (η_p^2)	**Interaction** p (η_p^2)
Delta			
Frontal left	.060 (.286)	.085 (.245)	.260 (.114)
Frontal median	.044 (.319)	.079 (.254)	.358 (.077)
Frontal right	.039 (.333)	.215 (.136)	.340 (.083)
Central left	.102 (.224)	.256 (.115)	.396 (.066)
Central median	.044 (.319)	.176 (.160)	.480 (.046)
Central right	.172 (.162)	.294 (.099)	.356 (.078)
Parietal left	.176 (.160)	.542 (.032)	.879 (.002)
Parietal median	.091 (.238)	.694 (.015)	.360 (.077)
Parietal right	.814 (.005)	.350 (.080)	.490 (.044)
Theta			
Frontal left	.233 (.127)	.172 (.162)	.250 (.118)
Frontal median	.176 (.160)	.518 (.039)	.635 (.021)
Frontal right	.178 (.159)	.426 (.058)	.550 (.033)
Central left	.759 (.009)	.134 (.192)	.352 (.079)
Central median	.842 (.004)	.234 (.126)	.719 (.012)
Central right	.657 (.019)	.081 (.251)	.735 (.011)
Parietal left	.943 (< .001)	.030 (.362)	.723 (.012)
Parietal median	.421 (.060)	.121 (.204)	.634 (.021)
Parietal right	.385 (.069)	.331 (.086)	.661 (.018)
Alpha			
Frontal left	.097 (.230)	.205 (.142)	.661 (.018)
Frontal median	.106 (.220)	.263 (.112)	.927 (.001)
Frontal right	.012 (.452)	.351 (.079)	.785 (.007)
Central left	.079 (.255)	.342 (.082)	.301 (.097)
Central median	.017 (417)	.452 (.052)	.436 (.056)
Central right	.006 (.511)	.319 (.090)	.543 (.035)
Parietal left	.006 (.509)	.322 (.089)	.734 (.011)
Parietal median	.002 (.591)	.503 (.042)	.377 (.071)
Parietal right	.003 (.555)	.455 (.052)	.648 (.020)
Beta			
Frontal left	.289 (.101)	.270 (.109)	.095 (.233)
Frontal median	.635 (.021)	.065 (.276)	.149 (.180)
Frontal right	.232 (.127)	.324 (.088)	.335 (.085)
Central left	.600 (.026)	.145 (.183)	.111 (.214)
Central median	.923 (.001)	.071 (.267)	.207 (.140)
Central right	.892 (.002)	.073 (.263)	.188 (.152)
Parietal left	.906 (.001)	.009 (.476)	.440 (.055)
Parietal median	.818 (.005)	.015 (.428)	.302 (.096)
Parietal right	.399 (.065)	.066 (.275)	.322 (.089)
Gamma			
Frontal left	.176 (.160)	.906 (.001)	.063 (.279)
Frontal median	.571 (.030)	.421 (.060)	.101 (.226)
Frontal right	.185 (.154)	.981 (< .001)	.246 (.120)
Central left	.317 (.091)	.998 (< .001)	.104 (.222)
Central median	.648 (.020)	.462 (.050)	.178 (.159)
Central right	.415 (.061)	.532 (.036)	.141 (.186)
Parietal left	.435 (.056)	.073 (.264)	.433 (.057)
Parietal median	.563 (.031)	.116 (.210)	.353 (.079)
Parietal right	.898 (.002)	.240 (.123)	.218 (.135)

Table S1. Changes in brain oscillation on delta, theta, alpha, beta, and gamma power for all regions of interest. Two-way repeated-measures 2 × 2 ANOVAs were used to test the effects of condition (Prolonged MI, Control) and time (First 5 min, Last 5 min) on delta, theta, alpha, beta, and gamma power during prolonged MI and documentary watching.

2.2 Synthèse

Lors de cette étude nous avons montré que la réalisation d'une tâche d'imagerie motrice prolongée pouvait induire de la fatigue mentale et induire une dégradation des performances lors d'une tâche physique subséquente. De plus, au cours de la tâche d'imagerie motrice prolongée la qualité de l'imagerie se dégradait avec temps. Ces résultats ont des implications pratiques, notamment il faudrait conseiller de limiter la durée des sessions en imagerie motrice afin de préserver la qualité des mouvements imaginés, mais aussi éviter l'instauration de fatigue mentale et de ses effets négatifs.

Nous avons observé une augmentation de la perception de l'effort au cours d'un exercice physique en présence de fatigue mentale. Cette augmentation de la perception de l'effort est largement admise dans la littérature. Plusieurs modèles ont été développés pour expliquer l'origine de la perception de l'effort, dont le modèle de la décharge corolaire. D'après ce modèle, au moment de la production de la commande motrice, une copie, nommée décharge corollaire, serait envoyée au niveau du cortex sensoriel. Cette copie de la commande motrice serait responsable de la perception de l'effort. Nous avons mis en évidence au cours de cette étude que l'augmentation de la perception de l'effort en présence de fatigue mentale était liée à l'augmentation de l'activité des aires motrices et prémotrices. Une augmentation de l'activité des aires motrices et prémotrices a également été observée lors de la tâche d'imagerie motrice prolongée. Lors de la réalisation des contractions imaginées, la perception de l'effort s'est avérée corrélée positivement avec l'activité des aires motrices et prémotrices, ce qui n'était pas le cas lors des contractions réelles pour lesquelles cette corrélation était seulement tendancielle. Il serait intéressant de pouvoir reproduire ces résultats en utilisant un exercice physique moins exigeant que des contractions des extenseurs du genou et/ou à moindre intensité afin de limiter les artefacts lors des enregistrements EEG. Cela permettrait d'avoir moins de variabilité lors des enregistrements et peut-être d'aboutir à des résultats statistiquement significatifs.

3 Etude 3

Effets de persistance de la fatigue mentale sur le contrôle moteur

Persistence effects of mental fatigue on motor control

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3.1 Résumé

Les effets de la fatigue mentale sur les performances cognitives et physiques sont bien décrits dans la littérature, mais les aspects de la récupération de la fatigue mentale ont été moins étudiés. Cette étude vise à combler cette lacune en examinant la persistance de la fatigue mentale sur le comportement et ces mécanismes électrophysiologiques. Quinze participants ont effectué une tâche de pointage consistant à atteindre une cible le plus rapidement possible, avant d'effectuer une tâche cognitive exigeante de 32 minutes (*Time Load Dual Back* - TLDB), puis immédiatement, 10 minutes, et 20 minutes après la fin de la tâche TLDB. Pendant l'expérience, l'électroencéphalographie a été enregistrée en continu. L'augmentation significative de la sensation de fatigue mentale après la tâche TLDB a été suivie d'une diminution pendant les 20 minutes de récupération sans retour aux valeurs initiale (i.e., avant la tâche de TLDB). Les oscillations cérébrales enregistrées au repos pendant la période de récupération ont montré une augmentation de la puissance thêta et alpha au fil du temps, ce qui suggère une persistance de la fatigue mentale. La durée des mouvements de pointage a augmenté progressivement au cours de la période de récupération, ce qui indique que les performances comportementales étaient de plus en plus altérées lors des 20 minutes suivant la tâche mentalement fatigante. En conclusion, les mesures subjectives ont indiqué une récupération partielle de la fatigue mentale après une tâche cognitive exigeante, tandis que les marqueurs électrophysiologiques et comportementaux ont suggéré que les effets de la fatigue mentale persistaient pendant au moins 20 minutes. Si l'évaluation subjective de la fatigue mentale est un moyen très pratique d'attester la présence d'une fatigue mentale, les mesures électrophysiologiques et comportementales semblent plus pertinentes pour évaluer l'évolution dans le temps des effets de la fatigue mentale.

Persistence of mental fatigue on motor control

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Keywords: Cognitive fatigue, Recovery effect, Electroencephalography (EEG), Brain oscillations, Event-related potentials, Fitts' law, Arm-pointing task.

ABSTRACT

The effects of mental fatigue on both cognitive and physical performance are well described in the literature, but the recovery aspects of mental fatigue have been less investigated. The present study aimed to fill this gap by examining the persistence of mental fatigue on behavior and electrophysiological mechanisms. Fifteen participants performed an arm-pointing task consisting of reaching a target as fast as possible, before carrying out a 32-min cognitively demanding task (Time Load Dual Back – TLDB - task), and immediately, 10 min, and 20 min after completion of the TLDB task. During the experiment, electroencephalography was continuously recorded. The significant increase in mental fatigue feeling after the TLDB task was followed by a decrease during the 20 min of recovery without returning to premeasurement values. Brain oscillations recorded at rest during the recovery period showed an increase in both theta and alpha power over time, suggesting a persistence of mental fatigue. Arm-pointing movement duration increased gradually over time during the recovery period, indicating that behavioral performance remained impaired 20 min after the end of the cognitively demanding task. To conclude, subjective measurements indicated a

partial recovery of mental fatigue following a cognitively demanding task, whereas electrophysiological and behavioral markers suggested that the effects of mental fatigue persisted for at least 20 min. While the subjective evaluation of mental fatigue is a very practical way to attest the presence of mental fatigue, electrophysiological and behavioral measures seem more relevant to evaluate the time course of mental fatigue effects.

1. INTRODUCTION

Mental fatigue, which is defined as a psychobiological state caused by prolonged and/or intense periods of demanding cognitive activity and characterized by subjective feelings of "tiredness" and "lack of energy" (Boksem and Tops, 2008; Rozand and Lepers, 2016), is a common problem in everyday life. It can affect patients with cancer, Alzheimer's or Parkinson's disease (Chaudhuri and Behan, 2000), as well as healthy individuals, in whom it can lead to a decrease in productivity, an increase in road accidents (Dinges, 1995), or even be involved in burnout or depression (Lavidor et al., 2002).

Mental fatigue is a very complex phenomenon, and its neural mechanisms are still poorly known. They likely involve changes in brain activity involving the anterior cingulate cortex (ACC), a brain area at the interface between cognition, emotion, and motor control (Müller and Apps, 2019). Several different theories have been proposed to explain the mental fatigue-induced performance decrements; these include underload theories (Manly et al., 1999), resource theories (Sanders, 1997), motivational control theories (Kurzban et al., 2013) and dual regulation system (Ishii et al., 2014). The present study falls within the framework of resource theories, and is close to ego-depletion theory (Baumeister et al., 1998; Hagger et al., 2010). In this background, performing a cognitively fatiguing task reduces, or even under certain circumstances, depletes cerebral and cognitive resources that cannot be replenished immediately and that cannot be fully available to perform a following task (cognitive or physical). This could result in performance decrement (although some compensatory mechanisms might maintain performance, (Hockey, 2013; Wang et al., 2016) and cerebral brain changes.

Since the middle of the 19th century (Davy, 1845), researchers have investigated mental fatigue in both laboratory and field conditions to better understand its effects and mechanisms. Under laboratory conditions, mental fatigue is generally induced by specific cognitive tasks. For example, the Stroop task (e.g., Rozand et al., 2015; Van Cutsem et al., 2017a), the AX-CPT

(e.g., Marcora et al., 2009; Pageaux et al., 2013) or computerized decision-making tasks (Otani et al., 2017) have been used, generally for a duration ranging from 45 min to 90 min, to induce mental fatigue. However, during prolonged cognitive tasks, both mental fatigue and boredom interfere, making it difficult to study mental fatigue per se. To differentiate between mental fatigue and boredom, shorter but more demanding cognitive tasks have been used to induce mental fatigue without boredom. For example, Borragan et al. (2016) used a cognitive task called the Time Load Dual Back (TLDB) task combining a traditional N-back working-memory updating task and an interfering second task (odd/even decision task) lasting 16 min. After completion of the TLDB task, the participants reported a significant increase in the feeling of mental fatigue, and their vigilance decreased during a subsequent psychomotor vigilance task (PVT; (Borragan et al., 2017). While subjective measures (e.g., visual analogue scale) can be used to evaluate mental fatigue (Smith et al., 2019), measures based on electrophysiological recordings can provide more objective evidence of mental fatigue.

Studies using electroencephalography (EEG) have shed light on the neural mechanisms involved in mental fatigue, notably changes in brain oscillations. Mainly an increase in alpha power has consistently been observed, which might reflect a decrease in arousal and alertness (Paus et al., 1997; Boksem et al., 2005; Zhao et al., 2012). Although alpha power changes are a robust marker of mental fatigue, a recent meta-analysis suggested that an increase in theta power would be a more reliable biomarker of the presence of mental fatigue (Tran et al., 2020). According to this meta-analysis, mental fatigue results in large increases in theta power through the whole brain (i.e., frontal, central, and posterior regions), while increases in alpha power are mainly observed in central and posterior regions and to a lesser extent in frontal regions. In addition to brain oscillations, event-related potentials (ERPs) have also been considered. Consistent effects of mental fatigue have been observed on N100, N2, and P300 components. For these three components, a decrease in amplitude over time has been observed and interpreted as reflecting a top-down modulation of sensory processing for the N100 (Boksem et al., 2005; Faber et al., 2012), a decrease in cognitive control for the N2 (Boksem et al., 2006; Möckel et al., 2015) and a decrease in attention for the P300 (Murata et al., 2005; Schmidt et al., 2009). In parallel with electrophysiological changes, performance can also be impaired by mental fatigue.

It has been established that mental fatigue may negatively impact subsequent cognitive (e.g., van der Linden et al., 2003; Boksem et al., 2005) or physical (for review: Van Cutsem et al., 2017b; Pageaux and Lepers, 2018) activities. Concerning physical performance, not all

physical activities are negatively impacted by mental fatigue. While previous studies have shown that mental fatigue impaired endurance performance (e.g., Marcora et al., 2009; Pageaux et al., 2014) as well as decision making (e.g., Smith et al., 2016; Harris and Bray, 2019) and motor skills (e.g., Rozand et al., 2015; Le Mansec et al., 2018), the maximal voluntary force/power production capacity seems to be preserved (e.g., Pageaux et al., 2013; Duncan et al., 2015). To evaluate the effects of mental fatigue on motor skills, Rozand et al. (2015) used an arm-pointing task consisting of reaching visual targets as fast as possible. Following mental fatigue, induced by 90 min of a modified Stroop task, these authors observed an ~10% increase in actual movement duration, indicating an impairment of motor skills following a prolonged cognitively demanding task.

While the effects of mental fatigue on motor performance have been clearly demonstrated, questions about the persistence of these effects and the time course of recovery from mental fatigue have been poorly investigated. To our knowledge, Rivers (1896) was one of the first to address this question by evaluating the effect of a 30- or 60-min rest period following 30 min of mental work (i.e., addition calculation). Results indicated that 30 min of total rest was insufficient to neutralize the effects of mental fatigue and that 60 min of total rest only partially eliminated the effects. More recently, Smith et al. (2019) investigated the effects of three different cognitive tasks (Stroop task, AX-CPT, and PVT), lasting 60 min, on reaction times, feeling of fatigue and electrophysiological markers, as well as their persistence over time. They observed that the feeling of mental fatigue (reported on a visual analogue scale) increased immediately after the three cognitive tasks but led to a decrease in vigilance only after the Stroop task and the AX-CPT task. The level of mental fatigue decreased gradually over time, suggesting that a recovery mechanism came into play. However, the feeling of mental fatigue remained high for 10 min after the PVT, 50 min after the Stroop task, and 60 min after the AX-CPT. Concerning performance, no negative effect of mental fatigue was reported on vigilance 30 min after completion of the three different cognitively demanding tasks. These observations suggest that performance may recover faster than the subjective feeling of mental fatigue.

The main objective of the present study was to investigate the time course of mental fatigue following a 32-min cognitively demanding task on both subjective (visual analogue scale; VAS) and electrophysiological (i.e., brain oscillations) markers, as well as on motor performance. An arm-pointing task was used to evaluate the impact of mental fatigue on motor performance, due to its involvement in many activities of daily living. We firstly hypothesized that during the completion of the TLDB task, an increase over time in both theta and alpha

power should be observed. It should concern all the brain regions for theta power, and more specifically central and parietal regions and to a lesser extend the frontal regions for alpha power. Concerning ERPs, we hypothesized that the amplitude of the N100, the N200, and the P300 should decrease over time as observed in previous studies (Boksem et al., 2005; Murata et al., 2005; Boksem et al., 2006; Faber et al., 2012). Secondly, we also expected that immediately after the cognitively demanding task the subjective feeling of mental fatigue would increase and the motor performance decrease. These alterations would be associated with an increase in both theta and alpha power during the rest period immediately following the cognitively demanding task. Finally, we assumed that, during the recovery period following the completion of the cognitively demanding task, a progressive decrease in the subjective feeling of mental fatigue would be associated with a return towards initial levels of brain oscillations recorded during rest period and motor performance.

2. MATERIALS AND METHODS

2.1. PARTICIPANTS

The study was conducted with 15 healthy active adults, eight males and seven females (mean ± SD; age: 21.9 ± 1.8 years). It included two sessions: a familiarization session and an experimental session. All participants reported normal or corrected-to-normal vision and none of them had a history of neurological disorders. They completed the Edinburgh questionnaire, which confirmed that all participants were right-handed. All participants were given instructions to sleep for at least 7 hr, not to consume alcohol, and to refrain from vigorous physical activity the day before each visit. Participants were also instructed not to consume caffeine and nicotine at least 3 hr before testing and were asked to declare if they had taken any medication or had any acute illness, injury, or infection. All the participants provided their written informed consent. The experiment was conducted in accordance with the Declaration of Helsinki (1964).

2.2. THE COGNITIVELY FATIGUING TASK: THE TIME LOAD DUAL BACK (TLDB) TASK

The Time Load Dual Back (TLDB) task is a dual task combining a classic N-back working- memory updating task (Kirchner, 1958) and an interfering second task (odd/even decision task). Stimuli were letters and digits displayed alternately on the screen (i.e., letter/digit/letter/…). When letters were presented, participants were instructed to press the

space bar with their left hand every time the displayed letter was the same as the previous one (1-back task). When digits were displayed, participants had to press a key on the numeric keypad, using their right index and middle fingers: "1" if it was an odd number, "2" if it was even. A total of eight letters (A, C, T, L, N, E, U, and P) and eight numbers (1, 2, 3, 4, 6, 7, 8, and 9) were used. Stimulus presentation was managed by the Experiment Builder software (SR Research). Stimuli were presented in Arial font size 120, in the center of a 16-inch computer screen (refresh rate 60 Hz). They were presented in blocks of 60 trials with a break of 30 s between each block.

2.3. THE PHYSICAL TASK: THE ARM-POINTING TASK

Participants had to point at a target as accurately and as fast as possible with a pencil held in their right hand. They were sitting down, and in the start position their arm was aligned with their right shoulder and all targets to be pointed at were located on a 45° diagonal to the left to limit joint stress. The targets were black squares displayed on a tactile screen in front of the participant (Fig. 1A). The targets had different indices of difficulty (Nitschke et al., 2006), which were calculated using the formula $ID = \log_2(\frac{2D}{\mathrm{W}})$, where D represents the center-to-center distance between the start point and the target, and W represents the width of the target. Using different distances (between 5 cm and 32 cm) and widths (between 0.5 cm and 2.5 cm), 40 targets were created with eight IDs ranging from 2.5 to 6 in steps of 0.5. Each ID included five different targets with different widths and distances from the start point.

The time measured for the pointing movement began when participants took the pen from the start point and stopped when the pen touched the tactile screen. If the participant landed on the target, the trial was considered as "correct"; if not, it was a miss. At each trial, the participant had to return to the start point. The pointing task lasted approximately 1.5 min.

The arm-pointing task was performed before the TLDB task, immediately after the TLDB task (Post), 10 min (Post 10) and 20 min (Post 20) after the TLDB task. For each arm-pointing task, the difficulty did not increase over time. The same trials were presented in pretest and in all the posttests, but with a different random order.

2.4. PSYCHOLOGICAL MEASUREMENT

The Saint Mary's Hospital Sleep Questionnaire was used to evaluate the participants' sleep quality the night before the experiment (at each session). It contains 14 items concerning sleep quality, such as depth, awakening in the middle of the night, satisfaction, refreshed feeling

upon awakening, difficulty in falling asleep, and early awakening. Participants reported that they slept on average 7 hr and 41 min (±12 min).

Motivation related to the entire protocol was measured at the beginning of the experiment, using the motivation questionnaire developed and validated by Matthews et al. (2001). It has two subscales, evaluating success motivation and intrinsic motivation. Each subscale has seven questions, with a choice of five answers: 0 = not at all, 1 = a little bit, 2 = somewhat, 3 = very much, 4 = extremely. Therefore, total scores for these motivation scales range between 0 and 28. A low score reveals low motivation, and a high score indicates high motivation. Participants' scores were 17.7 (±1.3) for success motivation and 23.3 (±0.9) for intrinsic motivation.

The participants also rated their level of mental fatigue on a Visual Analogue Scale (VAS) at four points of the experimental session: at the start of the session, after the TLDB task, and before Post 10 and Post 20 tests. The VAS was a line 100 mm long, with bipolar end anchors (0 mm = "Not mentally fatigued at all"; 100 mm = "Extremely mentally fatigued") on which participants placed a mark to estimate their level of mental fatigue.

2.5. PROCEDURE

The experiment included two sessions: a familiarization session and an experimental session (Fig. 1B). During the familiarization session, participants were shown the questionnaires used in the experiment, and were trained on both arm-pointing and TLDB tasks. The threshold of stimulation duration, corresponding to the highest level of TLDB task performance, was determined for each participant using the same procedure as previous studies (Borragan et al., 2016; Borragan et al., 2017). All participants started the familiarization session with a 1500 ms presentation of each event (i.e., letters and digits) without inter-stimulus intervals. At the end of each block, if the performance accuracy was equal to or greater than 85%, the duration of the presentation was reduced by 100 ms, and so on until the accuracy was lower than 85%. At this point, participants performed two more blocks with the same duration to pursue familiarization; the threshold for the experimental session was fixed at the last successful duration. The familiarization session also aimed to reduce learning effects, which could counteract the effect of mental fatigue on performance.

The experimental session took place 48 to 96 hr after the familiarization session, at the same time of day. Before installing the EEG recording system, participants were reminded how to perform the arm-pointing task and carried out another practice trial. While the EEG was

being set up, participants completed the Saint Mary's Hospital questionnaire and the motivation questionnaire. They were then installed on a comfortable chair in an acoustically and electrically isolated booth (Fig. 1A). First, EEG activity was recorded at rest for 2 min while the participants were sat in front of a black screen, and were asked to rest and not to think about anything. After that, they were asked to rate their level of mental fatigue on the VAS and to perform the first arm-pointing task. They then performed the TLDB task, which lasted 32 min[1] (excluding the rest periods between each block). Immediately after the TLDB task, the EEG activity was recorded at rest for 2 min, and participants rated their level of mental fatigue and performed the arm-pointing task again (Post). After 8 min of rest during which the experimenter talked with the participant, the same procedure was repeated (i.e., recording EEG activity at rest for 2 min, rating mental fatigue level and arm-pointing task; Post 10). Finally, after a second rest period of 8 min, the same procedure was repeated for the last time (Post 20; see Fig. 1B). During rest periods, the experimenter talked with the participant. Talking to the participant during the rest period was chosen as an ecological condition, mirroring what happens in daily life at work, for instance. The conversation was similar for each participant, and dealt with their job (or education), their hobbies (e.g., sport, nature), and their perspectives for the future (e.g., studies, jobs). These topics were always addressed in the same order.

[1] In a pilot experiment, 16 min of the TLDB task were used to induce mental fatigue as in Borragan et al. (2016). However, while 16 min of the TLDB task induced a subjective feeling of mental fatigue, it was not long enough to induce a decrement in arm-pointing task performance. The duration of the TLDB task was doubled to 32 min and, under these circumstances, both an increase in subjective mental fatigue and a decrement in arm-pointing task performance were observed.

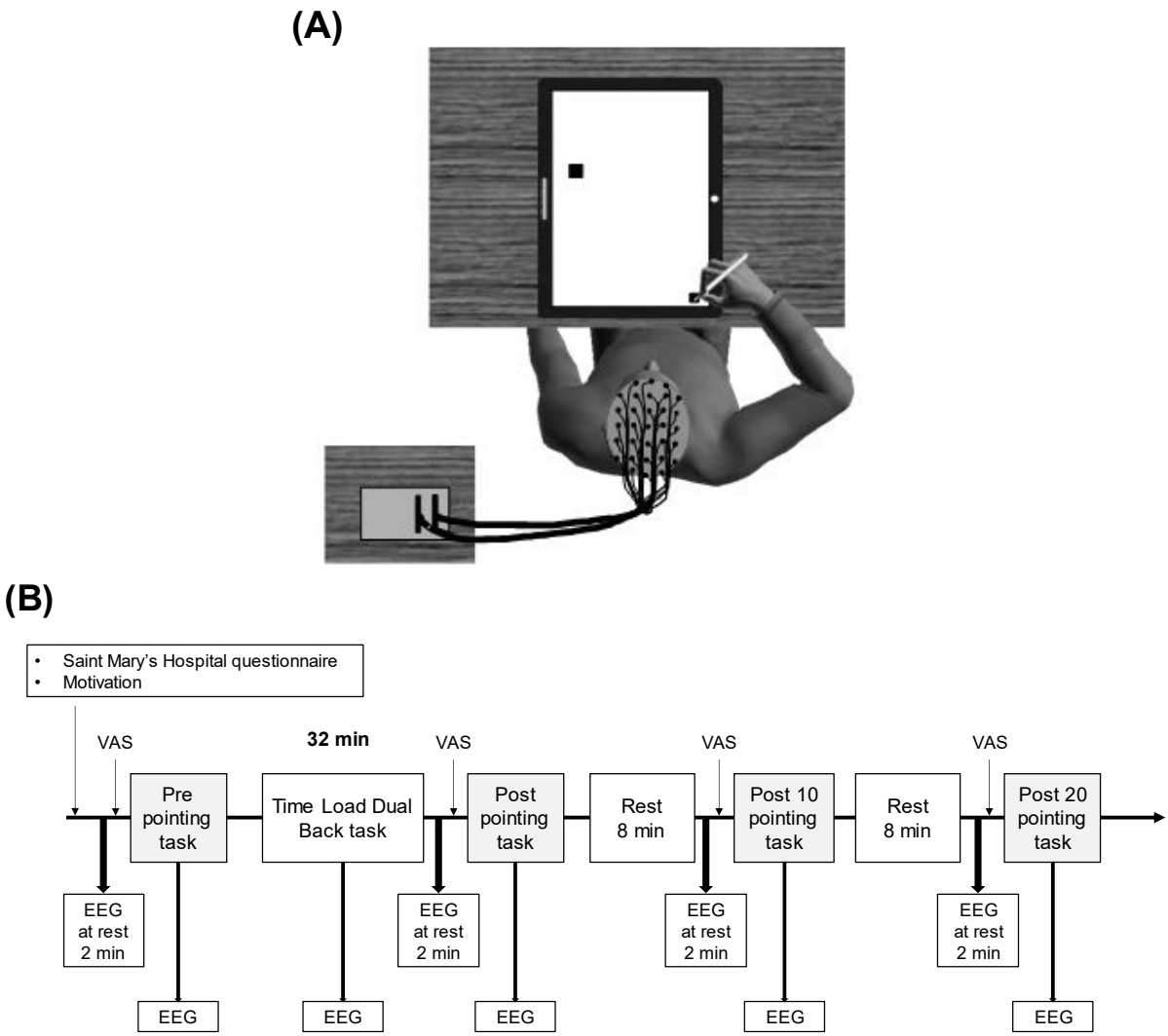

Figure 1. A schematic representation of the participants' position while performing the arm-pointing task (panel A), and an overview of the experimental protocol (panel B). VAS = fatigue visual analogue scale, EEG = electroencephalography.

2.6. EEG RECORDING AND PREPROCESSING

The electroencephalogram was recorded continuously through the Active Two BioSemi system from 64 electrodes in accordance with the 10-20 International system. Horizontal eye movements were monitored with electrodes placed on the outer left and right canthi, while eye blinks were monitored with an electrode placed under the left eye. Two additional electrodes were placed on the left and right mastoids (A1, A2). During recording, the BioSemi system's common-mode sense electrode served as the reference electrode. Electrophysiological signals

were digitized at 2048 Hz sampling rate and acquired with ActiView software. Offline data analyses were performed using MATLAB (MathWorks, Natick, MA, USA) and the EEGLAB toolbox (Delorme and Makeig, 2004). Continuous data were downsampled to 256 Hz, band-pass filtered at 0.01–100 Hz, and re-referenced to the average of A1 and A2. Noisy electrodes were identified with the probability and spectrum methods proposed in EEGLAB (threshold, Z = 5) and interpolated when necessary with a spherical method. To correct eye-movement artifacts, EEGLAB's Runica routine was used to perform independent component analyses, and components reflecting eye artifacts were removed by visual inspection. Continuous data were segmented into 500 ms epochs from 50 ms before to 450 ms after the onset of the stimuli and were baseline corrected using the pre-trial period from -25 ms to 0 ms.

2.7. DATA AND ANALYSIS

Pointing movement. Movement durations less than 100 ms and more than 1400 ms were excluded from the analysis. We estimated that movement duration below 100 ms and above 1400 ms were not coherent for the performed movements. Altogether, only 2 trials over 2400 were excluded from the data. Movement durations beyond two standard deviations (SDs) of the mean were also excluded. Analyses were performed on 88% of trials.

EEG data. For the TLDB task, only trials with correct responses (93% of trials) were considered for ERP analysis. Epochs were averaged separately for each condition and each participant. ERPs were obtained by computing the mean amplitude in the time window for each ERP component, and by grand-averaging data across participants. Because no studies have previously analyzed ERPs during the TLDB task and because ERPs are stimulus and task dependent, we determined our time windows for the ERP analyses based on visual inspection, according to the peak of the ERP and its shape, to be in complete adequation with the observed ERPs. Different time windows were used for ERP components for letters on fronto-central region (N100: 90-150 ms, N200: 230-315 ms, P300: 325-445 ms) and on parietal region (N200: 130-200 ms, P300: 325-445 ms). Using the same method, ERP components were also identified for digits on fronto-central region (P50: 25-75 ms) and parietal region (N200: 135-210 ms).

For EEG spectral analysis, during the TLDB task, the 2-min rest and the arm-pointing task, EEG power of individual epochs was computed by Fast Fourier Transform (FFT), using the *spectopo* function of the EEGLAB software. It was divided into five frequency bands: delta, 1–4 Hz; theta, 4–7 Hz; alpha, 8–12 Hz; beta 13–30 Hz; and gamma, 30–40 Hz to be analyzed. Spectral analyses during the TLDB task and the arm-pointing task were performed irrespective

of the occurrence of stimuli. Nine regions of interest (ROIs) were constituted to perform analysis on both ERPs and spectral data: Frontal Left (FL; mean of FP1, AF3, AF7, F3, F5, F7, FC3, FC5, FT7), Frontal Median (FM; mean of FPz, AFz, F1, Fz, F2, FC1, FCz, FC2), Frontal Right (FR: mean of FP2, AF4, AF8, F4, F6, F8, FC4, FC6, FT8), Central Left (CL: mean of C3, C5, T7, CP3, CP5, TP7), Central Median (CM: mean of C1, Cz, C2, CP1, CPz, CP2), Central Right (CR: mean of C4, C6, T8, CP4, CP6, TP8), Posterior Left (PL: mean of P9, P7, P5, P3, PO7, PO3, O1), Posterior Median (PM: mean of P1, Pz, P2, POz, Oz), and Posterior Right (PR: mean of P4, P6, P8, PO4, PO8, O2). Statistical evaluation was performed with repeated-measures ANOVAs on each ROI.

2.8. STATISTICS

All data are presented as means ± standard error of the mean. Degrees of freedom were corrected using the Greenhouse-Geisser procedure when sphericity was violated (corrected degree of freedom and *p*-values are reported). Only significant effects are reported, except when non-significance is relevant for the hypotheses being tested.

To evaluate mental fatigue effects on the VAS, one-way repeated measures ANOVA with time (Pre, Post, Post 10, and Post 20) as within-subject factor was conducted. The effects of mental fatigue on movement duration and errors on arm-pointing movements were evaluated using two-way repeated measures 4 × 8 ANOVAs with time (pre, post, post 10, and post 20) and ID (2.5, 3, 3.5, 4, 4.5, 5, 5.5 and 6) as within-subject factors.

For the TLDB task, analyses were performed separately for letters and digits. Two-way repeated measures 2 × 4 ANOVAs including the within-subject factors of Stimulus type (for letters: same/different; for digits: even/odd) and time-on-task (part 1, 0-8 min; part 2, 8-16 min; part 3, 16-24 min; and part 4, 24-32 min) were performed for RTs, accuracy, and ERPs. Only ERPs interesting for mental fatigue effects are reported in the Results section.

Brain oscillations were analyzed using one-way repeated measures ANOVAs with time-on-task (part 1, 0-8 min; part 2, 8-16 min; part 3, 16-24 min; and part 4, 24-32 min) as within-subject factor during the TLDB task and, with time (Pre, Post, Post 10, and Post 20) for the recordings at rest. Only results about theta and alpha power are reported in the Results section, the other brain oscillations are reported in supplementary data.

All analyses were performed using the Statistical Package for the Social Sciences, version 24 for Windows (SPSS Inc., Chicago, IL, USA). Significant main effects of time and significant interactions were followed up by contrast tests, and planned comparisons using t-tests with Bonferroni correction for multiple comparisons as appropriate. Only significant

results are reported, with adjusted p-values. For each ANOVA, partial eta squared is reported. Thresholds for small, moderate, and large effects were set at 0.01, 0.07 and 0.14, respectively (Cohen, 1988). Cohen's d was calculated for each paired t-test using JASP (Version 0.9.1.0) [Windows software]. Thresholds for small, moderate, and large effects were set at 0.2, 0.5, and 0.8, respectively (Cohen, 1988).

3. RESULTS

3.1. MENTAL FATIGUE ASSESSMENT

3.1.1. SUBJECTIVE MEASURE OF MENTAL FATIGUE

Visual Analogue Scale. As displayed in Figure 2, analysis revealed an increase in the feeling of fatigue over time [$F_{(3,42)}$ = 26.784, p < .001, η_p^2 = .657], qualified by a cubic trend [$F_{(1,14)}$ = 40.109, p < .001, η_p^2 = .741], with a significant increase in feeling-of-fatigue score between Pre and Post [$t_{(14)}$ = 6.629, p < .001, d = -1.711], followed by a reduction of the fatigue score between Post and Post 10 [$t_{(14)}$ = 4.601, p = .002, d = 1.188], but not between Post 10 and Post 20 [$t_{(14)}$ = 3.876, p > .05, d = 0.163]. The subjective feeling of fatigue was still significantly higher at Post 10 [$t_{(14)}$ = 4.713, p = .002, d = 1.217] and post 20 [$t_{(14)}$ = 5.863, p < .001, d = 1.514] compared to Pre.

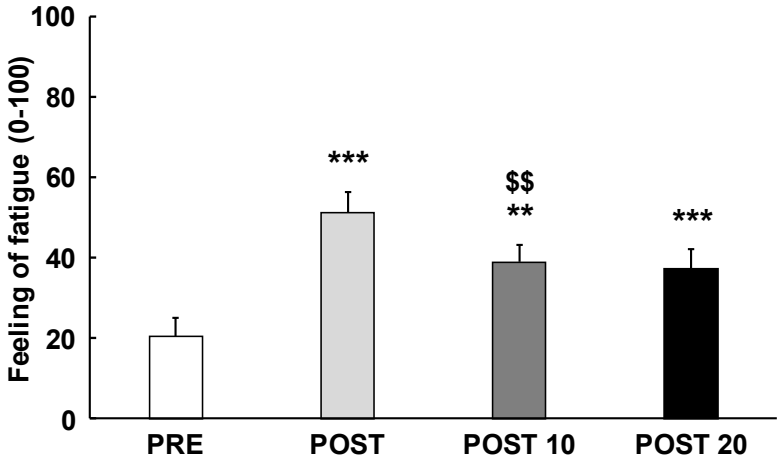

Figure 2. Time course of subjective feeling of mental fatigue. ** and ***: Significantly different from Pre (p < .01 and p < .001, respectively). $$: Significantly different from the previous measurement (p < .01). Data are presented as mean ± SE.

3.1.1. PERFORMANCE DURING THE TLDB TASK

Reaction time. Mean reaction time was 535.2 ms (±10.0) for digits and 498.8 ms (±11.0) for letters. No significant effect of time or interaction with the factor time was observed on reaction time during the TLDB task for letters or digits (all *ps* > .15, η_p^2 < .13).

Accuracy. Mean accuracy was 90.9% (±0.5) and 92.8% (±0.8) for digits and letters. No significant effect of time or interaction with the factor time was observed on reaction time during the TLDB task for letters or digits (*ps* > .35, η_p^2 < .07), suggesting that performance was maintained over time.

3.1.3. EEG DATA

3.1.3.1. Event-related potentials

N100. Analysis showed a significant time-on-task effect only for letters in CL region [$F_{(3,42)}$ = 4.019, p = .033, η_p^2 = .223], qualified by a linear trend [$F_{(1,14)}$ = 5.293, p = .030, η_p^2 = .293], reflecting a decrease in the N100 amplitude over time (Fig. 3).

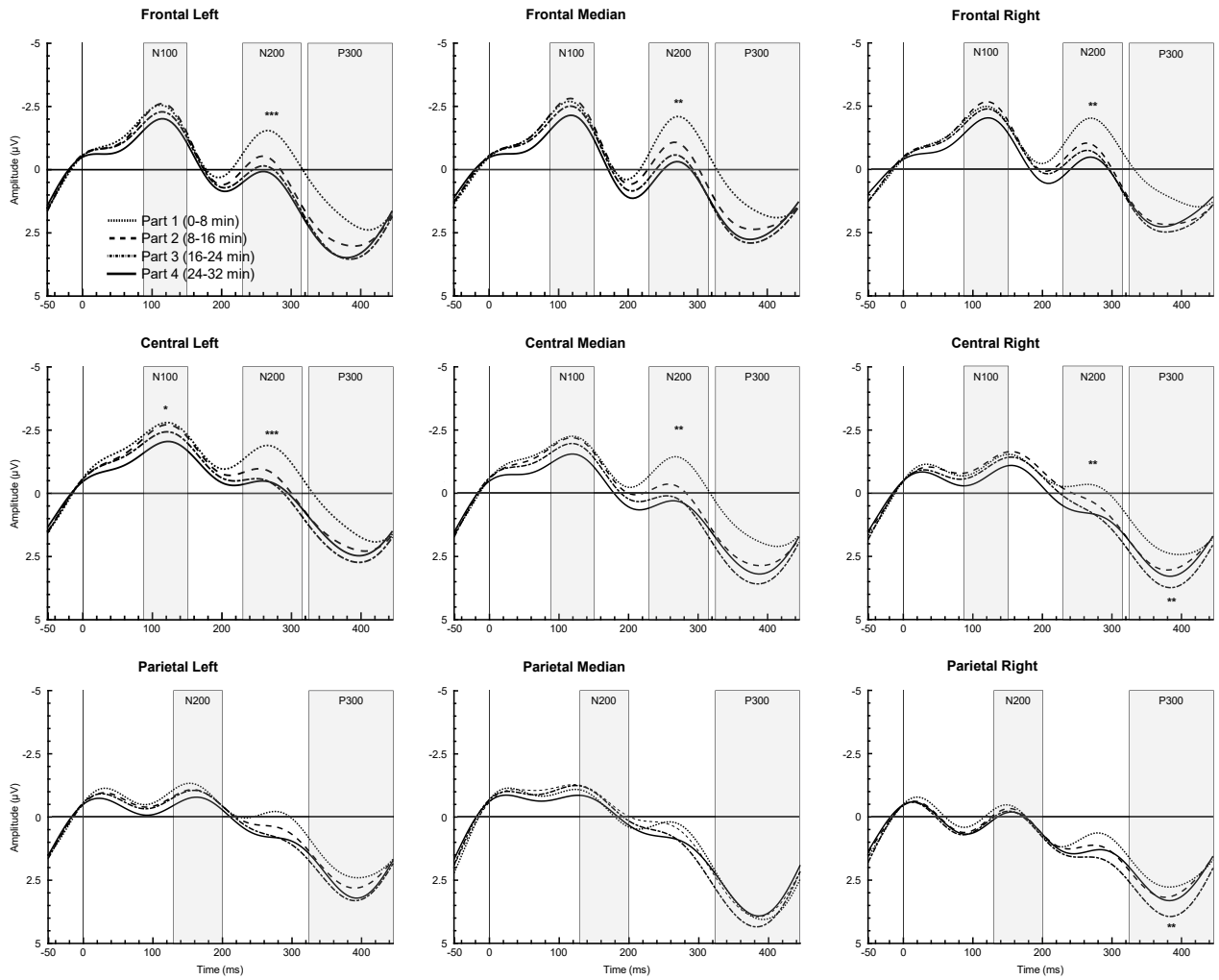

Figure 3. Time-on-task effect for letter stimuli during the 32-min time load dual back task in all regions of interest. *, ** and ***: Significantly time-on-task effect ($p < .05$, $p < .01$ and $p < .001$, respectively).

N200. For letters, ANOVA revealed a significant time-on-task effect for FL [$F_{(3,42)} = 6.755$, $p < .001$, $\eta_p^2 = .326$], FM [$F_{(3,42)} = 6.388$, $p = .001$, $\eta_p^2 = .313$], FR [$F_{(3,42)} = 5.755$, $p = .002$, $\eta_p^2 = .291$], CL [$F_{(3,42)} = 7.064$, $p < .001$, $\eta_p^2 = .335$], CM [$F_{(1.906,26.690)} = 6.623$, $p = .005$, $\eta_p^2 = .321$] and CR regions [$F_{(3,42)} = 6.274$, $p = .001$, $\eta_p^2 = .309$], indicating a linear decrease in N200 amplitude over time for all these regions (ps < .012, $\eta_p^2 > .378$). For digits, analysis showed a significant main effect of time-on-task for LF [$F_{(3,42)} = 4.278$, $p = .021$, $\eta_p^2 = .234$] and CL regions [$F_{(3,42)} = 4.090$, $p = .020$, $\eta_p^2 = .226$], qualified by a linear trend for both FL [$F_{(1,14)} = 7.576$, $p = .016$, $\eta_p^2 = .351$] and CL regions [$F_{(1,14)} = 7.882$, $p = .019$, $\eta_p^2 = .360$] indicating, as for letters, a decrease in the N200 amplitude over time (see Fig. 3 and 4).

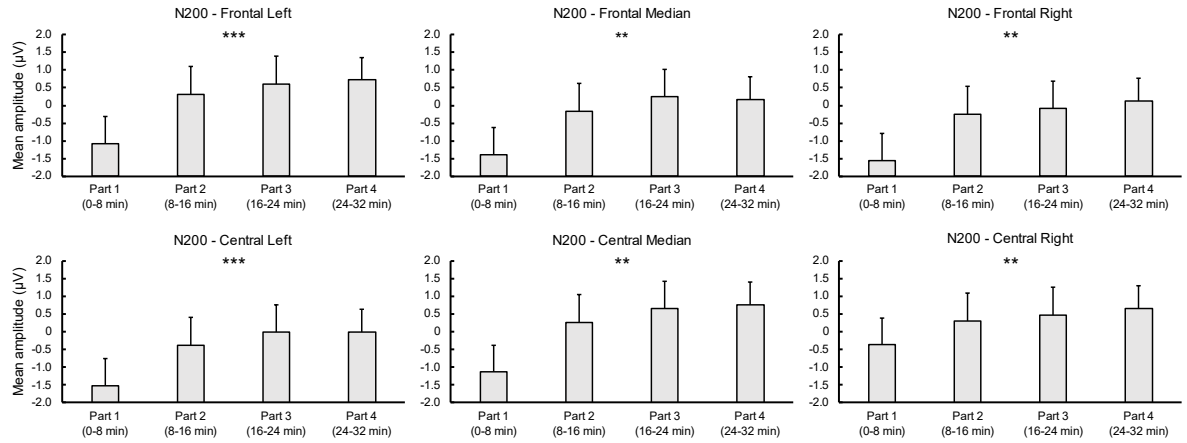

Figure 4. Time-on-task effect on N200 for letter stimuli during the 32-min time load dual back task in the frontal and central regions. ** and ***: Significantly time-on-task effect (p < .01 and p < .001, respectively).

P300. A significant time-on-task effect was reported only for letters on the P300 amplitude for CR [$F_{(3,42)}$ = 8.465, p = .002, η_p^2 = .377], qualified by a linear trend [$F_{(1,14)}$ = 11.415, p = .005, η_p^2 = .449], indicating an increase in the P300 amplitude over time. On PR region, analysis indicated a significant time-on-task effect on the P300 amplitude [$F_{(3,42)}$ = 5.854, p = .004, η_p^2 = .295], qualified by a quadratic trend [$F_{(1,14)}$ = 9.208, p = .009, η_p^2 = .397], reflecting an increase in P300 amplitude over time between the first and the second part [$t_{(14)}$ = -2.460, p = .028, d = -0.635], and between the second and the third part of the task [$t_{(14)}$ = -5.863 , p = .022, d = -0.667], but a decrease in the P300 amplitude between the third and the fourth part [$t_{(14)}$ = 2.164, p = .048, d = -0.559] (Fig. 3).

3.1.3.2. Brain oscillations

All the results of brain oscillations are presented in the Supplementary data (Table S1). Only significant differences related to brain oscillations useful to test our hypothesis, i.e. theta and alpha powers, are presented below.

Theta: Analysis showed a significant time-on-task effect on FL [$F_{(3, 42)}$ = 6.779, p < .001, η_p^2 = .326], FM [$F_{(3, 42)}$ = 12.828, p < .001, η_p^2 = .478], FR [$F_{(3, 42)}$ = 11.840, p < .001, η_p^2 = .458], CL [$F_{(3, 42)}$ = 13.411, p = .028, η_p^2 = .489], CM [$F_{(3,42)}$ = 13.570, p < .001, η_p^2 = .492], CR [$F_{(3,42)}$ =

9.616, $p < .001$, $\eta_p^2 = .407$], PM [$F_{(3,42)} = 7.754$, $p < .001$, $\eta_p^2 = .356$], and PR regions [$F_{(1.888, 26.438)} = 5.908$, $p = .008$, $\eta_p^2 = .297$] , qualified for all these regions by a linear trend (all *ps* < .011, $\eta_p^2 > .230$), indicating a decrease in theta power over time (see Fig. 5).

Alpha: ANOVA revealed a significant time-on-task effect on FL [$F_{(1.699, 23.781)} = 6.827$, $p = .006$, $\eta_p^2 = .328$], FM [$F_{(1.447, 20.253)} = 7.351$, $p = .007$, $\eta_p^2 = .344$], FR [$F_{(1.600, 22.397)} = 5.811$, $p = .013$, $\eta_p^2 = .293$], CL [$F_{(1.447, 20.256)} = 4.849$, $p = .028$, $\eta_p^2 = .257$], CM [$F_{(1.601, 22.426)} = 6.528$, $p = .008$, $\eta_p^2 = .318$],CR [$F_{(1.617, 22.634)} = 5.426$, $p = .016$, $\eta_p^2 = .279$], PL [$F_{(1.579, 22.108)} = 5.329$, $p = .018$, $\eta_p^2 = .276$], and PM regions [$F_{(1.621, 22.692)} = 7.779$, $p = .004$, $\eta_p^2 = .357$]. This main effect of time-on-task was qualified by a quadratic trend for all these regions (all *ps* < .020, $\eta_p^2 > .330$), highlighting a slight decrease in alpha power between the first and the second part of the TLDB task, followed by an increase in alpha power over time (see Fig. 5).

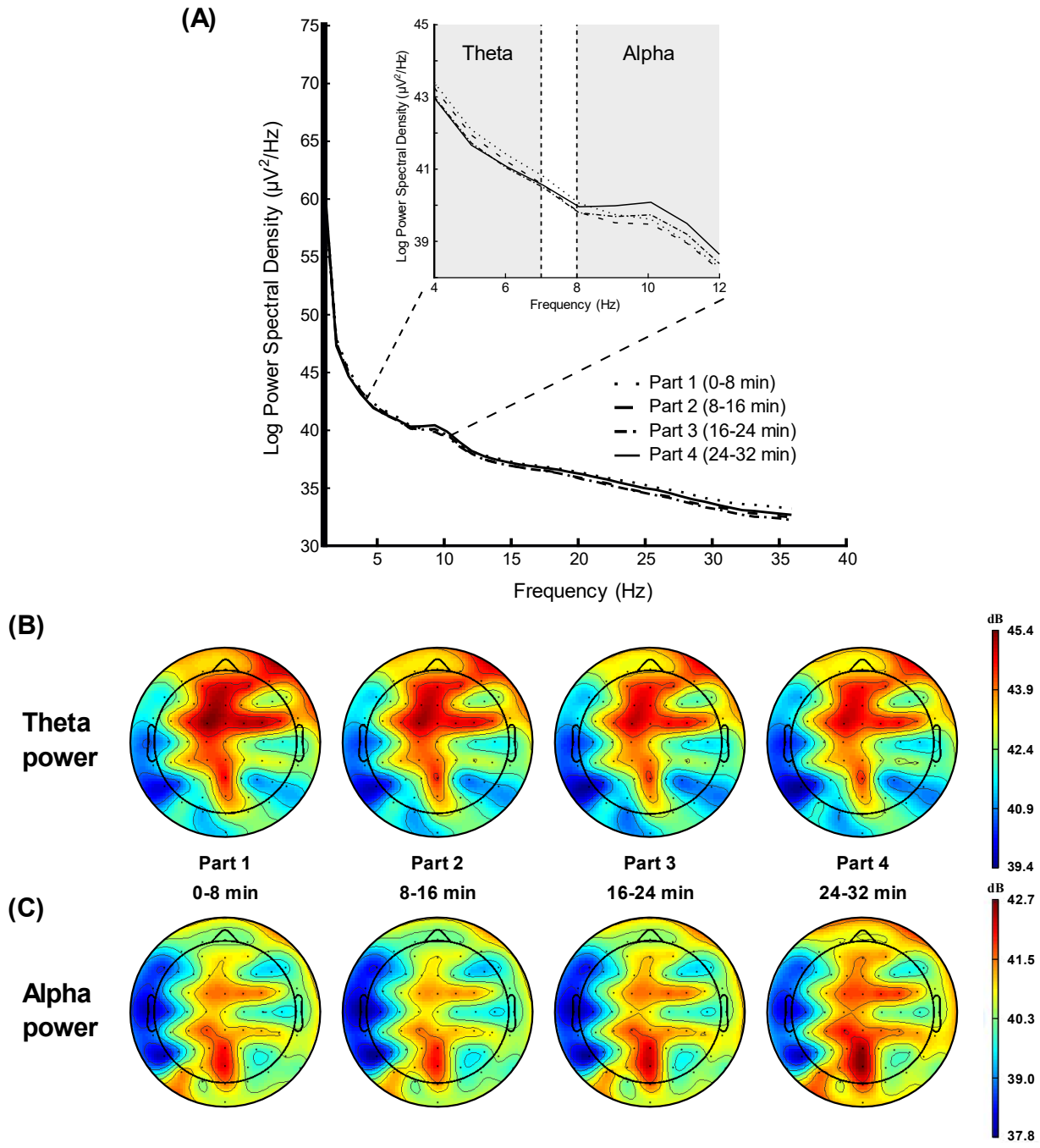

Figure 5. Modulation of brain power spectrum for part 1 (0-8 min), part 2 (8-16 min), part 3 (16-24 min), and part 4 (24-32 min) of the time load dual back task (panel A), with specifically time course of the theta power (panel B) and alpha power (panel C).

3.2. EFFECT OF MENTAL FATIGUE ON THE ARM-POINTING TASK

Movement duration. There was a significant main effect of ID [$F_{(1.245, 17.428)}$ = 136.045, p < .001, η_p^2 = .907] qualified by a linear trend [$F_{(1, 14)}$ = 10.607, p = .006, η_p^2 = .431], indicating an increase in movement duration with increasing ID, accompanied by a main effect of time [$F_{(3, 42)}$ = 5.259, p = .005, η_p^2 = .273]. The decomposition of this time effect revealed a linear increase in the duration of arm-pointing movements over time [$F_{(1, 14)}$ = 10.607, p = .006, η_p^2 = .431] as shown by comparison with Pre (*vs* Post: $t_{(14)}$ = -0.717, p = 1.000, d = -0.185; *vs* Post 10: $t_{(14)}$ = -2.527, p = .121, d = -0.653), up to significance at Post 20 measurement [$t_{(14)}$ = -2.977, p < .050, d = -0.769] (see Fig. 6).

Pointing errors. There was a significant main effect of ID on errors during the pointing task [$F_{(2.305, 32.275)}$ = 26.782, p < .001, η_p^2 = .657]. The decomposition of this main effect revealed a significant linear effect, with more errors as the ID of the target increased [$F_{(1, 14)}$ = 48.455, p < .001, η_p^2 = .776]. However, analyses showed no significant effect of time or ID × time interaction.

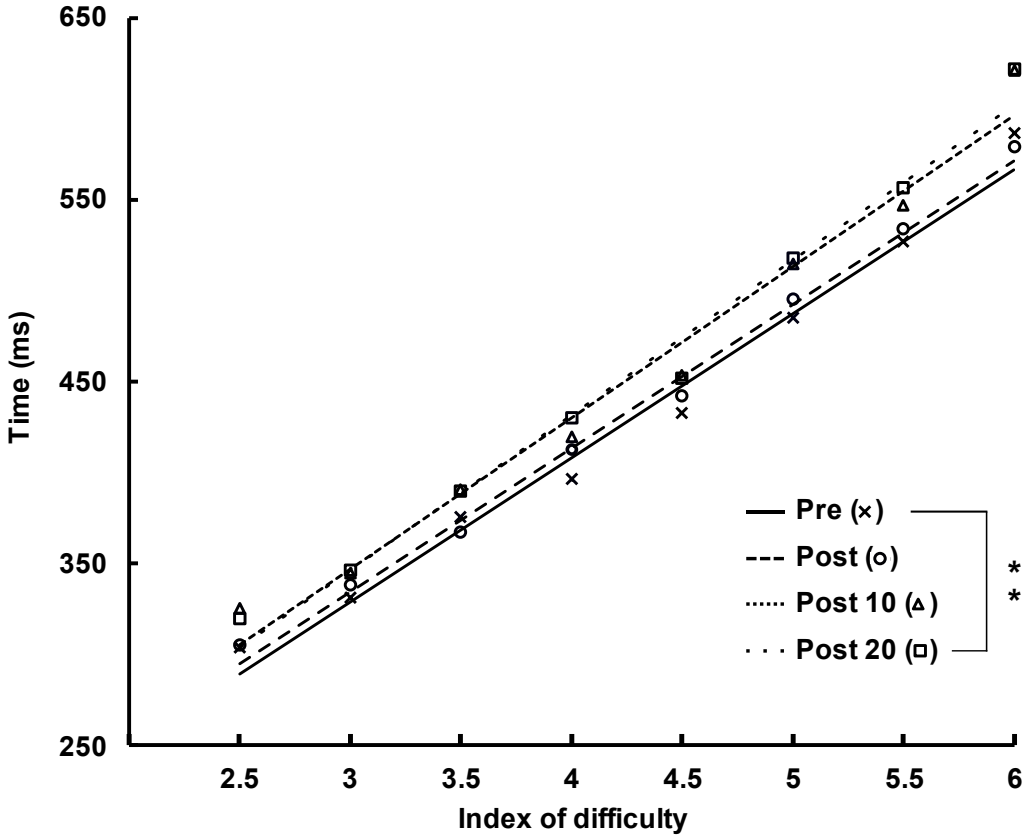

Figure 6. Time course of the duration of arm-pointing movement at Pre, Post, Post 10 and Post 20 with a significant effect of index of difficulty (ID) (p < .001). **: Significantly different from Pre (p < .01).

3.3. EFFECTS OF MENTAL FATIGUE ON BRAIN OSCILLATIONS AT REST

All the results of brain oscillations at rest are presented in the Supplementary data (Table S2). Significant differences related to alpha and theta powers are presented below.

Theta: Analysis showed a significant time effect on FL region [$F_{(3,42)} = 4.359$, $p = .009$, $\eta_p^2 = .237$], qualified by a linear trend [$F_{(1,14)} = 7.220$, $p = .018$, $\eta_p^2 = .340$], indicating an increase in theta power over time (see Fig. 7).

Alpha: ANOVA revealed a significant time effect on FL [$F_{(3,42)} = 4.641$, $p = .005$, $\eta_p^2 = .261$], FM [$F_{(3,42)} = 3.174$, $p = .034$, $\eta_p^2 = .185$], FR [$F_{(3,42)} = 4.177$, $p = .011$, $\eta_p^2 = .230$], CL [$F_{(3,42)} = 4.017$, $p = .013$, $\eta_p^2 = .223$], CR [$F_{(3,42)} = 3.107$, $p = .036$, $\eta_p^2 = .182$], PM [$F_{(3,42)} = 3.107$, $p = .037$, $\eta_p^2 = .312$], and PR regions [$F_{(3,42)} = 6.711$, $p = .021$, $\eta_p^2 = .324$]. This main effect of time-on-task was qualified by a linear trend for all these regions ($ps < .011$, $\eta_p^2 > .230$], indicating an increase in alpha power over time (see Fig. 7).

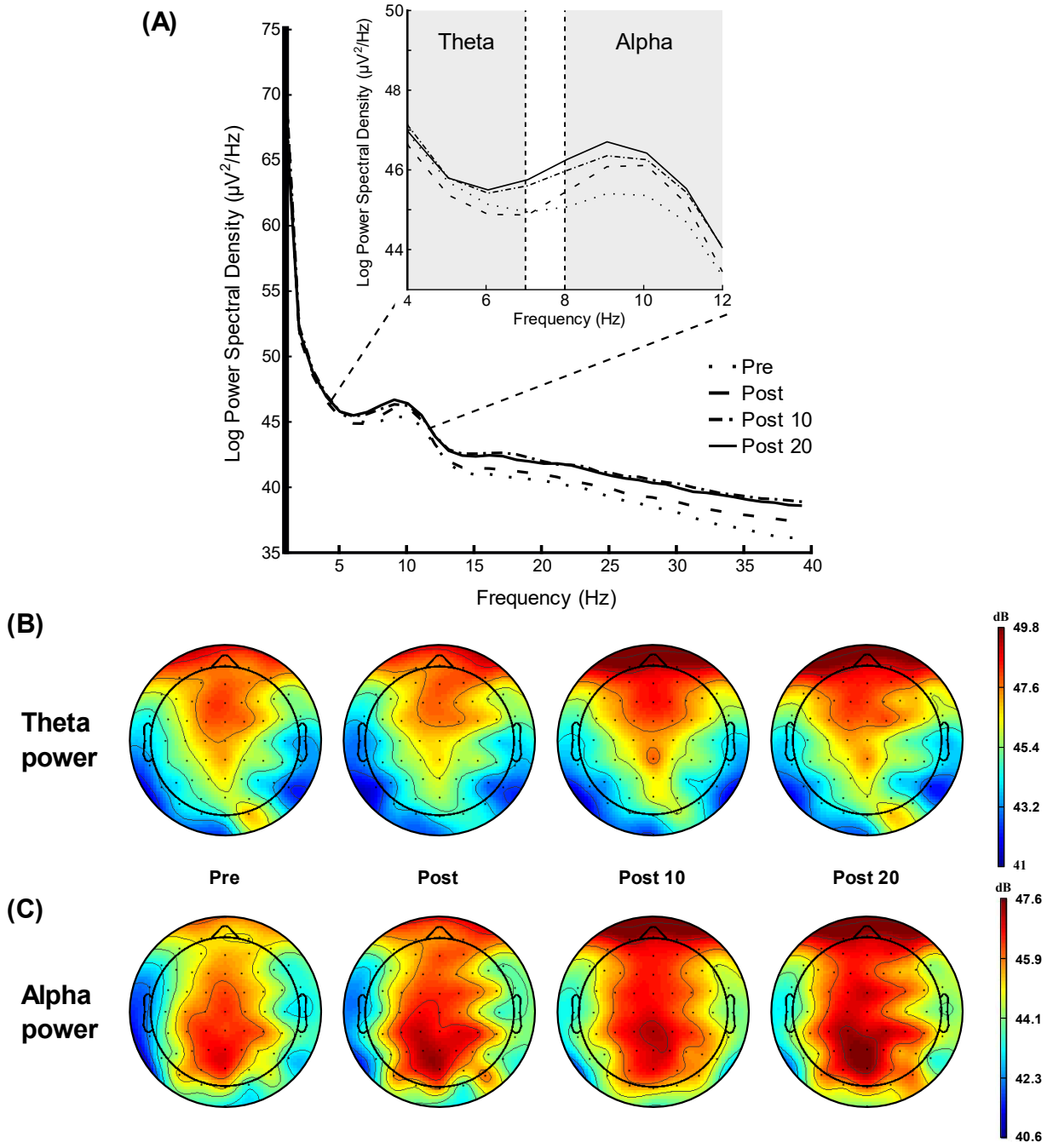

Figure 7. Modulation of brain power spectrum during the 2-min rest periods at Pre, Post, Post 10, and Post 20 (panel A), with specifically time course of the theta power (panel B) and alpha power (panel C).

4. DISCUSSION

The objective of the present study was to investigate the time course of mental fatigue effects following a cognitively demanding task (i.e., TLDB task) on subjective and electrophysiological markers as well as on arm-pointing task performance. The results showed that the subjective feeling of fatigue increased following the cognitively demanding task and then progressively decreased during the 20 min of recovery, but without returning to initial values. Brain oscillations during the rest periods showed a linear increase in both theta and alpha powers, suggesting that mental fatigue persisted after completion of the cognitively demanding task, and that no recovery mechanism really occurred. Contrary to expectations, motor control performance was worse during the recovery period than immediately after the cognitively demanding task, movements becoming even slower 20 min after completion of the task.

4.1. SUBJECTIVE FEELING OF MENTAL FATIGUE

In agreement with previous studies (Borragan et al., 2016; 2017), 32 min on the TLDB task induced an increase in the subjective feeling of mental fatigue, indicating that this cognitively demanding task successfully induced mental fatigue. The feeling of mental fatigue decreased 10 min after completion of the task and remained above the initial value 20 min later, indicating that recovery was not complete. Recently, similar effects were observed by Smith et al. (2019), who found that the subjective feeling of mental fatigue following 45 min performing mentally fatiguing tasks remained higher than pre-treatment values for 10 min after a PVT, 50 min after a Stroop task and 60 min after an AX-CPT task. These observations indicate that the recovery of the subjective level of mental fatigue may require more time than the duration of the cognitively demanding task itself.

4.2. PERFORMANCE DURING THE COGNITIVELY DEMANDING TASK

During the 32-min TLDB task, maintenance of performance (reaction time and accuracy) was observed, in contrast to previous studies by Borragan et al. (2016; 2017), who found a decrease in accuracy over time. It is worth noting that not all studies investigating mental fatigue found impaired performance during the cognitively demanding tasks used to induce mental fatigue; while some studies reported a decrease in performance (e.g., Marcora et al., 2009; Head et al., 2017), others found that it was maintained (e.g., Pageaux et al., 2015). Wang et al. (2016) postulated that the maintenance of performance despite mental fatigue could

be explained by a compensatory strategy reflected by an increase in anterior frontal brain activity during a prolonged cognitive task. Herlambang et al. (2019) found that performance of a prolonged cognitive task was maintained when participants had a high level of motivation, and decreased when their motivation was low. These observations suggest that motivation is an important factor when considering mental fatigue and its effects. In the present study, the participants showed high motivation to perform the experiment (success motivation = 17.7±1.3 and intrinsic motivation = 23.3±0.9 overall on a 0-28 scale), which could explain the maintenance of performance during the cognitively demanding task.

4.3. ELECTROPHYSIOLOGICAL MARKERS DURING THE COGNITIVELY DEMANDING TASK

In addition to subjective and behavioral measures, changes in ERP amplitude during the cognitively demanding task could provide an objective marker of mental fatigue, and explain the maintenance of behavioral performance over time. In the present study, the decrease in N100, considered as an indicator of mental fatigue (Boksem et al., 2005; Faber et al., 2012), might reflect an increase in mental workload. However, the maintenance of performance (i.e., reaction time and accuracy) suggests that a compensatory mechanism was involved during the cognitively demanding task. Previous studies reported a decrease in P300 amplitude (Koelega et al., 1992; Murata et al., 2005), interpreted as a decrease in attention over time during a prolonged cognitive task (Zhao et al., 2012), associated to a decline in behavioral performance with mental fatigue (Cheng et al., 2007; Guo et al., 2015). In the present study, the linear increase in P300 amplitude reported in central regions for letter stimulus could be attributed to an increase in cerebral resources needed to maintain task performance despite progressive mental fatigue.

In addition to the changes observed in the ERP components, brain oscillations also seemed to indicate a mental fatigue state. The increase in alpha power with mental fatigue induction has been widely reported in the literature and has been interpreted as reflecting a decrease in arousal and alertness (Paus et al., 1997; Lal and Craig, 2002; Boksem et al., 2005; Trejo et al., 2005; Zhao et al., 2012). Another interpretation of the increase in alpha power during the TLDB task could be that, in presence of mental fatigue, the participants had to allocate more cognitive resources to maintain their performance. However, an increase in alpha power has been also observed with performance impairment (Boksem et al., 2005; Zhao et al., 2012). The increase in alpha power was also observed when comparing rest periods (i.e., before

and after the cognitively demanding task) in the present study but also in previous studies (Li et al., 2020). These findings suggest that the increase in alpha power observed in mental fatigue studies, and more especially in time-on-task design, is likely not related to the allocation of more cognitive resources to maintain task performance. This increase in alpha power with mental fatigue has often been associated with an increase in theta power mainly over the prefrontal cortex (Lal and Craig, 2002; Trejo et al., 2005). Furthermore a recent meta-analysis suggests that an increase in theta power is a robust biomarker of mental fatigue, whereas an increase in alpha power is a second-line biomarker due to considerable individual variability (Tran et al., 2020). In the present study, a decrease in theta power was reported over time in frontal regions during the cognitively demanding task. Although theta power decrease has previously been attributed to boredom (Katahira et al., 2018), the relatively short duration of the cognitively demanding task used here (i.e., 32 min) limited the boredom effect.

4.4. BRAIN OSCILLATIONS AT REST

In contrast to the brain oscillations analyzed during the cognitively demanding task, those recorded at rest showed an increase in both theta and alpha powers, confirming previous results of the effects of mental fatigue on brain oscillations (Tran et al., 2020). This finding supports the importance of recording brain oscillations not only during the cognitively demanding task but also during the subsequent recovery period, in order to avoid confusion between changes due to the task per se, and those actually related to mental fatigue.

While the subjective feeling of mental fatigue decreased during the recovery period, the increase in both theta and alpha powers recorded at rest suggests that subjective (i.e., feeling of mental fatigue) and objective (i.e., brain oscillations) markers could provide contradictory data for interpreting the state of mental fatigue following a cognitively demanding task. Although evaluation of subjective mental fatigue using a VAS is considered to be the most practical way of assessing mental fatigue induction (Smith et al., 2019), it appears that objective electrophysiological markers of mental fatigue, such as changes in brain oscillations, could lead to a different conclusion than subjective evaluation. The present results suggest that when studying mental fatigue, it could be relevant to use different subjective and objective measures to have a more comprehensive view of the effects of mental fatigue.

4.5. ABSENCE OF MOTOR PERFORMANCE RECOVERY

In accordance with the literature, we observed an increase in the duration of movement

as the index of difficulty increased during an arm-pointing task (Rozand et al., 2015; Gueugneau et al., 2017) and maintenance of the speed/accuracy trade-off despite the presence of mental fatigue (Rozand et al., 2015; 2016).

In the present study, movement duration remained constant immediately after the demanding cognitive task, which differs from the results of Rozand et al. (2015). Those authors found that after 90 min of a modified Stroop task, the duration of arm-pointing movement increased by an average of 9%, irrespective of the index of difficulty of the target. The impairment of motor control under mental fatigue was confirmed in a second study by Rozand et al. (2016), who observed a 6% increase in movement duration after a cognitively demanding task inducing mental fatigue. However, the authors indicated that the negative effects of mental fatigue on movement duration seemed to be very short-lived. Indeed, from the second arm-pointing movement, movements were as fast as pretest measurements. In our study, the effects of mental fatigue on motor control were evaluated using the average time of 40 arm-pointing movements. Thus, if a mental fatigue effect occurred only on the first movement it was not enough to be observed on the average of 40 arm-pointing movements. It is worth noting that our experimental design does not allow us to verify this hypothesis, because movement times depend on the ID, and the ID associated with the first movement changed at each pointing task due to the use of different random orders.

When the arm-pointing task was repeated 10 min and 20 min after the cognitively demanding task, movement duration was more and more affected, becoming significantly slower 20 min after the task compared to initial performance. A possible interpretation could be that the deterioration of the pointing performance over time was related to muscular fatigue. However, in our pilot experiment the participants repeated five times an arm-pointing task, consisting in 40 movements, after 16 min of TLDB task without a deterioration of the performance. This observation suggested that the decrease in performance in this present study was not related to the repetition of arm-pointing movements or to a possible muscular fatigue, but rather to the effects of mental fatigue.

Neuroanatomically, one possible explanation could be the involvement of the ACC, one of the main brain structures involved in the mental fatigue process (Lorist et al., 2005; Boksem and Tops, 2008; Marcora et al., 2009). Although Tanaka et al. (2014) found reduced activation of the ACC with mental fatigue during a subsequent physical activity,Johnston et al. (2007) observed that switching tasks could lead to an increase in ACC activity. This increase could

lead to more resources being engaged to perform the new task. In the present study, the cognitively demanding task was different from the arm-pointing task, and as a consequence the task switching might have increased the activity of the ACC and, in the short term, could have counteracted the effect of mental fatigue. Immediately after the cognitively demanding task, this could result in more resources engaged in arm-pointing movements and could have boosted speed of movements, even in the presence of mental fatigue. During the recovery period, there was no longer task switching due to the repetition of the arm-pointing task. This might lead to a reduced ACC activity, which no longer counteracted the effect of mental fatigue. The persistence of mental fatigue could explain the impaired motor performance 20 min after completion of the cognitively demanding task.

4.6. CONCLUSION

The present study found that a 32-min cognitively demanding task induced mental fatigue. As predicted, the subjective feeling of mental fatigue decreased gradually during the 20 min recovery period but remained higher than before the cognitively demanding task. The increase in both theta and alpha power of brain oscillations during the recovery period suggests that participants remained mentally fatigued despite their lower subjective feeling of mental fatigue. The persistence of fatigue during the 20 min period following the cognitively demanding task is in accordance with behavioral results of the arm-pointing task indicating that motor control performance remained impaired. These findings indicate that even if subjective indicators of mental fatigue, such as visual analogue scales, are a practical method for assessing mental fatigue, objective indicators such as behavioral and electrophysiological markers are required to have a better characterization of the state of mental fatigue following cognitively demanding tasks.

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SUPPLEMENTARY DATA

Supplementary Table 1. Changes on brain oscillations during the time load dual back (TLDB) task on delta, beta, and gamma power for all regions of interest.

Time-on-task effect on brain oscillations during the TLDB task p (η_p^2)								
Delta								
Frontal Left	Frontal Median	Frontal Right	Central Left	Central Median	Central Right	Posterior Left	Posterior Median	Posterior Right
.288 (.084)	.235 (.095)	.229 (.097)	.147 (.129)	.259 (.092)	.319 (.079)	.494 (.048)	.254 (.093)	.178 (.118)
Interpretation: no significant time effect on delta power.								
Beta								
Frontal Left	Frontal Median	Frontal Right	Central Left	Central Median	Central Right	Posterior Left	Posterior Median	Posterior Right
.002 (.287)	.053 (.190)	.011 (.231)	< .001 (.459)	.025 (.226)	.007 (.244)	.074 (.165)	.114 (.143)	.041 (.202)
Interpretation: Decrease in beta power at the beginning of the TLDB task followed by an increase in beta power evidenced by a quadratic trend (all *ps* < .030; all η_p^2 > .30).								
Gamma								
Frontal Left	Frontal Median	Frontal Right	Central Left	Central Median	Central Right	Posterior Left	Posterior Median	Posterior Right
.007 (.244)	.058 (.183)	.013 (.224)	< .001 (.413)	.016 (.245)	.005 (.263)	.022 (.203)	.132 (.133)	.036 (.207)
Interpretation: Decrease in gamma power at the beginning of the TLDB task followed by an increase in gamma power evidenced by a quadratic trend (all *ps* < .045; all η_p^2 > .25).								

Supplementary Table 2. Changes on brain oscillations at rest on delta, beta, and gamma power for all regions of interest.

Time effect on brain oscillations at rest p (η_p^2)								
Delta								
Frontal Left	Frontal Median	Frontal Right	Central Left	Central Median	Central Right	Posterior Left	Posterior Median	Posterior Right
.209 (.101)	.090 (.141)	.186 (.107)	.679 (.035)	.200 (.104)	.253 (.091)	.235 (.095)	.401 (.067)	.874 (.016)
Interpretation: no significant time effect on delta power.								
Beta								
Frontal Left	Frontal Median	Frontal Right	Central Left	Central Median	Central Right	Posterior Left	Posterior Median	Posterior Right
.004 (.335)	.006 (.312)	002 (.298)	.004 (.337)	.029 (.237)	.001 (.321)	.001 (.319)	.034 (.224)	.009 (.238)
Interpretation: significant linear increase in beta power over time (all *ps* < .033; all η_p^2 > .286).								
Gamma								
Frontal Left	Frontal Median	Frontal Right	Central Left	Central Median	Central Right	Posterior Left	Posterior Median	Posterior Right
< .001 (.355)	.001 (.322)	.001 (.318)	< .001 (.355)	.002 (.303)	< .001 (.382)	< .001 (.381)	.001 (.304)	.001 (.252)
Interpretation: significant linear increase in gamma power over time (all *ps* < .015; all η_p^2 > .356).								

3.2 Synthèse

Cette troisième étude a montré que les effets de la fatigue mentale sur une tâche de contrôle moteur (i.e., une tâche de pointage) étaient persistants dans le temps. Bien que d'un point de vue subjectif, la sensation de fatigue mentale diminuait progressivement sur une période de 20 minutes suivant une tâche mentalement fatigante, les performances étaient de plus en plus altérées. L'EEG a également été utilisée dans cette étude afin d'évaluer de manière plus objective la présence de fatigue mentale. Les analyses EEG réalisées lors de la tâche cognitivement fatigante ont montré une diminution de l'amplitude de la N100, comme classiquement observé en présence de fatigue mentale, et pouvant traduire une augmentation de la charge mentale au cours de la tâche, indiquant donc que cette dernière devient de plus en plus exigeante. Concernant la P300, dans notre étude son amplitude croît avant de diminuer lors de la dernière partie de la tâche cognitivement fatigante, alors qu'habituellement en présence de fatigue la P300 décroît, reflétant ainsi une diminution des ressources attentionnelles allouées pour réaliser la tâche. Cette augmentation de l'amplitude de la P300 pourrait indiquer que les participants engageaient de plus en plus de ressources attentionnelles pour effectuer la tâche expliquant ainsi le maintien des performances, qui dans les études montrant une diminution de la P300 ont tendance à diminuer. Cela montre l'importance de mettre en relation les données comportementales et électrophysiologiques pour interpréter les résultats. Par ailleurs, l'analyse des ondes cérébrales enregistrées lors de la tâche cognitivement fatigante a montré une augmentation des ondes alpha comme largement rapporté dans la littérature, mais une diminution des ondes thêta ce qui va à l'encontre de cette même littérature. Lors des enregistrements au repos, les deux ondes alpha et thêta augmentaient comme attendu. Chaque tâche cognitive engendre des processus cognitifs spécifiques (i.e., ici une diminution des ondes thêta). Pour éviter cela, et identifier des marqueurs propres à la fatigue mentale, il faudrait effectuer des enregistrements au repos avant et après les tâches cognitivement fatigantes pour trouver des modulations d'ondes cérébrales spécifiques à la fatigue mentale et non-contaminées par les processus cognitifs impliquées dans la réalisation des tâches cognitives.

Les effets persistants de la fatigue mentale sur une tâche de contrôle moteur observés dans cette étude sont néanmoins à répliquer, et il serait intéressant d'observer si ces effets existent aussi sur d'autres type de tâches (e.g., attention, planification, prise de décision). De plus, en montrant qu'une simple pause ne suffit pas pour récupérer de la fatigue mentale, cette étude ouvre la voie à d'autres recherches concernant les stratégies de compensation possibles afin de récupérer plus rapidement après une tâche mentalement fatigante.

4 Étude 4

L’activité physique et la musique pour contrecarrer la fatigue mentale

Physical activity and music to counteract mental fatigue

Thomas Jacquet, Bénédicte Poulin-Charronnat, Patrick Bard, Joris Perra, and Romuald Lepers

A soumettre dans Neuroscience

4.1 Résumé

La fatigue mentale est un état psychobiologique causé par une tâche cognitive prolongée et/ou intense, qui entraîne une altération des performances cognitives et physiques. Certaines études ont déjà étudié l'utilisation de stratégies de compensation pour contrer les effets de la fatigue mentale, notamment en utilisant des substances bioactives comme la caféine. Cependant, les substances bioactives pourraient également avoir des effets secondaires. La présente étude vise à tester deux stratégies non-bioactives pour contrer la fatigue mentale : l'écoute de la musique et l'activité physique.

Dans l'Expérience 1, pour s'assurer que les effets de la fatigue mentale sont persistants dans le temps, quatorze participants ont effectué une tâche de pointage consistant à atteindre une cible le plus rapidement possible, avant d'effectuer une tâche cognitive exigeante de 32 minutes (*Time Load Dual Back* - TLDB), puis immédiatement, 10 minutes, et 20 minutes après la fin de la tâche de TLDB. Le niveau de fatigue mentale a été évalué à l'aide d'une échelle visuelle analogique avant chaque tâche de pointage. Dans l'Expérience 2, pour tester l'effet de nos deux stratégies de compensation, deux groupes de participants, les groupes "écoute de la musique" (n = 12) et "activité physique" (n = 11), ont été formés. Les participants ont effectué 32 minutes de la tâche de TLDB, suivies de 15 minutes consistant à écouter de la musique ou à faire du vélo à intensité modérée. Les participants ont effectué une tâche de pointage au début et à la fin de l'expérience. La sensation subjective de fatigue mentale et l'activité cérébrale ont été enregistrées avant chaque tâche de pointage et après la tâche de TLDB.

Les résultats de l'Expérience 1 ont montré que, si l'augmentation de la sensation de fatigue mentale après la tâche TLDB était suivie d'une diminution pendant les 20 minutes de récupération, la tâche de pointage était de plus en plus affectée par la fatigue mentale. Dans l'Expérience 2, l'effet négatif de la fatigue mentale a été compensé par les deux stratégies proposées, et après l'activité physique, les performances sur la tâche de pointage étaient encore meilleures qu'au début de l'expérience. Pour les deux groupes, la tâche cognitivement exigeante a augmenté la sensation subjective de fatigue mentale, et l'activité compensatoire l'a diminuée. Cependant, les analyses des oscillations cérébrales n'ont pas démontré une récupération de la fatigue mentale.

Les résultats ont suggéré que 15 minutes d'écoute de musique et d'activité physique pourraient être des stratégies efficaces pour contrer la fatigue mentale. Ces effets positifs ont été attribués à leur influence sur la production dopaminergique.

Physical activity and music to counteract mental fatigue

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Highlights

- Mental fatigue induced by cognitively demanding activity alters motor control.
- The negative effects of mental fatigue persist after 20 min of passive recovery.
- Listening to music or moderate physical activity counteract mental fatigue effects.
- Non-bioactive strategies could be used to reduce the effects of mental fatigue.

Abstract

Mental fatigue impairs both cognitive and physical performance. Previous studies have used bioactive substances such as caffeine to counteract mental fatigue. However, bioactive substances have side effects. The present study aimed to test two non-bioactive strategies to counteract mental fatigue: listening to music and physical activity.

In Experiment 1, to confirm the persistence of mental fatigue, participants performed an arm-pointing task, before completing a cognitively demanding task, immediately, 10 and 20 min after it. In Experiment 2, the cognitively demanding task was followed by 15 min of listening to music or cycling exercise. An arm-pointing task was performed before the cognitive task and after the compensation strategies. The subjective feeling of mental fatigue was assessed before each arm-pointing task and, for Experiment 2 brain activity was recorded at rest before each arm-pointing task and after the cognitive task.

Experiment 1 showed that, while the increase in the feeling of mental fatigue after the cognitive task was followed by a decrease during the 20 min of recovery, the arm-pointing task was increasingly affected by mental fatigue. In Experiment 2, the mental fatigue negative effect on the arm-pointing task was compensated by the two compensation strategies. For both groups, while subjective mental fatigue indicated a recovery after compensation, brain oscillations did not evidence this objectively.

The results suggested that both 15 min of listening to music and physical activity could be efficient strategies to counteract mental fatigue. These positive effects were attributed to their influence on dopamine production.

Keyword: Mental fatigue; Compensation; Motor control; Physical activity

Abbreviations

EEG: Electroencephalography, ERP: Event-related potential, fMRI: functional Magnetic Resonance Imaging, ID: Index of Difficulty, RPE: Rating of Perceived Exertion, TLDB: Time Load Dual Back, and VAS: Visual Analog Scale.

1. INTRODUCTION

Mental fatigue, which is defined as a psychobiological state caused by prolonged and/or intense periods of cognitively demanding activity and characterized by subjective feelings of "tiredness" and "lack of energy" (Boksem & Tops, 2008; Rozand & Lepers, 2016), could negatively impact daily life. A recent study conducted on the general population of Lausanne revealed that the prevalence of fatigue was 21.9% (Galland-Decker et al., 2019). This prevalence of mental fatigue affects everyday life and can lead to a decrease in productivity (Ricci et al., 2007), medical errors (Tawfik et al., 2018), or road accidents (Dinges, 1995). Moreover, mental fatigue is also a prevalent symptom in many diseases, such as cancers (Chang et al., 2000), brain injuries (Cantor et al., 2013), Parkinson's disease (Stocchi et al., 2014), Lyme disease (Shadick et al., 1994), or more recently in COVID-19 (Del Rio & Malani, 2020). Improved understanding of the neurophysiological mechanisms underlying mental fatigue is important to counteract its negative effects in both healthy individuals and patients.

In a laboratory environment, it has been demonstrated that mental fatigue significantly impairs cognitive (Lorist et al., 2000) and physical performance (for reviews: Pageaux & Lepers, 2018). When experiencing mental fatigue, impaired attention (Boksem et al., 2005), emotion regulation (Grillon et al., 2015), decision making (Guo et al., 2018), or executive functions (Lorist et al., 2000) have been observed. Concerning physical performance, mental fatigue has been shown to impair sport-related decision making (Head et al., 2017; Smith et al., 2016), technical skills (Le Mansec et al., 2018), motor control (Rozand et al., 2015), and endurance (Marcora et al., 2009).

To attest to the presence of mental fatigue, several subjective and objective markers can be used. It has recently been indicated that the use of a visual analog scale (VAS) appears to be the most practical method for assessing mental fatigue (Smith et al., 2019). Nonetheless, it seems necessary to use electrophysiological markers in addition to a subjective scale to characterize mental fatigue. Studies using electroencephalography (EEG) have notably highlighted that mental fatigue induces changes in brain oscillations. A recent meta-analysis suggests that an increase in theta power would be the most reliable biomarker of the presence of mental fatigue (Tran et al., 2020). Moreover, mental fatigue also induces an increase in alpha power (Arnau et al., 2017; Boksem et al., 2005), interpreted as reflecting decreased attention.

Mental fatigue has negative impacts on both cognitive and physical performances, thus some studies have investigated different compensation strategies to counteract the effects of this fatigue. Previous research has shown, for example, that chicken extract could help to compensate for the deleterious effects of mental fatigue (Nagai et al., 1996; Yamano et al., 2013). This positive effect was attributed to the various amino acids, peptides, and proteins contained in the chicken extract and their effects on levels of several brain neurotransmitters. However, the exact mechanisms to explain this remain to be clarified. Although chicken extract is very popular in Asia, it is not the case in Western countries. Caffeine is a more common bioactive substance that has been shown to be efficient to counteract the effects of mental fatigue (Azevedo et al., 2016). Franco-Alvarenga et al. (2019) showed that performance (20 km cycling time trial) in mentally fatigued cyclists was improved by 1.4% after ingesting caffeine (ingestion before the mentally fatiguing task). The beneficial effect of caffeine on endurance performance when mental fatigue is experienced could be attributed to the positive effect of caffeine on perceived effort (Doherty & Smith, 2005) and neuronal excitability (Davis et al., 2003). However, bioactive substances such as caffeine could also have side effects, such as abnormal heart rhythm, insomnia, shakiness, coronary heart diseases, arterial hypertension, arterial stiffness, or an elevation of cholesterol (Dworzański et al., 2009; Nawrot et al., 2003). To avoid these side effects, Van Cutsem et al. (2018) showed the effectiveness of rinsing the mouth with caffeine-maltodextrin to compensate for mental fatigue. However, although the use of a caffeine-maltodextrin mouth rinse is possible in laboratory settings, it is less practical in everyday life, especially at work for instance.

Other studies have chosen to use non-bioactive substances to compensate for the effects of mental fatigue. The intermittent release of certain odors (e.g., citral, green or menthol odor) (Kato et al., 2012) or listening to relaxing music (Guo et al., 2015) during mentally fatiguing tasks also appeared to be efficient strategies to limit the effects of mental fatigue on subsequent tasks. Finally, studies showed that other strategies such as taking a steam bath after mental effort (Mizuno et al., 2010), mindfulness (Axelsen et al., 2020), or auditory binaural beats (Axelsen et al., 2020) could also be efficient at counteracting the effects of mental fatigue.

Some non-bioactive strategies proposed to counteract mental fatigue may be difficult to apply in the context of daily life and/or present some limits. The present study thus aimed to test two different user-friendly strategies to counteract mental fatigue. The first strategy was listening to pleasant music. One of the most common effects of listening to music is the "Mozart effect". Previous work showed that performance was better on spatial reasoning tasks after

listening to a Mozart's sonata rather than silence or a relaxing sound (Rauscher et al., 1995). Levitin (2006) proposed that listening to music for 10 to 15 min before starting work would boost productivity. It is worth noting that the beneficial effects of listening to music on cognitive performance would be related more to changes in the listeners' emotional state than to the effects of the music itself (Schellenberg, 2012). Listening to music before completing an activity could also have a positive impact on physical exercise (Jarraya et al., 2012). In the present study and contrary to the study by Guo et al. (2015), listening to music was not proposed during the cognitively demanding task but after it, in order to counteract mental fatigue after its induction. It has been shown that music could be a distractor while completing a cognitive task and could lead to a decrease in performance (Dobbs et al., 2011). However, to induce a mental fatigue state, the participants needed to be engaged in the cognitively demanding task, without being disturbed.

The second compensation strategy tested in the present study was moderate physical exercise. An fMRI study evidenced that a 10-minute exercise session on a cycle ergometer at light intensity was sufficient to improve cognitive performance, and that this positive effect of physical activity was linked to an increase in arousal levels (Byun et al., 2014). In the literature, this beneficial effect of physical exercise has been largely reported for cognitive performance (Oberste et al., 2019), but also motor learning (Marin Bosch et al., 2020), or physical performance (Fradkin et al., 2010). In this context, conducting acute physical exercise could also be a promising and effective strategy to counteract mental fatigue.

We chose to evaluate the efficiency of these two compensation strategies on motor control (i.e., an arm-pointing task), which has previously been shown to be impacted by mental fatigue (Rozand et al., 2015). Rozand et al. (2015) showed that after 90 min of the Stroop task movement durations during an arm-pointing task were increased by ~4%, evidencing an impairment of motor control during mental fatigue. Recently, it has been shown that the effects of mental fatigue on motor control persisted for at least 20 min after the completion of the cognitively demanding task (Jacquet, Poulin-Charronnat, et al., 2021).

In this context, the first objective of the present study was to confirm that the effects of mental fatigue on motor control persist at least 15 min after inducing mental fatigue. We, therefore, performed a manipulation check in the first experiment to confirm that mental fatigue persisted over time following the cognitively demanding task in order to thereafter test the compensation strategies proposed. The second and main objective of the present study was to

evaluate the effectiveness of listening to music and acute physical activity to counteract the effects of mental fatigue on motor control. We hypothesized that both means could be efficient strategies to counteract mental fatigue. This effectiveness should be evidenced by maintaining performance on movement duration during an arm-pointing task after inducing mental fatigue followed by the compensation strategies. A possible recovery effect could also be evidenced on brain oscillations with a decrease in both theta and alpha power.

2. METHODS

2.1. PARTICIPANTS

The study involved 37 healthy active adults, with normal or corrected-to-normal vision and no history of neurological disease (age: 20.6 ± 0.7 years; 7 males and 30 females), who all gave written informed consent to perform the experiment. To check that they were all right-handed, participants completed the Edinburg questionnaire. All participants were given instructions to sleep for at least 6 h, not to consume alcohol, and not to practice vigorous physical activity the day before each visit. They were also instructed not to consume caffeine or nicotine for at least 3 h before testing and were asked to declare if they had taken any medication or had any acute illness, injury, or infection. The experiment was conducted in conformity with the latest version of the Declaration of Helsinki (1964).

2.2. EXPERIMENTAL DESIGN

For both Experiments 1 and 2, two sessions were performed: a familiarization and an experimental session. The familiarization session aimed to accustom the participants to the different questionnaires used and train them on both arm-pointing and Time Load Dual Back (TLDB) tasks (Borragan et al., 2016). The experimental session occurred between 48 h and 96 h after the familiarization session, at the same time of day.

Experiment 1

Experiment 1 included 14 participants (age: 21.1 ± 1.8 years; 2 males and 12 females). The participants started by completing the Saint Mary's Hospital questionnaire. Then, they reported their level of mental fatigue on a visual analog scale (VAS) and they performed the arm-pointing task (Pre measurement). Participants then conducted the cognitively demanding task consisting of 32 min of the TLDB task (excluding rest periods between blocks).

Immediately after the cognitively demanding task, they evaluated their level of mental fatigue on a VAS and repeated the arm-pointing task (Post measurement). The evaluation of the level of mental fatigue on a VAS and the arm-pointing task were repeated 10 min (Post 10 measurement) and 20 min (Post 20 measurement) after the completion of the cognitively demanding task (Fig. 1.A).

Experiment 2

Experiment 2, which was the main experiment, involved 11 participants for the "physical activity" group (age: 19.9 ± 0.8 years; 4 males and 7 females) and 12 participants for the "listening to music" group (age: 20.8 ± 0.5 years; 1 male and 11 females). As for Experiment 1, the session began with completing the Saint Mary's Hospital questionnaire. To record the brain activity of participants at rest, they were asked to stare at a black screen in front of them, to relax, and to think about nothing for 2 min. Following this rest period, the participants' subjective level of mental fatigue was evaluated on a VAS, and they carried out the arm-pointing task (Pre measurement). Participants then performed the cognitively demanding task consisting of 32 min of the TLDB task (excluding rest periods between blocks), following this their brain activity at rest was recorded for 2 min, and they completed a VAS to report their subjective level of mental fatigue ($Post_{CT}$ measurement). Then, participants performed a compensation task, which consisted of either 15 min of moderate physical activity (i.e., cycling at a moderate intensity) or 15 min of listening to music. After the compensation task, brain activity was recorded for 2 min at rest, and then the subjective level of mental fatigue was evaluated on a VAS, followed by the arm-pointing task ($Post_{comp}$ measurement; Fig 1.B).

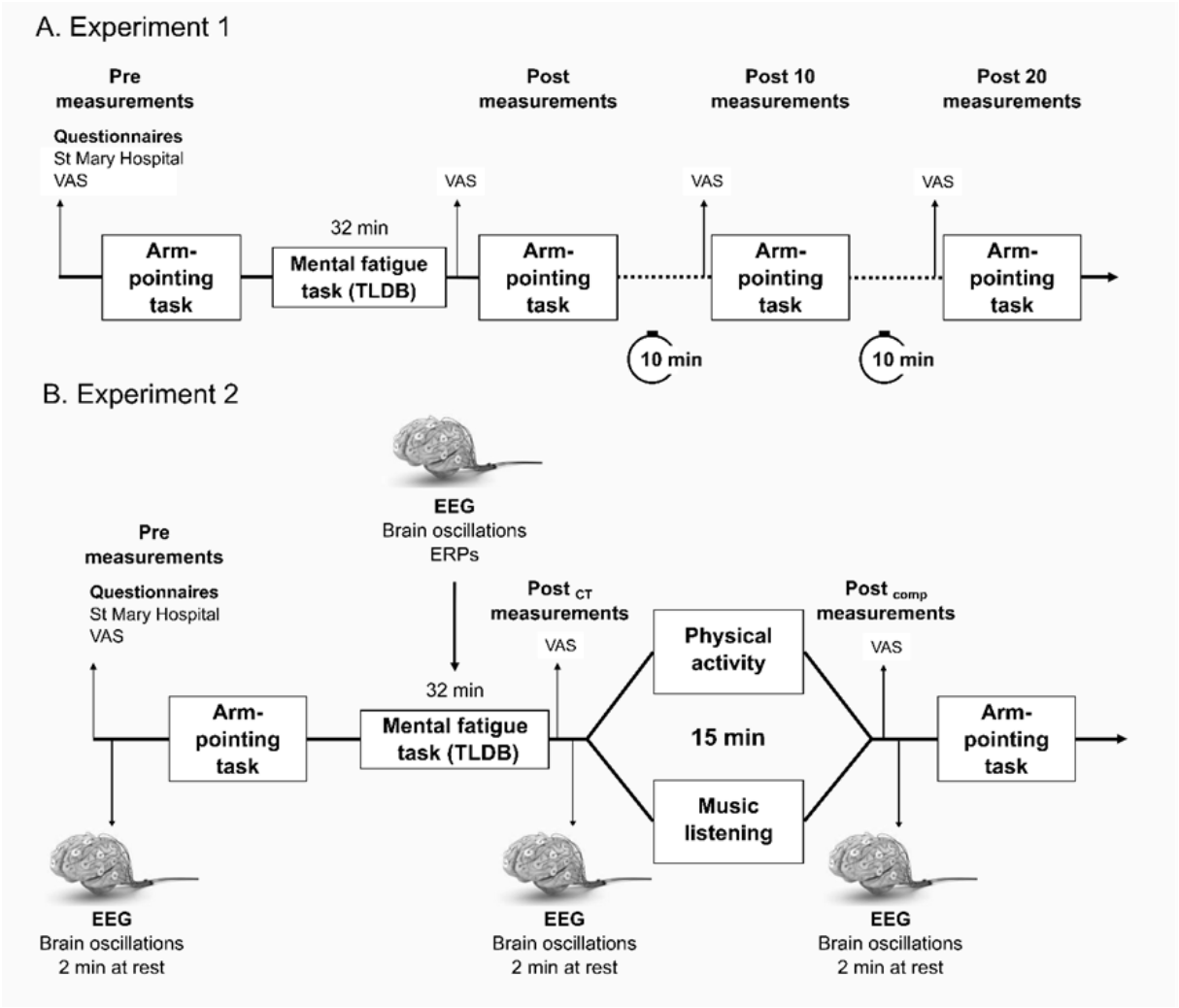

Figure 1. Overview of the experimental protocols for Experiment 1 (panel A) and Experiment 2 (panel B). EEG: electroencephalography. ERPs: Event-Related Potentials. $Post_{CT}$: Post cognitive task. $Post_{comp}$: Post compensation. TLDB: Time Load Dual Back. VAS: Visual Analogue Scale.

2.3. PSYCHOLOGICAL MEASUREMENTS

The sleep quality of each participant the night before the experiment was assessed using the Saint Mary's Hospital Sleep Questionnaire (Ellis et al., 1981). This questionnaire consists of 14 items concerning sleep quality such as depth, awakening in the middle of the night, satisfaction, refreshed feeling upon awakening, difficulty in falling asleep, and early awakening.

The subjective mental fatigue level of participants was evaluated using a VAS of mental fatigue. The VAS was a 100-mm-long line, with bipolar end anchors (0 mm = ''Not mentally

tired at all"; 100 mm = ''Extremely mentally tired"), on which participants had to place a mark to estimate their level of mental fatigue.

The pleasantness of the compensation strategies (i.e., listening to music or physical activity) was evaluated using a VAS of pleasantness. The VAS was a 100-mm-long line, with bipolar end anchors (0 mm = ''Not pleasant at all"; 100 mm = ''Extremely pleasant"), on which participants had to place a mark to estimate the pleasantness of the activity performed.

2.4. MENTAL FATIGUE TASK: THE TIME LOAD DUAL BACK (TLDB) TASK

The Time Load Dual Back (TLDB) task is a dual-task combining a classical N-back working memory-updating task (Kirchner, 1958) and an interfering second task. Letters and digits were alternately presented on a screen. For the digits (1, 2, 3, 4, 6, 7, 8, or 9), which constituted the interfering task, participants had to press the key "1" on the numeric keypad with their right index finger if the digit was odd and the key "2" if the digit was even. For the letters (A, C, T, L, N, E, U, or P), participants were instructed to press the space bar with their left hand every time the displayed letter was the same as the previous letter (1-back task). Experiment Builder software (SR Research) was used to monitor stimuli presentation. Stimuli were presented in Arial font size 60, centrally on a 16-inch computer screen (60 Hz refresh rate). Stimuli were presented by blocks of 60 with a break of 30 s between blocks.

For the familiarization session, we followed the procedure of Borragan et al. (2016) and Borragan et al. (2017) to determine individual thresholds of presentation duration. All participants started the TLDB task with a duration of 1500 ms for each event (i.e., letters and digits) with an inter-stimulus interval set at 0. At the end of each block, performance accuracy was calculated. If it was equal to or greater than 85%, the duration of the presentation was reduced by 100 ms. When performance accuracy became less than 85%, participants performed two more blocks with the same duration to pursue familiarization. For the experimental session, the threshold of stimulus presentation was fixed at the last successful level.

2.5. THE ARM-POINTING TASK

The arm-pointing task is a physical task used to evaluate motor control. The aim of this task is to reach a target presented on a touchscreen as accurately and fast as possible. Participants were sitting on a comfortable chair with a pencil in their right hand. At the starting position, shoulder abduction was 90° and movements were direct at 45° to the left.

In the start position, their arm was aligned with their right shoulder and all targets to be reached were located on a 45° diagonal to the left to limit joint stress. The targets were black squares displayed on a touchscreen in front of the participant. The targets presented several indexes of difficulty (IDs), which were calculated using the formula $ID = \log_2(\frac{2D}{W})$, where D represents the center-to-center distance between the start point and the target and W represents the width of the target.

For Experiment 1, using different distances (between 5 cm and 32 cm) and widths (between 1 cm and 2.5 cm), 53 targets were created with eight IDs ranging from 2 to 6.64.

For Experiment 2, in order to reduce task duration and to facilitate statistical analyses, 42 targets were created with eight IDs ranging from 3 to 6 by steps of 0.5 using different distances (between 5 cm and 32 cm) and widths (between 1 cm and 2.5 cm). Each ID included six different targets with different sizes and distances from the starting point.

The time recorded for the pointing movement began when the participant took the pen off the starting position and stopped when they put it back on the touchscreen. If the participant landed on the target the trial was considered as "correct", otherwise, it was a missed trial. For each trial, the participant had to return to the starting position. The pointing task lasted approximately 1.5 min.

2.6. COMPENSATORY TASKS

2.6.1. PHYSICAL ACTIVITY

The physical activity condition consisted of 15 min of exercise on an ergo-cycle. The intensity of the exercise was determined according to the Rating of Perceived Exertion (RPE) of each participant, and fixed at “moderate”, corresponding to a level of 12-13 on the Borg’s 6-20 RPE scale (Borg, 1998). The Borg’s RPE scale ranges from 6 (Nothing at all) to 20 (Maximal) and includes verbal anchors: No exertion at all (6), Extremely light (between 7 and 8), Very light (9), Light (9), Somewhat hard (13), Hard/Heavy (15), Very hard (17), Extremely heavy (19) or Maximal exertion (20). Perception of effort, which could be defined as the conscious sensation of “how hard, heavy and strenuous a physical task is” (Marcora, 2009), was assessed every 3 min by asking the following question to the participants: “How hard and intense is it for you to perform the exercise at this moment?”. To avoid any distractions during the physical exercise, participants were placed in front of a wall on which only the scale of RPE was posted.

During the familiarization session, participants included in the "physical activity" group were accustomed to the RPE scale. In addition, they performed 15 min of cycling on the ergo-cycle, at an identical intensity to that of the experimental session, to feel the effort it required.

2.6.2. MUSIC LISTENING

The music listening phase consisted of spending 15 min, sitting in front of a black screen, and listening to pleasant music. Because music preference is personal (Hargreaves and North, 2010), therefore the participants themselves selected the songs used as stimuli. In this study, we were not interested in the characteristics of the music (e.g., musical genre, tempo, rhythm or timbre) but only in its pleasant aspect for each participant. Participants brought their own music playlist the day of the familiarization session. In this way, the songs were assembled to form a single music track for the experimental session using Audacity software (Version 2.3.0 for Windows).

2.7. EEG RECORDING AND PREPROCESSING

Active Two BioSemi system from 64 electrodes was used to record the electroencephalogram according to the 10-20 International system. Horizontal eye movements were monitored with electrodes placed on the outer left and right canthi, while eye blinks were monitored with an electrode placed under the left eye. Two additional electrodes were placed on the left and right mastoids (A1, A2). During recording, the BioSemi system's common-mode sense electrode served as the reference electrode. Electrophysiological signals were digitized at a 2048 Hz sampling rate and acquired with ActiView software. Offline data analyses were performed using MATLAB (MathWorks, Natick, MA, USA) and the EEGLAB toolbox (Delorme & Makeig, 2004). Continuous data were downsampled to 256 Hz, band-pass filtered at 0.01–100 Hz, and re-referenced to the average of A1 and A2. Noisy electrodes were identified with the probability and spectrum methods proposed in EEGLAB (threshold, Z = 5) and interpolated when necessary with a spherical method. To correct eye-movement artifacts, EEGLAB's Runica routine was used to perform independent component analyses, and components reflecting eye artifacts were identified by visual inspection and removed. Continuous data were segmented into 500 ms epochs from 25 ms before to 475 ms after the onset of the stimuli and were baseline corrected using the pre-trial period from -25 ms to 0 ms.

2.8. DATA ANALYSES

2.8.1. POINTING MOVEMENT

Movements duration lower than 100 ms (0.1%) and higher than 1000 ms (0.4%) were excluded from the analysis. Movements duration beyond three standard deviations (SDs) of the mean were also excluded from the analysis (0.7%).

2.8.2. EEG DATA

For EEG data, nine regions of interest (ROIs) were constituted to perform analyses on both ERPs and spectral data (e.g., Arendsen et al., 2020; Jacquet et al., 2021a): Frontal Left (FL; mean of FP1, AF3, AF7, F3, F5, F7, FC3, FC5, FT7), Frontal Median (FM; mean of FPz, AFz, F1, Fz, F2, FC1, FCz, FC2), Frontal Right (FR: mean of FP2, AF4, AF8, F4, F6, F8, FC4, FC6, FT8), Central Left (CL: mean of C3, C5, T7, CP3, CP5, TP7), Central Median (CM: mean of C1, Cz, C2, CP1, CPz, CP2), Central Right (CR: mean of C4, C6, T8, CP4, CP6, TP8), Posterior Left (PL: mean of P9, P7, P5, P3, PO7, PO3, O1), Posterior Median (PM: mean of P1, Pz, P2, POz, Oz), and Posterior Right (PR: mean of P4, P6, P8, PO4, PO8, O2).

2.8.2.1. Spectral analysis

For spectral analysis, run on EEG recording during the TLDB task and at rest before each arm-pointing task, Fast Fourier Transform (FFT) was performed, using the *spectopo* function of the EEGLAB toolbox. EEG power was divided into five frequency bands: delta, 1–4 Hz; theta, 4–7 Hz; alpha, 8–12 Hz; beta 13–30 Hz; and gamma, 30–40 Hz.

2.8.2.2. Evoked-related potentials analyses

For ERP analyses during the TLDB task, only trials with correct responses (93.7% ±0.2 for digits and 92.9% ±0.5 for letters) were considered. Epochs were averaged separately for each condition and each participant. ERPs were obtained by computing the mean amplitude in the time window for each ERP component, and by grand-averaging data across participants.
During the TLDB task, based on visual inspection of peak amplitude, different time windows were used for ERP components. For letters, an N100 (110-190 ms) on the frontal and central regions, an N200 (250-340 ms) for frontal and CM regions, and a P300 (360-445 ms) for all regions were identified. For digits, an N100 (100-180 ms) and a P200 (180-260 ms) on the frontal and central regions, as well as a P300 (400-475 ms) for all regions were identified.

2.9. STATISTICS

All data are presented as means ± standard errors of the mean. Greenhouse-Geisser's correction to the degrees of freedom was applied when violations of sphericity were present (corrected p-values are reported). Only significant effects are reported, except when non-significance is relevant for the hypotheses being evaluated.

For Experiment 1, mental fatigue effects on the VAS were evaluated using one-way repeated measures ANOVA with time (Pre, Post, Post 10, and Post 20) as the within-subject factor. The effects of mental fatigue on movement durations and errors during the arm-pointing task were evaluated using two-way repeated-measures 4 × 53 ANOVAs with time (pre, post, post 10, and post 20) and ID (53 different IDs from 2 to 6.64) as within-subject factors. Missing values (due to errors or excluded using the method described in section 2.8) were computed from the linear equation obtained from the other points.

For Experiment 2, statistical analyses of mental fatigue effects on the VAS, brain oscillations, movement durations, and errors during the arm-pointing task were performed independently for each group (i.e., the "physical activity" and the "listening to music" group). Mental fatigue effects on the VAS were evaluated using independent one-way repeated measures ANOVAs with time (Pre, Post 1, and Post 2). The effects of mental fatigue on movement durations and errors during the arm-pointing task were evaluated using two-way repeated-measures 2 × 7 ANOVAs with time (Pre, and Post 2) and ID (3, 3.5, 4, 4.5, 5, 5.5, and 6) as within-subject factors. For brain oscillations recorded during rest periods, one-way repeated-measures ANOVAs with time on task (Pre, PostCT, and Postcomp) were used. Separate ANOVAs were performed for each frequency band. Only results about theta and alpha power, which are the power of interest, are reported in the Results section, the other brain oscillations are reported in supplementary data. Statistical evaluation was performed independently for each ROI. In Experiment 2, sleep and pleasantness were tested using paired t-tests.

For the TLDB task, analyses were performed separately for letters and digits. Two-way repeated measures 2 × 4 ANOVAs including the within-subject factors Stimulus type (for letters: same/different; for digits: even/odd) and time on task (part 1, 0-8 min; part 2, 8-16 min; part 3, 16-24 min; and part 4, 24-32 min) were performed for reaction times (RTs) and errors. Analyses were performed separately for Experiments 1 and 2. The same ANOVAs were used to analyze ERPs for Experiment 2. Brain oscillations during the TLDB task (only in Experiment

2) were analyzed using two-way repeated-measures ANOVAs with time on task (part 1, 0-8 min; part 2, 8-16 min; part 3, 16-24 min; and part 4, 24-32 min) as the within-subject factor. Group factor was not included in the ANOVA concerning the TLDB task for Experiment 2, similar results were expected and statistics were more powerful without this factor. As for the analyses of brain oscillations at rest, separate ANOVAs were performed for each frequency band and independently for each ROI. All results about the TLDB task are reported in supplementary data.

All analyses were performed using the Statistical Package for Social Sciences, version 24 for Windows (SPSS Inc., Chicago, IL, USA). Significant main effects of time and significant interactions were followed up with contrast tests with Bonferroni correction and only significant results are reported with adjusted p values. For each ANOVA, partial eta squared was calculated. Thresholds for small, moderate, and large effects were set at 0.01, 0.07 and 0.14, respectively (Cohen, 1988). Cohen's d was calculated for each t-test using JASP (Version 0.13.1.0) [Windows software]. Thresholds for small, moderate and large effects were set at 0.2, 0.5 and 0.8 respectively (Cohen, 1988).

3. RESULTS

3.1. EXPERIMENT 1

Visual analog scale. Fig 2. shows the VAS scores. ANOVA revealed a significant time effect on the subjective feeling of mental fatigue [$F_{(1.767,\ 22.973)}$ = 15.420, p < .001, η_p^2 = .543], qualified by a quadratic trend [$F_{(1,\ 13)}$ = 21.440, p < .001, η_p^2 = .623]. Paired comparisons revealed that the cognitively demanding task (*Pre vs. Post*) induced an increase in the subjective feeling of mental fatigue [$t_{(13)}$ = -5.290, p < .001, d = -1.413]. A decrease in the subjective feeling of mental fatigue was observed between Post and Post 10 measurements [$t_{(13)}$ = 3.680, p = .014, d = 0.984], but not between Post 10 and Post 20 measurements [$t_{(13)}$ = 2.235, p = .218, d = 0.597]. While the subjective feeling of mental fatigue was still higher 10 min after the completion of the cognitively demanding task (*Pre vs. Post 10*) [$t_{(13)}$ = -3.736, p = .012, d = -0.998], 20 min after the task it was no longer significantly different from its initial level (*Pre vs. Post 20*) [$t_{(13)}$ = -2.039, p = .312, d = -0.545].

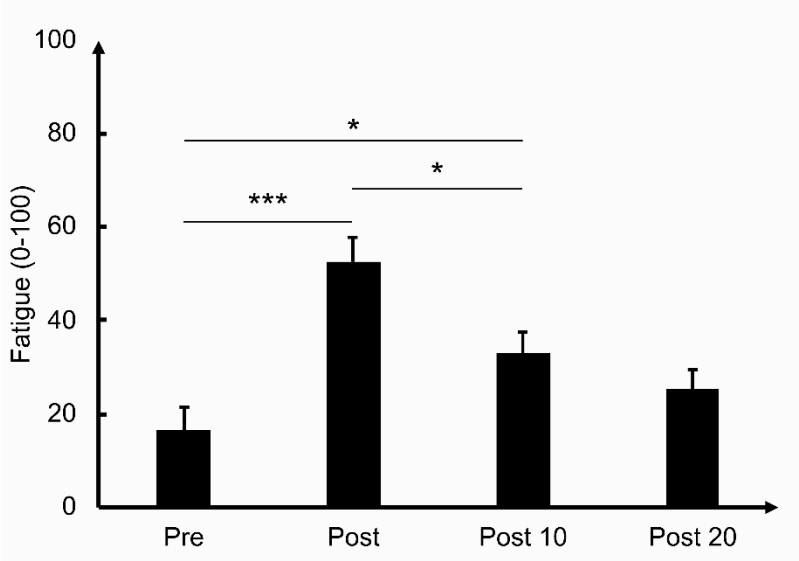

Figure 2. Time course of subjective feeling of mental fatigue for Experiment 1. * and ***: $p < .05$ and $p < .001$, respectively. Data are presented as mean ± SE.

Time Load Dual Back task. As the working hypotheses did not relate to the TLDB task, the data are not presented in this section. However, all behavioral data related to the cognitively demanding task are available in supplementary data.

Arm-pointing task. Fig. 3 shows the movement durations. Analyses performed on the arm-pointing task showed a significant ID effect [$F_{(52, 676)} = 136.396$, $p < .001$, $\eta_p^2 = .913$], qualified by a linear trend [$F_{(1, 13)} = 318.278$, $p < .001$, $\eta_p^2 = .961$], indicating that movement durations were slower with increasing IDs. A significant effect of time [$F_{(3, 39)} = 5.866$, $p < .001$, $\eta_p^2 = .311$], qualified by a linear trend [$F_{(1, 13)} = 6.991$, $p = .020$, $\eta_p^2 = .350$], showed an increase in movement durations over time. Arm-pointing movements were slower in Post [$t_{(13)} = -2.843$, $p = .042$, $d = -0.760$], Post 10 [$t_{(13)} = -3.983$, $p = .002$, $d = -1.064$] and Post 20 [$t_{(13)} = -3.665$, $p = .004$, $d = -0.980$] measurements compared to Pre measurement. Finally, a significant ID × time interaction was observed [$F_{(156, 2028)} = 1.553$, $p < .001$, $\eta_p^2 = .107$], qualified by a linear trend [$F_{(1, 13)} = 19.053$, $p < .001$, $\eta_p^2 = .594$], revealing that the increase in movement durations over time was more pronounced for the targets with the higher IDs.

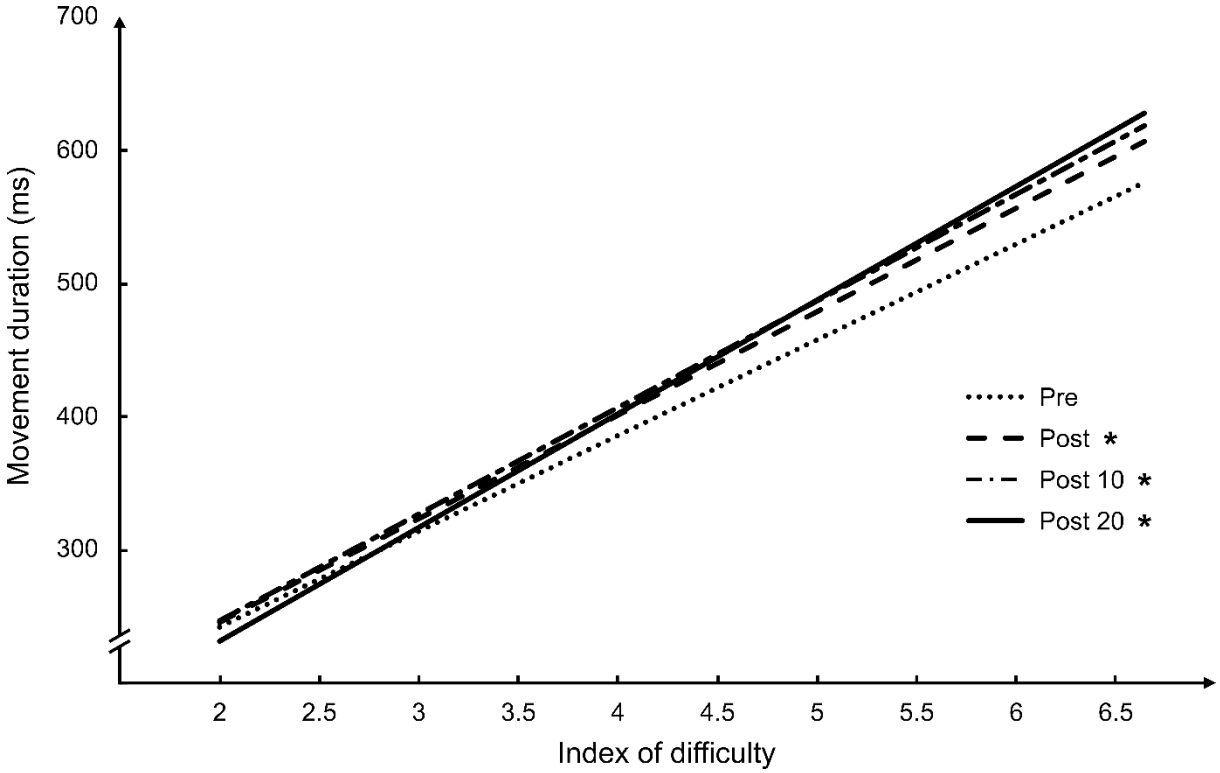

Figure 3. Time course of the duration of arm-pointing movement at Pre, Post, Post 10, and Post 20 measurements for Experiment 1, with a significant effect of the index of difficulty (ID; $p < .001$). *: Time effect: * = Significantly different from Pre ($p < .05$).

EXPERIMENT 2

Behavioral results

Sleep. No significant difference was observed in sleep duration between the two groups [$t_{(21)} = -1.859$, $p = .077$, $d = -0.776$]: "listening to music" group (465.4 min ± 12.2) and "physical activity" group (435.0 min ± 10.7).

Visual analog scale. For the "physical activity" group (Fig. 4.A), the ANOVA showed a significant time effect on the subjective feeling of mental fatigue [$F_{(2, 20)} = 38.453$, $p < .001$, $\eta_p^2 = .709$]. Post-hoc analyses showed an increase in the subjective feeling of mental fatigue between Pre and $Post_{CT}$ measurements [$t_{(10)} = -6.980$, $p < .001$, $d = -2.105$], followed by a decrease between $Post_{CT}$ and $Post_{comp}$ [$t_{(10)} = 3.499$, $p = .007$, $d = 1.055$]. However, the subjective feeling of mental fatigue still remained higher in $Post_{comp}$ than in Pre [$t_{(10)} = -1.050$, $p = .007$, $d = -1.050$].

For the "listening to music" group (Fig. 4.B), analyses revealed a significant time effect on the subjective feeling of mental fatigue [$F_{(2, 22)}$ = 17.502, p < .001, η_p^2 = .614]. Post-hoc analyses showed an increase in the subjective feeling of mental fatigue between Pre and $Post_{CT}$ measurements [$t_{(11)}$ = -5.549, p < .001, d = -1.602], followed by a decrease between $Post_{CT}$ and $Post_{comp}$ [$t_{(11)}$ = 4.553, p < .001, d = 1.314]. After listening to music, the subjective feeling of mental fatigue was not significantly different from that at the beginning of the experiment [$t_{(11)}$ = -0.996, p = .991, d = -0.287].

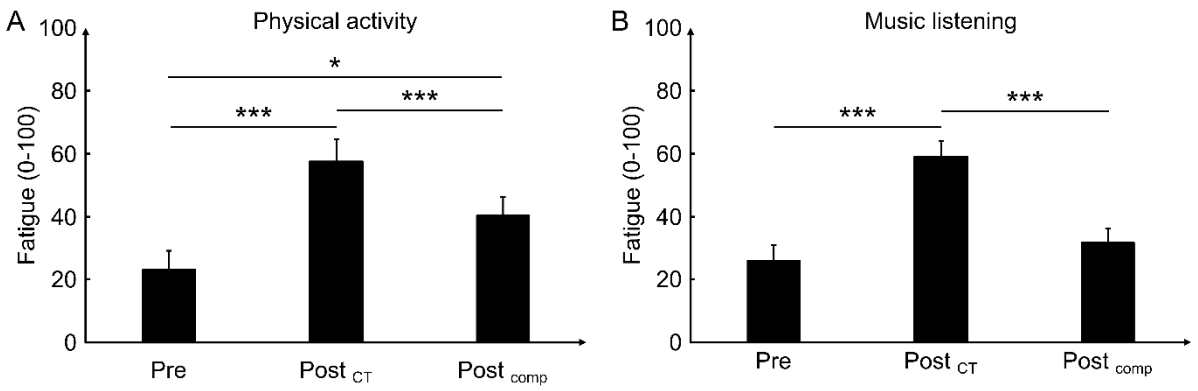

Figure 4. Time course of subjective feeling of mental fatigue for Experiment 2, for both the "physical activity" (panel A), and "listening to music" (panel B) groups. * and ***: Significantly different from Pre (p < .05 and p < .001, respectively). Data are presented as mean ± SE. $Post_{CT}$: Post cognitive task. $Post_{comp}$: Post compensation.

Pleasantness. Analyses showed that physical activity (56.6 ± 4.8) was perceived as less pleasant than listening to music (88.9 ± 2.2) [$t_{(21)}$ = 3.876, p < .001 .05, d = 2.600].

Time Load Dual Back task. As the working hypotheses did not relate to the TLDB task, the data is not presented in this section. However, all behavioral and EEG data related to the cognitively demanding task are available in supplementary data.

Arm-pointing task. For the "physical activity" group (Fig. 5.A), analyses performed on arm-pointing movements showed a significant ID effect [$F_{(1.546, 15.456)}$ = 112.013, p < .001, η_p^2 = .918], qualified by a linear trend [$F_{(1, 10)}$ = 162.731, p < .001, η_p^2 = .942], indicating that participants' movements were slower with increasing IDs. In addition, a significant effect of time [$F_{(1, 10)}$ = 4.983, p < .05, η_p^2 = .333] indicated that movement durations during the arm-pointing task were faster at the end of the experiment at $Post_{comp}$.

For the "listening to music" group (Fig. 5.B), a significant ID effect [$F_{(2.008,\ 22.083)}$ = 227.017, $p < .001$, $\eta_p^2 = .954$], qualified by a linear trend [$F_{(1,\ 10)} = 336.533$, $p < .001$, $\eta_p^2 = .968$], showed that participants' movement durations were slower with increasing IDs. However, no significant main effect of time or ID × time interaction were observed (all *ps* > .48; $\eta_p^2 < .08$), indicating that movement durations did not change over the experiment.

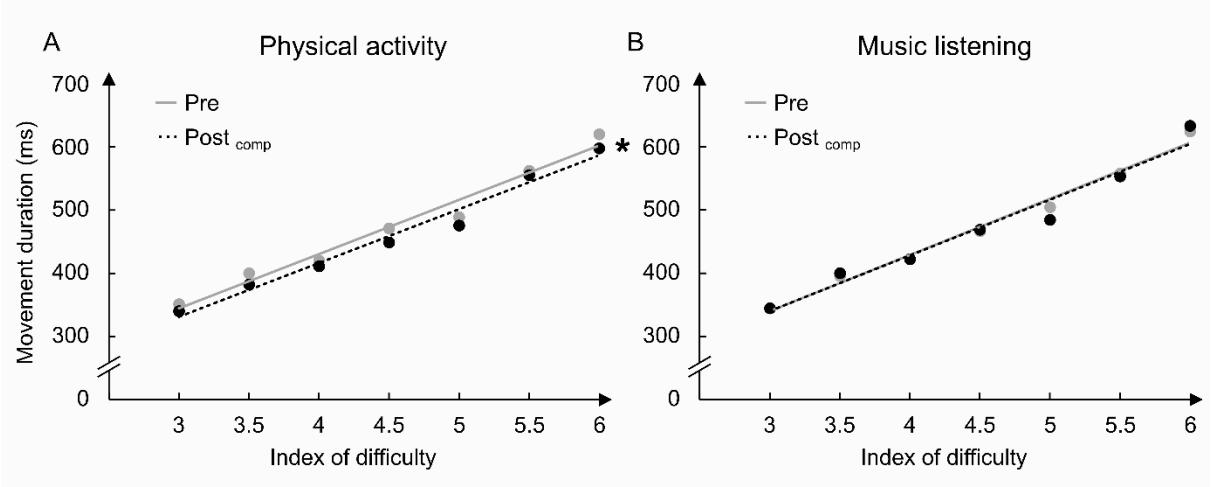

Figure 5. Time course of the duration of arm-pointing movement at Pre (before mentally fatiguing task), and $Post_{comp}$ (Post compensation) for Experiment 2, for both the "physical activity" (panel A), and "listening to music" (panel B) groups, with a significant effect of the index of difficulty (ID) for the physical activity group ($p < .001$). *: Significant time effect ($p < .05$).

EEG spectral analyses at rest

Theta. For both the "physical activity" (Fig 6.C), and "listening to music (Fig 6.D) groups, no significant time effect was observed on theta power.

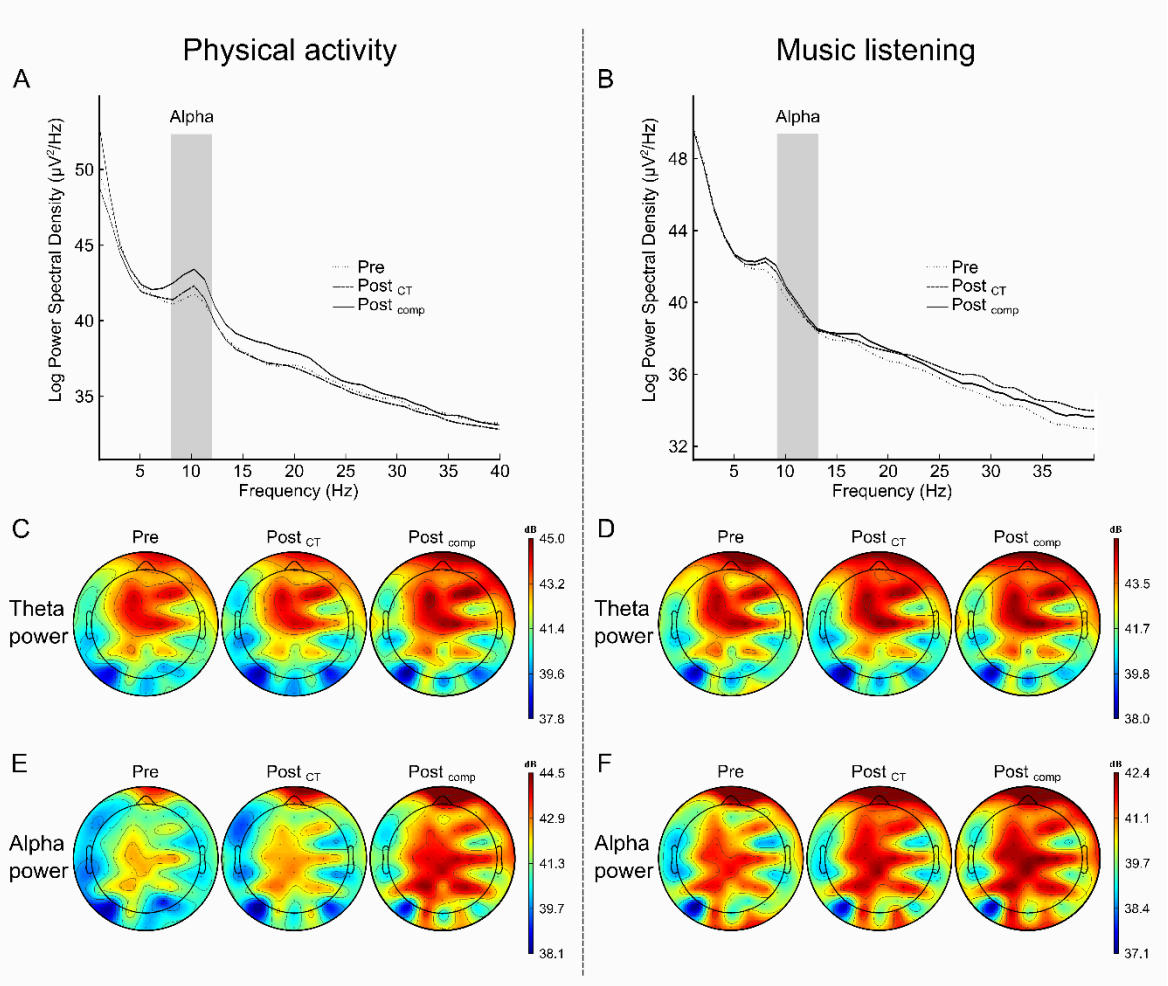

Figure 6. Brain oscillations of brain power spectrum during the 2-min rest periods at Pre, $Post_{CT}$, and $Post_{comp}$ for both the "physical activity" (panel A), and "listening to music" (panel B) groups, with specifically time course of the theta power for both the "physical activity" (panel C), and "listening to music" (panel D) groups, and the theta power for both the "physical activity" (panel E), and "listening to music" (panel F) groups. $Post_{CT}$: Post cognitive task. $Post_{comp}$: Post compensation

Alpha. For the "physical activity" group (Fig. 6.E), a significant effect of time was reported for all brain regions (all *ps* < .015; η_p^2 > .44), with a maximal effect in the CR region [$F_{(1.201,\ 12.013)}$ = 19.940, p < .001, η_p^2 = .666]. Post-hoc analyses revealed a significant increase in alpha power between $Post_{CT}$ and $Post_{comp}$ for all regions except the PR region (all *ps* < .037;

d < -0.825), and a significant increase in alpha power between Pre and $Post_{comp}$ for all brain regions (all *ps* < .037; d < -1.020).

For the "listening to music" group (Fig. 6.F), a significant effect of time was reported for the FM [$F_{(2, 22)}$ = 5.283, p = .013, η_p^2 = .324], CM [$F_{(1.239, 13.632)}$ = 5.375, p = .031, η_p^2 = .328], and CR regions [$F_{(2, 22)}$ = 5.078, p = .015, η_p^2 = .316]. Post-hoc analyses revealed a significant increase in alpha power between Pre and $Post_{CT}$ for the FM [$t_{(11)}$ = -2.649, p = .044, d = -0.765] and CR regions [$t_{(11)}$ = -2.611, p = .048, d = -0.754]. In addition, a more pronounced alpha power was observed in $Post_{comp}$ compared to Pre measurement for the FM [$t_{(11)}$ = -2.956, p = .022, d = -0.853], CM [$t_{(11)}$ = -3.271, p = .010, d = -0.944] and CR regions [$t_{(11)}$ = -2.888, p = .026, d = -0.834].

4. DISCUSSION

The present study aimed to (i) confirm the persistent effect of mental fatigue on arm-pointing task performance after a prolonged cognitively demanding task, and (ii) test two 15-min compensation strategies to counteract the negative effects of mental fatigue: listening to music and physical activity. Firstly, the results of Experiment 1 confirmed that the effects of mental fatigue were persistent and increasingly pronounced over time on arm-pointing movements for at least 20 min, despite a progressive decrease in the subjective feeling of mental fatigue. Secondly, Experiment 2 evidenced that listening to music and physical activity were efficient to counteract the negative effects of mental fatigue on an arm-pointing task.

4.1. MANIPULATION CHECK: MENTAL FATIGUE INDUCTION

A 16-min TLDB task has already been used successfully to induce a feeling of mental fatigue (Borragan et al., 2017; Borragan et al., 2016). However, it has been shown that 32 min of the TLDB task were necessary to induce deleterious effects related to mental fatigue on an arm-pointing task as used in the present study (Jacquet, Poulin-Charronnat, et al., 2021). In their study, Jacquet, Poulin-Charronnat, et al. (2021) used both electrophysiological (EEG) and subjective markers (VAS of mental fatigue) to attest to the presence of mental fatigue. As expected, the 32 min of the TLDB task increased the subjective feeling of mental fatigue in Experiment 1, as well as for both the "listening to music" and "physical activity" groups in Experiment 2. Moreover, analyses performed on brain oscillations and event-related potentials

in Experiment 2 (supplementary data) provided similar results as those observed by Jacquet, Poulin-Charronnat, et al. (2021) with notably a decrease in N200 amplitude over time as previously observed in studies on mental fatigue (Boksem et al., 2005; Guo et al., 2018). Altogether, these observations allow us to affirm that we succeeded in inducing mental fatigue with 32 min of the TLDB task.

4.2. PERSISTENCE OF THE EFFECTS OF MENTAL FATIGUE ON MOTOR CONTROL

The effects of mental fatigue on different physical performances are now well established in the literature (for review: Pageaux & Lepers, 2018), with motor control being one of the physical performances impacted. Rozand et al. (2015) evidenced that in the presence of mental fatigue, induced by 90 min of a modified Stroop task, the duration of arm-pointing movements increased by 4%, irrespective of the index of difficulty of the target. This result supporting impaired motor control with mental fatigue has been replicated with different cognitively demanding tasks (Jacquet, Poulin-Charronnat, et al., 2021; Rozand et al., 2016). A possible explanation for this negative effect of mental fatigue on motor control is that an increase in noise in the motor command would lead to slower movements to maintain task success (Rozand et al., 2015), as also suggested in case of physical fatigue (Missenard et al., 2009).

A recent study evidenced that motor control impaired with mental fatigue was persistent and could last at least 20 min after the completion of a mentally fatiguing task (Jacquet, Poulin-Charronnat, et al., 2021). However, despite a pioneer study conducted by Davis (1946), which evidenced only a partial recovery from mental fatigue after a calculation task of 30 min, few studies have evaluated the time course and persistence of the effect of mental fatigue. A previous study evidenced that a 12 min break following 90 min of a cognitively demanding task was not enough to observe a rebound in behavioral performances (a temporal discrimination task) despite a positive effect of this 12 min break on the subjective feeling of mental fatigue (Matuz et al., 2019). Our study also appears to indicate a dissociation of recovery effects between behavioral performances and the subjective feeling of mental fatigue. Although a decrease in the subjective feeling of mental fatigue seemed to indicate a recovery effect following a break, behavioral performances (i.e., motor task) were increasingly impacted by mental fatigue. This dissociation between subjective markers of mental fatigue and its growing effects on motor control has already been reported (Jacquet, Poulin-Charronnat, et al., 2021). Furthermore, Loch et al. (2020) also evidenced a decrease in subjective markers of mental

fatigue during the 20-min following a mentally fatiguing task, but without positive effects on cognitive performances. These observations show the importance of using different markers in order to improve the characterization of mental fatigue. While the VAS has recently been suggested as the most practical method to attest to mental fatigue (Smith et al., 2019), our results suggest that it is necessary to combine objective and subjective markers to highlight mental fatigue.

4.3. EXPLANATORY MECHANISMS OF MENTAL FATIGUE EFFECTS

While the effects of mental fatigue have been described widely in the literature, the explanatory mechanisms remain unclear. Several models have been developed to understand this phenomenon and explain its deleterious effects on performance: the model of ego depletion (Baumeister et al., 1998), the motivational control theory (Hockey, 1997, 2011), the model of costs and benefits (Boksem & Tops, 2008) and the model of the dual regulation of mental fatigue (Ishii et al., 2014). Despite some differences, these models suggested that a decrease in performance when there is mental fatigue is the result of a decrease in resources allocated to perform the required task. Among the brain areas involved in the allocation of resources is the anterior cingulate cortex (participating in the evaluation of the rewards; Parkinson et al., 2000). The activity of this brain area seems particularly impacted by mental fatigue (Tanaka et al., 2014). To account for this reduced anterior cingulate cortex activity, a theory in favor of a failure of the dopaminergic networks has been proposed (Chaudhuri & Behan, 2000). Prolonged neural activity can lead to an increase in adenosine concentration, due to the degradation of adenosine triphosphate (Lovatt et al., 2012). As the receptors of adenosine and dopamine (A2A and the D2 respectively) are colocalized adenosine would stop the dopaminergic signal (Schiffmann et al., 2007). The increase in the concentration of adenosine has already been proposed as a mechanism to explain the effects of mental fatigue (Pageaux et al., 2014).

4.4. COMPENSATION OF MENTAL FATIGUE BY PHYSICAL ACTIVITY AND MUSIC LISTENING

As previously found by Jacquet, Poulin-Charronnat, et al. (2021), Experiment 1 evidenced that arm-pointing movement performance was impaired with mental fatigue and that the performance was impaired even more during the 20-min period following mental fatigue induction. Experiment 2 showed that the negative effects of mental fatigue on the arm-pointing task could be counteracted by 15 min of listening to music or moderate physical activity.

Indeed, there was no longer any significant difference between the performance on the arm-pointing task before and after the mentally fatiguing task when it was followed by 15 min of listening to some pleasant music, selected by the participants. Following 15 min of cycling at a moderate intensity, the performance on the arm-pointing task was even better at the end compared to the beginning of the experiment. Concerning electrophysiological markers (i.e., brain oscillations at rest), the results did not seem to indicate a recovery effect. While listening to music did not induce any changes in brain oscillations, an increase in alpha power was observed after physical activity. As alpha power has been linked to mental fatigue (Tran et al., 2020), this observation suggests that participants could experience greater mental fatigue after the physical activity. However, this increase in alpha power might not be related to mental fatigue but rather to the physical fatigue resulting from the cycling exercise (Fumoto et al., 2010). Some authors have attributed the increase in alpha power to the increase in serotonin induce by physical activity (Chaouloff et al., 1986). In this context, alpha power was likely not to be relevant to assessing the presence of mental fatigue after physical exercise.

Both 15 min of listening to music and moderate physical activity thus appear efficient in counteracting the effects of mental fatigue. Previous studies have already demonstrated the beneficial effect of certain strategies to counter mental fatigue, such as caffeine (Azevedo et al., 2016; Franco-Alvarenga et al., 2019), or creatine intake (Van Cutsem et al., 2020). The positive effects on mental fatigue of both caffeine (Hsu et al., 2010; Huang et al., 2005) and creatine (Klivenyi et al., 2003; Matthews et al., 1999) have been attributed to dopamine secretion. An increase in dopamine could compensate for the decreased activity of the dopaminergic system induced by mental fatigue, preserve the activity of some brain areas despite mental fatigue, and consequently maintain performance. In the present experiment, the beneficial effect of listening to music and physical activity could therefore be attributed to their effects on dopamine production. It has already been demonstrated that both listening to music (Salimpoor et al., 2011) and practicing acute physical exercise (Hattori et al., 1994) could increase dopamine secretion, and as for caffeine or creatine, the resulting higher levels of dopamine could help to alleviate the effects of mental fatigue.

Furthermore, previous studies evidenced that both listening to music (Chabris, 1999) and acute physical activity (Byun et al., 2014) could lead to increased arousal levels and enhance performance. Although increased arousal levels do not seem to impact movement time (Ando et al., 2008), they may improve attentional processes (Heuer & Reisberg, 1990). This

could account for the compensation effect of mental fatigue from both listening to music and acute physical activity observed on the arm-pointing task. We also observed that 15 min of physical activity did more than just compensate for the effects of mental fatigue. Indeed, motor performance on the arm-pointing task was better after 15 min of moderate cycling following mental fatigue induction than its initial level. A similar result has already been observed in a study using caffeine intake to compensate for mental fatigue (Azevedo et al., 2016). This effect could be attributed to the generally positive effects of acute physical exercise. In parallel to the increase in dopamine, previous studies revealed that caffeine (Huang et al., 2005) and also acute physical exercise (Bauer et al., 2020) decreased the sensitivity of the adenosine receptors, increasing dopaminergic secretion even more. Through these combined effects on both dopamine and adenosine secretion, caffeine intake and acute moderate physical activity could not only compensate for the negative effects of mental fatigue but also improve performance.

4.5. CONCLUSION

The present study demonstrated that both listening to pleasant music and physical activity at a moderate intensity could be efficient strategies to counteract the negative effects of mental fatigue on motor performance. The positive effects of these two compensation strategies could be linked to their action on dopamine production, a neurotransmitter whose secretion is reduced by mental fatigue. It would be interesting to verify the positive effects of these compensation strategies on other cognitive processing (e.g., attention, planning and inhibition) or physical tasks (e.g., endurance exercise and technical skills for specific sports). Moreover, neuroimaging techniques such as fMRI could be interesting to examine further the mechanisms involved in the beneficial effects of both physical activity and listening to music to counteract mental fatigue.

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SUPPLEMENTARY DATA

Experiment 1

All results concerning the TLDB task performed during Experiment 1 are presented in this section.

Behavioral data

Mean RT was 533.2 ms (±8.9) for odd digits, 540.6 ms (±9.5) for even digits, and 484.4 ms (±9.8) for letters. For digits, a significant time-on-task effect was reported [$F_{(1.815, 23.590)} = 6.769$, $p = .006$, $\eta_p^2 = .342$], qualified by a linear trend [$F_{(1, 13)} = 9.392$, $p = .009$, $\eta_p^2 = .419$], evidencing faster RTs over time. No significant effect of parity, nor parity × time-on-task interaction were reported (*ps* > .24, $\eta_p^2 < .11$). Concerning letters, no significant effect was observed (*ps* > .13, $\eta_p^2 < .16$).

Mean accuracy was 92.6% (±0.7) for odd digits, 91.9% (±0.8) for even digits, 93.5% (±0.7) for same letters, and 98.8% (±0.2) for different letters. No significant effects of parity, nor time-on-task, nor parity × time-on-task interactions were reported for accuracy on digits, suggesting that performance was maintained over time (*ps* > .05, $\eta_p^2 < .17$). A significant stimulus type effect was observed for letters [$F_{(1, 13)} = 30.626$, $p < .001$, $\eta_p^2 = .702$], indicating a better accuracy for different letters compared to same letters. Moreover, a significant time effect [$F_{(3, 39)} = 4.378$, $p = .009$, $\eta_p^2 = .252$] qualified by a quadratic trend [$F_{(1, 13)} = 11.765$, $p = .004$, $\eta_p^2 = .475$] and a significant stimulus type × time-on-task interaction [$F_{(3, 39)} = 3.172$, $p = .035$, $\eta_p^2 = .196$], qualified by a quadratic trend [$F_{(1, 13)} = 6.380$, $p = .025$, $\eta_p^2 = .329$] were observed. The decomposition of this interaction evidenced that accuracy remained stable for different letters ($p > .06$, $\eta_p^2 < .17$], while its increase between Block 1 and Block 3 for same letters [$t_{(13)} = -2.017$, $p = .032$, $\eta_p^2 = .-.539$], and decrease between Block 3 and Block 4 [$t_{(13)} = 3.373$, $p = .020$, $\eta_p^2 = .902$].

Experiment 2

All results concerning the TLDB task performed during Experiment 2 are presented in this section.

Behavioral data

Mean RT was 554.5 ms (±4.0) for odd digits, 560.6 ms (±4.0) for even digits, and 494.5 ms (±4.9) for letters. For digits, a significant time-on-task effect was reported [$F_{(1.952, 42.946)} = 6.300$, $p = .004$, $\eta_p^2 = .223$], qualified by a linear trend [$F_{(1, 22)} = 9.071$, $p = .006$, $\eta_p^2 = .292$], evidencing faster RTs over time. Concerning letters, a significant time-on-task effect was observed [$F_{(3, 66)} = 4.090$, $p = .010$, $\eta_p^2 = .163$], qualified by a linear trend [$F_{(1, 22)} = 7.799$, $p = .011$, $\eta_p^2 = .262$], also indicating faster RTs over time.

Mean accuracy was 94.4% (±0.3) for odd digits, 93.1% (±0.3) for even digits, 86.9% (±0.9) for same letters, and 99.0% (±0.1) for different letters. Analyses revealed that the accuracy was greater for odd digits compared to even digits [$F_{(1, 22)} = 4.773$, $p = .040$, $\eta_p^2 = .178$]. No significant effect of time-on-task, nor parity × time-on-task interaction were reported for accuracy, suggesting that performance was maintained over time (*ps* > .15, $\eta_p^2 < .08$). A significant stimulus type effect was observed for letters [$F_{(1, 22)} = 41.367$, $p < .001$, $\eta_p^2 = .653$], indicating a better accuracy for different letters compared to same letters. However, neither significant effect of time on task nor stimulus type × time-on-task interaction (*ps* > .45, $\eta_p^2 <$ .04) were observed, indicating that performances were maintained over time.

EEG data

Event-related potentials for digits

N100. No significant change was observed for the N100 amplitude for digits.

P200. A significant time-on-task effect was reported for FL, FM, FR, CM, PL, and PR regions (all *ps* < .025; $\eta_p^2 > .17$), with a greater effect on frontal regions (all *ps* < .001; $\eta_p^2 > .28$), and more especially on FL region [$F_{(3, 63)} = 11.102$, $p <.001$, $\eta_p^2 = .335$]. For FL, FM, FR, CM, and PL regions, this main effect of time on task was qualified by a linear trend (all *ps* < .016; $\eta_p^2 >$ .24), revealing an increase in P200 amplitude over time, whereas the main effect of time on task was qualified by a quadratic trend on PR region [$F_{(1, 22)} = 10.889$, $p = .003$, $\eta_p^2 = .331$], indicating a decrease in P200 amplitude until the third part of the TLDB task, followed by an increase at the end of the TLDB task.

P300. Analyses revealed a greater P300 for odd digits compare to even digits in CR region [$F_{(1, 22)} = 5.057$, $p = .035$, $\eta_p^2 = .187$]. A significant time effect were reported in PL region [$F_{(2.196, 48.304)} = 3.690$, $p = .029$, $\eta_p^2 = .144$], indicating a linear decrease in P300 amplitude over time [$F_{(1, 22)} = 5.560$, $p = .028$, $\eta_p^2 = .202$].

Event-related potentials for letters

N100. Analyses revealed a significant effect of stimulus type for all regions (all *ps* < .001; η_p^2 > .45), indicating a greater N100 for same letters compared to different letters.

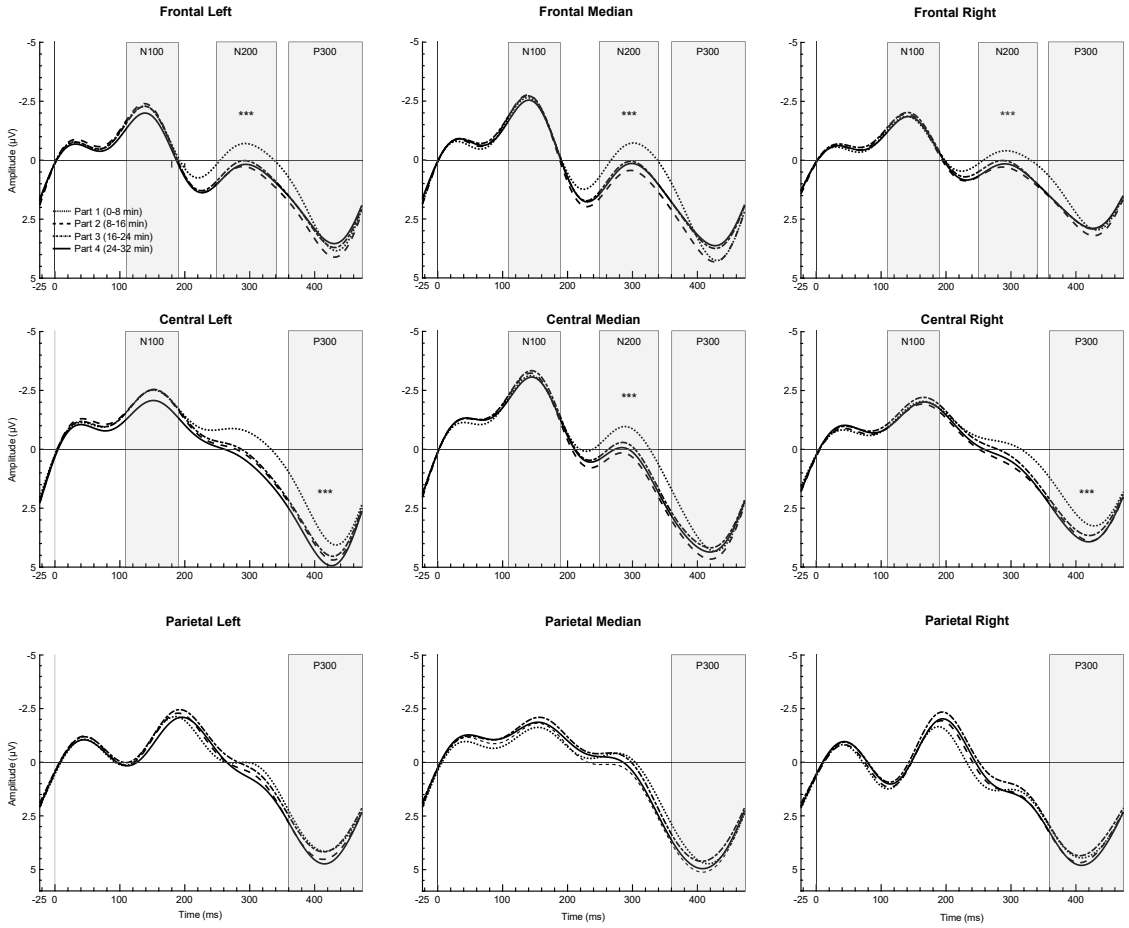

Figure S1. Time-on-task effect for letter stimuli during the 32-min TLDB task in all regions of interest. The gray rectangles show the time window used for event-related potential analyses. ***: Significant time-on-task effect (*p* < .001).

N200. A significant effect of stimulus type, revealing a greater N200 for different letters compared to same letters, was observed in all frontal regions (all *ps* < .04; η_p^2 > .18). A significant main effect of time on task was reported for all frontal and central regions (all *ps* < .001; η_p^2 > .21), with maximal effect in CM region [$F_{(2.141, 47.091)}$ = 10.286, p <.001, η_p^2 = .319], qualified by quadratic trends for all frontal regions (all *ps* < .015; η_p^2 > .24) with a decrease in N200 amplitude between the first and the second part of the TLDB task, followed by an increase in N200 amplitude during the end of the TLDB task. Finally, a significant stimulus type × time-on-task interaction was reported for all frontal and central regions (all *ps* < .003; η_p^2 > .20), with

maximal effect in CM region [$F_{(3, 66)}$ = 8.447, p <.001, η_p^2 = .277], qualified by quadratic trends for all regions (all *ps* < .003; η_p^2 > .36), highlighting that the decrease in N200 amplitude over time was more pronounced for same letters than different letters.

P300. A significant effect of the stimulus type was reported for all regions (all *ps* < .001; η_p^2 > .51), highlighting a greater P300 amplitude for same letters compared to different letters Analyses revealed a significant main effect of time on task in CL [$F_{(1.818, 40.004)}$ = 5.620, *p* =.009, η_p^2 = .203], and CR regions [$F_{(1.855, 40.810)}$ = 12.033, *p* < .001, η_p^2 = .354], qualified by a linear trend for CR region [$F_{(1, 22)}$ = 15.386, *p* = .001, η_p^2 = .423], and a cubic trend in CL region [$F_{(1, 22)}$ = 12.971, *p* =.002, η_p^2 = .382], indicating an overall increase in P300 amplitude over time. Finally, a significant stimulus type × time-on-task interaction was observed for all regions (all *ps* < .012; η_p^2 > .15), with a maximal effect on PL region [$F_{(3, 66)}$ = 5.450, *p* =.002, η_p^2 = .199]. This effect was qualified by a linear trend in CM, PL, PM, and PR regions (all *ps* < .040; η_p^2 > .17) and a cubic trend in FL, FM, FR, and CR regions, indicating that the P300 amplitude increased only for same letters, whereas it remained stable for different letters. A quadratic trend for CL region [$F_{(1, 22)}$ = 8.225, p = .009, η_p^2 = .272] highlighted that the P300 amplitude increased in the first part of the TLBD task and remained stable for the end of the task for same letters, whereas it remained stable over time for different letters.

Brain oscillations during the Time Load Dual Back task

Theta: Analyses showed a significant time-on-task effect for all frontal and central regions (all *ps* < .004, η_p^2 > .24), PL [$F_{(1.366,30.044)}$ = 3.860, *p* = .047, η_p^2 = .149], and PM regions [$F_{(1.462, 32.027)}$ = 10.937, *p* < .001, η_p^2 = .332], qualified by a quadratic trend for PL region [$F_{(1,22)}$ = 12.842, *p* = .002, η_p^2 = .369], indicating a decrease in theta power during the first parts of the TLDB task followed by maintenance in theta power at the end of the TLDB task. However, the trend was linear for all other regions (all *ps* < .007, η_p^2 > .29), indicating a decrease in theta power over time.

Alpha: Analyses showed a significant time-on-task effect for FM, FR, CM, PM, and PR regions (all ps < .05, η_p^2 > .13), with a maximal effect on PM region [$F_{(1.583, 34.833)}$ = 5.496, *p* = .013, η_p^2 = .200]. This main effect was qualified by a quadratic trend for all regions (all *ps* < .004, η_p^2 > .340), evidencing a decrease in alpha power between the first and the second part of the TLDB task followed by an increase in alpha power over time.

4.2 Synthèse

Cette étude a dans un premier temps permis de répliquer les effets de persistance de la fatigue mentale sur le contrôle moteur obtenus dans l'Étude 3. Comme dans cette étude précédente, malgré une sensation subjective de fatigue mentale qui décroit progressivement lors des 20 minutes suivant la tâche mentalement fatigante, les performances lors d'une tâche de pointage (évaluant le contrôle moteur) étaient de plus en plus dégradées.

Ayant répliqués ces effets de persistance, l'objectif principal de cette étude était de proposer des stratégies de compensation pour contrecarrer les effets de la fatigue mentale sur le contrôle moteur. Nous avons observé que l'écoute de musique et la pratique d'activité physique à intensité modérée étaient efficaces pour lutter contre la fatigue mentale car 20 minutes après ces deux activités les performances lors de la tâche de pointage n'étaient plus altérées. On a même noté que les performances étaient meilleures qu'au début de l'expérience (avant fatigue mentale) pour les participants ayant pratiqué 15 minutes d'activité physique. Les bienfaits de la pratique d'une activité physique et de l'écoute de musique ont été attribués à la libération de dopamine induite par chacune de ces deux activités. Nous savons que l'activité de certaines structures cérébrales comme le CCA est particulièrement impactée par la fatigue. Le CCA est particulièrement impliqué dans l'évaluation des récompenses, et son activation permet d'engager des ressources importantes pour mener à bien les tâches dans lesquelles nous nous engageons. La diminution de l'activité du CCA serait liée à une défaillance des réseaux dopaminergiques. La pratique d'une activité physique et l'écoute de musique pourrait palier cette défaillance des réseaux dopaminergiques et ainsi contrecarrer les effets de la fatigue mentale en permettant un maintien des performances.

Des études en neuroimagerie et en neurobiochimie sont cependant nécessaires afin de mieux comprendre les mécanismes explicatifs impliqués dans les effets bénéfiques de l'activité physique et de l'écoute de la musique sur la compensation de la fatigue mentale.

V. DISCUSSION GENERALE

À ce jour, la fatigue mentale représente un champ de recherche en plein essor. On trouve plus de 260 publications parues en 2020 sur cette thématique, preuve s'il en est de l'intérêt grandissant qu'elle suscite. Pourtant les études relatives à la fatigue mentale ne sont pas récentes. Dès 1845, le chimiste et physiologiste britannique John Davy s'est intéressé aux effets d'un effort cognitif soutenu sur plusieurs variables dont la température corporelle (Davy, 1845). Il montra qu'un effort cognitif soutenu engendrait une augmentation de la température corporelle. Ce fut la première preuve expérimentale, si l'on peut dire, indiquant qu'un effort cognitif soutenu, induisant à priori la fatigue mentale, pouvait engendrer des modifications physiologiques. Depuis, les études ont été nombreuses, et il est maintenant bien établi que la fatigue mentale peut impacter de façon négative non seulement les performances cognitives (e.g., Boksem et al., 2005; Lorist et al., 2005; van der Linden et al., 2003), mais également les performances physiques (e.g., Marcora et al., 2009; Pageaux & Lepers, 2018; Smith, Coutts, et al., 2016; Van Cutsem, Marcora, et al., 2017). Ces altérations peuvent avoir de nombreuses répercussions sur la vie quotidienne avec une augmentation des accidents de la route (Dinges, 1995; Karanikas & Nederend, 2019), des erreurs médicales (Nikpeyma & Gholamnejad, 2009; Tawfik et al., 2018), une baisse de la productivité au travail (Ricci et al., 2007) ou encore être impliquées dans certaines pathologies comme par exemple la dépression (Fuhrer & Wessely, 1995; Walford et al., 1993). Cependant, et alors même que les effets de la fatigue mentale sont bien établis, leurs origines et les mécanismes sous-jacents restent encore mal connus. Plusieurs modèles ont été proposés afin de formuler des hypothèses explicatives et mettre en évidence des origines physiologiques de la fatigue mentale (Boksem & Tops, 2008; Hockey, 2011; Ishii et al., 2014). À l'heure actuelle, il n'existe toujours pas de consensus permettant d'expliquer pourquoi et comment la fatigue mentale influence nos comportements. Ce travail de thèse s'inscrit donc dans ce contexte. Le premier objectif de ce travail était de mieux appréhender les mécanismes neurophysiologiques à l'origine de la fatigue mentale. Le second objectif était de s'intéresser aux effets de la fatigue mentale sur les performances cognitives et physiques et de tester des stratégies de compensation afin d'éviter ou de limiter les effets délétères de celle-ci.

1 Quelle(s) tâche(s) utiliser afin d'induire la fatigue mentale en laboratoire ?

Pour étudier le phénomène de fatigue mentale, le premier enjeu est de recréer cette sensation en laboratoire. Au cours de ce travail de thèse, nous avons utilisé plusieurs tâches

cognitives, précédemment utilisées dans la littérature. Nous avons, en particulier, utilisé une tâche prolongée d'imagerie motrice (e.g., Graham et al., 2014; Rozand et al., 2016; Talukdar et al., 2019), une tâche prolongée de Stroop modifié (e.g., Martin et al., 2016; Pageaux et al., 2015; Rozand et al., 2015) et une tâche de « *Time Load Dual Back* » (TLDB; e.g., Borragan et al., 2017; Borragan et al., 2016; O'Keeffe et al., 2020). Ces tâches cognitives, bien que de nature très différente et impliquant des processus cognitifs différents, ont toutes les trois permis d'induire des états de fatigue mentale. Elles ont cependant été utilisées sur des durées assez différentes allant de 32 min à 90 min. Lors d'une étude préliminaire conduite sur 16 participants, nous avions essayé d'induire de la fatigue mentale avec une tâche de TLDB de 16 min. Bien que cette durée de 16 min ait été suffisante pour induire une augmentation de la sensation subjective de fatigue mentale évaluée par une échelle de type VAS, aucun effet négatif n'a été observé sur une tâche de pointage subséquente impliquant le membre supérieur. L'instauration d'une sensation subjective de fatigue mentale à la suite de la réalisation d'une tâche de TLDB durant 16 min avait déjà été reportée dans d'autres études et pourrait refléter un mécanisme permettant d'alerter le sujet d'une baisse potentielle des performances (Borragan et al., 2017; Borragan et al., 2016; O'Keeffe et al., 2020). Afin de dépasser ce simple stade « d'alerte », et pour induire des effets significatifs de la fatigue mentale sur une performance motrice, nous avons choisi de doubler la durée de la tâche cognitivement exigeante. Avec 32 min de tâche de TLDB, nous avons réussi à induire non seulement une augmentation de la sensation subjective de fatigue mentale mais aussi une dégradation des performances lors de tâches de pointage. L'intérêt principal d'utiliser des tâches cognitivement plus coûteuses comme la tâche de TLDB plutôt que de tâches « plus classiques » telles que la tâche de Stroop ou d'AX-CPT, est de limiter la contagion des effets liés à la fatigue mentale par des phénomènes d'ennui. La tâche de TLDB permet de maintenir un niveau d'alerte plus important que lors des tâches de Stroop ou d'AX-CPT, créant ainsi un contexte moins favorable à l'apparition de somnolence (Borragan et al., 2017; O'Keeffe et al., 2020). Lors des études 3 et 4 nous avons choisi d'utiliser la tâche de TLDB afin de mieux appréhender les effets spécifiquement liés à la fatigue mentale.

Cependant, il est important de mentionner que la réalisation de la tâche de TLDB semble soumise à des processus d'apprentissage, et ce malgré la réalisation d'une session de familiarisation. Lors d'une étude préliminaire où nous souhaitions réaliser plusieurs sessions avec induction de fatigue mentale, nous avons demandé aux participants de réaliser à deux reprises, avec 2 à 5 jours d'intervalle entre chaque session, une tâche de TLDB de 32 min. Les

analyses statistiques menées sur la sensation subjective de fatigue mentale ont montré que, lors des deux sessions, la « quantité » de fatigue mentale induite était différente. Lors de la première session la tâche cognitive de TLDB a induit « plus » de fatigue mentale que lors de la seconde session. Cette différence pourrait s'expliquer par les effets d'apprentissage liés à la réalisation de la tâche. La tâche étant assez difficile, lors de la première session elle requière beaucoup plus de ressources cognitives, mais un phénomène d'apprentissage se met en place. Lors de la seconde session, l'apprentissage lié à la première session rend la tâche moins difficile et probablement moins fatigante mentalement. Les effets d'apprentissage sont d'autant plus importants pour des tâches plus difficiles. À l'inverse, l'utilisation de tâches plus longues mais moins complexes, comme 90 min de tâche de Stroop modifiée a provoqué une augmentation de la sensation subjective de fatigue mentale entre deux sessions espacées de 2 à 7 jours.

L'utilisation de tâches cognitives plus courtes, mais plus coûteuses et exigeantes sur le plan cognitif, semble donc particulièrement intéressante, non seulement pour avoir des protocoles expérimentaux plus courts et donc moins contraignants pour les participants et leur recrutement, mais également pour éviter l'apparition de la sensation d'ennui ou de somnolence dont les effets pourraient être confondus avec ceux de la fatigue mentale. En revanche, lors d'études avec des protocoles expérimentaux nécessitant d'induire la fatigue mentale lors de plusieurs sessions, les tâches plus longues comme la tâche de Stroop sont à privilégier pour induire un niveau similaire de fatigue mentale perçue entre sessions, au risque cependant d'induire également, comme nous l'avons vu précédemment, de l'ennui et/ou de la somnolence. Ces observations, uniquement basées sur l'évaluation subjective de la fatigue, mériteraient d'être approfondies par des évaluations objectives de la fatigue mentale.

2 Les marqueurs de fatigue mentale lors d'une tâche cognitive

Plusieurs méthodes peuvent être utilisées afin d'identifier la présence de fatigue mentale qu'elles soient subjectives (e.g., échelle visuelle analogique, BRUMS) ou objectives (e.g., électroencéphalographie, électrocardiographie, oculométrie). Une étude récente suggère d'utiliser préférentiellement une VAS afin d'identifier la présence et l'instauration de fatigue mentale (Smith et al., 2019). Parmi les arguments justifiant ce choix, on peut relever la simplicité de passation, ainsi que sa fiabilité. De plus, l'utilisation d'une VAS permet de mettre en évidence la présence de fatigue mentale avant que cette dernière n'ait des conséquences sur les performances comportementales. C'est donc pour cette raison que dans toutes nos études

nous avons utilisé la VAS pour détecter la présence de fatigue mentale. En parallèle, d'autres types de questionnaires et de mesures subjectives peuvent également être utilisés pour attester de la présence de fatigue mentale comme le BRUMS (e.g., Axelsen et al., 2020; Marcora et al., 2009), le POMS (e.g., Azevedo et al., 2016; Van Cutsem et al., 2018) ou encore le NASA-TLX (e.g., Filipas et al., 2019; Rozand et al., 2014).

On pourrait penser que les performances comportementales constituent un moyen objectif efficace d'évaluer la présence de fatigue mentale, mais ce n'est pas le cas. Bien que dans certaines situations les performances se détériorent avec le temps passé à réaliser une tâche cognitivement coûteuse (e.g., Faber et al., 2012; Lorist et al., 2000), dans d'autres contexte les performances sont maintenues, voire même parfois améliorées (e.g., Martin et al., 2016). Ces différents patrons de résultats ont été observés et sont connus depuis déjà bien longtemps (Martyn, 1913). Dans nos études, nous avons vu des performances cognitives maintenues ou améliorées au cours des tâches cognitivement coûteuses utilisées pour induire de la fatigue mentale. L'amélioration des performances au cours d'une tâche prolongée n'est pas étonnante et peut être associée à des effets d'apprentissage. De plus, plusieurs paramètres, dont la motivation, peuvent influencer le niveau de ressources engagées dans une tâche cognitivement coûteuse, et donc les performances comportementales (Boksem et al., 2006). Dans ce contexte, il semble important d'utiliser d'autres mesures, notamment des marqueurs électrophysiologiques, pour mettre en évidence de façon objective la présence de fatigue mentale. Dans ce travail de thèse, nous nous sommes concentrés sur l'utilisation de l'électroencéphalographie car il a été suggéré dans la littérature que cette technique serait la plus prometteuse pour identifier la présence de fatigue mentale (Lal & Craig, 2001).

Nous avons analysé, dans chacune de nos études, les modulations observées au niveau de l'activité cérébrale, que ce soit les potentiels évoqués ou les oscillations, lors de la tâche cognitivement coûteuse induisant la fatigue mentale. De façon globale au niveau des potentiels évoqués, dans toutes nos études nous retrouvons une décroissante de l'amplitude de la composante N100, ce qui est en accord avec la littérature (e.g., Boksem et al., 2005; Faber et al., 2012) et qui pourrait traduire une baisse de la capacité de discrimination visuelle. Les composantes plus tardives semblent, quant à elles, plus dépendantes de la tâche. Il est donc difficile de définir comment elles évoluent avec l'instauration de fatigue mentale. Cependant, la P300 est une composante souvent mesurée et dont l'amplitude a été reliée à la quantité de ressources attentionnelles engagées dans une tâche (i.e., plus la P300 est ample, plus les ressources attentionnelles sollicité sont importantes). Dans l'Étude 1, nous avons observé une

P300 qui décroissait au cours de la tâche prolongée de Stroop modifié, reflétant une diminution de l'attention comme classiquement observée dans les études sur la fatigue mentale (e.g., Möckel et al., 2015; Murata et al., 2005; Uetake & Murata, 2000; Zhao et al., 2012). Cependant, dans les Études 3 et 4, en utilisant la tâche de TLDB comme tâche mentalement fatigante, nous avons observé une augmentation de l'amplitude de la P300 avec le temps passé à réaliser la tâche. Une possible explication de ce résultat est qu'une augmentation des ressources attentionnelles a été nécessaire pour continuer à maintenir le niveau de performances tout au long de la tâche de TLDB. Nous suggérons donc que, lors d'une analyse des potentiels évoqués, les résultats soient toujours mis en relation avec les données comportementales.

Concernant les effets de la fatigue mentale sur les oscillations cérébrales, une récente revue de littérature a suggéré de s'intéresser en priorité aux ondes thêta et alpha, car elles seraient les marqueurs les plus robustes de la fatigue mentale (Tran et al., 2020). Nos observations dans l'Étude 1 ont montré une augmentation globale des ondes thêta et alpha comme classiquement rapporté (e.g., Katahira et al., 2018; Zhao et al., 2012) et mentionné dans la méta-analyse de Tran et al. (2020). Dans les Études 3 et 4, bien que nous ayons également rapporté une augmentation des ondes alpha au cours de la tâche cognitivement fatigante, nous avons noté une baisse de l'activité thêta avec le temps. Cette évolution inhabituelle pourrait être liée à la tâche de TLDB elle-même. Les ondes thêta ont été reliées à de nombreuses fonctions cognitives comme la mémoire de travail, les processus d'encodage et de récupération de la mémoire épisodique (Hsieh & Ranganath, 2014), fonctions impliquées lors de la tâche de TLDB. Une autre explication possible pourrait être liée à l'ennui. Les études s'intéressant à l'ennui ont montré que ce dernier provoquait une augmentation des ondes thêta (Katahira et al., 2018). L'augmentation des ondes thêta observée dans les études s'intéressant à la fatigue mentale, ne serait peut-être pas un marqueur spécifique de fatigue mentale mais seulement le reflet de l'ennui lié à la nature des tâches servant à induire la fatigue mentale (même si la tâche de TLDB nous semblait être une tâche relativement engageante et courte qui devait éviter l'apparition d'ennui). Ainsi afin de se focaliser uniquement sur les effets spécifiquement liés à la fatigue mentale, une étude récente a suggéré de s'intéresser uniquement aux modulations de l'activité cérébrale lors d'enregistrement effectués au repos avant et après la réalisation d'une tâche induisant la fatigue mentale (Li et al., 2020).

Bien que l'EEG semble prometteur et efficace pour mettre en avant la présence de fatigue mentale, l'utilisation concomitante de différentes mesures nous semble importante à considérer. Combiner différentes méthodes d'évaluation subjectives et objectives afin de mieux

décrire le phénomène de fatigue mentale devrait être la méthodologie utilisée par les études s'intéressant à la fatigue mentale et ses effets (e.g., Smith et al., 2019; Van Cutsem, De Pauw, et al., 2017).

3 Origine des effets de la fatigue mentale sur une tâche physique

Les premiers effets de la fatigue mentale sur les performances physiques ont été mis en évidence depuis bien longtemps. Dès la fin du 21ème siècle, Mosso (1891) a montré que la fatigue mentale pouvait altérer les performances en endurance musculaire des muscles des doigts. Les effets de la fatigue mentale ne se limitent pas seulement aux performances en endurance (pour revue : Brown et al., 2020; Pageaux & Lepers, 2018) car ils altèrent également le contrôle moteur (e.g., Rozand et al., 2015; Rozand et al., 2016) ou les prises de décision (e.g., Gantois et al., 2020; Harris & Bray, 2019; Kunrath et al., 2020), et impactent directement les performances sportives en football (e.g., Greco et al., 2018; Kunrath et al., 2020; Smith et al., 2017) ou tennis de table par exemple (Le Mansec et al., 2018). La durée et l'intensité de la tâche physique semblent être des facteurs importants dans la diminution des performances physiques due à la fatigue mentale (Van Cutsem, Marcora, et al., 2017). Alors qu'aucune des variables physiologiques traditionnellement associées aux performances d'endurance (fréquence cardiaque, lactatémie, consommation d'oxygène, débit ventilatoire) n'est affectée par les effets de la fatigue mentale (pour revue : Pageaux & Lepers, 2018; Van Cutsem, Marcora, et al., 2017), l'origine du déclin de la performance d'endurance semble liée à une perception de l'effort plus importante en présence de fatigue mentale.

Plusieurs modèles ont été proposés dans la littérature afin d'expliquer l'origine de la perception de l'effort. Deux modèles semblent émerger : le modèle des feedback afférents et le modèle de la décharge corollaire. Le modèle des feedback afférents soutient l'hypothèse selon laquelle la perception de l'effort serait d'origine périphérique. Cette hypothèse s'appuie sur les corrélations observées entre l'augmentation de l'effort perçu et l'augmentation de la concentration de la lactatémie et des métabolites dans le milieu musculaire (Noble & Robertson, 1996). Les informations seraient ensuite transmises au système nerveux central via les afférences musculaires des groupes III et IV, connues pour avoir des projections spinales et supra spinales, notamment vers le cortex sensoriel (Craig, 2002). Le modèle de la décharge corolaire, quant à lui, soutient la théorie selon laquelle la perception de l'effort est d'origine centrale (McCloskey, 2011). Au moment de la production de la commande motrice, une copie,

nommée décharge corollaire serait envoyée au niveau du cortex sensoriel, et c'est cette copie de la commande motrice qui serait responsable de la perception de l'effort. Plusieurs études semblent privilégier ce modèle de la décharge corollaire (Marcora, 2009). Pageaux et Gaveau (2016) ont suggéré que le fait de bloquer les afférences musculaires des groupes III et IV n'avait aucun impact sur la perception de l'effort. De plus, une corrélation entre la perception de l'effort et le potentiel cortical lié à la motricité, connu comme étant le reflet de l'activité des aires motrices et prémotrices, a été observée lorsque la perception de l'effort était manipulée par l'instauration de fatigue physique (de Morree et al., 2012), ainsi que par la consommation de caféine (de Morree et al., 2014).

Dans la plupart des études sur la fatigue mentale, aucune variable physiologique périphérique ne semble affectée par celle-ci (pour revue : Pageaux & Lepers, 2018; Van Cutsem, Marcora, et al., 2017). Dans l'Étude 2, nous avons montré que l'augmentation de la perception de l'effort en présence de fatigue mentale était liée à une augmentation de l'activité des aires motrices et prémotrices. De façon intéressante, lors des contractions imaginées, l'augmentation de l'effort perçu au cours de la tâche était également accompagnée d'une augmentation de l'activité des aires motrices et prémotrices. Cependant, que ce soit pour les contractions réelles ou imaginées, nous n'avons pas pu mettre en évidence une corrélation significative entre la perception de l'effort et l'activité des aires motrices et prémotrices. Cette absence de corrélation pourrait s'expliquer par la taille de notre échantillon (n =13), par la difficulté de l'exercice physique réalisé (i.e., 150 contractions isométriques des extenseurs du genou à 50 % de la MVC) générant parfois des artefacts au niveau EEG, ou encore par une variabilité assez importante. Une étude complémentaire, avec quelques ajustements du protocole (e.g., groupe musculaire sollicité moins important, intensité de contraction plus faible) serait nécessaire pour valider les résultats observés dans l'Étude 2.

4 Évolution de la sensation de fatigue mentale dans le temps et phénomène de récupération

L'évolution des effets de la fatigue mentale dans le temps a été peu étudiée jusqu'à présent. Pourtant dès la fin du 19ème siècle, Rivers (1896) s'était déjà intéressé à ces effets, ainsi qu'aux effets de récupération. Après 30 min de travail mental (i.e., additions), il montra que 30 min de repos total étaient insuffisantes pour neutraliser les effets de la fatigue mentale et que 60 min de repos total ne les éliminaient que partiellement. Cette étude semblait indiquer que les

effets de la fatigue mentale persistaient dans le temps. Peu d'études se sont par la suite intéressées à cette question. Lim et Kwok (2016) ont évalué l'influence de pauses d'une durée variée (1 min, 5 min et 10 min) sur une tâche d'attention auditive. Même si les pauses ne permettaient pas de retrouver le niveau de performance initial, elles permettaient de contrecarrer partiellement les effets de la fatigue mentale. De plus, plus la pause était longue plus elle s'avérerait efficace. Selon les auteurs, les effets bénéfiques étaient liés au fait que les participants engageaient davantage d'effort pour accomplir la tâche après une pause. Ces résultats, en faveur d'une récupération partielle, ont également été mis en évidence par d'autres études (e.g., Li et al., 2016; Matuz et al., 2019), confirmant que plus la pause est longue et plus elle serait bénéfique sur la récupération de la fatigue mentale (Chan et al., 2012). Smith et al. (2019) ont suivi, pendant 60 min, l'évolution des effets de la fatigue mentale sur sa sensation subjective (mesurée toutes les 10 min) et sur les capacités attentionnelles (mesurées toutes les 30 min). En ce qui concerne la sensation subjective de fatigue mentale, elle diminuait de façon progressive après une tâche cognitivement coûteuse mais pouvait malgré tout restée plus élevée qu'à son niveau initial même 60 min après la réalisation de la tâche mentalement fatigante. Ces observations sont cohérentes avec ce que nous avons pu observer dans nos Études 3 et 4 avec une sensation subjective de fatigue mentale qui décroissait progressivement durant les 20 min suivant nos tâches cognitivement coûteuses.

Dans l'étude de Smith et al. (2019), alors que les capacités attentionnelles étaient affectées par 90 min de Stroop ou de tâche d'AX-CPT, lors des évaluations de ces mêmes capacités attentionnelles 30 et 60 min après la fin de la tâche cognitivement coûteuse, les participants avaient retrouvé leurs capacités initiales. Plusieurs explications peuvent être avancées pour justifier les différences observées entre nos résultats et ceux de Smith et al. (2019). Une première explication est le délai de récupération. Dans nos études, nous avons évalué le phénomène de récupération des effets de la fatigue mentale sur 20 min, alors que Smith et al., (2019) ont évalué la récupération 30 min et 60 min après la fin de la tâche cognitivement coûteuse. Si nous avions mesuré de nouveau les performances de pointage 30 min après avoir fini la tâche cognitivement coûteuse, un rebond dans le niveau de performance aurait peut-être pu être observé. Deuxièmement, les capacités évaluées sont différentes. Dans nos études, nous nous sommes intéressés aux effets de la fatigue mentale sur le contrôle moteur (tâche de pointage) alors que Smith et al. (2019) se sont intéressés aux effets de la fatigue mentale sur l'attention. Troisièmement, les tâches cognitives utilisées pour induire la fatigue mentale étaient différentes. La fatigue mentale a été induite par des tâches cognitives longues

(i.e., Stroop et AX-CPT) dans l'expérience de Smith et al. (2019), ces tâches sont aussi connues pour provoquer plus l'ennui et/ou de la somnolence, que des tâches cognitivement plus coûteuse comme la tâche de TLDB que nous avons utilisée (O'Keeffe et al., 2020). La récupération peut être plus rapide sur ces phénomènes (i.e., ennui et somnolence), ce qui pourrait expliquer les différences observées au niveau des résultats entre les études.

Le dernier paramètre à prendre en considération est la nature de l'activité proposée lors de la récupération. Dans nos études nous avons utilisé lors de la phase de récupération des discussions verbales avec des sujets standardisées (e.g., hobbies, sport, avenir professionnel), afin de se rapprocher d'une situation écologique, dans une entreprise par exemple, lorsque nous faisons une pause. Dans l'étude de Smith et al. (2019), les participants lisaient des magazines lors de la récupération. Bien qu'il soit mentionné que les magazines étaient émotionnellement neutres, on ne peut pas exclure le fait que la lecture ait pu avoir un effet bénéfique sur la récupération de la fatigue mentale en lien avec le contenu des magazines (e.g., sujet intéressant, drôle, surprenant). De même, nous ne pouvons pas exclure que la discussion verbale avec nos participants ait pu induire de l'ennui, expliquant ainsi un déclin progressif des performances au cours de la phase de récupération.

Au regard des résultats et des questionnements exposés ci-dessus, nous pouvons constater que des interrogations concernant la persistance des effets de la fatigue mentale dans le temps et la récupération de ces effets subsistent. À ce jour, trop peu d'études ont été réalisées au vu du nombre important de paramètres à prendre en compte (e.g., nature de la tâche cognitive, capacité évaluée, nature de la pause), et ce champ d'investigation devra encore être approfondi dans de futures études.

5 Les stratégies pour compenser la fatigue mentale et contrecarrer ses effets

Comme nous l'avons vu dans ce travail de thèse, la fatigue mentale a fait l'objet de nombreuses études et ces effets commencent à être bien identifiés. Pourtant, bien qu'il soit communément admis que la fatigue mentale impacte de façon négative nos performances cognitives et physiques (e.g., Boksem et al., 2005; Pageaux & Lepers, 2018; van der Linden et al., 2003), peu d'études se sont penchées sur les stratégies pouvant y remédier. Parmi les études s'intéressant à cette problématique, nous pouvons dissocier deux grands types d'interventions : les interventions utilisant des substances bioactives (e.g., caféine, guarana, créatine, glucose),

et les interventions utilisant des stratégies non-bioactives (e.g., musique, odeurs, méditation). Les substances bioactives, et notamment la caféine, ont montré leur efficacité pour lutter contre la fatigue mentale et le déclin des performances qu'elle engendre (e.g., Azevedo et al., 2016; Franco-Alvarenga et al., 2019; Van Cutsem et al., 2018). L'utilisation de la caféine semble même faire mieux que contrer les effets de la fatigue mentale puisque les performances après prise de caféine en présence de fatigue mentale sont meilleures qu'avant l'induction de fatigue mentale (Azevedo et al., 2016). Les effets bénéfiques de la caféine seraient liés à l'activation de zones cérébrales spécifiques (notamment le CCA particulièrement impliqué dans le phénomène de fatigue mentale) et à l'augmentation de certains neurotransmetteurs comme la dopamine (Hsu et al., 2010; Volkow et al., 2015). Cependant, l'utilisation de substances bioactives comme la caféine peut entraîner des effets de dépendance ainsi que des effets secondaires néfastes comme des maladies coronariennes, du cholestérol, des troubles du rythme cardiaque et du sommeil, l'apparition d'anxiété ou des troubles gastro-intestinaux (Dworzański et al., 2009; McLellan et al., 2016; Nawrot et al., 2003). Pour ces raisons, l'utilisation de stratégies non-bioactives pourrait être particulièrement intéressante.

À ce jour, peu d'études ont testé les effets compensatoires de la fatigue mentale à travers l'utilisation de stratégies n'utilisant pas de substances bioactives. Dans l'Étude 4, nous avons proposé de contrer les effets délétères de la fatigue mentale par la pratique, pendant 15 min, d'une activité physique aérobie ou l'écoute de musique plaisante. Ces stratégies ont été choisies pour leurs effets analogues à ceux de la caféine sur la production de dopamine. En effet, il est connu que l'écoute de musique (Ferreri et al., 2019; Salimpoor et al., 2011), comme la pratique aiguë d'activité physique (Hattori et al., 1994; Meeusen et al., 1994) peuvent augmenter le niveau de dopamine. Les deux stratégies proposées dans notre étude ont été efficaces pour contrer les effets de la fatigue mentale. De façon intéressante, et à l'instar de la caféine (Azevedo et al., 2016), la pratique d'une activité physique à intensité modérée durant 15 min permet même d'obtenir de meilleures performances qu'avant induction de fatigue mentale. Une possible explication à ce résultat est l'effet bénéfique général de l'activité physique qui a déjà été montré sur les performances cognitives (Hillman et al., 2009; Oberste et al., 2019; Yanagisawa et al., 2010) et physiques (Fradkin et al., 2010; Hajoglou et al., 2005). Ces effets bénéfiques sont liés aux effets précédemment mentionnés sur la fonction dopaminergique, induisant non seulement une augmentation de la dopamine (Hattori et al., 1994; Meeusen et al., 1994), mais aussi une baisse de la sensibilité des récepteurs de l'adénosine (Bauer et al., 2020) ce qui provoque une meilleure sécrétion dopaminergique. L'augmentation de ce taux de

dopamine est connue pour améliorer de nombreuses fonctions cognitives comme la mémoire de travail (Murphy et al., 1996) ou l'attention (Noudoost & Moore, 2011). En régulant les processus liés à la charge cognitive, la dopamine permet d'engager plus de ressources pour réaliser une tâche est donc d'avoir de meilleurs performances (Westbrook et al., 2020)

6 Conclusions et perspectives

Les études réalisées lors de ce travail de thèse ont permis d'éclaircir en partie les origines électrophysiologiques de la fatigue mentale que ce soit lors d'une tâche mentalement fatigante ou bien lors d'un exercice physique en endurance subséquent. De plus, les travaux réalisés ont permis de mettre en évidence que les effets délétères de la fatigue mentale pouvaient persister dans le temps et que l'utilisation de certaines stratégies de compensation comme l'écoute de musique agréable ou la pratique d'une activité physique à intensité modérée pouvaient être efficaces pour contrecarrer ces effets. Cependant cette thématique autour de la fatigue mentale ouvre encore de nombreuses perspectives.

Ce travail de thèse a permis de mettre en avant les effets de la fatigue mentale sur certains marqueurs électrophysiologiques. Ainsi, lors de nos études nous avons mis en évidence une diminution de la N100 avec l'augmentation du temps passé sur la tâche et l'instauration de fatigue mentale. Ces résultats sont cohérents avec la littérature existante et l'on peut penser qu'il s'agit d'un marqueur fiable de fatigue mentale. Concernant la P300, les résultats divergent entre nos études. Lors de l'Étude 1, nous avons observé une diminution de l'amplitude de la P300 au cours de la tâche prolongée de Stroop modifiée, alors que dans les Études 3 et 4 nous avons observé une augmentation de l'amplitude de la P300 au cours de la tâche de TLDB. Cette divergence reflète des différences dans l'évolution de l'attention allouée à la réalisation de la tâche. Cette composante P300 ne nous semble alors pas la plus pertinente par attester de la présence de fatigue mentale. Grâce à l'EEG nous avons également pu mettre en évidence lors de l'Étude 2, que l'augmentation de la perception de l'effort lors d'un exercice d'endurance en présence de fatigue mentale était liée à une augmentation de l'activation des aires motrices et prémotrices. Les Études 3 et 4 ont montré que les effets de la fatigue mentale sur une tâche de contrôle moteur étaient persistants mais qu'ils pouvaient être compensés par la pratique aiguë d'une activité physique à intensité modérée ou l'écoute de musique plaisante. Enfin ces deux dernières études ont mis en lumière des divergences entre une évaluation subjective de la fatigue

mentale et ses répercussions sur une tâche de contrôle moteur, montrant ainsi l'importance d'utiliser différents types des marqueurs pour évaluer la fatigue mentale.

Les études investiguant les relations entre fatigue mentale et performances physiques montrent que la fatigue mentale ne semble pas impacter la capacité de production de force maximale, concluant à une absence d'effet de la fatigue mentale sur la fonction neuromusculaire (e.g., Pageaux et al., 2013; Rozand et al., 2014; Smith et al., 2015). Pourtant, l'analyse de la capacité de production de force maximale n'est pas le seul moyen d'évaluer la fonction neuromusculaire La fonction neuromusculaire peut également être évaluée par la vitesse d'atteinte d'une force ou la vitesse « de montée en force » (i.e., vitesse à laquelle on est capable d'atteindre un niveau de force donné). Ce paramètre semble être plus sensible à la détection de changements aigus et chroniques de la fonction neuromusculaire que la capacité de production de force (Angelozzi et al., 2012; Peñailillo et al., 2015). Il n'a pourtant été que très rarement étudié dans le cadre d'étude sur la fatigue mentale. Les rares études qui s'y sont intéressées, ont étudié ce paramètre comme une variable secondaire et n'ont pas observé d'effet de la fatigue mentale (Jacquet et al., 2021; Le Mansec et al., 2018). La vitesse à laquelle on est capable d'atteindre un niveau de force donné est pourtant liée à la plupart des performances impliquées dans les tâches de la vie quotidienne (Maffiuletti et al., 2016; Maffiuletti et al., 2010). Pour ces raisons, il serait intéressant d'examiner plus précisément les effets de la fatigue mentale sur la vitesse de montée en force. Ceci fera l'objet d'une future expérimentation conduite au laboratoire.

Un autre axe à développer est celui relatif aux stratégies pour compenser la fatigue mentale. Dans ce travail nous avons vu que l'utilisation d'écoute de musique agréable ou la pratique d'une activité physique durant 15 min pouvaient être efficaces pour contrer les effets de la fatigue mentale. Il pourrait être intéressant de voir si des stratégies utilisées plus précocement et de façon plus régulière (e.g., plusieurs fois par semaine pendant plusieurs semaines) pourraient s'avérer efficace pour prévenir l'apparition de fatigue mentale ou tout du moins limiter son apparition. Parmi les stratégies pouvant être utilisées à cet effet, nous pensons notamment à la pratique régulière d'activité physique en endurance. Proposer une activité physique modérée comme moyen de prévention pour la fatigue mentale pourrait être particulièrement pertinent du fait des effets de l'activité physique sur les fonctions dopaminergiques. En effet, l'activité physique, réalisée de manière régulière et à long terme, favorise l'activité dopaminergique (Bauer et al., 2020). Nous avons donc toutes les raisons de penser que cela pourrait s'avérer efficace pour lutter contre la fatigue mentale, d'autant plus

que Martin et al. (2016) ont montré que des sujets très entrainés (cyclistes professionnels) semblaient plus résistants à la fatigue mentale que des sujets peu entrainés. Il semble aussi pertinent de continuer à investiguer les effets de stratégies « aigues » de compensation de la fatigue mentale. Ainsi on pourrait proposer de compenser la fatigue mentale avec d'autres méthodes également connues pour avoir des effets bénéfiques sur le système dopaminergique comme la pratique du yoga (Newberg & Iversen, 2003). Dans l'Étude 4 de ce travail de thèse, nous avons mesuré les effets bénéfiques des stratégies de compensation sur une tâches de contrôle moteur, mais il pourrait être intéressant de tester ces effets sur d'autres types de tâches comme des tâches attentionnelles, de planification ou d'endurance.

La dernière perspective que nous souhaitons évoquer est la possibilité de réaliser des études dans des situations plus écologiques. Même si comme nous l'avons dit dans la partie introductive de ce travail, il est plus facile d'isoler les mécanismes de la fatigue mentale dans un milieu contrôlé et avec des tâches standardisées, il n'en reste pas moins pertinent de l'étudier dans un contexte écologique et représentatif de la vie quotidienne. Ainsi nous pourrions par exemple utiliser les smartphones, omniprésents dans la société actuelle pour induire de la fatigue mentale tout en restant dans un milieu de laboratoire contrôlé (Fortes et al., 2020; Greco et al., 2018). Une autre perspective intéressante à poursuivre serait d'exporter les études que nous réalisons en laboratoire dans le milieu professionnel en utilisant comme tâche mentalement fatigante une journée de travail afin d'en mesurer les effets sur différents types de d'activités cognitives et physiques. Dans la même logique, nous pourrions également tester l'utilisation de différentes stratégies de compensation de la fatigue mentale dans le milieu de l'entreprise afin d'observer les effets de ces dernières et voir si elles permettent d'améliorer le bien-être psychologique, physique et/ou la productivité de employés.

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VII. ANNEXES

Brunel Mood Scale

Vous trouverez ci-dessous une liste de mots pouvant décrire votre humeur actuelle. Merci de lire chacun d'entre eux avec attention. Ensuite, veuillez entourer les réponses de manière à pouvoir décrire au mieux l'humeur dans laquelle vous êtes à l'instant actuel.
Assurer vous de bien avoir répondu à toutes les questions.

0 = pas du tout 1 = un peu 2 = modérément 3 = beaucoup 4 = extrêmement

Paniqué	1	2	3	4
Vif	1	2	3	4
Embrouillé	1	2	3	4
Ereinté	1	2	3	4
Déprimé	1	2	3	4
Découragé	1	2	3	4
Agacé	1	2	3	4
Epuisé	1	2	3	4
Désorienté	1	2	3	4
Somnolent	1	2	3	4
Amer	1	2	3	4
Malheureux	1	2	3	4

Anxieux	1	2	3	4
Inquiet	1	2	3	4
Energique	1	2	3	4
Triste	1	2	3	4
Confus	1	2	3	4
Nerveux	1	2	3	4
Fâché	1	2	3	4
Dynamique	1	2	3	4
Fatigué	1	2	3	4
Irritable	1	2	3	4
Eveillé	1	2	3	4
Hésitant	1	2	3	4

NASA Task Load Index

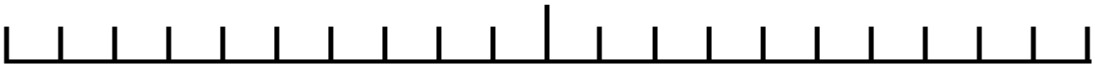
La méthode du NASA Task Load Index (TLX) de Hart et Staveland évalue la charge de travail sur 5 échelles de 7 points. Des incréments d'estimation élevée, moyenne et basse pour chaque point résultent en 21 graduations sur les échelles.

Ce questionnaire fait référence à la tâche que vous venez de réaliser

Exigence mentale — Comment était la difficulté mentale de la tâche ?

Très — Très

Exigence physique — Comment était la difficulté physique de la tâche ?

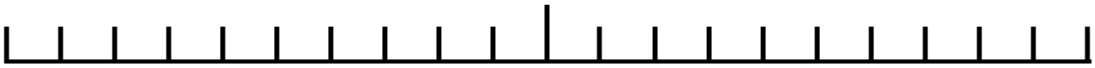


Très faible — Très

Exigence temporelle — Comment avez-vous ressenti la pression temporelle lors de l'exécution de la tâche ?

Très — Très

Performance — Avez-vous réussi à accomplir ce qui vous était demandé ?



ParfaitementParf — Pas du tout

Effort — À quel point l'exercice fut-il difficile à accomplir ?

Très — Très

Frustration — Etiez-vous stressé, découragé, agacé, inconfortable ?

Pas du tout — Extrêmement

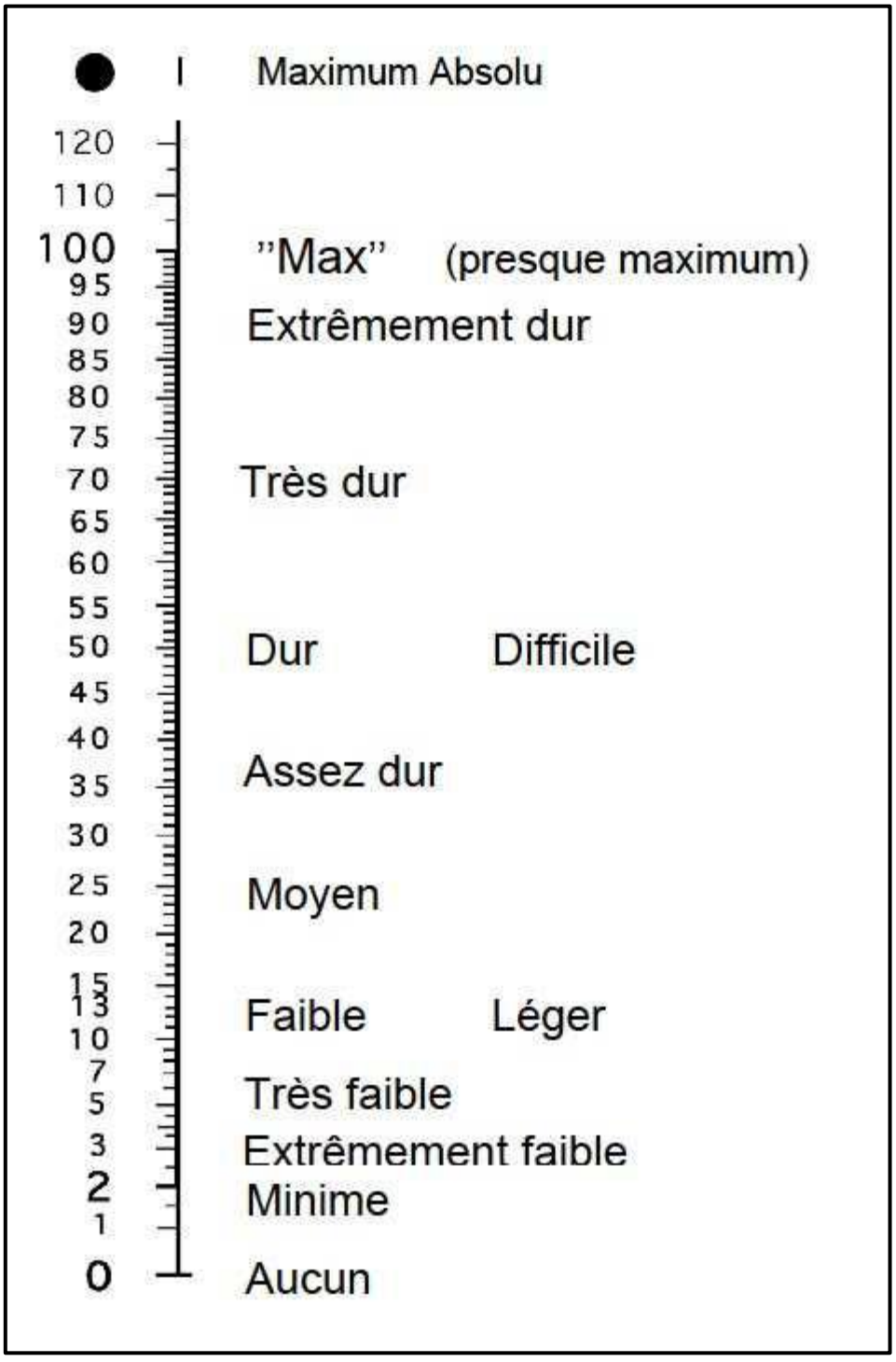
QUESTIONNAIRE DE MOTIVATION DE MATTHEWS

Merci de répondre aux questions traitant de votre motivation actuelle pour effectuer l'exercice que vous êtes sur le point de réaliser. Vous devez quantifier vos réponses via l'échelle mise à votre disposition, en entourant la réponse qui vous convient le mieux.

Assurez-vous d'avoir répondu à toutes les questions.

0 = pas du tout 1 = un peu 2 = modérément 3 = beaucoup 4 = extrêmement

Je m'attends à ce que l'exercice soit intéressant	0	1	2	3	4
Je fais cet exercice uniquement à cause d'une récompense extérieure (ex : argent…)	0	1	2	3	4
Je préfèrerais passer mon temps dédié à l'exercice à faire quelque chose d'autre	0	1	2	3	4
Je suis inquiet de ne pas faire aussi bien que ce que je peux faire	0	1	2	3	4
Je veux faire mieux que ce que la plupart des autres font	0	1	2	3	4
Je vais en avoir assez de cet exercice	0	1	2	3	4
Je souhaite faire de mon mieux	0	1	2	3	4
Je serais déçu si je ne fais pas de mon mieux pendant l'exercice	0	1	2	3	4
Je me suis engagé à réaliser une performance	0	1	2	3	4
Réaliser cet exercice en vaut la peine	0	1	2	3	4
Je m'attends à trouver l'exercice ennuyeux	0	1	2	3	4
Je me sens indifférent par rapport à ma performance future	0	1	2	3	4
Je veux réussir cet exercice	0	1	2	3	4
L'exercice va mettre en valeur mon aspect compétitif	0	1	2	3	4


Maximum Absolu
120
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"Max" (presque maximum)
Extrêmement dur
Très dur
Dur
Difficile
Assez dur
Moyen
Faible
Léger
Très faible
Extrêmement faible
Minime
Aucun

6	**Aucun**
7	**Extrêmement léger**
8	
9	**Très léger**
10	
11	**Léger**
12	
13	**Un peu dur**
14	
15	**Dur**
16	
17	**Très dur**
18	
19	**Extrêmement dur**
20	**Maximal**

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Mental fatigue induced by prolonged motor imagery increases perception of effort and the activity of motor areas

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ABSTRACT

Recent literature suggests that when prolonged, motor imagery (MI) induces mental fatigue and negatively impacts subsequent physical exercise. The aim of this study was to confirm this possibility with neurophysiological and self-reported measures. Thirteen participants performed 200 imagined isometric knee extension contractions (Prolonged MI condition) or watched a documentary (Control condition), and then performed 150 actual isometric knee extensions. Electroencephalography was continuously recorded to obtain motor-related cortical potential amplitude at Cz electrode (MRCP, index of motor area activity) for each imagined and actual contraction. Electromyography of the vastus lateralis muscle as well as the perceived effort required to perform prolonged MI, watch the documentary, and perform the actual contractions were measured. During prolonged MI, mental fatigue level, the effort required to imagine the contractions and MRCP amplitude increased over time. The increase in the effort required to imagine the contractions was significantly correlated with the MRCP amplitude. During the physical exercise, a significant condition × time interaction revealed a greater increase over time in perceived effort in the prolonged MI condition compared to the control condition, as well as a specific alteration in EMG RMS of the vastus lateralis muscle. These alterations observed in the presence of mental fatigue during actual contractions, combined with those observed during prolonged MI, suggest that prolonged MI may impair the motor command required to perform imagined or actual contractions. While the observed effect of mental fatigue on MRCP amplitude was clear during MI, future studies should tailor the physical exercise to minimize the exercise-induced decrease in force production capacity and control for its confounding effects on MRCP amplitude in the presence of mental fatigue.

1. Introduction

Mental fatigue is defined as a psychobiological state caused by prolonged periods of demanding cognitive activity and characterized by subjective feelings of "tiredness" and "lack of energy" (Boksem and Tops, 2008). Since the pioneer study of Marcora et al. (2009) demonstrating an impairment in cycling endurance performance following prolonged engagement in a demanding cognitive task, numerous studies confirmed the negative impact of mental fatigue on physical performances (for reviews see: Pageaux and Lepers, 2018; Brown et al., 2020). Mental fatigue impairs sport-related decision making (e.g., Head et al., 2017; Smith et al., 2016b), technical skills (e.g., Le Mansec et al., 2018; Smith et al., 2016a), motor control (e.g., Duncan et al., 2015; Rozand et al., 2015) and endurance (e.g., MacMahon et al., 2014; Pageaux et al., 2013) performances. Decrease in physical performances is generally associated with alteration in cardiorespiratory or metabolic responses and/or an inability of the brain to maximally recruit the working muscles (Taylor et al., 2016). However, mental fatigue does not

Abbreviations: EEG, Electroencephalography; EMG, Electromyography; MI, Motor Imagery; MRCP, Motor Related Cortical Potential; MVC, Maximal Voluntary Contraction; NASA-TLX, National Aeronautics and Space Administration Task Load Index; RFD, Rate of Force Development; RMS, Root Mean Square; RPE, Rating of Perceived Effort; VAS, Visual Analogue Scale.

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induce such alterations (Marcora et al., 2009; Pageaux et al., 2013). The only variable consistently associated with the decrease in physical performance was a greater perception of effort in the presence of mental fatigue (Brown et al., 2020; Le Mansec et al., 2018; Pageaux and Lepers, 2016, 2018).

Mental fatigue is traditionally induced by prolonged engagement in cognitive tasks involving the response inhibition process, such as the AX-CPT (Marcora et al., 2009; Pageaux et al., 2013; Smith et al., 2015) or the Stroop task (Rozand et al., 2015; Smith et al., 2016a). Interestingly, recent studies using motor imagery demonstrated that such cognitive exertion may also induce mental fatigue (Graham et al., 2014; Rozand et al., 2014, 2016). Motor imagery is defined as the internal simulation of movement without corresponding motor output (Decety, 1996a). Briefly, two main categories of motor imagery exist: visual motor imagery and kinesthetic motor imagery. Visual motor imagery consists of imagining seeing yourself performing the task and activates predominantly the occipital network (Chholak et al., 2019; Guillot et al., 2009). Kinesthetic motor imagery consists of imagining the sensations produced by the actual task and activates to a lesser extent similar brain areas than those activated during actual movements such as the premotor cortex, the parietal cortex and the cerebellum (e.g., Batula et al., 2017; Decety, 1996b; Ruffino et al., 2017; Solodkin et al., 2004; Stinear et al., 2006).

In a meta-analysis, Schuster et al. (2011) reported that ~17 min of motor imagery is optimal to observe positive effects on physical performance (e.g., Yue and Cole, 1992; Grosprêtre et al., 2018; Ranganathan et al., 2004), thus reinforcing the potential for its use in rehabilitation programs (e.g., Jackson et al., 2001; Lebon et al., 2012; Cho et al., 2013; Kumar, 2016). However, the positive effects of motor imagery seem to disappear when motor imagery is performed longer than the optimal duration proposed by Schuster et al. (2011). Indeed, Rozand et al. (2016) recently demonstrated that 100 imagined contractions (i.e., ~30 min) induced mental fatigue and increased movement duration during a pointing task. The involvement of the sustained attention and the inhibitory processes during a motor imagery task (Bart et al., 2020; O'Shea and Moran, 2017), as in cognitive tasks classically used to induce mental fatigue (e.g., AX-CPT, Stroop), could be one of the underlying mechanisms explaining the occurrence of mental fatigue. As mental fatigue could counteract the positive effects of motor imagery on subsequent performance, and therefore impair rehabilitation programs, it is important to investigate the occurrence of mental fatigue induced by prolonged motor imagery.

While the underlying mechanisms causing the decrease in physical performance in the presence of mental fatigue remain unclear, analysis of brain oscillations via electroencephalography (EEG) has been an efficient tool to identify mental fatigue-induced cerebral alterations during the completion of cognitive tasks (for review: Craig et al., 2012; Tran et al., 2020). Analyses of brain oscillations reveal a consistent increase in the theta power (e.g., Barwick et al., 2012) and alpha power (e.g., Shou and Ding, 2013) in the presence of mental fatigue. These changes were not only reported after cognitive tasks requiring predominantly the response inhibition process but also after cognitive tasks requiring concentration and attention (Lal and Craig, 2002; van der Linden et al., 2003). As these studies did not use prolonged motor imagery to induce mental fatigue, it remains unknown whether these alterations are transferable to mental fatigue induced by prolonged motor imagery.

When measuring cerebral activity with EEG, it is possible to monitor for each contraction (actual or imagined) a specific event-related potential called motor-related cortical potential (MRCP; e.g., Jankelowitz and Colebatch, 2002; do Nascimento et al., 2006). This potential was discovered during hand movements by Bates (1951) and recorded from the scalp overlying motor and premotor areas. MRCP amplitude is directly linked to the intensity of muscle contraction and has been extensively used in the literature as an index of the motor command (de Morree et al., 2012, 2014; Siemionow et al., 2000). In the presence of decreased maximal force production capacity, also known as muscle fatigue (Gandevia, 2001), previous studies observed an increased MRCP while the level of muscle force during each contraction remained constant (de Morree et al., 2012, 2014). As previous studies observed i) alterations in electromyographic signal of the working muscles during submaximal physical exercise following engagement in demanding cognitive tasks (Bray et al., 2008; Graham et al., 2014; Pageaux et al., 2015), and ii) longer duration of actual and imagined movements in the presence of mental fatigue (Rozand et al., 2015), it is plausible that mental fatigue may impact the regulation of the motor command and consequently alter MRCPs. This hypothesis is also supported by recent studies demonstrating an association between changes in MRCPs and perception of effort (de Morree et al., 2012, 2014). While an ongoing debate is still existing in the literature on the sensory signal generating perception of effort (peripheral vs. central origin; e.g., Amann and Light, 2014; Broxterman et al., 2018; Marcora, 2009; Pageaux, 2016; Smirmaul, 2014; Steele and Fisher, 2018), this perception has been classically used as a marker of the motor command for decades (Kjær et al., 1999; McCloskey et al., 1974; Mitchell et al., 1989), and its consistent increase in the presence of mental fatigue (Brown et al., 2020; Pageaux and Lepers, 2016, 2018) reinforces the possible interaction between mental fatigue and the motor command.

In this context, the primary aim of the present study was to induce mental fatigue using prolonged motor imagery. EEG was recorded during four blocks of fifty imagined contractions, and subjective feelings of fatigue, as well as the effort required to imagine the contractions were reported. We hypothesized that prolonged motor imagery will successfully induce mental fatigue evidenced by an increase in feelings of fatigue as well as in the effort required to imagine the contractions, and an increase in both alpha and theta power. Due to the known negative impact of mental fatigue on subsequent physical performance (for review see: Pageaux and Lepers, 2018; Brown et al., 2020), the secondary aim of our study was to identify, during a subsequent physical exercise, neurophysiological alterations caused by mental fatigue. Finally, as i) mental fatigue is known to increase the perception of effort during physical exercises (Pageaux and Lepers, 2018), and ii), previous studies demonstrated an association between changes in perceived effort and changes in MRCP (de Morree et al., 2012, 2014) we expect that prolonged motor imagery will increase the amplitude of MRCPs during both imagined and actual contractions.

2. Experimental procedures

2.1. Participants

Thirteen physically active right-handed adults (7 males and 6 females) volunteered in this study (mean ± SD; age: 25 ± 4 years, height: 182 ± 5 cm, weight: 77 ± 11 kg). This sample size was determined based on a previous study using a similar physical exercise with the knee extensors and investigating the relation between MRCP and physical fatigue in the presence and absence of caffeine (de Morree et al., 2014). All participants were involved in physical activity and declared to practice a physical activity at least one time per week. None of the participants had any known mental or somatic disorders or any injuries of the right leg during the last six months. All participants were given written instructions describing all procedures related to the study but were naive of its aims and hypotheses. The participants have never been informed prior to the experiment that motor imagery (MI) was used to generate mental fatigue. They were instructed that the aim of the study was to investigate the possible positive effects of motor imagery on a subsequent physical exercise. Each participant provided written informed consent. At the end of the last visit, participants were fully debriefed and asked not to discuss the real aims of the study with other participants. The study conformed to the standards set by the World Medical Association Declaration of Helsinki "Ethical Principles for Medical Research Involving Human Subjects" (2008). The experimental design of the

study was approved by the regional ethics committee (CPP EST: approval no. A00064-49).

2.2. Procedure

Participants visited the laboratory on three different occasions. Each participant completed all three visits over three weeks with a minimum of six days of recovery period between visits. All visits started between 8:30 a.m. and 10:00 a.m. All participants were given instructions to sleep for at least 7 h, refrain from the consumption of alcohol, and not to practice vigorous physical activity the day before each visit. Participants were also instructed not to consume caffeine and nicotine for at least 3 h before testing and were asked to declare if they had taken any medication or had any acute illness, injury, or infection. At the beginning of each session, the participants attested that they had complied with all instructions. For all the sessions, participants sat on the same isometric ergometer chair (Multi-form, la Roque d'Anthéron, France).

During the first visit, participants were familiarized with the laboratory and all the procedures. For all different questionnaires, oral and written instructions were provided during this familiarization (and recalled at the beginning of each visit). About the physical exercise, after a warm-up, participants performed 150 submaximal isometric knee extensions at 50% of their maximal voluntary contraction (MVC). If the physical exercise was too difficult during the familiarization session (i.e., excessive head movements and sweating) the target force was fixed at 45% of their MVC. On the contrary, if the physical exercise was too easy (i.e., low perceived effort at the end of the exercise and no muscular fatigue), the target force was fixed at 55% of their MVC. At the end of the familiarization, participants performed maximal imagined isometric contractions of the right knee extensors to get used to MI. After the familiarization, all participants reported that they successfully imagined the 50 contractions, felt associated sensations and reported a score of at least 5 on the Likert scale used to record the MI vividness (see section 2.4.4 Motor imagery vividness).

The second and third visits were randomized and counterbalanced. An overview of each visit is presented in Fig. 1. Each visit consisted of performing either prolonged MI or a control task (i.e., watching a documentary) for approximately 50 min, followed by a physical exercise (150 isometric knee extensions). In each visit, participants reported their level of mental fatigue and performed MVC with their right knee extensors to assess force production capacity before and after (Post 1, before the subsequent physical exercise) the prolonged MI or documentary watching, as well as after the physical exercise (Post 2). Motivation to perform prolonged MI or watch the documentary, and perform the subsequent physical exercise was measured before completion of each task. Participants reported their perceived workload of the prolonged MI session, documentary watching and physical exercise after completion of each task. Electromyographical (EMG) and electroencephalographic (EEG) signals were continuously recorded during all tasks; and the participants reported their perceived effort to perform MI, watch the documentary or perform the physical exercise.

Order and timing were the same for each participant and each session. VAS = fatigue visual analogue scale, RPE = rating of perceived effort, MI = motor imagery, MVC = maximal voluntary contraction, NASA-TLX = National Aeronautics and Space Administration Task Load Index.

2.3. Experimental tasks

2.3.1. Prolonged motor imagery

Prolonged MI consisted of four blocks of 12.5 min of kinesthetic MI for a total of approximately 50 min. During imagined maximal isometric knee extensions, participants were instructed to perform kinesthetic MI and to perceive muscle contractions and joint tension with the same sensations they experienced during the completion of the previous MVC. Each participant was instructed to not contract her/his quadricep muscles during MI. An experimenter was seated behind the participant to check the EMG signal of the vastus lateralis muscle in order to control that the participant did not contract her/his muscle during imagined contractions. Participants performed MI, with their eyes closed, seated on the same isometric ergometer chair than the one used for the MVCs and intermittent isometric extensions of the knee extensors.

Participants performed four blocks of 50 imagined contractions of 5 s, with a 10-s rest period between each imagined contraction and 1-min rest period between blocks (total duration of one block = 12.5 min, total duration of prolonged MI = 53 min). Three instructions were given during prolonged MI. Two seconds before starting the imagined contraction participants heard "Get ready", then "Push" to start the imagined contraction, and "Relax" to stop the imagined contraction. The Experiment Builder software was used to time the instructions for each imagined contraction (SR Research). At the end of each block, perceived effort to accomplish prolonged MI and MI vividness were assessed.

2.3.2. Control condition

The control condition consisted of watching an emotionally neutral documentary, "Home" by Y. Arthus-Bertrand, which was used as control condition in previous studies on mental fatigue (Le Mansec et al., 2018; Rozand et al., 2015). In these previous studies, it has been shown that this documentary did not induce any increase in subjective feeling of mental fatigue. Participants were sitting in a dark room on the same isometric ergometer chair than the one used for the intermittent MVCs of the knee extensors. The movie was projected on a screen placed 2 m in

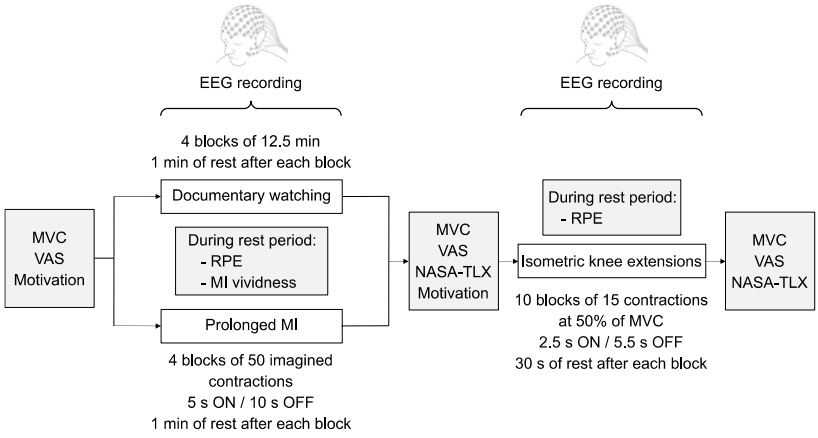

Fig. 1. Overview of the experimental protocol.

front of the participant. It was divided into four blocks of 12.5 min with 1 min of rest between each block to match with prolonged MI and to assess the perceived effort to watch the documentary.

2.3.3. Physical exercise

Following prolonged MI or watching the documentary, participants performed the physical exercise, which consisted in performing 150 submaximal isometric contractions of the right knee extensor muscles.

Beeps were presented as follows, a first beep to start the contractions and a second beep to stop the contractions. The contractions lasted 2.5 s with 5.5 s rest in between. Contractions were performed by blocks of 15 contractions interspaced by 30 s during which perception of effort was assessed.

Isometric contractions were performed at 50% of MVC (±5%). Visual feedback of the target strength was presented on a screen placed 2 m in front of the participant.

The Experiment Builder software was used to time the submaximal isometric contractions of the knee extensor muscles.

2.4. Psychological measures

2.4.1. Motivation

Motivation is defined as "the attribute that moves us to do or not to do something" (Gredler, 2001). Motivation has been proposed to influence performance (Richter et al., 2016) and interact with fatigue (Müller and Apps, 2019). Motivation to watch the documentary (control task), perform both motor imagery and physical exercise was measured with the motivation scale developed by Matthews et al. (2001). This questionnaire has seven questions on intrinsic motivation (e.g., "I wish to do my best") and seven questions on extrinsic motivation (e.g., "I performed this exercise only because of an outside reward"). For each question, there are five possible answers (0 = not at all, 1 = a little bit, 2 = somewhat, 3 = very much, 4 = extremely). The score of each motivation ranges between 0 and 28.

2.4.2. Subjective workload

The National Aeronautics and Space Administration Task Load Index (NASA-TLX) was used to evaluate subjective workload (Hart and Staveland, 1988). The NASA-TLX is composed of six subscales: mental demand (how much mental and perceptual activity was required?), physical demand (how much physical activity was required?), temporal demand (how much time pressure did you feel due to the rate or pace at which the task occurred?), performance (how much successful do you think you were in accomplishing the goals of the task set by the experimenter?), effort (how hard did you have to work to accomplish your level of performance?), and frustration (how much irritating, annoying did you perceive the task?). The participants had to score each of the items on a scale divided into 20 equal intervals anchored by a bipolar descriptor (e.g., high/low). This score was multiplied by 5, resulting in a final score between 0 and 100 for each of the subscales.

2.4.3. Mental fatigue level

A visual analogue scale (VAS) was used to measure feelings of mental fatigue before and after prolonged MI and documentary watching. The VAS consisted of a line measuring 100 mm in length, with bipolar end anchors (0 mm = "No tired at all"; 100 mm = "Extremely tired"). The following question was asked to access the level of mental fatigue: "What is your feeling of mental fatigue right now?". Participants were asked to place a mark along the line to indicate how they currently felt. VAS score is defined by the distance between the first anchor (0 mm: "No tired at all") and the mark placed by the participant.

2.4.4. Motor imagery vividness

MI vividness is defined as the clarity of the kinesthetic sensations elicited by MI (Saimpont et al., 2012). Participant had to evaluate their MI vividness on a Likert scale (1 = "Not clear at all'', 1 = "Very unclear'', 3 = "Unclear", 4 = "Moderately clear", 5 = "Quite clear'', 6 = "Clear'' 7 = "Very clear"). This measure, performed each 50 imagined contractions, allows monitoring the evolution of MI vividness.

2.4.5. Perception of effort

Perception of effort is defined as the conscious sensation of "how hard, heavy and strenuous a physical task is" (Marcora, 2009, 2010; Pageaux, 2016). During each task, participants reported the intensity of the effort invested. The intensity of perceived effort was reported with a modified version of the CR100 scale (Borg and Kaijser, 2006). This scale ranges from 0 (Nothing at all) to 100 (Maximal) and includes verbal anchors such as Weak/Light (13), Moderate (25), Strong/Heavy (50) or Very Strong (70). Modifications on the scale were made on the anchoring 0 and 100 to include the word effort in the description as follow: 0 = No effort at all; 100 = Maximal effort.

During prolonged MI and documentary watching, participants were asked each 12.5 min to answer the following question: "How hard and intense is it for you to imagine the contractions (or watch the documentary)?". During the physical task, participants were asked at the end of each block to answer the following question: "How hard and intense is it for you to drive your leg?".

The scale allows values above 100 to be specified if the participant perceives an effort higher than the "Maximal exertion" (i.e., rating 100). Each participant was provided verbal examples of "No exertion" (e.g., not doing any cognitive work or sitting on the couch relaxing) and "Maximal exertion" (e.g., the most intense effort experienced in their life during prior cognitive activities or the sensations perceived during an MVC).

2.5. Physiological measurements

2.5.1. Force recording

Right knee extension force was recorded using a homemade isometric ergometer that comprised a machine typically used for strength training connected to two strain gauges (STC 250 kg; sensitivity: 2.9997 mV/V; Celtron Technologies Inc., Santa Clara, CA, USA) (Matkowski et al., 2011). The signal force was recorded with a commercially available software (AcqKnowledge 4.1 for MP Systems, Biopac Systems Inc., Goleta, CA, USA). Knee angle was fixed at 100° to perform isometric knee extensions (0° = full knee extension).

Force data were analyzed offline using Matlab (The Mathworks, Natick, MA). The onset and offset of the muscle contractions were determined automatically based on the positive and negative peaks in the second differential of the force signal (5th-order Bessel low-pass filter). For each contraction (i.e., from the onset to the offset of muscle force signal), a time window of 500 ms was used to calculate the mean force. This 500 ms was defined as 250 ms around the middle of the contraction. Rate of Force Development (RFD) was calculated for each submaximal contraction as the average slope of the force-time curve (force/time) over the time interval 0–200 ms (Aagaard et al., 2002). The onset of force production was defined as the time point where the force exceeded the baseline by 2 SD. The baseline is calculated on a 1-s sliding window during the rest period previous each contraction. The offset of force production was defined as the point time where the force became lower than the baseline +2 SD Mean force and RFD during the submaximal trials were averaged over the first (contractions 1 to 75) and the second half (contractions 76 to 150) of the trials.

Force tremor, which represents the variability in force production during intermittent contractions, was calculated as the force coefficient of variation (CV). For each contraction (i.e., from the onset to the offset of muscle force signal), a time window of 1.5 s was used to calculate the force tremor. This 1.5 s was defined as 750 ms around the middle of the contraction.

2.5.2. EMG recording

Electromyography (EMG) activity of the vastus lateralis was

recorded with a pair of bipolar silver chloride circular (recording diameter of 10 mm) surface electrodes (Swaromed, Nessler Medizintechnik, ref 1066, Innsbruck, Austria) with an interelectrode (center-to-center) distance of 20 mm. The vastus lateralis muscle was chosen as representative of quadriceps muscle activity (Place et al., 2007). Low resistance between the two electrodes was obtained by shaving the skin and the skin was cleaned with alcohol. The electrodes were placed as close as possible to the patella for the vastus lateralis. The position of the electrodes followed the direction of the muscle fibers, according to the SENIAM recommendations (Hermens et al., 2000), and was aligned in the longitudinal direction of the muscle fibers. The reference electrode was placed on the ipsilateral patella. Myoelectrical signal was amplified with a bandwidth frequency ranging from 10 to 500 Hz (gain = 1000), digitized on-line at a sampling frequency of 2 kHz, and recorded with commercially available software (AcqKnowledge 4.1 for MP Systems, Biopac Systems Inc., Goleta, CA, USA).

The Root Mean Square (RMS) of the vastus lateralis EMG signal was calculated for each contraction from the onset to the offset of the EMG burst. The onset of muscle activity was considered to occur when the amplitude of the RMS-processed EMG exceeded +3 SD above the baseline EMG activity (mean activity calculated during a 400-ms time period immediately before impact). Thus, the contraction duration was defined as the time elapsed between the onset and the offset of EMG activation. The resulting values were averaged over the first half (contractions 1 to 75) and the second half (contractions 76 to 150) of the contractions.

2.5.3. EEG data

The electroencephalogram was recorded at 64-scalp sites using a 10–20 system (BioSemi ActiveTwo). Horizontal eye movements were monitored with electrodes placed on the outer left and right canthi. Vertical eye movements were monitored with an electrode placed under the left eye. Two additional electrodes were placed on the left and right mastoids (A1, A2). During recording, the BioSemi ActiveTwo system's common-mode sense electrode served as the reference electrode. Each electrode was filled with Signa gel for improving signal transduction. Electrophysiological signals were digitized at a 2048 Hz sampling rate and acquired with ActiView software. From the instructions given for imagined contractions and from the two beeps used for actual contractions, triggers were automatically reported on the EEG recording to signal the beginning and the end of each actual and imagined contraction. A trigger was also reported on the EEG recording when the participant had to prepare to imagine a movement. The EEG signals were analyzed using the EEGLAB (version 14.1) toolbox for Matlab (https://sccn.ucsd.edu/wiki/EEGLAB) (Delorme and Makeig, 2004).

Offline, data were re-referenced against the mean of electrodes A1 and A2 and downsampled to 512 Hz. EEG data were filtered with a 0.01–5 Hz band-pass filter for MRCP analysis, while a 1–40 Hz band-pass filter was performed for spectral analyses. To correct for eye movement artifacts, EEGLAB's runica routine was used to perform independent component analyses. Noisy electrodes were identified with the probability method in EEGLAB (Z = 5) and interpolated when necessary with a spherical method. EEG signals were segmented into 150 epochs of 8000 ms each (from 2500 ms before to 5500 ms after beep tone) for actual contractions, and into 200 epochs of 15,000 ms each (from 2500 ms before to 12,500 ms after contraction onset) for imagined contractions. All trials were baseline corrected with −2500 ms to −2000 ms. These epochs were used for MRCP analyses. During MI, MRCP amplitudes were averaged for each block (Block 1: imagined contractions 1 to 50, Block 2: imagined contractions 51 to 100, Block 3: imagined contractions 101 to 150, Block 4: imagined contractions 151 to 200). During actual contractions, MRCP amplitudes were averaged over the first half (contractions 1 to 75) and the second half (contractions 76 to 150) of the physical exercise. During the physical exercise, the MRCPs obtained during contractions producing a force above ±5% of the target force were excluded from the analysis. A visual inspection was also performed on all epochs, including actuals and imagined contractions, to remove contractions associated with movement artifacts (e.g., head movements).

EEG power was divided into five frequency bands: delta, 1–4 Hz; theta, 4–7 Hz; alpha, 8–12 Hz; beta 13–30 Hz; and gamma, 30–40 Hz. Spectral data were analyzed during the first 5 min and the last 5 min of the prolonged MI and documentary watching. To observe changes in brain activation all over the scalp, we used nine regions of interests (ROIs) as previously suggested by Arendsen et al. (2020): Anterior Left (mean of FP1, AF3, AF7, F3, F5, F7, FC3, FC5, FT7), Anterior Median (mean of FPz, AFz, F1, Fz, F2, FC1, FCz, FC2), Anterior Right (mean of FP2, AF4, AF8, F4, F6, F8, FC4, FC6, FT8), Central Left (mean of C3, C5, T7, CP3, CP5, TP7), Central Median (mean of C1, Cz, C2, CP1, CPz, CP2), Central Right (mean of C4, C6, T8, CP4, CP6, TP8), Posterior Left (mean of P9, P7, P5, P3, PO7, PO3, O1), Posterior Median (mean of P1, Pz, P2, POz, Oz), and Posterior Right (mean of P4, P6, P8, PO4, PO8, O2).

2.6. Statistics

All data are presented as means ± SE.

Paired *t*-tests were used to assess the effect of condition (Prolonged MI, Control) on motivation and NASA-TLX scores.

One-way repeated measures ANOVAs were used to test the effect of time (4 blocks of 12.5 min) on imagery vividness and MRCP amplitude during prolonged MI. Two-way repeated-measures 2 × 4 ANOVAs were used to test the effects of condition (Prolonged MI, Control) and time (4 blocks of 12.5 min) on perceived effort. Two-way repeated-measures 2 × 2 ANOVAs were used to test the effects of condition (Prolonged MI, Control) and time (First 5 min, Last 5 min) on delta, theta, alpha, beta, and gamma power during prolonged MI and documentary watching. To test the effects of prolonged MI on force production capacity, a two-way repeated-measures 2 × 2 ANOVA was used to test the effects of condition (Prolonged MI, Control) and time (Pre, Post 1) on MVC.

Two-way repeated-measures 2 × 2 ANOVAs were used to test the effects of condition (MI, Control) and time (First part: contractions 1 to 75, Second part: contractions 76 to 150) on the numbers of MRCPs analyzed, the MRCP amplitude, rating of perceived effort, force, RFD, tremor, and contraction duration during physical exercise. To test the effect of the physical exercise on force production capacity, a two-way repeated-measures 2 × 2 ANOVA was used to test the effects of condition (Prolonged MI, Control) and time (Post 1, Post 2) on MVC.

Greenhouse-Geisser correction to the degrees of freedom was applied when violations of sphericity were present (corrected degree of freedom and *p*-values are reported). For ANOVAs, when significant, main effects and condition × time interaction were followed up with Bonferroni tests as appropriate.

Partial eta squared are reported, and thresholds for small, moderate, and large effects were set at 0.01, 0.07, and 0.14, respectively (Cohen, 1988). Analyses were conducted using JASP (version 0.10.2.0 for Windows). For paired *t*-tests, Cohen's *dz* were calculated using G*Power software (version 3.1.6, Universität Düsseldorf, Germany) and thresholds for small, moderate and large effects were set at 0.2, 0.5, and 0.8 respectively (Cohen, 1988). Correlations were performed between perception of effort and MRCP amplitude for both the imagined and actual contractions, with the R package 'rmcorr' assessing repeated measures correlation (Bakdash and Marusich, 2017; Bland and Altman, 1995). Level of significance was set at $p < .05$ (two-tailed).

3. Results

Due to excessive head movements, one participant was excluded from the analyses related to the physical exercise. Therefore, the sample size was $N = 13$ for analyses related to the prolonged MI or the control condition (watching a documentary), and $n = 12$ for analyses related to the physical exercise.

3.1. Mental fatigue assessment

3.1.1. Effects of prolonged motor imagery on psychological measurements

Motivation to perform prolonged MI or watch the documentary did not differ for extrinsic ($t_{(12)} = -0.267$, $p = .794$, $dz = 0.077$; Prolonged MI: 15.9 ± 1.3, Control condition: 16.1 ± 1.2) and intrinsic ($t_{(12)} = -1.945$, $p = .076$, $dz = 0.538$; Prolonged MI: 17.6 ± 1.0, Control condition: 19.0 ± 0.9) motivation.

The effects of prolonged MI and the documentary watching on feelings of fatigue, perception of effort, subjective workload and MI vividness are displayed in Fig. 2. Feelings of fatigue (Fig. 2.A) increased over time ($F_{(1, 12)} = 18.306$, $p = .001$, $\eta_p^2 = 0.604$), with no significant main effect of condition ($F_{(1, 12)} = 1.563$, $p = .235$, $\eta_p^2 = 0.115$) or condition × time interaction ($F_{(1, 12)} = 3.464$, $p = .087$, $\eta_p^2 = 0.224$). Perception of effort (Fig. 2.B), was greater in the Prolonged MI condition compared to the Control condition ($F_{(1, 12)} = 10.518$, $p = .007$, $\eta_p^2 = 0.467$) and increased over time ($F_{(1.311, 15.732)} = 16.637$, $p < .001$, $\eta_p^2 = 0.581$). A condition × time interaction ($F_{(1.443, 17.319)} = 8.256$, $p = .006$, $\eta_p^2 = 0.408$) revealed that the effort required to imagine the contractions increased over time and was significantly higher at Block 3 ($t_{(12)} = -5.448$, $p < .001$, $dz = -1.248$) and Block 4 ($t_{(12)} = -8.141$, $p < .001$, $d = -1.117$) compared to Block 1. The effort reported to watch the documentary did not change over time (all $ps > .20$, all $dz < 0.95$). The effort reported to imagine contractions compared to watch the documentary was reported as significantly greater solely at Block 4 ($t_{(12)} = -8.141$, $p = .008$, $dz = -1.226$).

Analyses on the reported subjective workload (Fig. 2.C) revealed a greater mental demand ($t_{(12)} = 5.556$, $p < .001$, $dz = 1.541$), physical demand ($t_{(12)} = 2.456$, $p = .030$, $dz = 0.681$), temporal demand ($t_{(12)} = 2.379$, $p = .035$, $dz = 0.660$) and performance ($t_{(12)} = 4.573$, $p < .001$, $dz = 1.268$) following completion of prolonged MI compared to the documentary watching. However, the subscales frustration ($t_{(12)} = -0.623$, $p = .545$, $dz = -0.171$) and effort ($t_{(12)} = 2.060$, $p = .062$, $dz = 0.571$) did not change significantly.

MI vividness (Fig. 2.D) decreased over time ($F_{(1.490, 17.877)} = 8.163$, $p = .024$, $\eta_p^2 = 0.301$). As shown with the comparison with Block 1 (vs. Block 2: $t_{(12)} = 0.617$, $p = 1.000$, $dz = 0.171$; vs. Block 3: $t_{(12)} = 1.339$, $p = 1.000$, $dz = 0.385$; vs. Block 4: $t_{(12)} = 2.449$, $p = .184$, $dz = 0.679$), and Block 2 vs. Block 4 ($t_{(12)} = 3.395$, $p < .032$, $d = 0.942$), the decrease in MI vividness occurred towards the end of second half of the prolonged MI.

3.1.2. Effects of prolonged motor imagery on neurophysiological measurements

➢ Force production capacity

The force production capacity of the knee extensors decreased over time ($F_{(1, 12)} = 11.050$, p = .006, $\eta_p^2 = 0.479$) with no main effect of condition ($F_{(1, 12)} < 0.001$, p = .992, $\eta_p^2 < 0.001$) or condition × time interaction ($F_{(1, 12)} = 1.141$, p = .306, $\eta_p^2 = 0.086$; Prolonged MI condition: 206.9 ± 15.9 N to 195.6 ± 14.3 N, Control condition: 204.2 ± 16.6 N to 198.1 ± 16.9 N).

➢ Brain oscillations analysis

All the results on brain oscillations are presented in the Supplementary data (Table S1). Significant differences related to alpha power and theta power are presented below.

Theta (4–7 Hz). Theta power at the Parietal Left region decreased over time ($F_{(1, 11)} = 6.250$, $p = .030$, $\eta_p^2 = 0.362$). For all ROIs, no significant interaction was observed (all $ps > .25$, all $\eta_p^2 < 0.119$).

Alpha (8–12 Hz). A greater alpha power was observed in the Prolonged MI condition compared to the Control condition at the Frontal Median ($F_{(1, 11)} = 9.057$, $p = .012$, $\eta_p^2 = 0.452$), Central Median ($F_{(1, 11)} = 7.876$, $p = .017$, $\eta_p^2 = 0.417$), and Central Right ($F_{(1, 11)} = 11.477$, $p = .006$, $\eta_p^2 = 0.511$), Parietal Left ($F_{(1, 11)} = 11.423$, $p = .006$, $\eta_p^2 = 0.509$), Parietal Median ($F_{(1, 11)} = 15.867$, $p = .002$, $\eta_p^2 = 0.591$), and Parietal Right ($F_{(1, 11)} = 13.700$, $p = .003$, $\eta_p^2 = 0.555$) regions. However, for all ROIs, no significant interaction was reported (all $ps > .30$, all $\eta_p^2 < 0.098$).

➢ Motor and premotor area activity

99.8 ± 0.1% of imagined contractions were analyzed. During

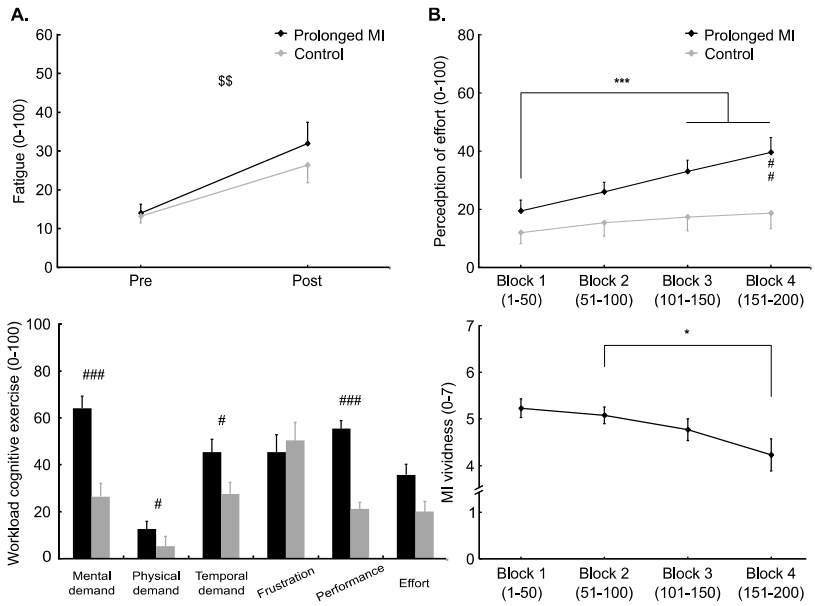

Fig. 2. Feelings of fatigue (panel A), rating of perceived effort to perform prolonged motor imagery (MI) and to watch the documentary (Control condition) (panel B), subjective workload of the prolonged MI and control task, and rating of MI vividness during prolonged MI evaluated with a Likert scale (panel D). $$: Significant main effect of time ($p < .01$). * and, ***: Significant difference between two time points within the same condition ($p < .05$ and, $p < .001$). #, ## and, ###: Significant difference between conditions at the same time of measurement ($p < .05$, $p < .01$ and, $p < .001$). Data are presented as means ± SE ($N = 13$).

prolonged MI, MRCP amplitude at Cz electrode (Fig. 3.) increased over time ($F_{(3,\ 36)} = 4.259$, $p = .011$, $\eta_p^2 = 0.262$). As shown with the comparison with Block 1 (vs. Block 2: $t_{(12)} = -0.569$, $p = 1.000$, $dz = -0.158$; vs. Block 3: $t_{(12)} = -3.050$, $p = .060$, $dz = -0.846$), MRCP amplitude at Cz progressively increased up to significance at Block 4 ($t_{(12)} = -4.358$, $p = .006$, $dz = -1.242$). The repeated measures correlation analysis revealed a significant correlation between MRCP amplitude and perception of effort during imagined contractions ($r(38) = 0.369$, $p = .019$).

3.2. Effects of mental fatigue induced by prolonged motor imagery on physical exercise

Motivation to perform physical exercise did not differ between conditions for intrinsic ($t_{(12)} = 0.217$, $p = .832$, $dz = 0.026$; Prolonged MI: 18.8 ± 1.3, Control condition: 18.7 ± 1.2) or extrinsic motivation ($t_{(12)} = -0.378$, $p = .713$, $dz = -0.111$; Prolonged MI: 16.9 ± 1.2, Control condition: 16.8 ± 1.5).

3.2.1. Psyghological changes

The NASA TLX scale (Fig. 4.A) revealed that in the Prolonged MI condition, participants reported a greater physical demand compared to the Control condition ($t_{(11)} = 2.185$, $p = .049$, $dz = 0.639$). No difference was reported for mental demand, temporal demand, performance, effort and frustration subscales (all $ps > .70$, all $|dz| < 0.45$).

Perception of effort (Fig. 4.B) increased over time ($F_{(1,\ 11)} = 65.466$, $p < .001$, $\eta_p^2 = 0.856$), and was higher in the Prolonged MI condition compared to the Control condition ($F_{(1,\ 11)} = 5.320$, $p = .042$, $\eta_p^2 = 0.326$). The condition × time interaction ($F_{(1,\ 11)} = 6.922$, $p = .023$, $\eta_p^2 = 0.386$) revealed a greater increase in perceived effort over time following prolonged MI ($t_{(11)} = -8.432$, $p < .001$, $dz = -2.458$) compared to watching a documentary ($t_{(11)} = -6.151$, $p < .001$, $dz = -1.758$). No significant difference between conditions ($t_{(11)} = -0.906$, $p = 1.000$, $dz = -0.262$) was observed during the first part of the physical exercise. During the second part of the physical exercise, perception of effort was higher in the Prolonged MI condition compared to Control

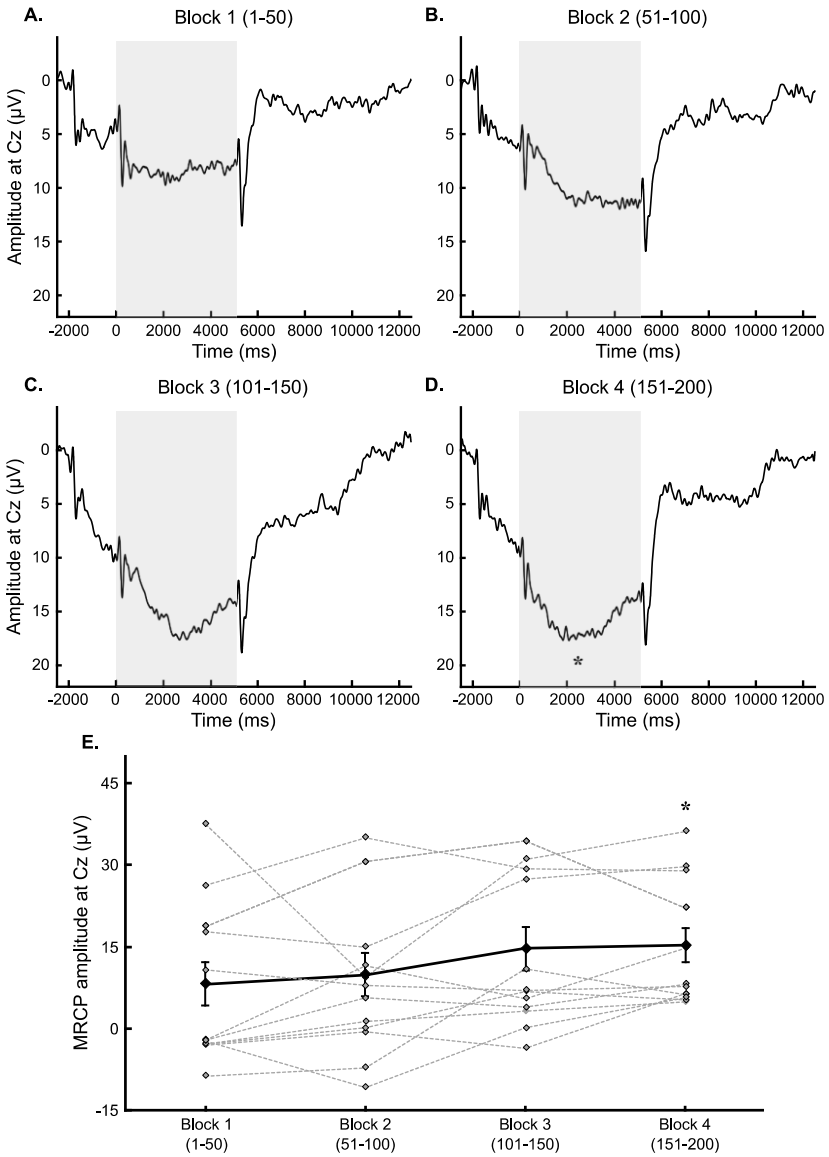

Fig. 3. Grand averages ($N = 13$) of the EEG signal amplitude at Cz electrode for the first block (panel A; imagined contractions 1 to 50), the second block (panel B; imagined contractions 51 to 100), the third block (panel C; imagined contractions 101 to 150), and the fourth block (panel D; imagined contractions 151 to 200) of the imagined isometric right knee extensions. Time 0 corresponds to the audio signal to start the contraction (panels A, B, C, and D), and the shaded area on the panels A, B, C and D represents the time window used for the analysis of the MRCP amplitude. Individual values of MRCP for each participants (panel E; grey bars indicate individual values and dark bars indicate averaged values). *: Significantly different from Block 1 ($p < .05$).

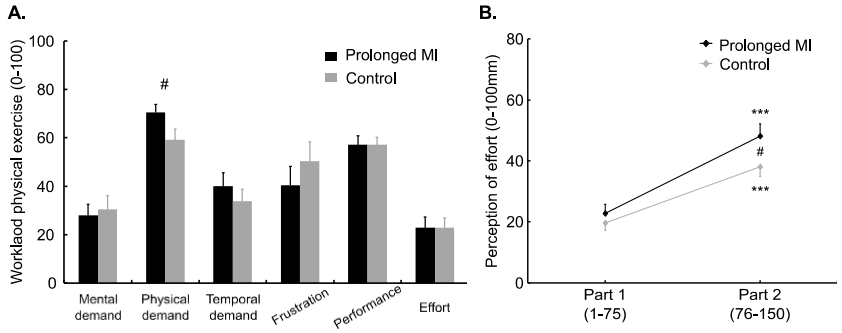

Fig. 4. Results for the subjective workload (NASA-TLX) (panel A) and the rating of perceived effort to perform the physical exercise following prolonged MI (black) and documentary watching (grey). #: Significant difference between conditions at the same time of measurement ($p < .05$). ***: Significant difference between two time points within the same condition ($p < .001$). Data are presented as means ± SE ($n = 12$).

condition ($t_{(11)} = -3.232$, $p = .031$, $dz = -0.933$).

3.2.2. Physiological changes

➢ Neuromuscular changes

The 150 right knee isometric contractions induced a decrease in force production capacity ($F_{(1, 11)} = 22.323$, $p < .001$, $\eta_p^2 = 0.670$) with no difference between conditions ($F_{(1, 11)} = 1.068$, $p = .324$, $\eta_p^2 = 0.088$) and no significant condition × time interaction ($F_{(1, 11)} = 3.522$, $p = .087$, $\eta_p^2 = 0.243$; Prolonged MI condition: 195.6 N ± 15.5–167.0 N ± 12.4, Control condition: 196.1 N ± 18.2–175.8 N ± 14.0).

Neuromuscular responses to the physical exercise, results of the ANOVAs, and the relevant follow-up tests are presented in Table 1. Neuromuscular responses did not differ between conditions, except for the VL EMG RMS. The condition × time interaction ($F_{(1, 11)} = 8.711$, $p = .013$, $\eta_p^2 = 0.442$) revealed an increase solely in the Prolonged MI condition ($t_{(11)} = -2.976$, $p = .054$, $dz = -0.859$) and not in the Control condition ($t_{(11)} = -0.377$, $p = .713$, $dz = -0.109$).

➢ Motor and premotor area activity

For the MRCP amplitude analysis, 18.3 ± 0.9 contractions per part of the exercise were excluded due to an incorrect force development and 2.4 ± 0.9 due to the presence of movement artifacts. In total, 72.4 ± 1.3% of the total number of contractions were included in the statistical analysis. The numbers of contractions analyzed did not differ between the experimental conditions ($F_{(1,11)} = 4.009$, $p = .071$, $\eta_p^2 = 0.267$) and did not change over time ($F_{(1,11)} = 0.920$, $p = .358$, $\eta_p^2 = 0.077$). The condition × time interaction was also not significant ($F_{(1,11)} = 0.044$, $p = .838$, $\eta_p^2 = 0.004$).

MRCP amplitude at Cz during the physical exercise (Fig. 5) increased over time ($F_{(1,11)} = 10.325$, $p = .008$, $\eta_p^2 = 0.484$) with no main effect of condition ($F_{(1,11)} = 2.222$, $p = .164$, $\eta_p^2 = 0.168$) or condition × time interaction ($F_{(1,11)} = 3.832$, $p = .076$, $\eta_p^2 = 0.258$). As shown in Fig. 5B and C, MRCP amplitude responses to the actual contractions presented a notable variability. The repeated measures correlation analysis failed to reveal a significant correlation between MRCP amplitude and perception of effort for actual contractions ($r(35) = 0.311$, $p = .060$).

4. Discussion

The main aim of the present study was to confirm that, when prolonged, motor imagery could induce a state of mental fatigue. The progressive increase in motor and premotor area activity required to imagine the contractions, in combination with the decreased quality of motor imagery and the increased feelings of fatigue, confirms that prolonged motor imagery induces mental fatigue. The secondary aim of the study was to identify during a subsequent physical exercise neurophysiological alterations caused by mental fatigue. While this study confirms previous observations that perception of effort during a physical exercise is increased in the presence of mental fatigue (for review see: Pageaux and Lepers, 2018; Brown et al., 2020), the results of the analysis of the MRCP amplitude cannot firmly confirm that this higher perceived effort is related to greater activation of the motor and premotor areas required to perform the isometric knee extensions. As discussed thereafter, this study needs to be replicated with specific adjustments on the physical exercise protocol to limit the exercise-induced decrease in force production capacity. Such adjustments will facilitate the possibility to observe clearer specific alterations in MRCP amplitude related to mental fatigue during an actual physical exercise.

4.1. Evidence of motor imagery

When requiring participants to engage in motor imagery, it is difficult to assess whether they actually imagine and execute the task. The greater alpha power during the prolonged motor imagery condition compared to the control condition, as well as the higher effort and

Table 1
Mean force, rate of force development (RFD), tremor, contraction duration, and vastus lateralis (VL) EMG RMS during the isometric knee extensions, during the first part (contractions 1 to 75) and the second part (contractions 76 to 150) of the physical exercise in Prolonged MI and Control conditions. Data are presented as means ± SE ($n = 12$).

Variables	Prolonged MI		Control		Condition	Time	Interaction
	Part 1 (0–75)	Part 2 (76–150)	Part 1 (0–75)	Part 2 (76–150)	p (η_p^2)	p (η_p^2)	p (η_p^2)
Force (N)	105.7 ± 8.1	104.9 ± 7.9	104.4 ± 7.9	104.1 ± 7.8	.473 (.048)	.297 (.098)	.405 (.064)
RFD mean (N/s)	271.8 ± 40.7	272.8 ± 45.3	286.2 ± 30.2	273.9 ± 39.1	.798 (.006)	.721 (.012)	.576 (.029)
Tremor (%)	2.23 ± 0.40	2.33 ± 0.31	2.15 ± 0.29	2.17 ± 0.23	.736 (.011)	.802 (.006)	.905 (.001)
Contraction duration (s)	2.88 ± 0.04	2.85 ± 0.03	2.91 ± 0.05	2.93 ± 0.05	.405 (.064)	.844 (.004)	.110 (.215)
VL EMG RMS (% RMS max)	30.3 ± 2.2	32.7 ± 2.6	30.9 ± 2.7	31.2 ± 2.9	.827 (.005)	.089 (.241)	.013 (.442)

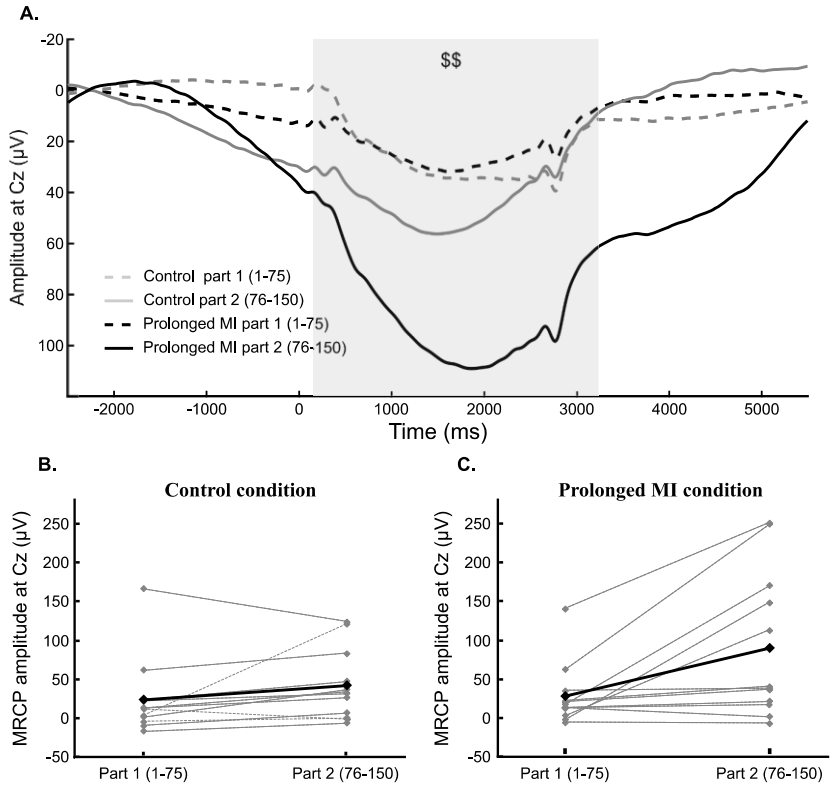

Fig. 5. Grand average (n = 12) of the EEG signal amplitude at Cz electrode for the first part (contractions 1 to 75) and the second part (contractions 76 to 150) of the submaximal isometric right knee extensions in both Prolonged MI and Control conditions. Time 0 corresponds to the audio signal to start the contraction (panel A), and the shaded area on the panel A represents the time window used for the analyse of the MRCP amplitude as presented in panels B and C. Individual mean amplitude of MRCP for the first and the second part of isometric knee extensions in the Control condition (panel B) and in the Prolonged MI condition (panel C). $$: Significant main effect of time on MRCP amplitude ($p < .01$).

mental demand experienced during the prolonged motor imagery condition, suggest the involvement of different cognitive processes during both prolonged motor imagery and documentary watching (Beyer et al., 1990). As previously observed, the imagination of maximal voluntary contractions was associated with the presence of MRCPs, confirming a specific activation of motor and premotor areas (do Nascimento et al., 2006; Jankelowitz and Colebatch, 2002). The MRCP amplitudes at Cz electrode during the imagined contractions were smaller than during the actual contractions (M = 12.00 μV vs. M = 45.56 μV). This result is in line with neuroimaging studies reporting lower activation of motor and premotor areas during imagined contractions compared to actual contractions (Batula et al., 2017; Porro et al., 1996). Furthermore, it is important to note that the absence of EMG activity during the imagination of contractions confirms that the participants imagined without activating their knee extensors. The integration of these results altogether confirms that the participants accurately performed motor imagery.

4.2. *Evidence of mental fatigue induced by prolonged motor imagery*

Mental fatigue is characterized by subjective feelings of "tiredness" and "lack of energy", associated or not with a decrease in cognitive performance (Boksem and Tops, 2008; Brown et al., 2020; Pageaux and Lepers, 2018). Mental fatigue is also known to increase the effort required to perform cognitive or physical activities (Nolte et al., 2008; Pageaux and Lepers, 2016). In the present study, feelings of fatigue increased over time, and the quality of motor imagery measured with the report of motor imagery vividness decreased during the prolonged motor imagery session, suggesting that prolonged motor imagery induces mental fatigue. The induction of mental fatigue by engagement in prolonged motor imagery is also confirmed by the progressive increase in the effort required to imagine the contractions over time.

In the present study, both the prolonged motor imagery and documentary watching increased feelings of fatigue. While the lack of significant condition × time interaction on the reported feelings of fatigue refrains the firm conclusion that the prolonged motor imagery condition induced a greater level of mental fatigue than the control condition, it is important to note that the participants experienced more effort to perform the subsequent physical exercise in the prolonged motor imagery condition compared to the control condition. A higher than normal perception of effort during a physical exercise is a well-reported alteration induced by the presence of mental fatigue (for review see: Pageaux and Lepers, 2018; Brown et al., 2020). Therefore, by considering that i) the effort required to perform motor imagery or watching a documentary increased solely in the prolonged motor imagery condition, and ii) the effort required to perform the subsequent physical exercise increased solely in the prolonged motor imagery condition, we are confident that the level of mental fatigue was greater following prolonged motor imagery compared to watching a documentary for the same duration. As boredom and sleepiness are proposed to interact with mental fatigue, it cannot be excluded that the observed increase in feelings of fatigue in the control condition confounds with changes in boredom and/or sleepiness, as recently suggested (O'Keeffe et al., 2020). As feelings of fatigue and boredom (Pattyn et al., 2008), as well as feelings of fatigue and sleepiness (Shen et al., 2006), can be dissociated from each other, future studies inducing mental fatigue should monitor the changes in these three constructs during prolonged engagement in demanding cognitive tasks. Such approach is likely to open new opportunities for researchers interested in better understanding the neurophenomenological differences between the experience of fatigue, boredom and sleepiness.

4.3. Are brain oscillations a good marker of mental fatigue induced by prolonged motor imagery?

The analysis of brain oscillations recorded with electroencephalography is a well-used marker of mental fatigue induced by prolonged engagement in demanding cognitive tasks. A recent meta-analysis reported that changes in brain oscillations on the theta and alpha power are consistently observed in the presence of mental fatigue (Tran et al., 2020). Prolonged engagement in demanding cognitive tasks has been shown to increase the oscillations on both alpha (e.g., Craig et al., 2012) and theta (e.g., Wascher et al., 2014) power. In the present study, no significant main effect of time or condition × time interaction was reported for the oscillations of the alpha power, suggesting that the completion of prolonged motor imagery did not induce a specific change over time in this parameter. Also, contrary to the hypothesis expecting an increased theta power in the presence of mental fatigue, the oscillations of the theta power decreased over time in the left parietal region. The observed changes in the oscillations of the theta power and the lack of changes in the oscillations of the alpha power do not support the possibility to use changes in brain oscillations as a marker of mental fatigue induced by prolonged motor imagery. These results are in line with a recent study showing that the engagement in different cognitive tasks leading to mental fatigue (psychomotor vigilance task, AX-CPT and Stroop task) does not elicit clear effects on EEG responses (Smith et al., 2019). The integration of our results with those of Smith et al. (2019) suggests that future studies should aim at identifying EEG-markers of mental fatigue that could provide coherent responses between different tasks known to induce a state of mental fatigue.

4.4. Prolonged motor imagery increases the motor and premotor area activity required to imagine muscle contractions

While the analysis of brain oscillations was not successful to identify the presence of mental fatigue, this study is to the best of our knowledge, the first to identify a neurophysiological alteration caused by mental fatigue induced by prolonged motor imagery. The progressive increase in MRCP amplitude suggests that a greater motor and premotor area activity is required to imagine muscle contractions in the presence of mental fatigue. It is therefore plausible that mental fatigue induces alterations in the motor command required to accurately perform imagined or actual muscle contractions. The hypothesis of an altered motor command in the presence of mental fatigue has been originally reported in a previous study demonstrating alterations in the speed-accuracy trade-off in the presence of mental fatigue (Rozand et al., 2015). In this study, the authors observed a longer duration of actual and imagined movements during a pointing task performed following 90 min of an incongruent Stroop task, compared to watching an emotionally neutral documentary for the same duration. In the present study, the observed increase in MRCP amplitude in the presence of mental fatigue, as well as the correlation between MRCP amplitude and perception of effort, provides neurophysiological evidence that mental fatigue could increase the magnitude of the motor command required to imagine a movement, and supports the hypothesis of an altered motor command in the presence of mental fatigue proposed by Rozand et al. (2015).

While the present study confirms that prolonged motor imagery induces mental fatigue, it is crucial to acknowledge that motor imagery is an efficient tool in rehabilitation when its use is not prolonged. By integrating the results of the objective (increase in MRCP amplitude over time) and subjective (increase in the effort required to imagine the contractions over time and decreased motor imagery vividness) markers of mental fatigue, our results reconcile with the recent meta-analysis of Schuster et al. (2011) suggesting that ~17 min of motor imagery is optimal to observe positive effects on physical performance. Indeed, in the present study, significant alterations in the effort required to perform imagined contractions was apparent after 25 min of motor imagery (i.e., from Block 3). By integrating the results of the meta-analysis of Schuster et al. (2011) with the results of the present study, future studies willing to use motor imagery and control for mental fatigue induction should use motor imagery sessions lasting no longer than 20 min.

4.5. Effects of mental fatigue induced by prolonged motor imagery on a subsequent physical exercise

As observed in previous studies, performing repeated muscle contractions for a prolonged duration induces a decrease in force production capacity that in turn increases the effort required to perform the physical exercise (Gandevia, 2001). This decrease in force production capacity highlights the presence of neuromuscular fatigue (Gandevia, 2001) and explains the increase in perception of effort and MRCP amplitude during the second half of the physical exercise in both prolonged motor imagery and control conditions (de Morree et al., 2012, 2014). Indeed, as perception of effort during physical exercise reflects the neuronal process of the motor command (de Morree et al., 2012, 2014; Pageaux, 2016; Pageaux and Gaveau, 2016), producing the same absolute level of force in the presence of neuromuscular fatigue requires an increased motor command to counteract the negative effects of neuromuscular fatigue on the corticospinal pathway and recruit additional muscle fibers (de Morree et al., 2012; Pageaux, 2016).

Contrary to previous studies demonstrating a higher perceived effort at the onset of the physical exercise performed in the presence of mental fatigue (Pageaux et al., 2013, 2014, 2015), in the present study the effort reported by the participants during the first half of the physical exercise did not differ between the prolonged motor imagery and the control conditions. Perception of effort was greater in the presence of mental fatigue solely in the second half of the physical exercise. As the studies observing a higher effort at the onset of the physical exercise used cognitive tasks predominantly involving the response inhibition process and not prolonged motor imagery, the discrepancy in these results suggests that mental fatigue may have different effects on a physical exercise depending on the method used to induce it. It can be speculated that, the absence of difference in perceived effort in the first half of the physical exercice could be due to the positive immediate effects of an acute motor imagery session on corticospinal plasticity (Ruffino et al., 2019). It cannot be excluded that the positive effects of motor imagery on the corticospinal pathway could counteract at the onset of the physical exercise the negative effects of mental fatigue on subsequent physical performance. Further studies should investigate a duration-response relationship on the effects of a single session of motor imagery on subsequent physical performance.

4.6. Effect of mental fatigue on motor and premotor area activity

Perception of effort is proposed to be generated by the neuronal process of a corollary discharge of the motor command (de Morree et al., 2012, 2014; Pageaux, 2016; Pageaux and Gaveau, 2016), and is traditionally used in the neurophysiology literature as a marker of the central motor command (e.g., Kjær et al., 1999; McCloskey et al., 1974; Mitchell et al., 1989; Seed et al., 2019). Muscle activation measured with EMG is traditionally used as a marker of the motor command sent to the working muscles in studies interested in the regulation of muscle contractions and movements (e.g., Carrier et al., 2011; Thoroughman and Shadmehr, 1999). The vastus lateralis EMG RMS increased solely in the prolonged motor imagery condition and not in the control condition. The specific alterations in objective (EMG) and subjective (perception of effort) indices of the motor command suggest that prolonged motor imagery alters the motor command in a subsequent physical exercise, and that underlying neurophysiological alterations progressively develop over time. However, both the nonsignificant condition × time interaction on the analysis of the MRCP amplitude and the nonsignificant correlation between MRCP amplitude and perception of effort do not allow to clearly conclude on that point. The observed variability in changes in MRCP amplitude during the physical exercise performed

following prolonged motor imagery (Fig. 5.C) also suggests between-participant differences in response to mental fatigue. Although all participants declared to engage in a physical activity at least one time per week, their exact training status and sport expertise was not collected. As expertise in endurance sports seems to be associated with greater resistance to mental fatigue (Martin et al., 2016), the variability observed in changes in MRCP amplitude could be due to differences between participant in training status, sport expertise or physical activity level. In this context, studies interested in investigating mental fatigue should carefully record at least the physical activity level of their participants, and if possible their sport expertise and associated performance level (Decroix et al., 2016; Pauw et al., 2013).

As previous studies also observed alterations in EMG signal of the working muscles during submaximal physical exercices following engagement in demanding cognitive tasks (Bray et al., 2008; Graham et al., 2014; Pageaux et al., 2015), we believe that the absence of significance in the condition × time interaction is likely due to the confounding effects of neuromuscular fatigue on MRCP amplitude (de Morree et al., 2012, 2014) rather than the absence of a true effects of mental fatigue on this parameter. Indeed, as a reduction in force production capacity is known to increase MRCP amplitude (de Morree et al., 2012), and our physical exercise induced a decrease in force production capacity, future studies should be conducted by tailoring the physical exercise to limit as much as possible the presence of exercise-induced neuromuscular fatigue. As the magnitude of neuromuscular fatigue is known to be intensity and contraction duration dependent (Burnley et al., 2012; Mendez-Villanueva et al., 2009), such tailoring could be done by decreasing the level of the relative force target to reach during each contraction or the duration of the contractions, as well as by increasing the recovery period between the contractions. Such changes in the physical exercise protocol are also likely to reduce the number of excluded MRCPs due to head or body movement during the muscle contractions. Even if knee extensions were investigated for their relevance to locomotion and other activities of the daily life in this study, these contractions involve a large muscle group and generate large artifacts on the EEG signal. Therefore, we also suggest that future studies should consider involving a smaller muscle group and perform movements such as elbow flexions, wrist flexions or handgrip contractions. Involving a smaller muscle group compared to the knee extensors, or decreasing the intensity of the physical exercise, will also reduce cardiorespiratory responses to the physical exercise (Mitchell et al., 1980) and render the physical exercise more accessible to various populations and not only physically active and healthy young adults. Finally, we acknowledge that the limit of our sample size does not allow to clearly conclude on the condition × time interaction on the MRCP amplitude during the physical exercise ($p = .076$, $\eta_p^2 = 0.258$) performed following the prolonged motor imagery. An increased sample size in future studies is i) likely to overcome this limitation and ii) of great importance for studies interested in gender and sex differences in the effect of mental fatigue on subsequent physical performance.

4.7. Conclusion and perspectives

The present study confirms that, when prolonged, motor imagery induces a state of mental fatigue. The presence of mental fatigue was evidenced by the progressive increase in motor and premotor area activity required to imagine the contractions (i.e., increase in MRCP amplitude over time), in combination with the decreased quality of motor imagery and the increased feelings of fatigue. In the presence of mental fatigue induced by prolonged motor imagery, the subsequent physical exercise was perceived as being more effortful in the second part of the exercise and was associated with a specific increase in EMG RMS of the vastus lateralis muscle. These alterations suggest that mental fatigue induced by prolonged motor imagery may alter the motor command required to perform imagined and actual contractions. However, due to the marked decrease in knee extensors force production capacity induced by the physical exercise and consequently its confounding effects on the observed increase in MRCP amplitude (de Morree et al., 2012), future studies will be necessary to replicate and reinforce the results of the present study, notably by tailoring the physical exercise to avoid, or at least minimize, neuromuscular fatigue.

Credit author statement

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Appendix A. Supplementary data

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Persistence of Mental Fatigue on Motor Control

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The effects of mental fatigue on both cognitive and physical performance are well described in the literature, but the recovery aspects of mental fatigue have been less investigated. The present study aimed to fill this gap by examining the persistence of mental fatigue on behavior and electrophysiological mechanisms. Fifteen participants performed an arm-pointing task consisting of reaching a target as fast as possible, before carrying out a 32-min cognitively demanding task [Time Load Dual Back (TLDB) task], and immediately, 10 and 20 min after completion of the TLDB task. During the experiment, electroencephalography was continuously recorded. The significant increase in mental fatigue feeling after the TLDB task was followed by a decrease during the 20 min of recovery without returning to premeasurement values. Brain oscillations recorded at rest during the recovery period showed an increase in both theta and alpha power over time, suggesting a persistence of mental fatigue. Arm-pointing movement duration increased gradually over time during the recovery period, indicating that behavioral performance remained impaired 20 min after the end of the cognitively demanding task. To conclude, subjective measurements indicated a partial recovery of mental fatigue following a cognitively demanding task, whereas electrophysiological and behavioral markers suggested that the effects of mental fatigue persisted for at least 20 min. While the subjective evaluation of mental fatigue is a very practical way to attest the presence of mental fatigue, electrophysiological and behavioral measures seem more relevant to evaluate the time course of mental fatigue effects.

Keywords: cognitive fatigue, recovery effect, electroencephalography (EEG), brain oscillations, event-related potentials, Fitts' law, arm-pointing task

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INTRODUCTION

Mental fatigue, which is defined as a psychobiological state caused by prolonged and/or intense periods of demanding cognitive activity and characterized by subjective feelings of "tiredness" and "lack of energy" (Boksem and Tops, 2008; Rozand and Lepers, 2016), is a common problem in everyday life. It can affect patients with cancer, Alzheimer's or Parkinson's disease (Chaudhuri and Behan, 2000), as well as healthy individuals, in whom it can lead to a decrease in productivity, an increase in road accidents (Dinges, 1995), or even be involved in burnout or depression (Lavidor et al., 2002).

Mental fatigue is a very complex phenomenon, and its neural mechanisms are still poorly known. They likely involve changes in brain activity involving the anterior cingulate cortex (ACC), a brain area at the interface between cognition, emotion, and motor control (Müller and Apps, 2019).

Several different theories have been proposed to explain the mental fatigue-induced performance decrements; these include underload theories (Manly et al., 1999), resource theories (Sanders, 1997), motivational control theories (Kurzban et al., 2013), and dual regulation system (Ishii et al., 2014). The present study falls within the framework of resource theories, and is close to ego-depletion theory (Baumeister et al., 1998; Hagger et al., 2010). In this background, performing a cognitively fatiguing task reduces, or even under certain circumstances, depletes cerebral and cognitive resources that cannot be replenished immediately and that cannot be fully available to perform a following task (cognitive or physical). This could result in performance decrement (although some compensatory mechanisms might maintain performance, Hockey, 2013; Wang et al., 2016) and cerebral brain changes.

Since the middle of the 19th century (Davy, 1845), researchers have investigated mental fatigue in both laboratory and field conditions to better understand its effects and mechanisms. Under laboratory conditions, mental fatigue is generally induced by specific cognitive tasks. For example, the Stroop task (e.g., Rozand et al., 2015; Van Cutsem et al., 2017a), the AX-CPT (AX-continuous performance test; e.g., Marcora et al., 2009; Pageaux et al., 2013) or computerized decision-making tasks (Otani et al., 2017) have been used, generally for a duration ranging from 45–90 min, to induce mental fatigue. However, during prolonged cognitive tasks, both mental fatigue and boredom interfere, making it difficult to study mental fatigue *per se*. To differentiate between mental fatigue and boredom, shorter but more demanding cognitive tasks have been used to induce mental fatigue without boredom. For example, Borragan et al. (2016) used a cognitive task called the Time Load Dual Back (TLDB) task combining a traditional N-back working-memory updating task and an interfering second task (odd/even decision task) lasting 16 min. After completion of the TLDB task, the participants reported a significant increase in the feeling of mental fatigue, and their vigilance decreased during a subsequent psychomotor vigilance task (PVT; Borragan et al., 2017). While subjective measures [e.g., visual analog scale (VAS)] can be used to evaluate mental fatigue (Smith et al., 2019), measures based on electrophysiological recordings can provide more objective evidence of mental fatigue.

Studies using electroencephalography (EEG) have shed light on the neural mechanisms involved in mental fatigue, notably changes in brain oscillations. Mainly an increase in alpha power has consistently been observed, which might reflect a decrease in arousal and alertness (Paus et al., 1997; Boksem et al., 2005; Zhao et al., 2012). Although alpha power changes are a robust marker of mental fatigue, a recent meta-analysis suggested that an increase in theta power would be a more reliable biomarker of the presence of mental fatigue (Tran et al., 2020). According to this meta-analysis, mental fatigue results in large increases in theta power through the whole brain (i.e., frontal, central, and posterior regions), while increases in alpha power are mainly observed in central and posterior regions and to a lesser extent in frontal regions. In addition to brain oscillations, event-related potentials (ERPs) have also been considered. Consistent effects of mental fatigue have been observed on N100, N2, and P300 components. For these three components, a decrease in amplitude over time has been observed and interpreted as reflecting a top–down modulation of sensory processing for the N100 (Boksem et al., 2005; Faber et al., 2012), a decrease in cognitive control for the N2 (Boksem et al., 2006; Möckel et al., 2015) and a decrease in attention for the P300 (Murata et al., 2005; Schmidt et al., 2009). In parallel with electrophysiological changes, performance can also be impaired by mental fatigue.

It has been established that mental fatigue may negatively impact subsequent cognitive (e.g., van der Linden et al., 2003; Boksem et al., 2005) or physical (for review: Van Cutsem et al., 2017b; Pageaux and Lepers, 2018) activities. Concerning physical performance, not all physical activities are negatively impacted by mental fatigue. While previous studies have shown that mental fatigue impaired endurance performance (e.g., Marcora et al., 2009; Pageaux et al., 2014) as well as decision making (e.g., Smith et al., 2016; Harris and Bray, 2019) and motor skills (e.g., Rozand et al., 2015; Le Mansec et al., 2018), the maximal voluntary force/power production capacity seems to be preserved (e.g., Pageaux et al., 2013; Duncan et al., 2015). To evaluate the effects of mental fatigue on motor skills, Rozand et al. (2015) used an arm-pointing task consisting of reaching visual targets as fast as possible. Following mental fatigue, induced by 90 min of a modified Stroop task, these authors observed an ∼10% increase in actual movement duration, indicating an impairment of motor skills following a prolonged cognitively demanding task.

While the effects of mental fatigue on motor performance have been clearly demonstrated, questions about the persistence of these effects and the time course of recovery from mental fatigue have been poorly investigated. To our knowledge, Rivers (1896) was one of the first to address this question by evaluating the effect of a 30- or 60-min rest period following 30 min of mental work (i.e., addition calculation). Results indicated that 30 min of total rest was insufficient to neutralize the effects of mental fatigue and that 60 min of total rest only partially eliminated the effects. More recently, Smith et al. (2019) investigated the effects of three different cognitive tasks (Stroop task, AX-CPT, and PVT), lasting 60 min, on reaction times, feeling of fatigue and electrophysiological markers, as well as their persistence over time. They observed that the feeling of mental fatigue (reported on a VAS) increased immediately after the three cognitive tasks but led to a decrease in vigilance only after the Stroop task and the AX-CPT task. The level of mental fatigue decreased gradually over time, suggesting that a recovery mechanism came into play. However, the feeling of mental fatigue remained high for 10 min after the PVT, 50 min after the Stroop task, and 60 min after the AX-CPT. Concerning performance, no negative effect of mental fatigue was reported on vigilance 30 min after completion of the three different cognitively demanding tasks. These observations suggest that performance may recover faster than the subjective feeling of mental fatigue.

The main objective of the present study was to investigate the time course of mental fatigue following a 32-min cognitively demanding task on both subjective (VAS) and electrophysiological (i.e., brain oscillations) markers, as well as on motor performance. An arm-pointing task was used to evaluate the impact of mental fatigue on motor performance,

due to its involvement in many activities of daily living. We firstly hypothesized that during the completion of the TLDB task, an increase over time in both theta and alpha power should be observed. It should concern all the brain regions for theta power, and more specifically central and parietal regions and to a lesser extend the frontal regions for alpha power. Concerning ERPs, we hypothesized that the amplitude of the N100, the N200, and the P300 should decrease over time as observed in previous studies (Boksem et al., 2005, 2006; Murata et al., 2005; Faber et al., 2012). Secondly, we also expected that immediately after the cognitively demanding task the subjective feeling of mental fatigue would increase and the motor performance decrease. These alterations would be associated with an increase in both theta and alpha power during the rest period immediately following the cognitively demanding task. Finally, we assumed that, during the recovery period following the completion of the cognitively demanding task, a progressive decrease in the subjective feeling of mental fatigue would be associated with a return toward initial levels of brain oscillations recorded during rest period and motor performance.

MATERIALS AND METHODS

Participants

The study was conducted with 15 healthy active adults, eight males and seven females (mean ± SD; age: 21.9 ± 1.8 years). It included two sessions: a familiarization session and an experimental session. All participants reported normal or corrected-to-normal vision and none of them had a history of neurological disorders. They completed the Edinburgh questionnaire, which confirmed that all participants were right-handed. All participants were given instructions to sleep for at least 7 h, not to consume alcohol, and to refrain from vigorous physical activity the day before each visit. Participants were also instructed not to consume caffeine and nicotine at least 3 h before testing and were asked to declare if they had taken any medication or had any acute illness, injury, or infection. All the participants provided their written informed consent. The experiment was conducted in accordance with the Declaration of Helsinki (1964).

The Cognitively Fatiguing Task: The Time Load Dual Back Task

The TLDB task is a dual task combining a classic N-back working-memory updating task (Kirchner, 1958) and an interfering second task (odd/even decision task). Stimuli were letters and digits displayed alternately on the screen (i.e., letter/digit/letter/. . .). When letters were presented, participants were instructed to press the space bar with their left hand every time the displayed letter was the same as the previous one (1-back task). When digits were displayed, participants had to press a key on the numeric keypad, using their right index and middle fingers: "1" if it was an odd number, "2" if it was even. A total of eight letters (A, C, T, L, N, E, U, and P) and eight numbers (1, 2, 3, 4, 6, 7, 8, and 9) were used. Stimulus presentation was managed by the Experiment Builder software (SR Research). Stimuli were presented in Arial font size 120, in the center of a 16-inch computer screen (refresh rate 60 Hz). They were presented in blocks of 60 trials with a break of 30 s between each block.

The Physical Task: The Arm-Pointing Task

Participants had to point at a target as accurately and as fast as possible with a pencil held in their right hand. They were sitting down, and in the start position their arm was aligned with their right shoulder and all targets to be pointed at were located on a 45° diagonal to the left to limit joint stress. The targets were black squares displayed on a touch screen in front of the participant (**Figure 1A**). The targets had different indices of difficulty (Nitschke et al., 2006), which were calculated using the formula $ID = \log_2(\frac{2D}{W})$, where D represents the center-to-center distance between the start point and the target, and W represents the width of the target. Using different distances (between 5 and 32 cm) and widths (between 0.5 and 2.5 cm), 40 targets were created with eight IDs ranging from 2.5 to 6 in steps of 0.5. Each ID included five different targets with different widths and distances from the start point.

The time measured for the pointing movement began when participants took the pen from the start point and stopped when the pen touched the touch screen. If the participant landed on the target, the trial was considered as "correct"; if not, it was a miss. At each trial, the participant had to return to the start point. The pointing task lasted approximately 1.5 min.

The arm-pointing task was performed before the TLDB task, immediately after the TLDB task (Post), 10 min (Post 10) and 20 min (Post 20) after the TLDB task. For each arm-pointing task, the difficulty did not increase over time. The same trials were presented in pretest and in all the posttests, but with a different random order.

Psychological Measurement

The Saint Mary's Hospital Sleep Questionnaire was used to evaluate the participants' sleep quality the night before the experiment (at each session). It contains 14 items concerning sleep quality, such as depth, awakening in the middle of the night, satisfaction, refreshed feeling upon awakening, difficulty in falling asleep, and early awakening. Participants reported that they slept on average 7 h and 41 min (±12 min).

Motivation related to the entire protocol was measured at the beginning of the experiment, using the motivation questionnaire developed and validated by Matthews et al. (2001). It has two subscales, evaluating success motivation and intrinsic motivation. Each subscale has seven questions, with a choice of five answers: 0 = not at all, 1 = a little bit, 2 = somewhat, 3 = very much, 4 = extremely. Therefore, total scores for these motivation scales range between 0 and 28. A low score reveals low motivation, and a high score indicates high motivation. Participants' scores were 17.7 (±1.3) for success motivation and 23.3 (±0.9) for intrinsic motivation.

The participants also rated their level of mental fatigue on a VAS at four points of the experimental session: at the start of the session, after the TLDB task, and before Post 10 and Post 20

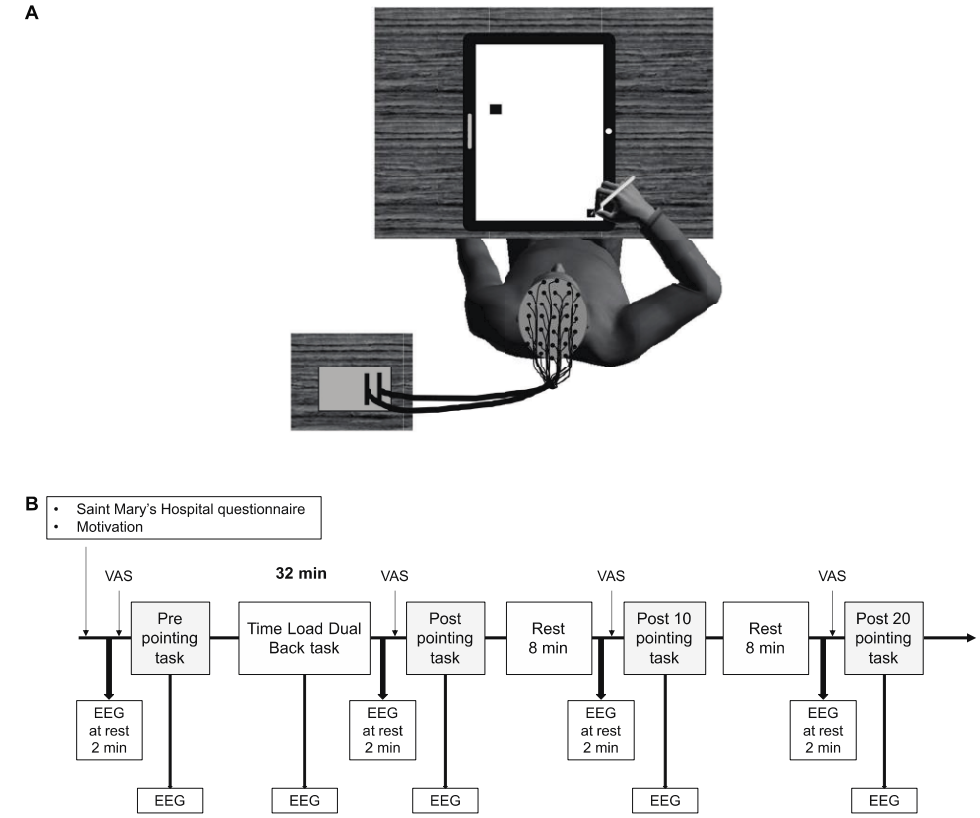

FIGURE 1 | A schematic representation of the participants' position while performing the arm-pointing task **(A)**, and an overview of the experimental protocol **(B)**. VAS, fatigue visual analog scale; EEG, electroencephalography.

tests. The VAS was a line 100 mm long, with bipolar end anchors (0 mm = "Not mentally fatigued at all"; 100 mm = "Extremely mentally fatigued") on which participants placed a mark to estimate their level of mental fatigue.

Procedure

The experiment included two sessions: a familiarization session and an experimental session (**Figure 1B**). During the familiarization session, participants were shown the questionnaires used in the experiment, and were trained on both arm-pointing and TLDB tasks. The threshold of stimulation duration, corresponding to the highest level of TLDB task performance, was determined for each participant using the same procedure as previous studies (Borragan et al., 2016, 2017). All participants started the familiarization session with a 1500 ms presentation of each event (i.e., letters and digits) without inter-stimulus intervals. At the end of each block, if the performance accuracy was equal to or greater than 85%, the duration of the presentation was reduced by 100 ms, and so on until the accuracy was lower than 85%. At this point, participants performed two more blocks with the same duration to pursue familiarization; the threshold for the experimental session was fixed at the last successful duration. The familiarization session also aimed to reduce learning effects, which could counteract the effect of mental fatigue on performance.

The experimental session took place 48–96 h after the familiarization session, at the same time of day. Before installing the EEG recording system, participants were reminded how to perform the arm-pointing task and carried out another practice trial. While the EEG was being set up, participants completed the Saint Mary's Hospital questionnaire and the motivation questionnaire. They were then installed on a comfortable chair in an acoustically and electrically isolated booth (**Figure 1A**). First, EEG activity was recorded at rest for 2 min while the participants were sat in front of a black screen, and were asked to rest and not to think about anything. After that, they were asked to rate their level of mental fatigue on the VAS and to perform the first arm-pointing task. They then performed the TLDB task, which lasted 32 min[1] (excluding the

[1] In a pilot experiment, 16 min of the TLDB task were used to induce mental fatigue as in Borragan et al. (2016). However, while 16 min of the TLDB task induced a subjective feeling of mental fatigue, it was not long enough to induce a decrement in arm-pointing task performance. The duration of the TLDB task was doubled

rest periods between each block). Immediately after the TLDB task, the EEG activity was recorded at rest for 2 min, and participants rated their level of mental fatigue and performed the arm-pointing task again (Post). After 8 min of rest, the same procedure was repeated (i.e., recording EEG activity at rest for 2 min, rating mental fatigue level and arm-pointing task; Post 10). Finally, after a second rest period of 8 min, the same procedure was repeated for the last time (Post 20; see **Figure 1B**). During rest periods, the experimenter talked with the participant. Talking to the participant during the rest period was chosen as an ecological condition, mirroring what happens in daily life at work, for instance. The conversation was similar for each participant, and dealt with their job (or education), their hobbies (e.g., sport, nature), and their perspectives for the future (e.g., studies, jobs). These topics were always addressed in the same order.

EEG Recording and Preprocessing

The electroencephalogram was recorded continuously through the Active Two BioSemi system from 64 electrodes in accordance with the 10–20 International system. Horizontal eye movements were monitored with electrodes placed on the outer left and right canthi, while eye blinks were monitored with an electrode placed under the left eye. Two additional electrodes were placed on the left and right mastoids (A1, A2). During recording, the BioSemi system's common-mode sense electrode served as the reference electrode. Electrophysiological signals were digitized at 2048 Hz sampling rate and acquired with ActiView software. Offline data analyses were performed using MATLAB (MathWorks, Natick, MA, United States) and the EEGLAB toolbox (Delorme and Makeig, 2004). Continuous data were downsampled to 256 Hz, band-pass filtered at 0.01–100 Hz, and re-referenced to the average of A1 and A2. Noisy electrodes were identified with the *probability* and *spectrum* methods proposed in EEGLAB (threshold, Z = 5) and interpolated when necessary with a spherical method. To correct eye-movement artifacts, EEGLAB's Runica routine was used to perform independent component analyses, and components reflecting eye artifacts were removed by visual inspection. Continuous data were segmented into 500 ms epochs from 50 ms before to 450 ms after the onset of the stimuli and were baseline corrected using the pre-trial period from −25 ms to 0 ms.

Data and Analysis

Pointing Movement

Movement durations less than 100 ms and more than 1400 ms were excluded from the analysis. We estimated that movement duration below 100 ms and above 1400 ms were not coherent for the performed movements. Altogether, only two trials over 2400 were excluded from the data. Movement durations beyond two standard deviations (SDs) of the mean were also excluded. Analyses were performed on 88% of trials.

to 32 min and, under these circumstances, both an increase in subjective mental fatigue and a decrement in arm-pointing task performance were observed.

EEG Data

For the TLDB task, only trials with correct responses (93% of trials) were considered for ERP analysis. Epochs were averaged separately for each condition and each participant. ERPs were obtained by computing the mean amplitude in the time window for each ERP component, and by grand-averaging data across participants. Because no studies have previously analyzed ERPs during the TLDB task and because ERPs are stimulus and task dependent, we determined our time windows for the ERP analyses based on visual inspection, according to the peak of the ERP and its shape, to be in complete adequation with the observed ERPs. Different time windows were used for ERP components for letters on fronto-central region (N100: 90–150 ms, N200: 230–315 ms, P300: 325–445 ms) and on parietal region (N200: 130–200 ms, P300: 325–445 ms). Using the same method, ERP components were also identified for digits on fronto-central region (P50: 25–75 ms) and parietal region (N200: 135–210 ms).

For EEG spectral analysis, during the TLDB task, the 2-min rest and the arm-pointing task, EEG power of individual epochs was computed by Fast Fourier Transform (FFT), using the *spectopo* function of the EEGLAB software. It was divided into five frequency bands: delta, 1–4 Hz; theta, 4–7 Hz; alpha, 8–12 Hz; beta 13–30 Hz; and gamma, 30–40 Hz to be analyzed. Spectral analyses during the TLDB task and the arm-pointing task were performed irrespective of the occurrence of stimuli. Nine regions of interest (ROIs) were constituted to perform analysis on both ERPs and spectral data: Frontal Left (FL; mean of FP1, AF3, AF7, F3, F5, F7, FC3, FC5, FT7), Frontal Median (FM; mean of FPz, AFz, F1, Fz, F2, FC1, FCz, FC2), Frontal Right (FR: mean of FP2, AF4, AF8, F4, F6, F8, FC4, FC6, FT8), Central Left (CL: mean of C3, C5, T7, CP3, CP5, TP7), Central Median (CM: mean of C1, Cz, C2, CP1, CPz, CP2), Central Right (CR: mean of C4, C6, T8, CP4, CP6, TP8), Posterior Left (PL: mean of P9, P7, P5, P3, PO7, PO3, O1), Posterior Median (PM: mean of P1, Pz, P2, POz, Oz), and Posterior Right (PR: mean of P4, P6, P8, PO4, PO8, O2). Statistical evaluation was performed with repeated-measures ANOVAs on each ROI.

Statistics

All data are presented as means ± standard error of the mean. Degrees of freedom were corrected using the Greenhouse–Geisser procedure when sphericity was violated (corrected degree of freedom and *p*-values are reported). Only significant effects are reported, except when non-significance is relevant for the hypotheses being tested.

To evaluate mental fatigue effects on the VAS, one-way repeated measures ANOVA with time (Pre, Post, Post 10, and Post 20) as within-subject factor was conducted. The effects of mental fatigue on movement duration and errors on arm-pointing movements were evaluated using two-way repeated measures 4 × 8 ANOVAs with time (pre, post, post 10, and post 20) and ID (2.5, 3, 3.5, 4, 4.5, 5, 5.5, and 6) as within-subject factors.

For the TLDB task, analyses were performed separately for letters and digits. Two-way repeated measures 2 × 4 ANOVAs

including the within-subject factors of Stimulus type (for letters: same/different; for digits: even/odd) and time-on-task (part 1, 0–8 min; part 2, 8–16 min; part 3, 16–24 min; and part 4, 24–32 min) were performed for RTs, accuracy, and ERPs. Only ERPs interesting for mental fatigue effects are reported in the "Results" section.

Brain oscillations were analyzed using one-way repeated measures ANOVAs with time-on-task (part 1, 0–8 min; part 2, 8–16 min; part 3, 16–24 min; and part 4, 24–32 min) as within-subject factor during the TLDB task and, with time (Pre, Post, Post 10, and Post 20) for the recordings at rest. Only results about theta and alpha power are reported in the "Results" section, the other brain oscillations are reported in **Supplementary Data**.

All analyses were performed using the Statistical Package for the Social Sciences, version 24 for Windows (SPSS Inc., Chicago, IL, United States). Significant main effects of time and significant interactions were followed up by contrast tests, and planned comparisons using *t*-tests with Bonferroni correction for multiple comparisons as appropriate. Only significant results are reported, with adjusted *p*-values. For each ANOVA, partial eta squared is reported. Thresholds for small, moderate, and large effects were set at 0.01, 0.07, and 0.14, respectively (Cohen, 1988). Cohen's *d* was calculated for each paired *t*-test using JASP (Version 0.9.1.0) [Windows software]. Thresholds for small, moderate, and large effects were set at 0.2, 0.5, and 0.8, respectively (Cohen, 1988).

RESULTS

Mental Fatigue Assessment

Subjective Measure of Mental Fatigue

Visual analog scale

As displayed in **Figure 2**, analysis revealed an increase in the feeling of fatigue over time [$F_{(3,42)} = 26.784$, $p < 0.001$, $\eta_p^2 = 0.657$], qualified by a cubic trend [$F_{(1,14)} = 40.109$, $p < 0.001$, $\eta_p^2 = 0.741$], with a significant increase in feeling-of-fatigue score between Pre and Post [$t_{(14)} = 6.629$, $p < 0.001$, $d = -1.711$], followed by a reduction of the fatigue score between Post and Post 10 [$t_{(14)} = 4.601$, $p = 0.002$, $d = 1.188$], but not between Post 10 and Post 20 [$t_{(14)} = 3.876$, $p > 0.05$, $d = 0.163$]. The subjective feeling of fatigue was still significantly higher at Post 10 [$t_{(14)} = 4.713$, $p = 0.002$, $d = 1.217$] and post 20 [$t_{(14)} = 5.863$, $p < 0.001$, $d = 1.514$] compared to Pre.

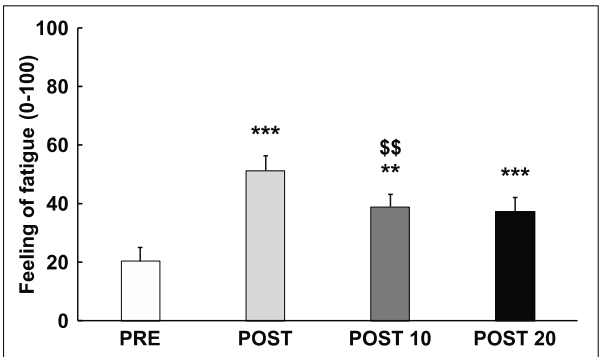

FIGURE 2 | Time course of subjective feeling of mental fatigue. ** and ***: Significantly different from Pre ($p < 0.01$ and $p < 0.001$, respectively). $$: Significantly different from the previous measurement ($p < 0.01$). Data are presented as mean ± SE.

Performance During the TLDB Task

Reaction time

Mean reaction time was 535.2 ms (±10.0) for digits and 498.8 ms (±11.0) for letters. No significant effect of time or interaction with the factor time was observed on reaction time during the TLDB task for letters or digits (all $ps > 0.15$, $\eta_p^2 < 0.13$).

Accuracy

Mean accuracy was 90.9% (±0.5) and 92.8% (±0.8) for digits and letters. No significant effect of time or interaction with the factor time was observed on reaction time during the TLDB task for letters or digits ($ps > 0.35$, $\eta_p^2 < 0.07$), suggesting that performance was maintained over time.

EEG Data

Event-related potentials

N100. Analysis showed a significant time-on-task effect only for letters in CL region [$F_{(3,42)} = 4.019$, $p = 0.033$, $\eta_p^2 = 0.223$], qualified by a linear trend [$F_{(1,14)} = 5.293$, $p = 0.030$, $\eta_p^2 = 0.293$], reflecting a decrease in the N100 amplitude over time (**Figure 3**).

N200. For letters, ANOVA revealed a significant time-on-task effect for FL [$F_{(3,42)} = 6.755$, $p < 0.001$, $\eta_p^2 = 0.326$], FM [$F_{(3,42)} = 6.388$, $p = 0.001$, $\eta_p^2 = 0.313$], FR [$F_{(3,42)} = 5.755$, $p = 0.002$, $\eta_p^2 = 0.291$], CL [$F_{(3,42)} = 7.064$, $p < 0.001$, $\eta_p^2 = 0.335$], CM [$F_{(1.906,26.690)} = 6.623$, $p = 0.005$, $\eta_p^2 = 0.321$], and CR regions [$F_{(3,42)} = 6.274$, $p = 0.001$, $\eta_p^2 = 0.309$], indicating a linear decrease in N200 amplitude over time for all these regions ($ps < 0.012$, $\eta_p^2 > 0.378$). For digits, analysis showed a significant main effect of time-on-task for LF [$F_{(3,42)} = 4.278$, $p = 0.021$, $\eta_p^2 = 0.234$] and CL regions [$F_{(3,42)} = 4.090$, $p = 0.020$, $\eta_p^2 = 0.226$], qualified by a linear trend for both FL [$F_{(1,14)} = 7.576$, $p = 0.016$, $\eta_p^2 = 0.351$] and CL regions [$F_{(1,14)} = 7.882$, $p = 0.019$, $\eta_p^2 = 0.360$] indicating, as for letters, a decrease in the N200 amplitude over time (see **Figures 3**, **4**).

P300. A significant time-on-task effect was reported only for letters on the P300 amplitude for CR [$F_{(3,42)} = 8.465$, $p = 0.002$, $\eta_p^2 = 0.377$], qualified by a linear trend [$F_{(1,14)} = 11.415$, $p = 0.005$, $\eta_p^2 = 0.449$], indicating an increase in the P300 amplitude over time. On PR region, analysis indicated a significant time-on-task effect on the P300 amplitude [$F_{(3,42)} = 5.854$, $p = 0.004$, $\eta_p^2 = 0.295$], qualified by a quadratic trend [$F_{(1,14)} = 9.208$, $p = 0.009$, $\eta_p^2 = 0.397$], reflecting an increase in P300 amplitude over time between the first and the second part [$t_{(14)} = -2.460$, $p = 0.028$, $d = -0.635$], and between the second and the third part of the task [$t_{(14)} = -5.863$, $p = 0.022$, $d = -0.667$], but a decrease in the P300 amplitude between the third and the fourth part [$t_{(14)} = 2.164$, $p = 0.048$, $d = -0.559$] (**Figure 3**).

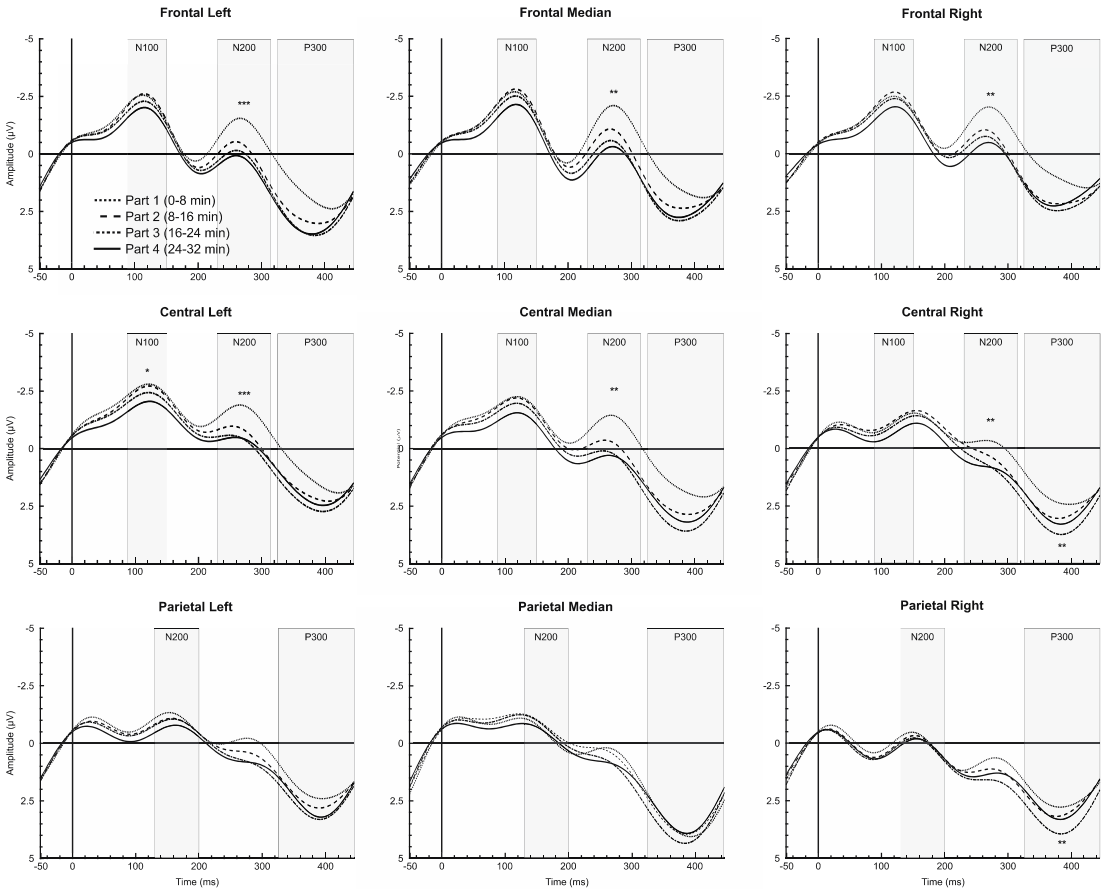

FIGURE 3 | Time-on-task effect for letter stimuli during the 32-min time load dual back task in all regions of interest. *, ** and ***: Significantly time-on-task effect ($p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively).

Brain oscillations

All the results of brain oscillations are presented in the **Supplementary Table S1**. Only significant differences related to brain oscillations useful to test our hypothesis, i.e., theta and alpha powers, are presented below.

Theta. Analysis showed a significant time-on-task effect on FL [$F_{(3,42)} = 6.779$, $p < 0.001$, $\eta_p^2 = 0.326$], FM [$F_{(3,42)} = 12.828$, $p < 0.001$, $\eta_p^2 = 0.478$], FR [$F_{(3,42)} = 11.840$, $p < 0.001$, $\eta_p^2 = 0.458$], CL [$F_{(3,42)} = 13.411$, $p = 0.028$, $\eta_p^2 = 0.489$], CM [$F_{(3,42)} = 13.570$, $p < 0.001$, $\eta_p^2 = 0.492$], CR [$F_{(3,42)} = 9.616$, $p < 0.001$, $\eta_p^2 = 0.407$], PM [$F_{(3,42)} = 7.754$, $p < 0.001$, $\eta_p^2 = 0.356$], and PR regions [$F_{(1.888,26.438)} = 5.908$, $p = 0.008$, $\eta_p^2 = 0.297$], qualified for all these regions by a linear trend (all $ps < 0.011$, $\eta_p^2 > 0.230$), indicating a decrease in theta power over time (see **Figure 5**).

Alpha. ANOVA revealed a significant time-on-task effect on FL [$F_{(1.699,23.781)} = 6.827$, $p = 0.006$, $\eta_p^2 = 0.328$], FM [$F_{(1.447,20.253)} = 7.351$, $p = 0.007$, $\eta_p^2 = 0.344$], FR [$F_{(1.600,22.397)} = 5.811$, $p = 0.013$, $\eta_p^2 = 0.293$], CL [$F_{(1.447,20.256)} = 4.849$, $p = 0.028$, $\eta_p^2 = 0.257$], CM [$F_{(1.601,22.426)} = 6.528$, $p = 0.008$, $\eta_p^2 = 0.318$], CR [$F_{(1.617,22.634)} = 5.426$, $p = 0.016$, $\eta_p^2 = 0.279$], PL [$F_{(1.579,22.108)} = 5.329$, $p = 0.018$, $\eta_p^2 = 0.276$], and PM regions [$F_{(1.621,22.692)} = 7.779$, $p = 0.004$, $\eta_p^2 = 0.357$]. This main effect of time-on-task was qualified by a quadratic trend for all these regions (all $ps < 0.020$, $\eta_p^2 > 0.330$), highlighting a slight decrease in alpha power between the first and the second part of the TLDB task, followed by an increase in alpha power over time (see **Figure 5**).

Effect of Mental Fatigue on the Arm-Pointing Task

Movement Duration

There was a significant main effect of ID [$F_{(1.245,17.428)} = 136.045$, $p < 0.001$, $\eta_p^2 = 0.907$] qualified by a linear trend [$F_{(1,14)} = 10.607$,

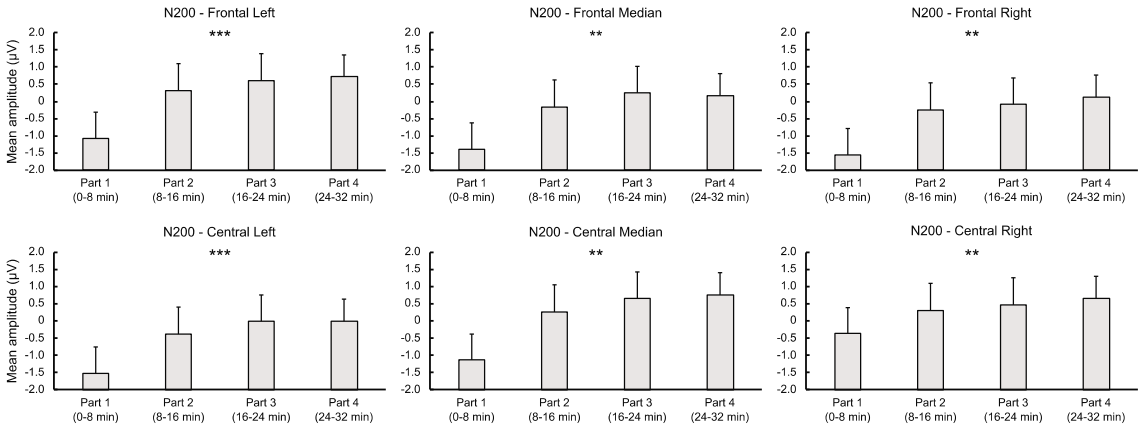

FIGURE 4 | Time-on-task effect on N200 for letter stimuli during the 32-min time load dual back task in the frontal and central regions. ** and ***: Significantly time-on-task effect ($p < 0.01$ and $p < 0.001$, respectively).

$p = 0.006$, $\eta_p^2 = 0.431$], indicating an increase in movement duration with increasing ID, accompanied by a main effect of time [$F_{(3,42)} = 5.259$, $p = 0.005$, $\eta_p^2 = 0.273$]. The decomposition of this time effect revealed a linear increase in the duration of arm-pointing movements over time [$F_{(1,14)} = 10.607$, $p = 0.006$, $\eta_p^2 = 0.431$] as shown by comparison with Pre [*vs.* Post: $t_{(14)} = -0.717$, $p = 1.000$, $d = -0.185$; *vs.* Post 10: $t_{(14)} = -2.527$, $p = 0.121$, $d = -0.653$], up to significance at Post 20 measurement [$t_{(14)} = -2.977$, $p < 0.050$, $d = -0.769$] (see **Figure 6**).

Pointing Errors

There was a significant main effect of ID on errors during the pointing task [$F_{(2.305,32.275)} = 26.782$, $p < 0.001$, $\eta_p^2 = 0.657$]. The decomposition of this main effect revealed a significant linear effect, with more errors as the ID of the target increased [$F_{(1,14)} = 48.455$, $p < 0.001$, $\eta_p^2 = 0.776$]. However, analyses showed no significant effect of time or ID × time interaction.

Effects of Mental Fatigue on Brain Oscillations at Rest

All the results of brain oscillations at rest are presented in the **Supplementary Table S2**. Significant differences related to alpha and theta powers are presented below.

Theta

Analysis showed a significant time effect on FL region [$F_{(3,42)} = 4.359$, $p = 0.009$, $\eta_p^2 = 0.237$], qualified by a linear trend [$F_{(1,14)} = 7.220$, $p = 0.018$, $\eta_p^2 = 0.340$], indicating an increase in theta power over time (see **Figure 7**).

Alpha

ANOVA revealed a significant time effect on FL [$F_{(3,42)} = 4.641$, $p = 0.005$, $\eta_p^2 = 0.261$], FM [$F_{(3,42)} = 3.174$, $p = 0.034$, $\eta_p^2 = 0.185$], FR [$F_{(3,42)} = 4.177$, $p = 0.011$, $\eta_p^2 = 0.230$], CL [$F_{(3,42)} = 4.017$, $p = 0.013$, $\eta_p^2 = 0.223$], CR [$F_{(3,42)} = 3.107$, $p = 0.036$, $\eta_p^2 = 0.182$], PM [$F_{(3,42)} = 3.107$, $p = 0.037$, $\eta_p^2 = 0.312$], and PR regions [$F_{(3,42)} = 6.711$, $p = 0.021$, $\eta_p^2 = 0.324$]. This main effect of time-on-task was qualified by a linear trend for all these regions ($ps < 0.011$, $\eta_p^2 > 0.230$], indicating an increase in alpha power over time (see **Figure 7**).

DISCUSSION

The objective of the present study was to investigate the time course of mental fatigue effects following a cognitively demanding task (i.e., TLDB task) on subjective and electrophysiological markers as well as on arm-pointing task performance. The results showed that the subjective feeling of fatigue increased following the cognitively demanding task and then progressively decreased during the 20 min of recovery, but without returning to initial values. Brain oscillations during the rest periods showed a linear increase in both theta and alpha powers, suggesting that mental fatigue persisted after completion of the cognitively demanding task, and that no recovery mechanism really occurred. Contrary to expectations, motor control performance was worse during the recovery period than immediately after the cognitively demanding task, movements becoming even slower 20 min after completion of the task.

Subjective Feeling of Mental Fatigue

In agreement with previous studies (Borragan et al., 2016, 2017), 32 min on the TLDB task induced an increase in the subjective feeling of mental fatigue, indicating that this cognitively demanding task successfully induced mental fatigue. The feeling of mental fatigue decreased 10 min after completion of the task and remained above the initial value 20 min later, indicating that recovery was not complete. Recently, similar effects were observed by Smith et al. (2019), who found that the subjective feeling of mental fatigue following 45 min performing mentally fatiguing tasks remained higher than pre-treatment values for 10 min after a PVT, 50 min after a Stroop task and 60 min after an AX-CPT task. These observations indicate

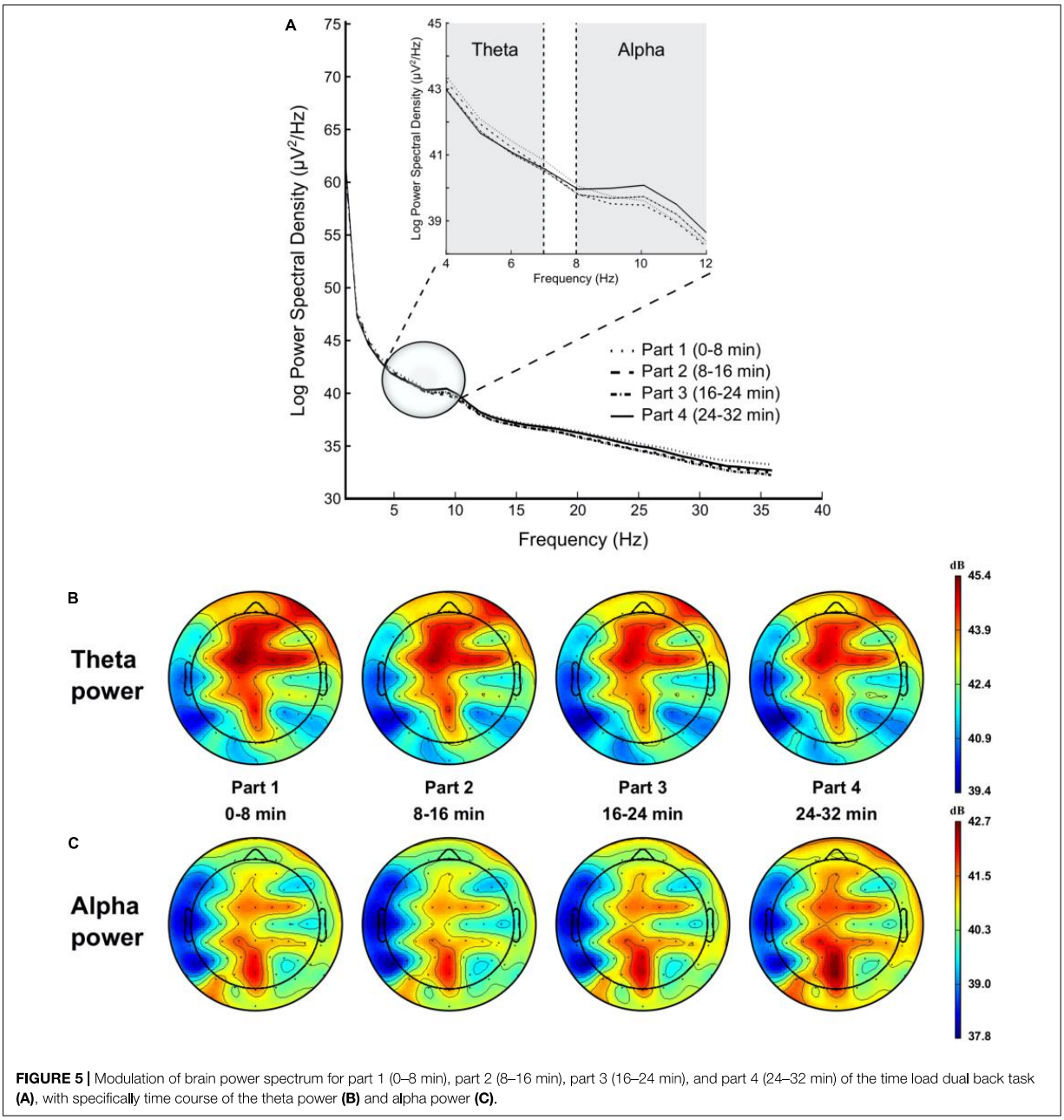

FIGURE 5 | Modulation of brain power spectrum for part 1 (0–8 min), part 2 (8–16 min), part 3 (16–24 min), and part 4 (24–32 min) of the time load dual back task **(A)**, with specifically time course of the theta power **(B)** and alpha power **(C)**.

that the recovery of the subjective level of mental fatigue may require more time than the duration of the cognitively demanding task itself.

Performance During the Cognitively Demanding Task

During the 32-min TLDB task, maintenance of performance (reaction time and accuracy) was observed, in contrast to previous studies by Borragan et al. (2016, 2017), who found a decrease in accuracy over time. It is worth noting that not all studies investigating mental fatigue found impaired performance during the cognitively demanding tasks used to induce mental fatigue; while some studies reported a decrease in performance (e.g., Marcora et al., 2009; Head et al., 2017), others found that it was maintained (e.g., Pageaux et al., 2015). Wang et al. (2016) postulated that the maintenance of performance despite mental fatigue could be explained by a compensatory strategy

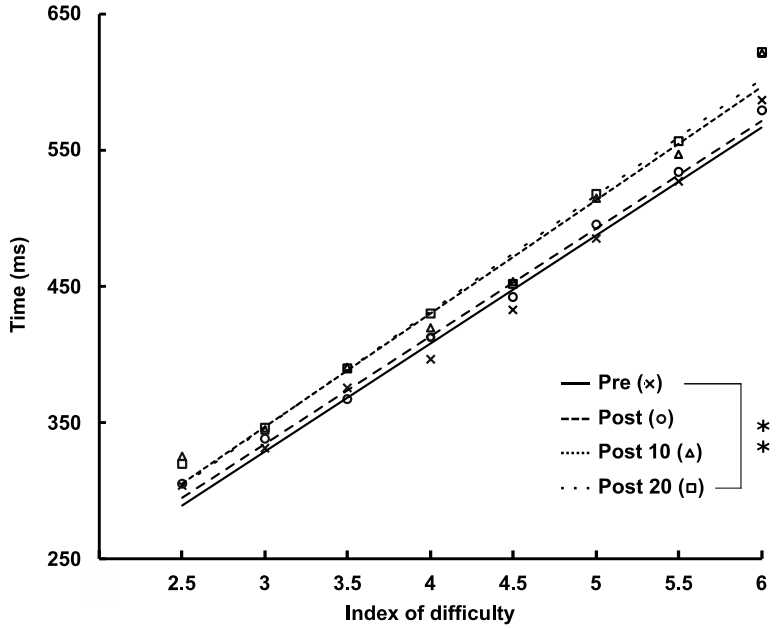

FIGURE 6 | Time course of the duration of arm-pointing movement at Pre, Post, Post 10, and Post 20 with a significant effect of index of difficulty (ID) ($p < 0.001$). **: Significantly different from Pre ($p < 0.01$).

reflected by an increase in anterior frontal brain activity during a prolonged cognitive task. Herlambang et al. (2019) found that performance of a prolonged cognitive task was maintained when participants had a high level of motivation, and decreased when their motivation was low. These observations suggest that motivation is an important factor when considering mental fatigue and its effects. In the present study, the participants showed high motivation to perform the experiment (success motivation = 17.7 ± 1.3 and intrinsic motivation = 23.3 ± 0.9 overall on a 0–28 scale), which could explain the maintenance of performance during the cognitively demanding task.

Electrophysiological Markers During the Cognitively Demanding Task

In addition to subjective and behavioral measures, changes in ERP amplitude during the cognitively demanding task could provide an objective marker of mental fatigue, and explain the maintenance of behavioral performance over time. In the present study, the decrease in N100, considered as an indicator of mental fatigue (Boksem et al., 2005; Faber et al., 2012), might reflect an increase in mental workload. However, the maintenance of performance (i.e., reaction time and accuracy) suggests that a compensatory mechanism was involved during the cognitively demanding task. Previous studies reported a decrease in P300 amplitude (Koelega et al., 1992; Murata et al., 2005), interpreted as a decrease in attention over time during a prolonged cognitive task (Zhao et al., 2012), associated to a decline in behavioral performance with mental fatigue (Cheng et al., 2007; Guo et al., 2015). In the present study, the linear increase in P300 amplitude reported in central regions for letter stimulus could be attributed to an increase in cerebral resources needed to maintain task performance despite progressive mental fatigue.

In addition to the changes observed in the ERP components, brain oscillations also seemed to indicate a mental fatigue state. The increase in alpha power with mental fatigue induction has been widely reported in the literature and has been interpreted as reflecting a decrease in arousal and alertness (Paus et al., 1997; Lal and Craig, 2002; Boksem et al., 2005; Trejo et al., 2005; Zhao et al., 2012). Another interpretation of the increase in alpha power during the TLDB task could be that, in presence of mental fatigue, the participants had to allocate more cognitive resources to maintain their performance. However, an increase in alpha power has been also observed with performance impairment (Boksem et al., 2005; Zhao et al., 2012). The increase in alpha power was also observed when comparing rest periods (i.e., before and after the cognitively demanding task) in the present study but also in previous studies (e.g., Li et al., 2020). These findings suggest that the increase in alpha power observed in mental fatigue studies, and more especially in time-on-task design, is likely not related to the allocation of more cognitive resources to maintain task performance. This increase in alpha power with mental fatigue has often been associated with an increase in theta power mainly over the prefrontal cortex (Lal and Craig, 2002; Trejo et al., 2005). Furthermore a recent meta-analysis suggests that an increase in theta power is a robust biomarker of mental fatigue, whereas an increase in alpha power is a second-line biomarker due

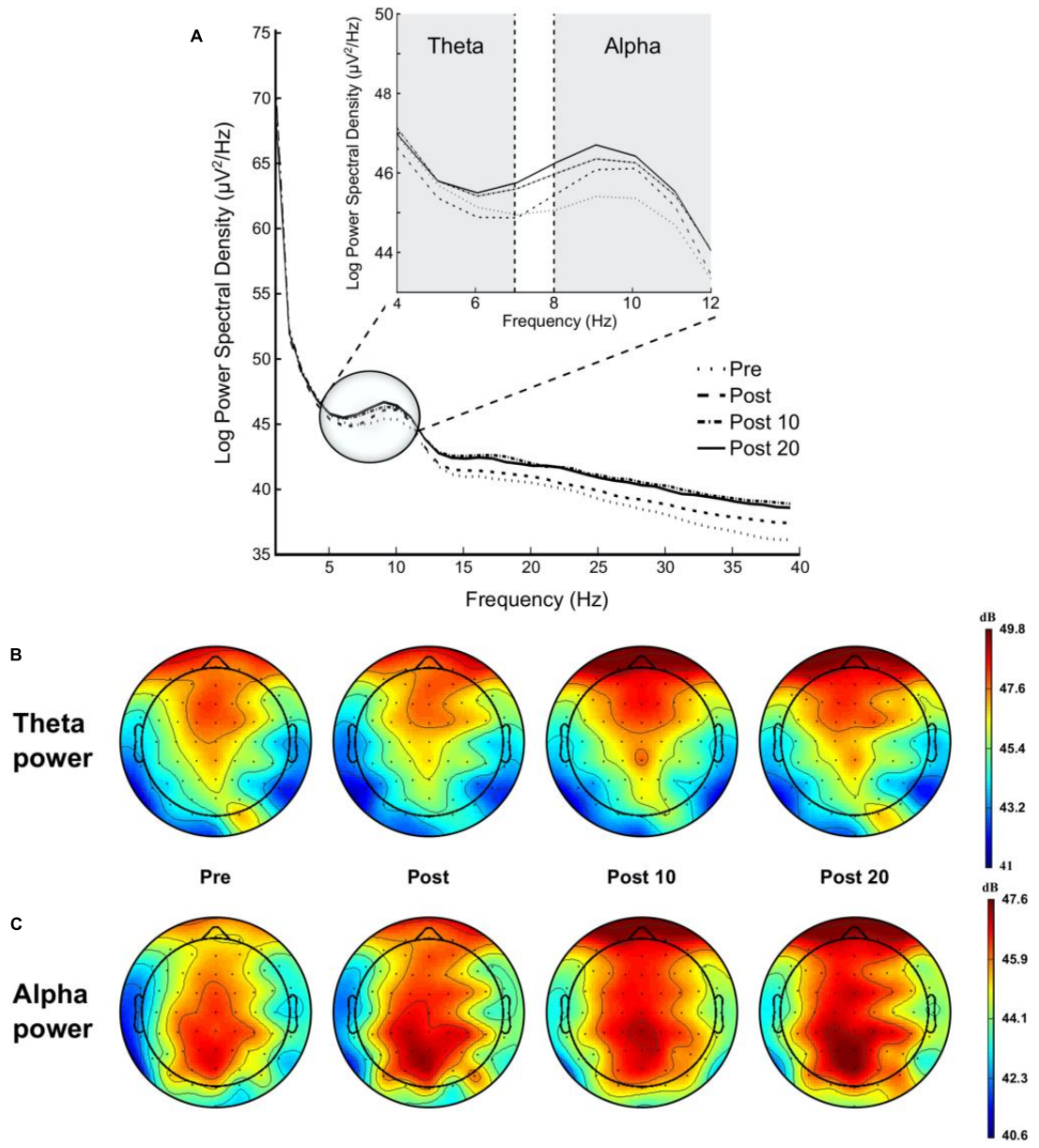

FIGURE 7 | Modulation of brain power spectrum during the 2-min rest periods at Pre, Post, Post 10, and Post 20 **(A)**, with specifically time course of the theta power **(B)** and alpha power **(C)**.

to considerable individual variability (Tran et al., 2020). In the present study, a decrease in theta power was reported over time in frontal regions during the cognitively demanding task. Although theta power decrease has previously been attributed to boredom (Katahira et al., 2018), the relatively short duration of the cognitively demanding task used here (i.e., 32 min) limited the boredom effect.

Brain Oscillations at Rest

In contrast to the brain oscillations analyzed during the cognitively demanding task, those recorded at rest showed an increase in both theta and alpha powers, confirming previous results of the effects of mental fatigue on brain oscillations (Tran et al., 2020). This finding supports the importance of recording brain oscillations not only during the cognitively demanding task

but also during the subsequent recovery period, in order to avoid confusion between changes due to the task *per se*, and those actually related to mental fatigue.

While the subjective feeling of mental fatigue decreased during the recovery period, the increase in both theta and alpha powers recorded at rest suggests that subjective (i.e., feeling of mental fatigue) and objective (i.e., brain oscillations) markers could provide contradictory data for interpreting the state of mental fatigue following a cognitively demanding task. Although evaluation of subjective mental fatigue using a VAS is considered to be the most practical way of assessing mental fatigue induction (Smith et al., 2019), it appears that objective electrophysiological markers of mental fatigue, such as changes in brain oscillations, could lead to a different conclusion than subjective evaluation. The present results suggest that when studying mental fatigue, it could be relevant to use different subjective and objective measures to have a more comprehensive view of the effects of mental fatigue.

Absence of Motor Performance Recovery

In accordance with the literature, we observed an increase in the duration of movement as the index of difficulty increased during an arm-pointing task (Rozand et al., 2015; Gueugneau et al., 2017) and maintenance of the speed/accuracy trade-off despite the presence of mental fatigue (Rozand et al., 2015, 2016).

In the present study, movement duration remained constant immediately after the cognitively demanding task, which differs from the results of Rozand et al. (2015). Those authors found that after 90 min of a modified Stroop task, the duration of arm-pointing movement increased by an average of 9%, irrespective of the index of difficulty of the target. The impairment of motor control under mental fatigue was confirmed in a second study by Rozand et al. (2016), who observed a 6% increase in movement duration after a cognitively demanding task inducing mental fatigue. However, the authors indicated that the negative effects of mental fatigue on movement duration seemed to be very short-lived. Indeed, from the second arm-pointing movement, movements were as fast as pretest measurements. In our study, the effects of mental fatigue on motor control were evaluated using the average time of 40 arm-pointing movements. Thus, if a mental fatigue effect occurred only on the first movement it was not enough to be observed on the average of 40 arm-pointing movements. It is worth noting that our experimental design does not allow us to verify this hypothesis, because movement times depend on the ID, and the ID associated with the first movement changed at each pointing task due to the use of different random orders.

When the arm-pointing task was repeated 10 and 20 min after the cognitively demanding task, movement duration was more and more affected, becoming significantly slower 20 min after the task compared to initial performance. A possible interpretation could be that the deterioration of the pointing performance over time was related to muscular fatigue. However, in our pilot experiment the participants repeated five times an arm-pointing task, consisting in 40 movements, after 16 min of TLDB task without a deterioration of the performance. This observation suggested that the decrease in performance in this present study was not related to the repetition of arm-pointing movements or to a possible muscular fatigue, but rather to the effects of mental fatigue.

Neuroanatomically, one possible explanation could be the involvement of the ACC, one of the main brain structures involved in the mental fatigue process (Lorist et al., 2005; Boksem and Tops, 2008; Marcora et al., 2009). Although Tanaka et al. (2014) found reduced activation of the ACC with mental fatigue during a subsequent physical activity, Johnston et al. (2007) observed that switching tasks could lead to an increase in ACC activity. This increase could lead to more resources being engaged to perform the new task. In the present study, the cognitively demanding task was different from the arm-pointing task, and as a consequence the task switching might have increased the activity of the ACC and, in the short term, could have counteracted the effect of mental fatigue. Immediately after the cognitively demanding task, this could result in more resources engaged in arm-pointing movements and could have boosted speed of movements, even in the presence of mental fatigue. During the recovery period, there was no longer task switching due to the repetition of the arm-pointing task. This might lead to a reduced ACC activity, which no longer counteracted the effect of mental fatigue. The persistence of mental fatigue could explain the impaired motor performance 20 min after completion of the cognitively demanding task.

CONCLUSION

The present study found that a 32-min cognitively demanding task induced mental fatigue. As predicted, the subjective feeling of mental fatigue decreased gradually during the 20 min recovery period but remained higher than before the cognitively demanding task. The increase in both theta and alpha power of brain oscillations during the recovery period suggests that participants remained mentally fatigued despite their lower subjective feeling of mental fatigue. The persistence of fatigue during the 20 min period following the cognitively demanding task is in accordance with behavioral results of the arm-pointing task indicating that motor control performance remained impaired. These findings indicate that even if subjective indicators of mental fatigue, such as VASs, are a practical method for assessing mental fatigue, objective indicators such as behavioral and electrophysiological markers are required to have a better characterization of the state of mental fatigue following cognitively demanding tasks.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

TJ was involved in the design of the study, data collection, analysis, and interpretation, as well as in the draft of the main document. BP-C participated to the elaboration of the experimental design, data collection, analysis, data interpretation, and in drafting the document. PB took part in study programming and data analyses. RL participated to the elaboration of experimental design, the data interpretation, and had also an active role in the manuscript writing. All the authors approved the final version and agree to be accountable for all aspects of the work.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.588253/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Résumé

La fatigue mentale est un phénomène courant dans la société actuelle provoquant une altération des performances cognitives comme physiques. Elle peut conduire à une augmentation des risques d'accident, une baisse de productivité, et à certaines pathologies comme la dépression. L'objectif de ce travail de thèse était d'étudier le phénomène de fatigue mentale en examinant plus spécifiquement ses marqueurs électrophysiologiques, ainsi que de trouver des stratégies de compensation pour limiter et/ou éviter ses effets délétères.

La première étude a identifié des modulations de l'activité cérébrale lors d'une tâche prolongée de Stroop modifiée. Une augmentation globale des ondes thêta et alpha, ainsi qu'une diminution de l'amplitude des ondes N100 et P300 interprétées comme reflétant une baisse de l'attention ont été observées. La seconde étude a mis en évidence que l'augmentation de la perception de l'effort lors d'un exercice physique d'endurance en présence de fatigue mentale était liée à une augmentation de l'activité des aires motrices et prémotrices (lors de contractions réelles et imaginées). Dans une troisième étude, nous avons montré que les effets de la fatigue mentale persistaient dans le temps. Les performances lors d'une tâche de pointage étaient de plus en plus altérées après la tâche mentalement fatigue, et ce malgré un effet de récupération sur le niveau de fatigue mentale perçue. La quatrième étude a montré que l'utilisation de stratégies de compensation, comme l'écoute de musique agréable ou la pratique d'une activité physique durant 15 min étaient efficaces pour contrer les effets liés à la fatigue mentale et maintenir le niveau de performance motrice. Ces travaux ont montré que la fatigue mentale engendre des modifications de l'activité cérébrale au cours d'une tâche cognitivement exigeante mais également lors d'une exercice physique subséquent. De plus, le phénomène de fatigue mentale semble persister dans le temps et impacter de plus en plus nos performances. Cependant des stratégies de compensation comme l'écoute de musique ou la pratique d'une activité physique semblent efficaces pour contrecarrer ses effets délétères.

Mots clés : fatigue mentale, électroencéphalographie, compensation, performance physique, conflit vitesse/précision, perception de l'effort.

Abstract

Mental fatigue is a common phenomenon in modern society, causing an alteration in both cognitive and physical performances. It can lead to an increased risk of accidents, a drop in productivity, and certain disorders such as depression. The objective of this thesis work was to study this phenomenon of mental fatigue by investigating more specifically its electrophysiological markers, and to find compensatory strategies to limit and/or avoid its deleterious effects.

The first study identified brain activity modulations during a prolonged modified Stroop task. An increase in theta and alpha waves, as well as a decrease in N100 and P300 amplitude reflecting a decrease in attention were observed. The second study showed that the increase in the perception of effort during physical endurance exercise in the presence of mental fatigue was linked to an increase in the activity of the motor and premotor areas (during actual and imagined contractions). In a third study, we highlighted that the effects of mental fatigue were persistent over time. Performance during an arm-pointing task was increasingly impaired after the mentally fatiguing task, despite a recovery effect on the level of perceived mental fatigue. Finally, the fourth study showed that the use of compensatory strategies such as listening to pleasant music or practicing a physical activity for 15 min were effective in countering the effects of mental fatigue and maintaining the level of motor performance. This work showed that mental fatigue leads to changes in brain activity during a cognitively demanding task, and during subsequent physical exercise. Moreover, the phenomenon of mental fatigue seems to persist over time and increasingly impact performance. However, compensatory strategies such as listening to music or practicing a physical activity seem to be effective in counteracting its deleterious effects.

Keywords: mental fatigue, electroencephalography, compensation, physical performance, speed/accuracy trade-off, perception of effort.