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Sensations spontanées : soubassements cognitifs et électroencéphalographiques de l'expérience subjective du corps

Sara Salgues

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Sensations spontanées : soubassements cognitifs et électroencéphalographiques de l'expérience subjective du corps.

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UNIVERSITE LUMIERE LYON 2

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THESE

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Sensations spontanées : soubassements cognitifs et électroencéphalographiques de l'expérience subjective du corps

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*“Home is behind, the world ahead,
And there are many paths to tread
Through shadows to the edge of night,
Until the stars are all alight.
Then world behind and home ahead,
We’ll wander back and home to bed.
Mist and twilight, cloud and shade,
Away shall fade! Away shall fade!”*

J.R.R. Tolkien, *The Fellowship of the Ring*

Résumé

De récentes études ont dévoilé l'existence d'un phénomène somatosensoriel au repos lorsque l'attention est dirigée sur le corps : la perception spontanée de sensations à la surface de la peau. Ce phénomène intrigue par plusieurs aspects. En effet, la phénoménologie de ces sensations est identique à la perception tactile. Pourtant, rien ne semble les provoquer, puisqu'elles sont ressenties sur le corps immobile et préservé de tout contact externe. Quelle est donc la source de ces signaux ? Comment ces sensations si discrètes arrivent-elles à entrer en conscience ? Et surtout, pourquoi les percevons-nous ? La confrontation à la littérature de la conscience corporelle nous a permis de détecter un manque de connaissance fondamentale : les divers modèles existants conçoivent majoritairement la conscience du corps comme le traitement de signaux physiologiques périphériques, et entretiennent un flou artistique sur les étapes amenant ces signaux à la conscience. Seule la théorie attentionnelle de la conscience corporelle postule l'existence d'un environnement interne de sensations corporelles, dont les traces reflèteraient l'activité de mécanismes somatosensoriels centraux.

Ce travail de thèse a ainsi porté de front deux objectifs : mieux comprendre la nature des sensations spontanées, et décrire les mécanismes à l'œuvre dans leur perception. Par ce biais, nous avons ainsi cherché à enrichir les connaissances théoriques fondamentales sur les tenants et aboutissants de la conscience corporelle. Trois axes ont été proposés. Le premier confronte l'origine périphérique et centrale des sensations spontanées, le deuxième s'intéresse au rôle de certains mécanismes cognitifs responsable de l'accès en conscience corporelle, et le troisième approfondit la question des corrélats neuraux des sensations spontanées. Dans ces différents travaux nous avons adopté une approche unique : corréler les caractéristiques de sensations spontanées perçues à un instant T à des traits cognitifs/comportementaux ou électroencéphalographiques (EEG) extraits séparément. Outre l'approche cognitive, nous avons donc aussi emprunté à la physiologie et aux neurosciences, afin de diversifier nos mesures et d'apporter des éléments de réponses suffisants à nos interrogations. Les résultats obtenus nous permettent de défendre l'existence d'un phénomène somatosensoriel hallucinatoire chez l'individu lambda, mais nécessaire à la conscience corporelle. Nous montrons également que l'émergence de ce phénomène dépend de mécanismes non-spécifiques au corps : nous spécifions le rôle des processus attentionnels centraux, et apportons pour la première fois des preuves de l'investissement de la mémoire de travail visuospatiale. Nous

concluons ce travail en proposant un modèle de la conscience corporelle, intégrant l'ensemble des travaux présentés dans un tout cohérent.

Mots clefs : conscience corporelle, sensations spontanées, représentations, attention, mémoire de travail visuospatiale, corrélats neuraux, électroencéphalographie.

Abstract

Recent studies have revealed the existence of a somatosensory phenomenon at rest when attention is directed to the body: the spontaneous perception of sensations on the skin surface. This phenomenon fascinates in many ways. Indeed, the phenomenology of these sensations is identical to tactile perception. However, nothing seems to provoke them, since they are felt on the motionless and preserved from any external contact body. What is the cause of these sensations? How do these discreet signals enter our awareness ? And above all, why do we perceive them? The confrontation with the literature on body awareness has allowed us to detect a fundamental lack of knowledge: the various existing models conceive body awareness mainly as the processing of peripheral physiological signals and keep vague the steps that bring these signals to awareness. Only the attentional theory of body awareness postulates the existence of an internal environment of bodily sensations, whose traces would reflect the activity of central somatosensory mechanisms.

Thus, this thesis work had two objectives: improve our understanding of the nature of spontaneous sensations and describe the mechanisms at work in their perception. By this means, we have sought to enrich the fundamental theoretical knowledge on the ins and outs of body awareness. Three axes have been proposed. The first one confronts the peripheral and central origin of spontaneous sensations, the second one is interested in the role of specific cognitive mechanisms responsible for the access to body awareness, and the third one deepens the question of the neural correlates of spontaneous sensations. In these different works we have adopted a unique approach: correlating the characteristics of spontaneous sensations perceived at a given time with separately extracted cognitive/behavioral or electroencephalographic (EEG) features. In addition to the cognitivist approach, we have therefore also borrowed from physiology and neuroscience, to diversify our measurements and to provide sufficient elements of answers to our interrogations. The results obtained allow us to defend the existence of a hallucinatory phenomenon in the lambda individual, but necessary to the body consciousness. We also show that the emergence of this phenomenon depends on mechanisms non-specific to the body: we specify the role of central attentional processes and provide for the first-time evidence of the investment of visuospatial working memory. We conclude this work by proposing a model of body awareness, integrating all the presented work into a coherent whole.

Keywords: body awareness, spontaneous sensations, representations, attention, visuospatial working memory, neural correlates, electroencephalography.

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Acronymes et abréviations

ADCL <i>Activation/deactivation checklist</i>	IRMf <i>Imagerie par résonance magnétique fonctionnelle</i>
AI <i>Anterior insula</i>	MAM <i>Master activation map</i>
ANOVA <i>Analysis of variance</i>	MNI <i>Montreal Neurological Institute templates</i>
ARBS <i>Attention-related body sensations</i>	NSU <i>Négligence Spatiale Unilatérale</i>
BMI <i>Body mass index</i>	PT <i>Perceptual threshold</i>
BP <i>Brown-Peterson</i>	RD <i>Resources difficulty</i>
CI <i>Confidence interval</i>	ROI <i>Region of interest</i>
CL <i>Cognitive load</i>	RT <i>Response time</i>
CS <i>Complex span</i>	SCL <i>Skin conductance level</i>
DEC <i>Decay</i>	SD <i>Standard deviation</i>
EBA <i>Extrastriate body area</i>	SEM <i>Standard error of the mean</i>
EEG <i>Electroencephalography</i>	SI <i>Primary somatosensory cortex</i>
eLORETA <i>Exact low resolution electromagnetic tomography</i>	SII <i>Secondary somatosensory cortex</i>
EOG <i>Electrooculography</i>	sLORETA <i>Standardized low resolution electromagnetic tomography</i>
fMRI <i>Voir IRMf</i>	SPS <i>Spontaneous sensations</i>
HB <i>Beat/pulse</i>	TG <i>Tingling</i>
ID <i>Inhibition difficulty</i>	TPJ <i>Temporo-parietal junction</i>
INT <i>Interference</i>	WM <i>Warming</i>
IRM <i>Imagerie par résonance magnétique</i>	

INTRODUCTION GENERALE

De l'existence des sensations spontanées et de leurs liens avec la conscience corporelle

« On est encore très loin d'appréhender la densité et la diversité de l'ensemble constitué par les couches superposées et mutuellement influentes du courant de conscience, tel qu'il traverse l'esprit tout en se renouvelant en permanence. Même l'art le plus puissant – qu'il s'exprime dans un film, une pièce de théâtre ou un récit littéraire – laisse à peine pressentir ce à quoi la conscience humaine ressemble véritablement. »

Oliver Sacks, *Le Fleuve de la Conscience*

Les philosophes aiment opposer la conscience du *Self*, cette entité abstraite rassemblant tous les aspects de notre individualité, à celle du corps, une forme de conscience moins « élevée » puisqu'elle consisterait uniquement à percevoir les sensations corporelles. Pour ces raisons, le corps fut parfois délégué au rang d'enveloppe matérielle principalement destinée à permettre les interactions avec l'environnement. Les neurosciences, la neuropsychologie et la psychologie cognitive mettent un point d'honneur à le remettre au cœur du développement du *Self*.

De grands modèles défendent la prédominance de la perception intéroceptive et somatosensorielle dans la conscience du corps. On associe une conscience développée de son propre corps à des compétences de détection des signaux internes ou provoqués à sa surface. Ces deux dernières décennies pourtant, de nouveaux travaux s'intéressent aux sensations perçues sur la peau en l'absence de stimulations cutanées ou de mouvements du corps. Ce phénomène fut baptisé sensations spontanées (SPS), et son étude soulève de nombreuses questions. Comment peut-on percevoir des sensations que rien ne semble provoquer ? Pourquoi certains y sont plus « sensibles » que d'autres ? Quels facteurs expliquent les caractéristiques de ces sensations ? On comprendra très vite l'intérêt majeur que présentent les SPS pour étudier la subjectivité du rapport au corps.

Cette thèse s'attache donc à investiguer les facteurs contribuant au phénomène des SPS, et à apporter une meilleure compréhension de leur implication dans la conscience corporelle. Néanmoins, face à l'aspect novateur de ce phénomène, il est primordial d'identifier ces pistes d'exploration. A cette fin, nous nous attarderons d'abord sur les différentes conceptions de la conscience corporelle et définirons le cadre théorique de nos recherches. Dans un second temps nous présenterons les SPS, les connaissances que nous possédons déjà, et les points d'ombres que nous cherchons à éclaircir. Une fois ces objectifs de recherche définis, nous argumenterons le choix des facteurs cognitifs et neuraux qui sont au cœur de nos études.

I. La conscience de soi et du corps

A. Définitions

La conscience est un concept plus difficile à définir qu'à comprendre. Et pour cause, il possède une double facette plus présente dans le langage anglophone qu'en français. Lorsqu'on parle de la conscience *consciousness*, on entend l'ensemble des connaissances sur l'individu, notamment l'état physiologique et physique de son corps, ses pensées et ses souvenirs, ou ses interactions dans l'espace. En ce sens, cette conscience est une forme de mémoire autobiographique du corps, fondation du *Self* (c'est-à-dire notre individualisme, notre personnalité). Ces connaissances sur son corps et soi-même, qu'elles soient publiques (c'est-à-dire notre aspect visuel, notre comportement ou notre discours) ou privées (celles accessibles uniquement par l'introspection, la remémoration, le discours interne) offriraient une trame au *Self* narratif (le « je »), l'ancrant dans le temps et le liant au passé (Asai et al., 2016; Morin, 2006). Bien qu'elle ne soit pas constamment au centre de nos préoccupations, cette conscience est continuellement présente, linéaire et non-fragmentée (James, 1890), nous permettant de garder le sentiment d'exister et d'être indépendant de l'environnement.

L'autre facette, *conscious awareness*, pourrait être mieux traduite par la prise de conscience. On entend par là une expérience subjective limitée dans le temps, dont l'émergence dépend de l'état d'éveil. Elle est située sur un continuum allant de l'inconscience, tout état d'éveil bas où l'information ne peut être perçue et ne peut accéder à la conscience (Berry, 2012; Shah & Shah, 2017), à la méta-conscience, un état d'éveil élevé où l'individu prend conscience de son état de conscience actuel (Morin, 2006). Bien que cette forme de conscience dépende de processus perceptuels de bas niveaux, elle est à dissocier de la perception pure et brute. Lorsqu'une information entre en conscience après avoir été perçue, l'individu est alors capable de la conceptualiser, de l'appréhender et de la manipuler mentalement, de façon explicite, déclarative et volontaire (Corbetta & Shulman, 2011; Vallar & Calzolari, 2018). Afin de souligner cet aspect, Craig lui donne le nom de *material me* (A. D. Craig, 2009a, 2010b). A nouveau, cette prise de conscience du corps serait intrinsèquement liée au *Self*, à travers deux dimensions qui élaborent le sentiment d'incarner le corps. Tout d'abord le sens du corps, c'est-à-dire la perception de sensations corporelles qui permet de délimiter les frontières avec l'environnement et de faire naître le sentiment d'appartenance : « c'est ma main car je ressens les caresses qui y sont prodiguées » (Serino et al., 2013; Tsakiris, 2010). Et ensuite l'agentivité, qui correspond au contrôle de l'action, à l'élaboration

d'intentions motrices et à l'attribution des mouvements du corps à soi (Asai et al., 2016). De la même façon que sens du corps et agentivité participent à l'élaboration du *Self* narratif, conscience corporelle et prise de conscience du corps sont étroitement intriquées et interdépendantes. On s'intéressera donc tout autant au *body awareness*, la conscience corporelle continuellement présente, qu'au *conscious body awareness* ou *material me*, la prise de conscience à un instant T du corps, de son état et de ses sensations.

B. Schéma corporel, homoncule somatosensoriel et d'autres termes compliqués

Les altérations de la conscience corporelle sont rassemblées sous la dénomination de troubles du schéma corporel. Il s'agit d'un ensemble de manifestations pathologiques caractérisées par une perturbation des processus cognitifs à l'œuvre vis-à-vis du corps uniquement. Les asomatognosies (*a-* privatif, *soma* le corps, et *gnosies*, les connaissances) sont une catégorie particulière de modèles pathologiques où les capacités à prendre conscience de son corps ou à garder en mémoire ses changements sont défectueuses. Ces troubles peuvent résulter d'atteintes périphériques comme dans le cas de l'amputation ou de la déafférentation, ou de mécanismes centraux défectueux comme dans le cas de l'agnosie digitale. Les difficultés éprouvées sont diverses et multiples : perception, identification, localisation, et contrôle volontaire des membres sont distinctement altérés, et s'accompagnent invariablement d'une incapacité à éprouver un sentiment d'appartenance et de familiarité vis-à-vis du corps. Il n'est pas rare d'observer une anosognosie – l'incapacité à réaliser le dysfonctionnement –, une anosodiaphorie – la minimisation du dysfonctionnement – ou une somatoparaphrénie – un discours délirant où le patient affirme qu'une partie de son corps appartient à une personne tierce. Les troubles sont, dans la grande majorité des cas, restreints à un membre ou à un hémicorps, et n'interfèrent pas avec le traitement du corps d'autrui (Haggard & Wolpert, 2005). Différentes conceptions théoriques seront avancées dans le but de théoriser la conscience corporelle tout en respectant les contraintes présentées par les cas d'asomatognosies.

L'appellation schéma corporel est un héritage des *schemata*. Head et Holmes (1911), pionniers du domaine, soulèvent la question de l'indépendance des mécanismes à l'œuvre dans la conscience du corps. En effet, seule la perception du corps s'accompagne de sentiments subjectifs d'appartenance et de familiarité. Par ailleurs, différents mécanismes sont à l'œuvre dans le

traitement de notre propre corps et dans celui d'autrui : ainsi, le patient atteint d'autotopagnosie n'éprouve aucune difficulté à localiser les parties du corps sur un schéma, une photo, ou sur une autre personne, alors qu'il est incapable de faire de même sur sa propre personne. Head et Holmes introduisent le *schemata*, une unité cognitive qui garde une trace instantanée des changements du corps. Deux *schemata* principaux sous-tendent la conscience du corps : un proprioceptif, qui intègre les mouvements du corps, et un de surface, qui localise les stimulations tactiles sur le corps. Ces unités trouvent leur force dans leur indépendance et leur organisation topographique. Ainsi l'atteinte d'un *schemata* provoque un dysfonctionnement isolé à une modalité sensorielle ou à une partie du corps, conformément à ce qu'on observe dans la littérature des asomatognosies. Dans le cas de l'agnosie digitale, le patient est incapable de localiser des stimulations sur ses doigts sans retours visuels (Haggard & Wolpert, 2005). Ces *schemata* sont repris dans le modèle emblématique des *body schema* et *body image* (Gallagher, 2005; Haggard & Wolpert, 2005; Paillard, 1999). Le *body schema* est une carte sensorimotrice générée à partir des efférences proprioceptives, kinesthésiques et tactiles, et reposant sur les représentations structurales du corps. Cette carte encode la position du corps dans l'espace, la position des membres les uns par rapport aux autres, et se met constamment à jour avec les mouvements afin de garder une connaissance de l'état actuel du corps. Le *body image* quant à lui dépeint l'image du corps d'un point de vue externe, canonique, principalement grâce aux afférences visuelles. Dans cette conception théorique, ces deux unités cognitives sont hiérarchiquement organisées. En effet, le *body schema* n'est pas accessible à la conscience, au contraire du *body image*. Cependant, le *body image* reçoit des afférences du *body schema* lui permettant d'avoir un retour sur le corps et de contrôler consciemment les mouvements. Ces deux unités sont les fondements de la conscience corporelle, mais seul le *body image* permet de prendre activement conscience du corps.

Malheureusement ces conceptions souffrent d'une faille de taille : on n'identifie pas de soubassement neural aux *schemata*. Par ailleurs la distinction entre *body schema* et *body image*, très floue, ouvre la porte à de nombreux mésusages et détournements (Berlucchi & Aglioti, 1997, 2010). Ce manque de précision dessert la modélisation théorique de la conscience corporelle et complique l'étude des asomatognosies. Par exemple, le syndrome du membre fantôme est catégorisé par Ramachandran comme une atteinte du *body image* (Ramachandran, 1998) avant d'être intégré dans les troubles du *body schema* par Haggard et Wolpert (Haggard & Wolpert, 2005). Actuellement, on distingue les altérations du *body schema*, des dysfonctionnements cognitifs qui entravent la conscience du corps (Haggard & Wolpert, 2005), et les altérations du *body image*, des

troubles psychiatriques ou psychologiques affectant le rapport au corps et pouvant notamment provoquer des perturbations du comportement alimentaire (Sakson-Obada et al., 2018). On abandonne donc les *schemata*, ces unités qui ne trouvent une utilité que dans le contexte du corps, et de nouvelles conceptions mettent en avant le rôle de représentations du corps.

Les modèles des *schemata* admettent déjà l'existence de représentations structurales du corps : il n'y a pas une représentation unique, chaque partie du corps est sous-tendue par une trace neurale codant les dimensions du membre et sa disposition par rapport au reste du corps. Il s'agit alors des prémisses de l'homuncule somatosensoriel, ce corps dans le cerveau (Kinsbourne, 1998; Kinsbourne & Lempert, 1980). Ces représentations se distinguent en fonction de leur modalité et contribuent différemment à la conscience du corps. Sirigu défend ainsi l'existence de deux systèmes de représentations du corps, un visuospatial et un lexico-sémantique – chacun sous-tendu par un hémisphère – (Gallace & Spence, 2010; Sirigu et al., 1991), de telle sorte qu'il est possible d'éprouver une incapacité à localiser les membres de son propre corps, sans atteinte des capacités de définition et de dénomination, comme il est fait état dans l'autotopoagnosie (Haggard & Wolpert, 2005).

Par ailleurs, la théorisation en termes de représentations ouvre la porte à de nouvelles considérations : puisqu'elles sont déjà mises en évidence dans le fonctionnement mnésique, on peut distinguer les représentations du corps stables, stockées à long terme, des représentations plus modulables, destinées à manipuler l'information sur le moment. Dans le modèle de Sirigu (Sirigu et al., 1991), des représentations dynamiques sont générées à partir des homuncules et des afférences sensorielles, de sorte à rendre perceptible l'état actuel du corps ou à permettre le contrôle moteur volontaire. Hors de la logique des homuncules, Carruthers (2008) dissocie les représentations *inline*, qui permettent de prendre conscience de l'état actuel du corps, et les représentations *offline*, qui maintiennent la connaissance du corps tel qu'il est habituellement. Les représentations *inline* sont mises à jour fréquemment via les afférences sensorielles, et sont maintenues en conscience pendant un court laps de temps afin de rendre les mouvements du corps perceptibles et contrôlables. Les représentations *offline* au contraire sont plus stables, mises à jour uniquement lors de changements majeurs dans l'état physique ou fonctionnel du corps. Puisqu'elles sont élaborées à partir des afférences sensorielles et des représentations stockées en mémoire, elles sont accessibles à la conscience de manière immédiate et différée.

Mais les conceptions théoriques de la conscience corporelle ont fréquemment été décriées, et à raison. D'une part, l'abondance de termes aux définitions floues empêche les consensus et

pénalise la cohérence globale. D'autre part, le postulat selon lequel la conscience corporelle est une sphère cognitive isolée, ainsi que la volonté de décomposer chacune de ses facettes, mènent à une conception passive. La conscience est réduite à avoir des connaissances sur son corps et à les mettre à jour en mémoire, et peu d'intérêt est porté aux mécanismes perceptifs et processus cognitifs permettant de prendre conscience des sensations corporelles. D'autres modèles sont plus pertinents sur ce point.

C. *The ever-present background of bodily sensations*

Le corps possède une dualité qui le distingue des stimuli classiquement traités par notre système nerveux central : nous pouvons l'appréhender à la fois grâce à notre extéroception et à notre intéroception. On entendra par extéroception la perception grâce aux organes sensoriels externes (vision, audition, olfaction, gustatif et toucher) classiquement dévouée aux interactions avec l'environnement, et par intéroception la perception grâce aux systèmes sensoriels internes (intérocepteurs, propriocepteurs, système vestibulaire). Par cette dualité, les afférences sensorielles provenant du corps ne se limitent pas aux interactions avec l'environnement. Mais surtout, alors que nous pouvons adopter des comportements dans le but d'empêcher notre extéroception, tels que nous déplacer pour ne pas être en contact avec un objet, fermer les yeux, ou boucher nos oreilles, nous ne pouvons pas *physiquement* éteindre le sens intéroceptif. Des mécanismes cognitifs nous permettent de prendre plus ou moins conscience du corps, de certaines de ses parties, et de ses sensations.

Des conceptions philosophiques font état que le contenu de la conscience dépend de ce à quoi nous portons attention (Morin, 2006). On y oppose ainsi la conscience de soi et celle de l'environnement sur l'observation que l'on ne peut être pleinement conscient de nos pensées ou de notre corps si l'on ne se « déconnecte » pas du monde extérieur. Grâce au modèle pathologique de la négligence spatiale unilatérale (NSU), on établit une relation causale entre la lésion des réseaux attentionnels et l'incapacité à prendre conscience de l'hémi-environnement ou de l'hémicorps controlatéral (Corbetta & Shulman, 2011). Dans cette lignée, Kinsbourne (1998) et O'Shaughnessy (2003) défendent l'implication de l'attention dans la conscience corporelle.

O'Shaughnessy, philosophe et auteur de la conception sous-attentionnelle du corps (O'Shaughnessy, 1986), place la proprioception au centre de la conscience corporelle. La raison de

ce choix est la nature particulière des signaux proprioceptifs, qui n'informent pas sur des interactions ponctuelles avec l'environnement mais sur le corps en lui-même : ses mouvements, la disposition des membres les uns par rapport aux autres, sa forme et ses limites avec l'environnement. Lorsque nous sommes engagés dans l'environnement, nous n'avons pas besoin de regarder ou de prêter attention au corps pour acquérir ces connaissances : la proprioception n'a pas vocation à être perceptible pour contribuer à la conscience corporelle. Dans cette vision, le *body schema* est donc un environnement proprioceptif continuellement présent, qui maintient une conscience du corps subliminale, non-médiée par l'attention. En certaines instances, nous pouvons prendre conscience de ces afférences, ce qu'O'Shaughnessy nomme une « introspection proprioceptive » : dès lors, nous accédons au *body image*, une mémoire à court terme du corps. Rendre le corps, plus particulièrement une partie, perceptible requiert cependant d'y diriger l'attention, car « *the attention culls what it needs, and discards what it does not out* » (O'Shaughnessy, 1998, p. 182). De manière générale le modèle d'O'Shaughnessy est apprécié car il apporte de nombreux arguments d'une mémoire du corps. Mais en raison de l'approche philosophique, il résiste aux neurosciences en de nombreux points. D'une part, le postulat d'une prépondérance de la proprioception sur les autres signaux corporels est source de dissensions – par exemple, Gallace et Spence (Gallace & Spence, 2008, 2009, 2010) avancent de nombreux arguments d'un rôle tout aussi important du toucher et de la perception tactile en continu dans la conscience corporelle, et de nombreux travaux relèvent l'importance des mécanismes d'intégration multi-sensorielle (Arzy et al., 2006; Ionta et al., 2011, 2014; Lenggenhager et al., 2009). L'idée d'un environnement proprioceptif continuellement présent et non-médié par l'attention pose également un problème. Qu'en est-il des cas de NSU dirigées vers le corps (Dieguez et al., 2007), où les troubles attentionnels ne se répercutent pas uniquement sur la prise de conscience de l'hémicorps, mais affectent aussi le comportement moteur volontaire et involontaire, et donc la proprioception ?

Quant à Kinsbourne (1998), il décrit une conscience corporelle ancrée dans l'attention. Kinsbourne affirme l'existence d'un *ever-present background of bodily sensations*, un flux de sensations corporelles continuellement présent en périphérie de notre conscience. Contrairement à O'Shaughnessy, Kinsbourne ne restreint pas ce *background* perpétuellement présent à la perception, et propose que certaines sensations naissent de représentations du corps. C'est donc ce flux constant d'afférences sensorielles et de traces de représentations neurales qui sous-tend la programmation motrice sans contrôle volontaire, et permet la génération des sentiments subjectifs d'appartenance, de familiarité du corps, et l'impression de continuité dans le temps. Prêter attention à notre corps

revient à diriger notre attention dans ce *background* : à la manière de Posner (Posner et al., 1980), le focus attentionnel se déplace tel un spot lumineux dans le *background of bodily sensations* en n'en éclairant qu'une portion restreinte à la fois. Lorsque ce spot est porté sur la représentation d'un membre du corps, il l'active et la maintient en conscience, rendant certaines sensations corporelles perceptibles. Ainsi, en fonction de comment nous dirigeons ce spot, il nous est possible – ou non – de prendre conscience de l'existence même de notre corps, de capter des événements et changements majeurs le concernant, et de mettre à jour les représentations correspondantes afin de garder une trace en mémoire de son état. En conséquence, le corps paraît complet tant que nous n'avons pas la preuve du contraire, un présupposé qui fait sens face aux fréquentes occurrences d'anosognosie, anosodiaphorie et somatoparaphrénie dans les asomatognosies.

Kinsbourne s'éloigne des dichotomies théoriques entre *body schema* et *body image*. Au contraire des conceptions théoriques développées précédemment, il met l'accent sur les mécanismes et non pas sur la modalité des signaux corporels. Par cette approche, il est plus facile d'appréhender et de décrire les interactions entre la conscience continue du corps, et la prise de conscience du corps à un instant T, qui semblent intrinsèquement liées et se déterminer l'une l'autre. Outre l'avantage d'aborder enfin pleinement l'aspect actif de la conscience corporelle, il est possible de comprendre la malléabilité de la subjectivité comme une résultante de ces processus cognitifs et de comment l'individu les engage lorsqu'il s'intéresse à son corps.

II. Les sensations spontanées

A. L'état de l'art

La littérature des asomatognosies regorge de cas typiques où le patient témoigne de sensations qu'il n'aurait vraisemblablement pas *dû* ou *pu* ressentir. Le syndrome du membre fantôme est l'exemple le plus fréquemment dépeint : l'individu perçoit le battement de son cœur à travers les veines du membre absent, se plaint de démangeaisons et de douleurs récurrentes, et ressent le membre absent effectuer des actions. Ces sensations alimentent l'impression vivace et difficile à supprimer que le membre est intact et bien rattaché au reste du corps. C'est un phénomène qui surgit aussi bien après amputation que dans l'agénésie/amélie – une condition congénitale qui se manifeste par le non-développement d'un membre ou d'un organe – et qui opère tout aussi bien sur les parties externes du corps que les organes internes (Halligan, 2002; Ramachandran, 1998). Moins connues mais tout aussi pertinentes, les hallucinations tactiles et distorsions perceptuelles du corps sont relevées dans de nombreux contextes : épilepsies du lobe temporal, spectre de la schizophrénie, maladie de Parkinson, diabète, ou encore l'utilisation de certaines substances psychotropes comme le LSD (Berrios, 1982; Freudenmann et al., 2010; Hoch et al., 1952; Isbell, 1959; Jacobs & Trulson, 1979; Jalal, 2018; Kataoka & Ueno, 2017). On entend par là un phénomène perceptuel aberrant, où l'individu perçoit une sensation persistante sur sa peau que rien n'explique et dont il ne peut se détacher. Ces hallucinations adoptent de multiples formes, allant de la persistance d'une démangeaison au sentiment d'avoir des insectes grouillants sous ou sur la peau (une hallucination portant le doux nom de *delusional parasitosis* ou *delusional infestation*, Freudenmann et al., 2010). Bien évidemment, le syndrome du membre fantôme et les hallucinations tactiles sont caractérisés par un fort affect négatif, sont fréquemment associés à une perturbation de la perception somatosensorielle et douloureuse, et interfèrent avec les capacités de raisonnement ou le comportement de l'individu. On associe donc classiquement la perception spontanée de sensations à une conscience anormale du corps.

Jusqu'au 21^e siècle on ne s'interroge pas sur l'existence d'un phénomène similaire chez l'individu lambda. Pourtant, dans deux études portant sur le *gating* – la suppression tactile par le mouvement du corps (R. F. Schmidt, Schady, et al., 1990; R. F. Schmidt, Torebjörk, et al., 1990) – Schmidt fait état de sensations perçues spontanément à la surface de la peau et les nomme paresthésies. En 2011, dans le tout premier article qui en fait son objet d'étude principal, Michael

et Naveteur écriront « *Everyone knows what it is like to feel spontaneous sensations (SPS)* » (Michael & Naveteur, 2011). Car en effet, tout un chacun est susceptible de détecter ces fourmillements, vibrations, pulsations ou réchauffements à la surface de la peau, qui apparaissent lorsque l'attention est portée sur le corps alors que ce dernier est au repos et préservé de toute stimulation. Mais ce phénomène est discret, peu inquiétant, et surtout privé : or les outils expérimentaux de la psychophysiologie sont inadaptés pour étudier la perception de sensations qui apparaissent en l'absence de stimulations cutanées. Un protocole expérimental pour recueillir les SPS est proposé pour la première fois en 2005, en tant qu'expérience contrôlée, lorsque Naveteur, Honoré et Michael (2005) s'intéressent aux biais de réponses dans la perception tactile. Dans une première expérience, ils relèvent les effets des interactions vision-attention sur la détection de stimulations électrocutanées subliminales qui, en réalité, ne sont jamais délivrées. La question se pose alors de savoir si les chocs subliminaux supposément détectés sont liés à la manipulation expérimentale, ou s'il s'agit de sensations apparaissant spontanément sur la peau même en l'absence de dispositif. Ils demandent aux participants de porter attention pendant dix secondes aux sensations qu'ils perçoivent sur leur main alors que celle-ci est laissée immobile et dénuée de tout matériel expérimental, et découvrent (1) que les participants ressentent très rapidement des SPS, (2) qu'ils sont capables de les identifier, de les localiser sur la main et d'évaluer leur intensité, et surtout (3) que leurs caractéristiques ne correspondent en rien à celles des sensations induites par le biais de réponse (Naveteur et al., 2005). Cette première étude motivera de nombreuses autres, puisqu'on réalise qu'on peut étudier la perception sur la peau en l'absence de stimulation, et qu'on ne sait absolument rien des SPS.

1. L'étude des sensations spontanées

Plusieurs protocoles expérimentaux ont été développés par différents auteurs dans l'optique d'étudier la perception des SPS chez l'individu lambda. A notre connaissance, seuls trois méthodologies expérimentales investiguant la perception de SPS ont été publiées. Nous les aborderons dans l'ordre chronologique.

1. Naveteur et collaborateurs (2005) développent la tâche standard de SPS. Dans cette première version, la tâche consiste à porter attention aux SPS perçues sur et dans la main, pendant une période d'attention de 10 secondes. Dès 2011 la tâche porte uniquement sur

la surface glabre de la main, afin d'en faciliter la récolte et les futures analyses (Michael & Naveteur, 2011). Les SPS sont introduites en amont aux participants à l'aide d'une liste de 11 descripteurs, développée sur la base des travaux de Ochoa & Torebjörk (1983). Les conditions standard d'expérimentation requièrent un focus attentionnel et visuel sur la main pendant la période d'attention. Une étude préliminaire permettra d'établir que, dans ces conditions expérimentales, les premières SPS sont perçues dès 3 secondes, et que tous les participants reportent des SPS après 20 secondes. La période d'attention de 10 secondes permet donc d'induire une variabilité interindividuelle dans la fréquence de perception des SPS, et limite les potentiels effets plafond et plancher. Dans les premières études publiées (Beaudoin & Michael, 2014; Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2005, 2015), le participant est assis face à une table, et les mains sont posées paume à plat sur une feuille de papier. En 2011, dans une expérience contrôle, le participant est assis sur un fauteuil, la main posée paume vers le haut sur la cuisse. Cette position empêche tout contact entre la surface investiguée de la main et tout autre objet, permet un focus visuel direct vers la main, et est adaptée pour créer le moins de tensions musculaires et articulaires possibles. Pour ces raisons, les études de 2015 adaptent le protocole avec cette nouvelle posture. Directement après chaque période de focalisation, et seulement si les participants ont perçu des SPS, ils rapportent leur localisation et leur étendue en grisant les zones correspondantes sur des cartes de main. On récolte également l'intensité de chaque sensation, le type de sensation, et la confiance des participants vis-à-vis de la localisation et de l'étendue sur la main. Les analyses portent sur la distribution topographique de la fréquence des SPS, ainsi que sur leurs caractéristiques non-topographiques (i.e., intensité, variété, nombre de zones, étendue en pourcentage, confiance du participant).

2. Bauer et collaborateurs demandent à leur participants de porter attentions aux SPS sur leur pouce pendant 60 secondes, avec les yeux fermés et l'instruction explicite de ne pas chercher à visualiser le pouce (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014). Il n'est pas précisé cependant quelles instructions sont fournies aux participants afin de définir les SPS. Le ressenti subjectif de l'individu est récolté seulement à des fins descriptives. Le protocole étant adapté pour les passations en Imagerie par Résonance Magnétique (IRM), les analyses consistent uniquement en des comparaisons de conditions et ne prennent pas en compte la fréquence des SPS. Le choix de la période d'attention

s'appuie sur une étude préliminaire menée par Bauer et collaborateurs, où ils reportent 20 à 40 secondes nécessaires avant de percevoir des SPS nettes et distinctes. Le choix de prolonger la période, jusqu'à 60 secondes, offre la possibilité d'étudier l'activité neurale pendant l'attention portée aux SPS chez tous les participants. Mais peu d'analyses sont réalisées directement sur les résultats comportementaux à cette tâche, de telle sorte que l'on ne sait rien de ces qualités intrinsèques. On peut en effet se demander si, en raison de la période prolongée d'attention, les différences interindividuelles dans la propension à ressentir spontanément des sensations ne seraient pas effacées par l'effet plafond que nous avons évoqué précédemment.

3. Tihanyi et Köteles s'attachent à étudier l'effet de l'entraînement au yoga sur la capacité à détecter les SPS – qu'ils nomment *attention-related body sensations* (ARBS; Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017). Le test *ARBS* est dérivé de la tâche standard de SPS. Plusieurs périodes d'attention de 15 secondes sont effectuées les yeux fermés, sur sept régions successives : les deux paumes, les épaules, le visage, le ventre, le torse, puis une partie du corps au choix. Dans une première version du protocole, seule une question est posée aux participants : « Pendant ces 15 secondes, avez-vous ressenti des SPS, comme des fourmillements ? ». Dans la deuxième et dernière version, aucun exemple de SPS n'est donné et plus d'informations sont récoltées : le type de sensation, la partie du corps sur laquelle elles ont été perçues, la latence d'apparition, l'intensité, et l'agréabilité. Un item supplémentaire demande aux participants de fournir une potentielle explication de la cause des SPS perçues. Tihanyi et Köteles restreignent leurs analyses aux sensations de fourmillements et de réchauffement, et ciblent particulièrement l'augmentation de leur fréquence et de leur intensité avec l'entraînement au yoga.

Les travaux présentés dans cette thèse empruntent la méthodologie expérimentale de la tâche standard de SPS (Michael et al., 2015, 2017). A ce jour, elle se montre la plus satisfaisante pour la collecte de données, à la fois quantitativement et qualitativement, et montre le plus de succès pour explorer toute la complexité des SPS.

2. Le gradient proximo-distal

L'effet le plus remarquable des SPS est leur distribution inégale sur la face interne de la main. C'est notamment grâce à la tâche standard de SPS que cet effet a été mis en évidence, sans faille à ce jour. Au niveau de l'individu, les SPS peuvent être perçues sur n'importe quelle région de la main, et leur répartition à la surface de la peau pourrait être régie par la loi du hasard puisqu'aucune stimulation cutanée ne vient inférer leur localisation. Pourtant, en compilant les cartes de mains remplies par une certaine quantité d'individus ayant réalisé la tâche, on relève un gradient proximo-distal : la fréquence des SPS est maximale sur les phalanges distales, et diminue à mesure qu'on se rapproche de la base de la paume. A ce jour, un gradient local aussi précis n'a été mis en exergue que sur la face interne des mains, seule partie du corps étudiée à l'aide de la tâche standard de SPS. Certaines études relèvent ce gradient dans l'intensité des SPS, plus intenses sur les phalanges distales et moins intenses vers la base de la paume (Echalier et al., 2020; Michael et al., 2015, 2017). Mais si l'on prête plus attention aux données de Tihanyi (Tihanyi, 2019), on peut également supposer l'existence d'un gradient global, car les SPS sont plus fréquentes sur les extrémités (mains et pieds) que sur le tronc et la tête.

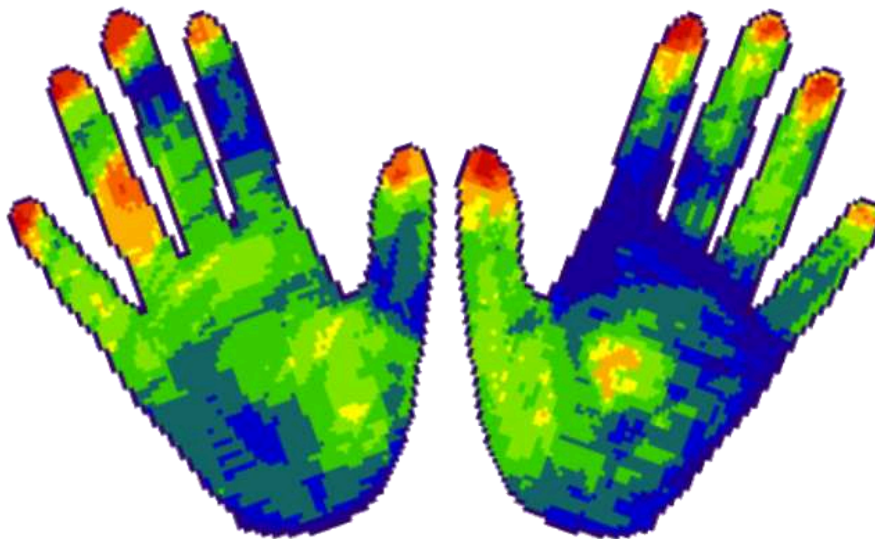


Figure 1 : Illustration du gradient proximo-distal des SPS.
Les couleurs rouges / chaudes indiquent la fréquence élevée,
les couleurs bleues / froides la fréquence basse. Sara Salgues®

La distribution topographique des SPS n'est donc pas hasardeuse. De plus, elle ne peut pas être expliquée par les contacts de la main avec une surface - comme c'était le cas dans la première version

de la tâche standard de SPS - puisque le gradient persiste lorsque la face interne de la main est laissée à l'air libre (Michael & Naveteur, 2011). L'intérêt d'étudier principalement la distribution topographique des SPS est très vite saisi, puisque des différences y sont induites par les conditions expérimentales (Beaudoin & Michael, 2014; Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015) et émergent en fonction des caractéristiques individuelles (Borg et al., 2015; Michael et al., 2015, 2017; Naveteur et al., 2015). Cette variable est la plus susceptible de refléter l'implication des processus responsables des SPS. Mais aucune preuve n'a été avancée concernant la nature de cette distribution, et comme nous l'aborderons plus tard, plusieurs facteurs seraient susceptibles de l'expliquer. Malheureusement, on ne sait pas ce que cette organisation topographique reflète exactement.

3. Une richesse de sensation

Quelles sensations peuvent être perçues spontanément ? Classiquement, la sensation que nous identifions est déterminée par l'événement qui la provoque, de telle sorte que la manipulation d'un objet crée des sensations de pression, des contractions musculaires et articulaires, et peut susciter des sensations thermales en fonction de sa température. Dans le phénomène des SPS, il est beaucoup plus difficile de prédire les sensations qui vont être identifiées, d'autant plus que les participants ne manquent pas de descripteurs pour décrire la richesse de leur expérience perceptive. La nature des SPS semble être aussi variée que la perception somatosensorielle. En cette raison, l'étude des SPS a été rapprochée très tôt des études psychophysiologiques, notamment des travaux de Ochoa & Torebjörk (1983) explorant la qualité des sensations provoquées par la stimulation de récepteurs sensoriels cutanés. Si cet aspect est prolifique pour l'examen des SPS, puisqu'il est possible de présenter des exemples guidant le participant dans la tâche comme le font Michael et Naveteur (Michael et al., 2012; Michael & Naveteur, 2011), il est encore trop peu appréhendé dans la recherche. Tihanyi et Köteles (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017) prennent par exemple le parti de n'étudier que les fourmillements et les réchauffements. Ils argumentent ce choix sur la prééminence de ces sensations dans leurs données, mais leurs études souffrent de cette contrainte et peu d'effets sont reportés avec cette procédure. Dans les études employant la tâche standard de SPS, l'intérêt est progressivement porté non pas sur les descripteurs employés, mais sur le type de sensations auxquels ces descripteurs appartiennent. De cette façon, les études les plus récentes (Borg et al., 2015; Echalié et al., 2020; Michael et al., 2015, 2017;

Michael, Guyot, et al., 2020; Naveteur et al., 2015) ont observé la prédominance des sensations de surface (comme le fourmillement, la vibration), profondes (le battement du cœur, la circulation sanguine) et thermales (le réchauffement et le refroidissement), et la rareté des sensations parétiques (engourdissements) et douloureuses (picotements). Grâce à cette manipulation, on observe que les facteurs modulant la distribution des SPS n'affectent pas équitablement tous les types de SPS (Beaudoin & Michael, 2014; Borg et al., 2015; Echalié et al., 2020; Michael et al., 2012, 2015, 2017; Michael, Guyot, et al., 2020; Michael & Naveteur, 2011; Naveteur et al., 2015). Mais avec les méthodes expérimentales actuelles, l'aspect qualitatif des SPS semble le moins indiqué pour explorer les tenants et aboutissants de leur perception. Néanmoins, la question de l'origine même de cette richesse et variabilité dans la qualité des SPS se doit d'être abordée.

B. La dépendance au contexte

Au-delà des facettes topographiques et qualitatives inhérentes aux SPS, leur perception est dépendante des conditions expérimentales. En théorie, le phénomène des SPS est optimal lorsque le corps est au repos, et que l'attention est dirigée vers ce dernier. D'autres paramètres, comme la posture – assise dans notre protocole, allongé chez Tihanyi et collaborateurs (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017) – ainsi que la température ambiante sont contrôlés afin d'en mitiger les effets. En conséquence, très peu de manipulations expérimentales peuvent être mises en place pendant la tâche de SPS sans risquer d'induire ou d'altérer leur perception. Les quelques études empruntant cette logique expérimentale le firent donc dans le but d'explorer les effets induits par le mouvement du corps et le focus sur la perception des SPS.

Le repos du corps est une condition sine qua non de l'expérimentation des SPS. La raison étant que toute sensation perçue en parallèle d'un mouvement du corps ou d'une stimulation de la peau peut potentiellement être provoquée par ces déformations cutanées. Ce présupposé induit une certaine origine périphérique aux SPS, que Beaudoin & Michael (2014) s'attachent à étudier. La tâche est légèrement modifiée en deux instances pour étudier l'effet du mouvement et de la pression cutanée : sur la main en focus, et pendant la période d'attention aux SPS, le pouce effectue un mouvement gauche-droite continu, ou porte un anneau serré en restant immobile. Et à l'instar de la perception tactile, les SPS sont sensibles à ces phénomènes : leur perception diminue avec le mouvement du pouce, et est facilitée par la pression de l'anneau. La présence d'un phénomène de *gating*, c'est-à-dire une inhibition somatosensorielle provoquée par le mouvement, renforce les

similarités entre la perception des SPS et l'extéroception (S. R. Jones et al., 2010; Kissin et al., 1987; Malinen et al., 2006; R. F. Schmidt, Schady, et al., 1990; R. F. Schmidt, Torebjörk, et al., 1990). Le *gating* opérant sur les doigts selon un gradient latéral avec un effet de la distance, et n'affectant pas les sensations thermales, la question se pose de mécanismes inhibiteurs de bas niveaux : avec un tel degré de précision et de spécificité dans la suppression des SPS, il serait possible qu'une inhibition soit effective au niveau cutané (Kissin et al., 1987), et donc par inférence que les SPS dépendent de facteurs périphériques.

Mais la perception de SPS repose également fortement sur le focus attentionnel. Et malheureusement, les différents protocoles expérimentaux explorant les SPS divergent essentiellement sur la présence d'un focus visuel, une inconsistance bien trop importante puisque les interactions entre vision et attention sont particulièrement connues pour induire des différences dans la perception tactile (Kennett et al., 2001; Press et al., 2004; Serino et al., 2007; Taylor-Clarke et al., 2002, 2004). Ces interactions furent longuement étudiées par Michael et Naveteur (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015), afin de décrire le plus précisément possible les effets induits par les subtiles différences de focus sur la perception des SPS. Le focus attentionnel et visuel de la main provoque des phénomènes complémentaires d'amplification et de suppression des SPS. Et alors que la perception des SPS est facilitée dès que l'attention est dirigée sur la main, la suppression n'opère plus lorsque la vision est dirigée sur un autre objet, ou est obstruée à l'aide d'un masque. Cependant, en l'absence d'entrée visuelle, l'amplification des SPS opère si les yeux sont dirigés vers la main en focus attentionnel. En décrivant ces effets, Michael et Naveteur révèlent également deux caractéristiques propres aux SPS. En premier lieu, l'existence d'une dissociation entre les doigts et la paume, une dissociation déjà relevée dans les études physiologiques et psychophysiologiques (Johansson & Vallbo, 1976; Vallbo & Johansson, 1976). Ici, les phénomènes d'amplification sont relevés sur les doigts, tandis que la suppression n'opère que sur la paume. En second lieu, une préférence de la main gauche à la fois pour la fréquence des SPS et dans l'émergence des phénomènes de suppression et d'amplification. Comme nous le développerons par la suite, ces phénomènes suggèrent la dépendance des SPS à des facteurs périphériques et/ou centraux.

Il est compliqué d'établir que le repos et le focus visuel déterminent l'émergence des SPS. Il reste évident néanmoins que ces conditions modulent la perception et prise de conscience de ces signaux. Si les SPS ne sont pas provoquées par des événements externes au corps, elles semblent pourtant soumises aux mécanismes périphériques/de bas niveaux et aux processus de haut niveau

habituellement impliqués dans la perception tactile. Et bien que leur mise en évidence fût menée minutieusement, les processus responsables de ces phénomènes ainsi que la raison de ces mécanismes n'ont pas été identifiés à ce jour.

C. Des différences interindividuelles

1. Caractéristiques intrinsèques

Si le repos et le focus offrent un environnement favorable à la perception des SPS, nous ne sommes pas tous égaux face à ce phénomène. Ces différences sont liées d'une part aux caractéristiques individuelles intrinsèques comme l'âge, le genre ou l'IMC (Naveteur et al., 2015), qui sont déjà connues pour induire une variabilité dans la perception tactile (Boles & Givens, 2011; Brodoehl et al., 2013; Genetta-Wadley & Swirsky-Sacchetti, 1990; Kozłowska, 1998; Peters et al., 2009; Thornbury & Mistretta, 1981). La fréquence des SPS diminue sur les doigts et augmente sur la paume chez les personnes âgées, un pattern qui suit l'émoussement de la sensibilité tactile sur les extrémités et le recul du gradient proximo-distal (Kozłowska, 1998; Thornbury & Mistretta, 1981). Également, les hommes reportent plus fréquemment des SPS que les femmes. Or, si jusqu'à présent on liait les SPS à la perception somatosensorielle, l'effet du sexe vient questionner ce présupposé puisque les femmes ont une sensibilité tactile plus fine (Inami et al., 2005; Peters et al., 2009), tandis que les hommes sont meilleurs intérocepteurs (Harver et al., 1993; Katkin, 1985; Whitehead & Drescher, 1980). D'autre part, les habiletés cognitives interagissent avec ces caractéristiques intrinsèques. Par exemple, le bénéfice du focus visuel est réduit avec l'âge, et plus particulièrement chez les femmes. Percevoir les SPS semble mobiliser une variété de processus cognitifs au-delà du focus attentionnel et visuel. En considérant le biais vers la main gauche, il serait cohérent que ces processus soient sous-tendus par l'hémisphère droit, qui assure entre autre l'attention, le traitement visuospatial et l'intéroception (Joseph, 1988). Assurément, les individus plus sensibles aux SPS devraient présenter d'aussi bonnes compétences dans ces domaines cognitifs.

2. Traits attentionnels

Puisque porter attention à soi rime aussi bien avec ressentir le corps qu'explorer ses pensées (Scheibner et al., 2017; Vaitl, 1996), il n'est pas invraisemblable que les individus reportant

aisément des SPS exhibent également une grande aisance vis-à-vis des autres signaux privés. Cette allégation a été vérifiée en plusieurs instances : la pratique du yoga ou de la méditation (Tihanyi, 2019; Tihanyi & Köteles, 2017), tout comme les habiletés intéroceptives (Michael et al., 2015) ou la propension à avoir la tête dans les nuages (Michael et al., 2017), sont bénéfiques pour la perception des SPS. D'une part, l'entraînement au yoga amène une plus grande aisance à reporter des SPS sur tout le corps. Et localement, l'intéroception et le vagabondage de pensées déterminent le locus des SPS : car, si classiquement leur fréquence est importante sur les doigts, les individus bons intérocepteurs ou ayant tendance à être dans leurs pensées y préfèrent celles sur la paume. Ces effets suggèrent qu'avec l'habitude de diriger l'attention vers soi vient une aisance à explorer le corps et donc à percevoir des SPS plus rares.

3. Modèles pathologiques

Certaines pathologies sont caractérisées par un focus constant sur le corps, et d'autres par un détournement du focus loin de ce dernier. On retrouve ces manifestations dans les syndromes douloureux, dont les distorsions somatosensorielles affectent la perception des SPS (Borg et al., 2015; Echalié et al., 2020). Prenons pour exemple le modèle pathologique de la fibromyalgie, qui serait expliqué par une hypervigilance dirigée sur le corps. Cette attention constante entraîne une diminution du seuil perceptuel et du seuil douloureux, de telle sorte qu'on relève chez les patients une amplification somatosensorielle et une anxiété exacerbée vis-à-vis du corps. Il est donc assez cohérent que ces patients soient plus sensibles aux SPS douloureuses, et reportent des SPS plus intenses que les individus lambda. Mais l'effet le plus impressionnant reste l'amplification massive de leur fréquence, sur l'entièreté de la main – à l'exception des phalanges distales, qui exhibent déjà un effet plafond chez l'individu lambda – au point de compromettre tout gradient proximo-distal (Figure 2; Borg et al., 2015).

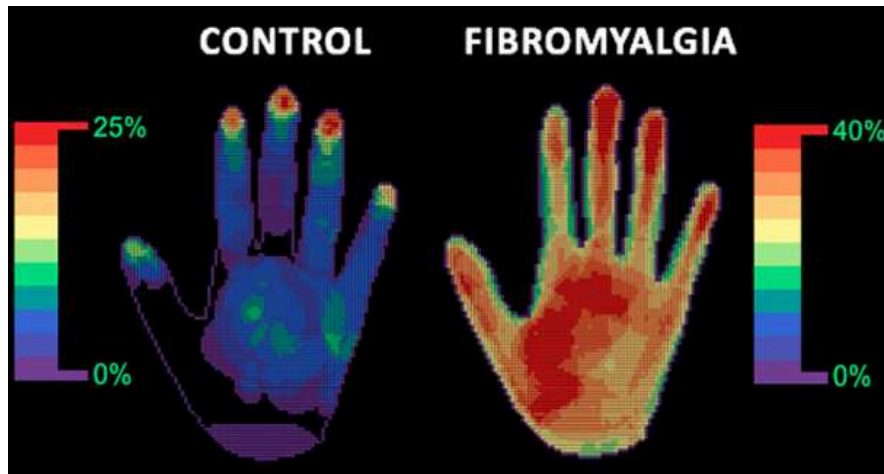


Figure 2 : Illustration des distorsions perceptuelles observées dans la fibromyalgie à l'aide des SPS. Sont présentées les cartes de fréquence du groupe contrôle (gauche) et des patients (droite) selon une échelle colorée graduée. Les couleurs rouges / chaudes indiquent la fréquence élevée, les couleurs bleues / froides la fréquence basse.

Tiré de Borg et al., 2015.

Au contraire, dans le syndrome douloureux régional complexe, les douleurs neuropathiques étant restreintes à une partie du corps, l'attention en est constamment détournée. En conséquence, on observe des perturbations des SPS uniquement sur la main ipsilatérale au membre inférieur atteint : un pattern atypique, où les SPS sur les doigts sont peu reportées, tandis que celles sur la périphérie de la paume sont plus fréquentes que chez les contrôles (Echalier et al., 2020).

L'étude du spectre de la schizophrénie permet de soulever d'autres considérations. On associe à cette pathologie des distorsions de la conscience corporelle et du *Self* d'un autre ordre, telles que hallucinations tactiles et autoscopiques, trouble de l'agentivité, et l'incroyable capacité à s'auto-chatouiller (Frith, 2005; Lemaitre et al., 2016; Sakson-Obada et al., 2018). Et on y identifie également des difficultés attentionnelles, notamment dans le contrôle inhibiteur et la régulation des ressources cognitives (Michael, Dorey, et al., 2020). Récemment, des travaux de Michael et collaborateurs (2020) ont démontré que les SPS reposaient sur ces processus d'incarnation qui sont affectés dans le spectre de la schizophrénie. Ces travaux montrent ainsi que l'habileté à opérer une rotation mentale de son corps réduit la fréquence des SPS, mais également que la possession de traits schizotypiques – le pendant lambda du spectre de la schizophrénie – mène à des distorsions perceptuelles du corps se traduisant par une augmentation anormale de la fréquence des SPS.

En somme, l'attention est le point commun de ces effets. En effet, l'intéroception et le vagabondage de pensée sont associés à de meilleures performances attentionnelles (Kane et al., 2016; Kane & McVay, 2012; Matthias et al., 2009; Pollatos, Matthias, et al., 2007), tandis que les

syndromes douloureux et le spectre de la schizophrénie exhibent des difficultés attentionnelles (Birklein & Kingery, 2009; Jensen et al., 2009; Michael, Dorey, et al., 2020). Ces modèles pathologiques résultent également de mécanismes somatosensoriels dysfonctionnels et d'altérations neurales spécifiques (Blakemore et al., 2000; Borg et al., 2018; Flor, 2003; Frith, 2005; Kim et al., 2017; Lemaitre et al., 2016; Lewis et al., 2007) concernant des aires clés de la somesthésie et de l'attention. Les caractéristiques des SPS rendraient ainsi compte de l'état des représentations du corps, mais également des mécanismes cognitifs à l'œuvre dans la conscience corporelle.

III. Points d'ombre et objectifs de recherche

Nous avons pu voir dans une première partie que la conscience du corps est un construit théorique complexe, requérant un accès aux afférences sensorielles, des représentations du corps, et des processus cognitifs élaborant et maintenant cette expérience en conscience. Vraisemblablement, les SPS contribueraient à cette conscience du corps. Mais force est d'admettre que nous ne savons ni en quelle qualité, ni par quels moyens.

En premier lieu, l'origine des SPS est inconnue. Si, selon les mots de Kinsbourne (1998), elles appartiennent au *background of bodily sensations*, leur nature n'est pas clairement établie. Sont-elles des signaux sensoriels provoqués par l'activité physiologiques cutanée, ou au contraire par l'activité spontanée du cortex somatosensoriel ? Il est vrai que ce phénomène partage beaucoup de points communs avec la perception tactile et semble influencé par des mécanismes périphériques (Beaudoin & Michael, 2014; Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015). Mais on ne peut ignorer la possibilité que ces effets soient dus à des processus de haut niveau influençant l'activité physiologique (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017). Et alors que les SPS exhibent des distorsions perceptuelles en l'absence d'atteintes physiques (Borg et al., 2015; Echalié et al., 2020; Michael, Guyot, et al., 2020), on pourrait supposer qu'elles sont indépendantes de l'activité périphérique, à l'instar des hallucinations tactiles. Un premier objectif principal est donc d'explorer les potentiels soubassements périphériques et centraux des SPS.

Une seconde problématique que nous aborderons est le rôle de la cognition dans la perception des SPS. Pour ne pas déplaire à Kinsbourne et sa théorie attentionnelle (Kinsbourne, 1998), la perception des SPS est modulée par le focus visuel sur le corps. Mais de nombreux éléments laissent à penser qu'une plus grande variété de processus attentionnels et cognitifs sont impliqués dans leur perception. C'est le cas du biais vers la main gauche, qui suggère la prédominance de processus latéralisés à droite. Mais également de la relation entre SPS et compétences intéroceptives ou penchant au vagabondage de pensée – des construits cognitifs reposant sur un ensemble de processus perceptuels, attentionnels, mnésiques, et d'intégration multimodale (Fiacconi et al., 2017; Kane et al., 2016; Perrone-Bertolotti et al., 2014; Smeekens & Kane, 2016; Tsakiris et al., 2011). Au niveau théorique, de nombreux modèles suggèrent l'implication de processus mnésiques à court terme, que ce soit dans la création d'une mémoire du

corps comme le décrit O'Shaughnessy (1986, 2003), ou dans le maintien en conscience comme le précise Kinsbourne (1998). Ces processus cognitifs, ainsi que leur contribution dans la prise de conscience du corps, ne sont identifiés ni dans la théorie ni dans l'étude des SPS. Le deuxième objectif de recherche principal est donc d'identifier les processus attentionnels et mnésiques déterminant la perception des SPS.

Un dernier objectif, sous-jacent aux deux précédents, est d'enrichir la compréhension théorique fondamentale de la conscience corporelle. L'étude des SPS, et notamment de leur topographie qui est particulièrement sensible aux distorsions perceptuelles, se révèle être un véritable atout pour appréhender la subjectivité de l'individu vis-à-vis de son corps. En investiguant leur perception sur les mains pendant un court laps de temps à un moment donné, nous récoltons un instantané de ce dont l'individu est capable de prendre conscience lorsqu'il prête attention à son corps, un polaroid qui dépeint l'image que nous nous projetons de notre propre corps et avec lequel nous nous familiarisons. Les travaux que nous présenterons auront ainsi tous cet intérêt commun, comprendre ce qui détermine la subjectivité même de l'expérience perceptuelle du corps.

PROLOGUE

Les facteurs périphériques, centraux et cognitifs au sein de la conscience
corporelle

Les mécanismes de la conscience corporelle

Au-delà des conceptions théoriques, la recherche expérimentale et en imagerie cérébrale cherche à apporter une meilleure compréhension des composantes cognitives et neurales de la conscience corporelle. Malheureusement, ces études soulèvent surtout la multitude de mécanismes et d'aires neurales à l'œuvre. Il nous fut donc primordial d'identifier les facteurs contribuant à la conscience corporelle et pouvant contribuer à la perception des SPS – au vu de ce que nous savons déjà sur ce phénomène. Sans prétendre proposer une revue exhaustive de la littérature, nous nous intéresserons aux facteurs susceptibles d'être à l'origine des SPS, de déterminer leur accès à la conscience, ou les deux. Nous développerons donc dans cette partie les différents mécanismes et processus cognitifs qui seront au cœur de nos recherches tout au long de ce manuscrit.

I. La somesthésie

Nous avons décrit en Introduction générale les nombreuses caractéristiques des SPS les rapprochant de la perception tactile. Il serait logique d'en déduire que le phénomène des SPS dépend en partie de mécanismes somesthésiques. Deux niveaux de traitement des afférences somatosensorielles sont mis en exergue dans la littérature. La recherche en physiologie décrit l'implication du système nerveux périphérique dans la détection et la reconnaissance d'événements cutanés, tandis que les neurosciences identifient des mécanismes centraux à l'œuvre dans le codage des afférences somatosensorielles. Nous aborderons donc ces deux champs de littérature.

A. Sur le bout des doigts : les mécanismes somesthésiques périphériques

La peau humaine est constituée en partie de neurones sensoriels, également appelés unités réceptives, qui réagissent aux événements cutanés et informent le système nerveux central via un réseau de fibres. Un premier codage des événements cutanés a déjà lieu en périphérie. On distingue classiquement trois types de neurones sensoriels, les mécanorécepteurs, les nocicepteurs et les thermorécepteurs, qui – en théorie – réagissent sélectivement aux événements cutanés de surface, thermiques et douloureux. En réalité, ces unités codent différentes dimensions des événements cutanés, parfois indépendamment de leur nature.

Les travaux de Vallbo et Johansson (Johansson & Vallbo, 1976, 1979a, 1979b; Vallbo & Johansson, 1976, 1984) ont grandement contribué aux connaissances sur les mécanorécepteurs de surface dans la perception tactile. Ces unités sont issues de fibres myélinisées fines $A\delta$ et larges $A\beta$ innervant principalement la peau glabre. Elles contribuent aussi bien à l'identification des événements tactiles à la surface de la peau que des mouvements du corps grâce aux déformations cutanées. Quatre types de mécanorécepteurs ont été identifiés, chacun caractérisé par la taille de son champ récepteur et sa vitesse d'adaptation aux événements cutanés. Leurs caractéristiques sur la main glabre sont décrites dans la Table 1.

Table 1: Tableau récapitulatif des propriétés des mécanorécepteurs innervant la main glabre, à partir des travaux de Vallbo et Johansson (Johansson & Vallbo, 1976, 1979a, 1979b; Vallbo & Johansson, 1976, 1984).

	Corpuscules de Meissner (RA ou FA I)	Corpuscules de Merkel (SA I)	Corpuscules de Pacini (PC ou FAII)	Corpuscules de Ruffini (SA II)
Localisation	Derme papillaire	Épiderme	Derme et tissus sous-cutanés	Derme
Proportion	43%	25%	13%	19%
Densité	Inégale : 140/cm ² sur phalange distale vs 25/cm ² sur paume	Inégale : 70/cm ² sur phalange distale vs 8/cm ² sur paume	Uniforme	
Diamètre médian du champ récepteur	12.6mm ²	11.0mm ²	101mm ²	59mm ²
Limites du champ récepteur	Bien définies		Floues	
Résolution spatiale	Haute		Basse	
Déformations cutanées détectées	Indentation		Vibration, indentation et étirement	
Sensibilité à la direction	Non		Oui	
Seuil psychophysiologique	13.8µm	56.5µm	9.2µm	331µm
Adaptation	Événements dynamiques	Événements statiques	Événements dynamiques	Événements statiques
Détection de décharge unique	Oui	Non		

Les corpuscules de Meissner et de Merkel, aux champs récepteurs étroits, sont inégalement distribués sur la main : leur densité augmente graduellement sur les segments de la main et est maximale sur les phalanges distales (Figure 3). Cette organisation selon un gradient proximo-distal sous-tend un codage spatial plus précis sur les segments aux extrémités du corps.

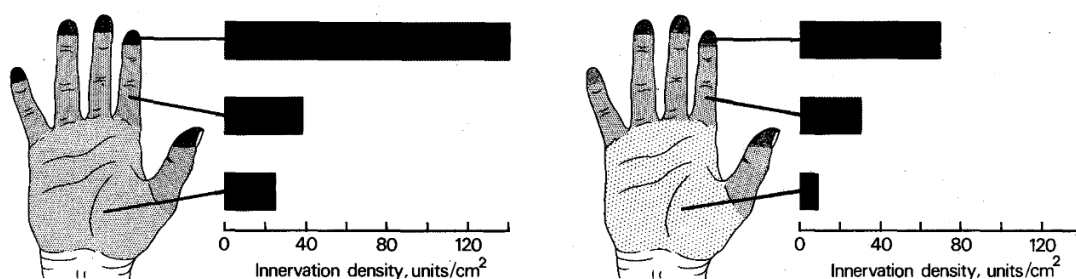


Figure 3: Illustration de la densité moyenne des corpuscules de Merkel (gauche) et de Meissner (droite) sur la peau glabre de la main. Tiré de Vallbo & Johansson, 1984.

Par ailleurs, s'il n'y a pas de différence dans le seuil physiologique des mécanorécepteurs de surface, le seuil perceptuel varie entre ces unités et détermine la perception d'événements discrets. Seuls les corpuscules de Meissner, particulièrement denses sur les régions distales des doigts, possèdent la caractéristique de ne pas avoir un seuil perceptuel différent du seuil physiologique : une seule impulsion dans le champ récepteur de ces unités suffit pour provoquer la perception d'une sensation. Dû à cette caractéristique, l'acuité tactile aux extrémités du corps repose majoritairement sur les paramètres physiologiques (Peters et al., 2009; Vallbo & Johansson, 1976). Au contraire, sur le reste du corps, la perception tactile dépend de mécanismes neuraux – qui seront abordés dans la section suivante.

D'autres unités réceptives issues de fibres non-myélinisées C, à la conductance plus lente, contribuent au codage de dimensions plus qualitatives des événements cutanés. Ces unités sont particulièrement présentes sur la peau poilue, et seraient plus éparses sur la peau glabre (Olausson et al., 2010; Watkins et al., 2021). Néanmoins, disposant également d'un seuil physiologique bas et innervant des couches cutanées plus profondes, leur mise en évidence sur des régions déjà denses en mécanorécepteurs de surface est particulièrement difficile. Ces unités ne sont pas discriminées sur leur vitesse d'adaptation ou la taille de leur champ récepteur, qui sont intermédiaires en référence aux mécanorécepteurs de surface. Mais une catégorisation se fait sur la base des événements cutanés auxquels ces unités réagissent. Des mécanorécepteurs CT sont mis en évidence, sensibles aux mêmes déformations cutanées que les mécanorécepteurs de surface mais modulés par l'intensité et la valence des événements cutanés (Liljencrantz & Olausson, 2014; McGlone et al., 2012; Watkins et al., 2021). L'étude de la thermoception permet d'identifier le rôle de thermorécepteurs C2 dans la détection de la chaleur, tandis que des mécanorécepteurs issus de fibres finement myélinisées A δ seraient requis dans la détection du froid (Darian-Smith et al., 1979; Filingeri, 2016; Granovsky et al., 2005; Johnson et al., 1979; Paricio-Montesinos et al., 2020; Schepers & Ringkamp, 2009). Des nocicepteurs C également, au seuil physiologique plus haut, réagiraient aux stimuli mécaniques et thermaux douloureux.

Ainsi, des mécanismes physiologiques déterminent déjà les aspects topographiques et qualitatifs de l'expérience somatosensorielle, et certains suffisent à provoquer la perception d'une sensation à la surface de la peau. Ces mécanismes périphériques seraient primordiaux à la conscience corporelle. C'est ce que suggèrent les cas de déafférentation, où le patient ne ressent pas ou trop peu son corps, et doit le regarder régulièrement afin de s'assurer qu'il est toujours là (Haggard & Wolpert, 2005; Lucci & Pazzaglia, 2015; Paillard, 1999). Il serait possible que les SPS soient

déterminées par l'activité spontanée de facteurs physiologiques cutanés. Cette hypothèse fut déjà proposée par Michael et Naveteur (2011) et par Tihanyi et Köteles (Tihanyi, 2019; Tihanyi & Köteles, 2017). Nous la développerons plus précisément dans l'Acte I : L'origine. Néanmoins, la perception somatosensorielle ne dépend pas uniquement de mécanismes périphériques, et d'autres mécanismes neuraux pourraient tout autant être responsables de la perception des SPS.

B. Le système nerveux central

A l'aide d'un paradigme en IRMf, Bauer et collègues (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014) mettent en exergue l'activation de régions cérébrales spécifiques pendant l'attention portée aux SPS sur le pouce, notamment les cortex somatosensoriels, l'insula et la région temporo-pariétale. Ces régions étant fréquemment associées à la perception somesthésique et à la conscience corporelle (Blanke & Arzy, 2005; A. D. Craig, 2009a, 2010b, 2011; Gallace & Spence, 2008, 2009, 2010; Hiromitsu et al., 2020; Igelström et al., 2015; Sperduti et al., 2011; Strigo & Craig, 2016; Yu et al., 2018), il est donc plutôt rassurant de relever leur activation pendant la perception de SPS. Nous ne savons pas pour autant quels mécanismes cognitifs sont reflétés par cette activité, et encore moins comment ces mécanismes déterminent la perception des SPS.

En effet, les cortex somatosensoriels, l'insula et la jonction temporo-pariétale constituent différentes étapes clés du chemin neural amenant les signaux somatosensoriels en conscience. Comme le décrivent Gallace et Spence (2010), le traitement des afférences sensorielles va du plus local et modalité spécifique au plus global et intermodal. Ce flux d'informations depuis les aires perceptuelles jusqu'aux aires d'intégration multimodales serait donc nécessaire à la perception des signaux du corps. Néanmoins, en plusieurs instances la littérature fait état de distorsions perceptuelles du corps ou d'hallucinations somatosensorielles provoquées par un dysfonctionnement de ces régions (Bär et al., 2002; Flor, 2003; Lemaitre et al., 2016; Moseley & Flor, 2012; Perez et al., 2015; Yu et al., 2018). Par ailleurs, ces régions sous-tendent une variété de processus cognitifs variés dont certains furent déjà associés aux SPS, comme l'attention et l'intéroception (Carter & Huettel, 2013; A. D. Craig, 2009a; García-Cordero et al., 2017; Ionta et al., 2011). En conséquence, ces mécanismes neuraux peuvent tout aussi bien amener les SPS en conscience, moduler leur perception, ou être leur origine même. Pour ces raisons, nous allons interroger la contribution de chacune de ces régions à la perception des SPS.

1. Les cortex somatosensoriels

Les cortex somatosensoriels primaire (SI) et secondaire (SII), des régions pariétales localisées dans le cortex post-central, sont les aires perceptuelles somesthésiques. En cette qualité, on y retrouve une organisation somatotopique rostro-caudale des activations neurales en lien avec les afférences tactiles. Ces activations représentent chaque segment du corps en fonction du nombre et de la taille des champs récepteurs qui l'innervent. On associe cette organisation fonctionnelle à l'homoncule somatosensoriel (Figure 4).

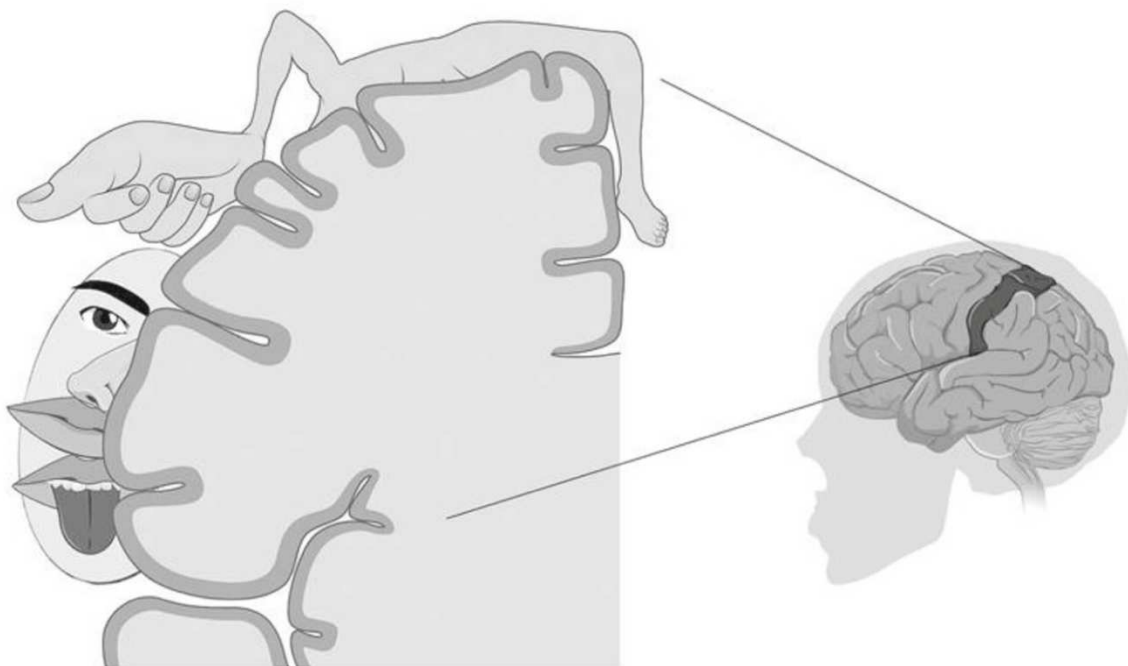


Figure 4 : Représentation visuelle de l'homoncule somatosensoriel.

Tiré de Hochstetter, 2016.

SI et SII reçoivent tout deux des afférences somatosensorielles depuis le système nerveux périphérique, et sont réciproquement connectées, à la fois ipsi- et controlatéralement. Il est donc difficile de déduire le sens de l'information somatosensorielle à partir de cette organisation structurale, mais l'activité fonctionnelle permet de supposer une primauté de SI sur SII. D'une part, la somatotopie est particulièrement précise en SI et plus floue en SII (Huang & Sereno, 2018; Kinsbourne & Lempert, 1980; Martuzzi et al., 2014; Overduin & Servos, 2004; Ruben et al., 2001). D'autre part, les activations neurales sont controlatérales à l'hémicorps stimulé en SI, mais bilatérales en SII. L'activité en SI résulterait du traitement local de signaux transmis par les mécanorécepteurs en périphérie, tandis que les efférences de SI activeraient les aires correspondantes

en SII, préservant l'organisation somatotopique initiale mais avec un traitement plus global (Barba et al., 2002; Gallace & Spence, 2008, 2009, 2010). Logiquement, SI serait dédié au décodage de bas niveau des afférences somatosensorielles, et SII intégrerait les informations somatosensorielles entre les deux hémicorps à des fins de coordination.

Bien que SI et SII soient des aires perceptuelles somesthésiques, elles sont pourtant sensibles aux afférences visuelles. En SI, la vision du corps semble faciliter le traitement de signaux corporels si elle apporte des informations complémentaires, telles que la localisation sur le corps, la surface sur la peau, ou l'occurrence dans le temps. Au contraire, en SII les effets de la vision sont indépendants du traitement tactile en cours, ce qui reflèterait la mobilisation de processus attentionnels centraux sur la perception tactile (Forster & Eimer, 2005; Naveteur, 2007; Press et al., 2004; Taylor-Clarke et al., 2002, 2004). D'un point de vue expérimental, tout un champ de littérature adresse ces interactions visuo-tactiles et notamment les perturbations de la conscience corporelle qu'elles peuvent induire. Par exemple, l'illusion de la main en caoutchouc : il est très aisé d'induire un sentiment d'appartenance vis-à-vis d'une fausse main, pour peu que celle-ci soit visible de l'individu et que les stimulations qui y sont appliquées par l'expérimentateur soient cohérentes avec celles administrées sur la véritable main (Armel & Ramachandran, 2003; Limanowski et al., 2014; Tsakiris, 2010; Wawrzyniak et al., 2018). Cette importance de la vision a également été relevée dans la nature même de l'homoncule somatosensoriel : les représentations du corps reflètent l'acuité tactile, mais sont élaborées à partir de représentations visuelles du corps (Kinsbourne & Lempert, 1980; Longo, 2017; Sirigu et al., 1991).

Les différences entre SI et SII s'observent également dans les mécanismes perceptuels. Ainsi l'activation de SI seule ne suffit pas à la perception tactile ; du fait de ses nombreuses connections avec les régions pariétales et préfrontales, SII tiendrait ce rôle en plus de contribuer à d'autres expériences subjectives telle que se représenter le corps dans l'espace (Bretas et al., 2020; Gallace & Spence, 2010). Cependant, tout dysfonctionnement de SI anéantit toute possibilité de conscience tactile (Gallace & Spence, 2010). De plus, la réorganisation corticale et l'activité spontanée de SI ont été avancées comme cause du membre fantôme chez l'individu amputé, à la fois pour les sensations douloureuses et non-douloureuses (Andoh et al., 2017; Flor, 2003; Gallace & Spence, 2008; Moseley & Flor, 2012; Ramachandran, 1998), alors que de telles avancées n'ont pas été proposées pour SII. Dans leurs deux études, Bauer et collaborateurs (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014) insistent d'ailleurs sur l'importance de SI, dont l'activation seule suffirait à éliciter la perception des SPS.

On peut supposer que l'activité de SI et SII reflète des processus somesthésiques à l'œuvre dans le traitement de SPS codés par les neurones périphériques. L'hypothèse que les SPS soient un construit perceptuel sans base physiologique et généré par ces mêmes régions n'est pas négligeable pour autant. Nous nous attacherons donc à apporter des éléments de réponse à ces deux points dans l'Acte I : L'origine et l'Acte III : ETUDE approfondie des corrélats cognitifs et neuraux.

2. L'insula antérieure

L'insula, ce morceau de cortex plié entre le lobe temporal et le lobe frontal, possède plusieurs cordes à son arc. Cette pluralité est abordée à travers les nombreuses revues de littérature proposées par Craig (A. D. Craig, 2003a, 2003c, 2004, 2009a, 2010a, 2010b, 2011, 2013; A. D. Craig et al., 1996, 2000). A l'instar des cortex somatosensoriels, l'insula est somatotopiquement organisée mais uniquement pour les événements thermiques ; en raison, Craig et autres auteurs (A. D. Craig et al., 2000; Hua et al., 2005) lui attribuent le titre de cortex perceptuel thermal. L'insula est ainsi clivée en deux, avec une préférence antérieure pour le réchauffement et postérieure pour le refroidissement. Malgré cette spécialisation, l'insula est également sensible à l'intensité des événements somatosensoriels et douloureux, et serait investie dans le codage de dimensions plus qualitatives et subjectives de la somesthésie (Casey et al., 1996; A. D. Craig, 2009a; Lenoir et al., 2018; Moayedi & Weissman-Fogel, 2009). Cela lui confère l'habileté de coder l'agréabilité des sensations corporelles, mais également de réagir aux événements potentiellement nocifs. Enfin, l'insula est un nœud clef de la perception cardiovasculaire et viscéro-gastrique, d'où sa prépondérance dans l'étude de l'intéroception (Herman et al., 2021; Khalsa et al., 2009; Nagai et al., 2004; Pollatos, Schandry, et al., 2007; Walter et al., 2020). On suppose que le traitement des signaux intéroceptifs et somesthésiques dans l'insula contribuerait notamment à l'homéostasie (A. D. Craig, 2003b; Strigo & Craig, 2016), c'est-à-dire la gestion des mécanismes physiologiques régulant le corps en fonction de ses besoins.

On accorde un intérêt plus particulier encore à l'insula antérieure (AI), locus du *material me*, c'est-à-dire l'expérience consciente et subjective du corps et du *Self* (A. D. Craig, 2003c, 2009a, 2010b). Cet intérêt naît d'une part des intrications insulaires avec les systèmes perceptuels : AI élaborerait des représentations plus ou moins complexes sur la base de ces afférences sensorielles, lesquelles seraient à la base de l'expérience subjective du corps (Berlucchi & Aglioti, 2010; A. D. Craig, 2009a; Khalsa et al., 2009). D'autre part, de son implication dans des processus centraux

tels que l'attention ou le contrôle cognitif, que l'on sait liés à la prise de conscience (Critchley et al., 2004; Krolak-Salmon et al., 2003; Mars et al., 2012; Menon & Uddin, 2010; Modinos et al., 2009; Sadaghiani et al., 2010). A travers des modulations de l'arousal, AI maintiendrait le focus attentionnel vers le corps ou le *Self*, et les dysfonctionnements insulaires – fréquemment répertoriés dans les syndromes douloureux – seraient à l'origine de l'hypervigilance vers le corps, laquelle provoque douleurs et amplification somatosensorielle (Borg et al., 2015; R. E. Harris et al., 2009). On associe ainsi à AI la perception consciente, notamment intéroceptive, visuelle et auditive. Mais cette région se montre également nécessaire à l'émergence d'expériences subjectives requérant l'intégration des afférences sensorielles et de haut niveaux, telle que la conscience du mouvement, la perception du temps ou la conscience émotionnelle (A. D. Craig, 2009b). Enfin, à partir de ces construits subjectifs, AI intervient dans l'évaluation des risques, l'anticipation et la prise de décision (A. D. Craig, 2008, 2009a, 2009b, 2011). L'étude de AI permet de saisir les mécanismes responsables de l'expérience subjective du corps, mais également d'appréhender la variété de construits subjectifs élaborés à partir des signaux corporels. Pour ces raisons, l'Acte III : ETUDE approfondie des corrélats cognitifs et neuraux abordera son rôle dans le phénomène des SPS.

Enfin, une littérature plus récente met en exergue le rôle de l'insula dans certaines distorsions perceptuelles du corps, appelées hallucinations autoscopiques : ces expériences particulières sont caractérisées par le sentiment vivace d'être en dehors de son corps, et s'accompagnent également de sensations de fourmillements sur le corps (Yu et al., 2018). Ces hallucinations seraient principalement liées à un dysfonctionnement temporo-pariétal, une région que l'on retrouve fréquemment associée à l'insula.

3. La jonction temporo-pariétale

La jonction temporo-pariétale (TPJ) est une entité fonctionnelle plus que structurelle : ses limites physiques étant plutôt floues, on suppose qu'elle comprend les gyri supramarginal et angulaire, et empiète sur le lobule pariétal inférieur et la scissure temporale supérieure postérieure. Il s'agit d'une aire d'intégration supramodale particulièrement connectée à de grands réseaux cérébraux et soutenant une très grande variété de processus cognitifs (Arzy et al., 2006; Carter & Huettel, 2013; Eddy, 2016; Igelström & Graziano, 2017; Ionta et al., 2011, 2014; Mars et al., 2012; Wu et al., 2015). On y relève entre autres la cognition sociale, la mémoire épisodique, l'incarnation et l'attention.

L'intérêt pour TPJ est multiple. Gallace et Spence promeuvent d'une part son implication dans la perception somatosensorielle (Gallace & Spence, 2008, 2009, 2010). Ses connexions réciproques avec les cortex somatosensoriels et l'insula sous-tendraient des échanges à la fois *bottom-up* et *top-down*. Dans un premier temps, l'intégration multimodale des afférences somatosensorielles et insulaire en TPJ contribuerait au développement de représentations destinées à maintenir une mémoire somatosensorielle à court terme du corps. Ces représentations seraient également à la base de construits cognitifs complexes comme l'incarnation, le sentiment d'être localisé dans les limites physiques de son propre corps (Arzy et al., 2006; Ionta et al., 2011; Wang et al., 2016). Dans un second temps, les afférences de TPJ vers les aires perceptuelles moduleraient directement l'activité neurale de ces régions. Des processus attentionnels mobilisés par TPJ seraient à l'origine de ces modulations, et seraient vraisemblablement destinés à adapter la perception somatosensorielle sur la base des signaux déjà perçus (Donaldson et al., 2015; Igelström & Graziano, 2017; Kucyi et al., 2012).

Cependant, une certaine ambiguïté naît de son implication dans des processus antithétiques. Avec l'insula, TPJ est un nœud commun au réseau cérébral par défaut et au réseau de saillance (Buckner et al., 2008; Fox et al., 2005; Power et al., 2011; Scheibner et al., 2017). Ces deux réseaux promeuvent respectivement l'attention vers soi et vers l'environnement, mais ne peuvent être fonctionnels que si l'autre est désengagé. On retrouve une ambiguïté tout à fait semblable dans la prise de perspective, où TPJ est associée à la fois à la perspective en première et troisième personne – deux mécanismes qui ne peuvent être mis en place en parallèle et contribuent différemment au sentiment d'incarnation (Babo-Rebelo et al., 2019; Ionta et al., 2014; Martin et al., 2020; Vogeley & Fink, 2003; Zhang et al., 2014). On attribue donc généralement à TPJ le rôle d'interrupteur, chargé de déterminer la direction attentionnelle (interne vs externe) et la perspective de l'individu. Cette ambivalence cognitive reflète la flexibilité certaine des processus attentionnels et d'incarnation dans la conscience du corps. Si au moment où nous prenons conscience de notre corps nous avons l'impression de l'incarner, il nous est profitable de savoir « sortir de notre corps » pour nous projeter à la place des autres (Eddy, 2016; R. Harris, 2019; Kessler & Braithwaite, 2016; Zahavi, 2010). Ainsi, nous avons déjà évoqué les perturbations somatosensorielles provoquées par des dysfonctionnements attentionnels, mais d'autres altérations de la conscience corporelle naissent de mécanismes d'incarnation défailants.

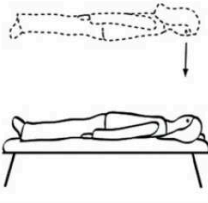
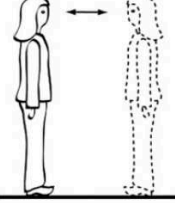
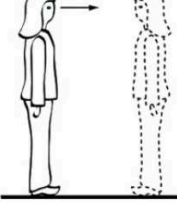
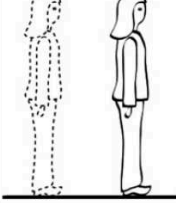
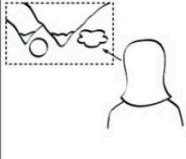
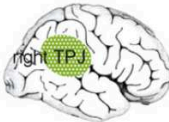


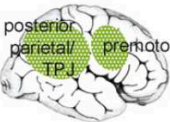
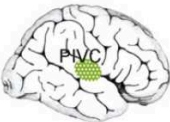
	expérience de sortie du corps	héautoscopie	hallucinations autoscopiques	sentiment de présence	illusion de la pièce inclinée
Phénoménologie					
perturbations vestibulaires	+++	++	-	+	+++
désintégration dans l'espace personnel	+++	+++	+++	+++	-
désintégration entre l'espace personnel et extrapersonnel	+++	++	-	+	+++
trouble	incarnation sens du corps	incarnation sens du corps	-	sens du corps	-
mécanismes neuraux					

Figure 5 : Expériences hallucinatoires liées aux dysfonctionnements de TPJ.

Tiré de Lopez et al., 2008.

Les dysfonctionnements de TPJ sont à l'origine de nombreuses distorsions perceptuelles caractérisées par une désincarnation (Figure 2; Blanke & Mohr, 2005; Hiromitsu et al., 2020; Lopez et al., 2008; Persinger et al., 2010; Persinger & Makarec, 1992; Serino et al., 2013). Les hallucinations autoscopiques prennent plusieurs formes. Les plus classiques (et les plus impressionnantes) sont les expériences de sortie du corps, où l'individu perçoit son corps depuis une position élevée. Les héautoscopies sont presque semblables, à la différence que l'individu perçoit son corps face à lui, mais ne sait pas quel perçoit est le vrai. Certains de ces phénomènes sont plus discrets et courants chez l'individu lambda. C'est le cas du sentiment de présence, ou conscience parasitaire, où sa propre présence est perçue sur, derrière ou devant l'épaule, un phénomène qui peut être interprété – selon les croyances de l'individu – comme une expérience religieuse ou paranormale. Les travaux de Persinger approfondissent particulièrement les comportements anormaux liés aux dysfonctionnements de TPJ (Persinger, 2001; Persinger et al., 2010, 2013; Persinger & Makarec, 1992; Persinger & Saroka, 2013; Saroka et al., 2014; Saroka & Persinger, 2013). Il défend une sensibilité temporo-pariétale à l'activité électromagnétique externe au corps, qui serait variable d'un individu à l'autre et expliquerait l'occurrence d'hallucinations autoscopiques chez l'individu lambda, ainsi que la prépondérance des populations schizotypiques à rapporter ces distorsions perceptuelles. La question se pose alors de l'implication de ces mécanismes dans la

perception des SPS, leur perception étant affectée par les traits schizotypiques (Michael, Guyot, et al., 2020). Ses travaux relèvent également la forte intrication entre expériences autoscopiques et hallucinations tactiles. Les expériences de sortie du corps et les phénomènes de conscience parasitaire dans un contexte d'épilepsie temporale s'accompagnent de fourmillements sur le corps (Persinger et al., 2013; Saroka & Persinger, 2013). Les lésions de TPJ peuvent également être à l'origine de psychose somatosensorielle, comme dans l'infestation délirante, où les hallucinations tactiles font émerger le ressenti d'avoir des insectes dans la peau (Eccles et al., 2015; Freudenmann et al., 2010).

Cet entraperçu de la TPJ soulève de nombreuses pistes d'exploration. Son implication dans la perception des SPS pourrait résulter de mécanismes dévoués à la perception somesthésique, mais également de processus attentionnels destinés à adapter le contenu en conscience, ou encore de processus d'intégration multimodaux contribuant à l'incarnation. Ces pistes seront abordées dans l'Acte III : ETUDE approfondie des corrélats cognitifs et neuraux. Néanmoins, cette revue de la littérature sur les mécanismes neuraux met également l'accent sur des processus attentionnels et mnésiques dont dépendraient l'accès en conscience et l'intégrité de la conscience corporelle. Nous nous étendrons spécifiquement sur ces composantes cognitives.

II. L'accès à la conscience

Les mécanismes de conscience sont distincts des processus perceptuels, attentionnels et mnésiques. Néanmoins, l'accès à la conscience dépend cruellement du bon fonctionnement de ces composantes cognitives. Dans la théorie attentionnelle de la conscience corporelle, Kinsbourne (1998) établit comme fondement de l'accès à la conscience du corps le focus attentionnel et le maintien des représentations en conscience. D'un point de vue fonctionnel, des processus attentionnels top-down promus par l'insula et la TPJ modulerait le construit perceptuel en SI et SII, et des processus mnésiques élaborant et mettant à jour des représentations dans les aires perceptuelles et d'intégration multimodales contribueraient à une mémoire à court terme du corps (Gallace & Spence, 2008, 2009, 2010). L'ensemble de ces opérations contribuerait à la prise de conscience du corps.

A. L'attention

1. L'arousal physiologique et l'état attentionnel

Le déterminant premier de la perception, et par extension de la conscience, est l'état attentionnel ou état d'éveil. L'attention, sphère cognitive centrale et majeure de la cognition humaine, assume l'intensité de l'effort cognitif réalisé. Cette compréhension naît de la relation étroite entre l'arousal, c'est-à-dire l'activation physiologique de l'organisme, et les capacités attentionnelles : un arousal élevé est signe d'énergie, d'éveil cognitif ou d'activation physique, tandis qu'un arousal bas accompagne un état de digestion ou de repos (Thayer, 1967, 1970). L'arousal physiologique varie avec les interactions des systèmes sympathiques et parasympathiques, augmentant avec l'activité du premier et diminuant avec celle du second. L'arousal élevé est donc un marqueur de réactivité attentionnelle aux signaux de l'environnement, et son enregistrement permet d'étudier le niveau de conscience associé au traitement cognitif (Smythies, 1997). Mais l'arousal varie également avec la cognition du *Self*, puisque le vagabondage de pensée, le discours interne (la petite voix dans notre tête que nous utilisons pour raisonner, élaborer et conceptualiser nos pensées), le traitement émotionnel et l'intéroception sont associées à des variations de l'activité physiologique (Chapell, 1994; Critchley et al., 2000; Deuter et al., 2018; Hoehn-Saric & McLeod, 2000; Nagai et al., 2004; Nikula, 1991; Pollatos, Schandry, et al., 2007; Tsakiris & De Preester, 2019). Ainsi, partir

dans ses pensées ou explorer les sensations sur son corps ne serait pas plus reposant qu'être attentif à l'environnement.

La loi Yerkes-Dodson établit une relation en U inversée entre l'arousal et les performances cognitives, loi selon laquelle la qualité de la performance souffre lorsque l'arousal est trop bas (sommeil) ou trop élevé (anxiété). Sur la base de cette loi, Kahneman développe le modèle des ressources cognitives (Egeth & Kahneman, 1975), des ressources limitées dont la quantité varie avec le niveau d'arousal, et dont l'engagement détermine le succès des opérations cognitives. Les tâches automatisées requièrent très peu de ressources car elles ne nécessitent pas de contrôle volontaire et pas d'accès en conscience ; elles les accaparent automatiquement très tôt. Au contraire, plus une tâche nécessite l'engagement de mécanismes contrôlés et plus elle est coûteuse. Ces tâches non-automatisées sont donc en compétition pour les ressources cognitives restantes.

Lorsque la demande cognitive est trop élevée, des mécanismes feedback peuvent agir soit sur l'arousal dans le but d'augmenter les ressources cognitives à disposition, soit sur l'allocation des ressources afin de les mobiliser en priorité sur les tâches répondant aux objectifs internes. Un arousal trop élevé ou trop bas interfère avec l'allocation des ressources cognitives, mais aussi avec l'évaluation de la demande en ressources. On comprendra alors que notre état d'éveil détermine le succès des opérations en conscience – coûteuses – mais également que des différences interindividuelles dans la réussite de ces tâches naît de l'expertise, c'est-à-dire de l'habitude à s'engager dans certaines opérations cognitives (Figure 6).

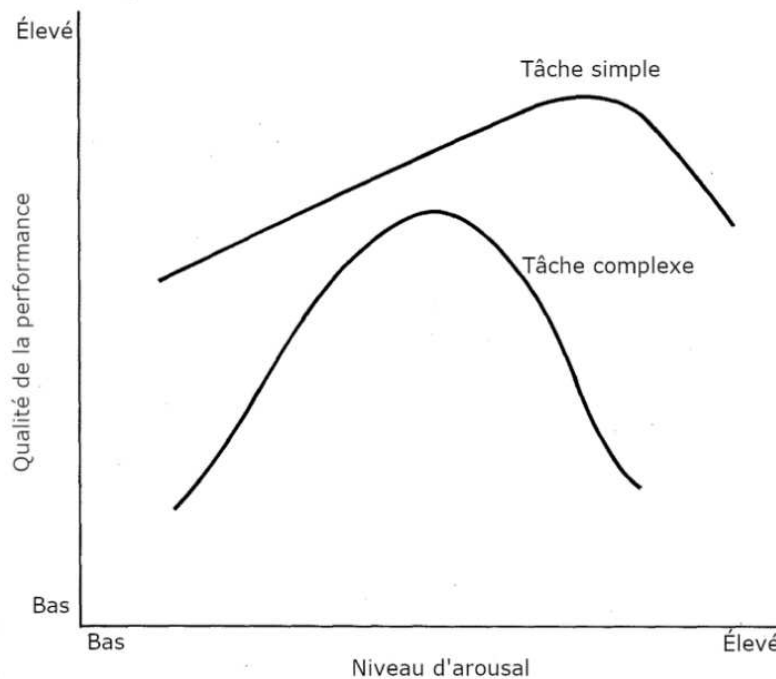


Figure 6 : Relation entre arousal, performances et cout de la tâche.
Tiré de Egeth & Kahneman, 1975.

2. La sélectivité attentionnelle

Le second déterminant de la conscience est l'objet sur lequel l'attention se porte. Car, rappelons-le, nos capacités cognitives sont inadéquates face à la multitude d'informations sensorielles à notre disposition. Et comme le dit Kinsbourne (1998), nous ne prenons conscience que d'une portion du *background of bodily sensations*, celle en focus.

Easterbrook (1959) développe une théorie liant arousal et sélectivité attentionnelle sur la base de la loi Yerkes-Dodson : avec un arousal bas, la sélectivité est inopérante et les signaux sensoriels sont traités indépendamment de leur signifiante ; alors que l'arousal augmente, l'attention devient plus sélective et les performances s'améliorent du fait du rejet correct des signaux non-pertinents et distracteurs ; lorsque l'arousal est trop élevé, la sélection devient trop exigeante et des signaux pertinents incorrectement rejetés mènent à une baisse des performances.

Le modèle Master Activation Map (MAM; Michael et al., 2007; Michael, Dorey, et al., 2020; Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014; Michael & Gálvez-García, 2011) approfondit le modèle des ressources cognitives (Egeth & Kahneman, 1975) et identifie les processus attentionnels et leur coordination dans la sélection des signaux sensoriels accédant en conscience. Selon ce modèle deux cartes représenteraient les éléments saillants dans

l'environnement sur la base de leurs caractéristiques physiques, ainsi que ceux répondant aux besoins de l'individu. La carte de saillance serait générée uniquement à partir des afférences sensorielles et celle de pertinence serait modulée par des processus de haut niveau. Une carte principale, la MAM, intègre ces éléments en une seule représentation unifiée de l'espace, et sert d'interface aux processus d'orientation et d'inhibition. Ces deux mécanismes sont indépendants et contribuent de façon complémentaire à la sélection : guidée par la carte MAM, l'orientation dirige le focus attentionnel à travers l'environnement sensoriel, tandis que l'inhibition agit directement sur le contenu de la carte MAM en supprimant les signaux distracteurs ou non-pertinents pour les objectifs internes. En parallèle des unités de régulation des ressources cognitives gèrent la quantité de ressources engagée dans les opérations cognitives, et assurent l'efficacité des processus inhibiteurs en leur allouant une certaine quantité de ressources.

Plusieurs études sur les SPS portent sur l'attention. Trois études de Michael et Naveteur (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015) abordent les interactions visuo-attentionnelles et mettent en exergue des mécanismes facilitateurs et supprimeurs reflétant la sélection des SPS. D'autres renforcent le poids du focus attentionnel dirigé vers le corps dans leur perception, par le biais d'habiletés cognitives (Michael et al., 2015, 2017) ou de modèles pathologiques (Borg et al., 2015; Echalié et al., 2020) impliquant cette composante de l'attention. De leur côté, Bauer et collègues (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014) observent que l'insula et TPJ, les bases neurales de l'orientation attentionnelle vers le *Self* et l'environnement (Corbetta et al., 2008; Corbetta & Shulman, 2011), sont activées lors de l'attention portée aux SPS. Pourtant, nous venons de voir la complexité des mécanismes attentionnels derrière ce focus attentionnel, en passant par l'arousal qui reflète l'éveil cognitif, jusqu'à l'interaction des processus inhibiteurs et régulateurs des ressources cognitives qui déterminent la sélectivité de l'attention. Ces questions seront donc abordées dans l'Acte II : Les déterminants cognitifs, mais également dans l'Acte III : ETUDE approfondie des corrélats cognitifs et neuraux à travers TPJ et AI.

B. La mémoire de travail

Un dernier point que nous aborderons est celle du maintien de la conscience. D'une part, les conceptions théoriques de la conscience corporelle argumentent en faveur d'une mémoire du corps, et particulièrement d'une mémoire à court terme fondamentale à sa prise de conscience (Carruthers,

2008; Gallace & Spence, 2009; O'Shaughnessy, 2003; Sirigu et al., 1991). Kinsbourne (1998) quant à lui aborde le rôle de l'attention dans le maintien de la conscience et la mise à jour des représentations corporelles.

La conception de la mémoire proposée par Cowan (1999) se rapproche par bien des aspects de la théorie attentionnelle de la conscience corporelle (Kinsbourne, 1998) et des modèles attentionnels (Egeth & Kahneman, 1975; Michael et al., 2007; Michael, Dorey, et al., 2020; Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014; Michael & Gálvez-García, 2011) auxquels nous nous référons. La mémoire à long terme et à court terme ne sont pas dissociées, elles sont intriquées et interdépendantes. Des représentations forment un stock mnésique à long terme, lequel est sensible aux afférences sensorielles qui activent certaines de ces représentations en fonction de leurs similarités. Une fois actives, les représentations sont à portée du focus attentionnel qui assure leur entrée en mémoire de travail. La mémoire de travail est ici un paradigme où des mécanismes à la fois attentionnels et mnésiques contribuent au maintien et à la manipulation de représentations en conscience sur le court terme. Cowan (1999) décrit des échanges réciproques entre le stock à long terme et la mémoire de travail. Du côté ascendant, la portion de représentations actives en focus est maintenue en mémoire de travail, et dès lors que le focus attentionnel est désengagé de ces représentations, elles s'évanouissent de la conscience et retournent à leur état d'activation précédent. Les modifications des représentations en mémoire de travail en lien avec les afférences sensorielles peuvent être implémentées en mémoire à long terme. Du côté descendant, des processus mnésiques en mémoire de travail peuvent récupérer des représentations hors du focus en fonction des buts et du contenu en conscience, tandis que des mécanismes attentionnels peuvent inhiber les représentations actives susceptibles d'interférer avec le traitement en mémoire de travail. Ces interactions expliquent comment la perception peut être influencée par la conscience. Elles montrent également que des mécanismes contrôlés et volontaires luttent pour sauvegarder le contenu en mémoire de travail autant qu'il est nécessaire.

Le mécanisme fondamental de la mémoire de travail serait l'oubli. Dans la lignée de Cowan (1999), le modèle *Time-Based Resources Sharing* (Barrouillet et al., 2004, 2012; Barrouillet & Camos, 2012; Vergauwe et al., 2014) défend que la mémoire de travail est limitée par le temps : l'activation des représentations suit un déclin temporel normal, jusqu'à redevenir inaccessibles au focus attentionnel. D'autres facteurs peuvent accroître cet oubli, notamment la multiplicité des opérations cognitives en cours, ainsi que leur difficulté. Barrouillet défend l'existence d'un mécanisme, le rafraichissement attentionnel, dédié à contrecarrer le déclin des représentations en

les replaçant au cœur du focus. Ce mécanisme utilisant les mêmes ressources cognitives que celles allouées au traitement en mémoire de travail, on ne pourrait pas maintenir et manipuler des représentations différentes en parallèle mais seulement en alternance. Le nombre d'opérations en cours et leur difficulté limite par ailleurs la quantité de représentations pouvant être maintenues en conscience, ainsi que la qualité des informations que nous récupérons.

Ainsi, si prendre conscience du corps repose sur des mécanismes attentionnels, il est fort à parier que la mémoire du corps requiert les mêmes mécanismes que ceux engagés en mémoire de travail. On pourrait supposer que ces mécanismes mnésiques seraient nécessaires à construire et maintenir l'expérience subjective du corps, à mettre à jour la mémoire à long terme du corps, et également à protéger la conscience du corps des interférences causées par d'autres représentations internes (A. D. Craig, 2009a; Modinos et al., 2009) ou externes au corps. On pourrait également relever que l'expérience consciente du corps est limitée dans le temps, et que nous devons « l'oublier » (le faire disparaître du contenu en conscience) afin de pouvoir nous engager dans d'autres opérations. Selon cette logique, la conscience corporelle serait sujette aux mêmes limitations que la mémoire de travail. Or, il est déjà fait état d'un cas d'asomatognosie particulier, où l'individu est capable de prendre conscience de son corps, mais perd cette conscience très rapidement s'il ne garde pas le membre affecté au centre de son champ visuel (Haggard & Wolpert, 2005; Wolpert et al., 1998). Signifiant ainsi que la conscience du corps n'est pas juste élicitée, et doit être continuellement maintenue pour en prévenir l'oubli. D'autre part, le syndrome du membre fantôme illustre les dysfonctionnements résultant de l'inadéquation entre les représentations du corps stockées en mémoire et l'état du corps actuel (Flor, 2003; Haggard & Wolpert, 2005; Moseley & Flor, 2012). D'où le besoin de mécanismes pouvant manipuler et transformer les traces en mémoire pour sauvegarder la conscience corporelle. Mais rapprocher conscience du corps et mémoire de travail n'a pas été fait jusqu'à présent, et nous l'aborderons donc dans l'Acte II : Les déterminants cognitifs.

III. Articulation du manuscrit

En développant le phénomène des SPS en introduction, nous avons mis en avant trois objectifs de recherche, dont deux principaux : explorer la nature et le rôle des SPS, identifier les mécanismes qui les amènent en conscience, et apporter de nouveaux éléments de compréhension concernant la conscience corporelle chez l'individu lambda. Les éléments que nous avons présenté dans ce contexte théorique ne suffisent pas à la conscience corporelle. Néanmoins, ils relèvent tous d'un intérêt particulier, certains car ils pourraient être à l'origine des SPS, d'autres car ils détermineraient leur accès à la conscience, et quelques-uns car ils tiendraient ces deux rôles. L'organisation du manuscrit suit ainsi cette logique. L'Acte I cherchera à mettre en évidence les soubassements périphériques et centraux des SPS, par le biais de la sensibilité tactile et de l'activité oscillatoire de SI et SII. L'Acte II portera sur les mécanismes attentionnels et en mémoire de travail et leur rôle spécifique dans l'accès à la conscience des SPS. L'Acte III clôturera ce travail en mêlant l'étude des mécanismes corticaux à l'origine des SPS et contribuant à la conscience corporelle. Nous nous intéresserons à TPJ et AI à travers deux interrogations : en premier, nous approfondirons le rôle de l'attention via leur connectivité fonctionnelle et des mesures déclaratives et psychophysologiques d'arousal ; en second, en incluant les cortex somatosensoriels, nous étudierons les mécanismes centraux déterminant la perception des SPS selon leur type. Si les facteurs que nous appréhendons sont déjà bien discutés dans la littérature de la conscience corporelle, certains comme la mémoire de travail ou les mécanismes attentionnels en sont absents ou sont sources de débat. Nous espérons donc que les études présentées contribueront aussi bien à la popularisation des SPS dans la recherche qu'à une meilleure compréhension des processus cognitifs à l'œuvre dans la conscience corporelle.

Cependant, l'étude des SPS n'est pas simple. Leur récolte nécessite repos du corps, absence d'événements externes pouvant induire la perception d'une sensation sur la peau, et focus attentionnel et visuel sur la partie du corps ciblée. En somme, toute manipulation expérimentale dans le but d'étudier les soubassements du phénomène est susceptible de l'altérer directement. Néanmoins, les différences que l'on observe dans leur perception sont liées à des traits individuels, qu'ils soient physiques (Naveteur et al., 2015), cognitifs (Michael et al., 2015, 2017) ou neuraux (Borg et al., 2015; Echalié et al., 2020). Recueillir les SPS, ce serait vraisemblablement obtenir un polaroid d'un environnement mouvant, un aperçu représentatif de la conscience corporelle de chacun, nous permettant d'ouvrir une fenêtre sur les habitudes cognitives de l'individu vis-à-vis de son corps. Les travaux que nous présentons partent tous de ce postulat. En raison, nous explorerons

les relations entre des traits individuels et les caractéristiques des SPS reportées à un instant T. Nous emprunterons à la psychologie cognitive, aux neurosciences, et même parfois à la psychophysiologie, en proposant des tâches comportementales, des enregistrements électroencéphalographiques (EEG) et psychophysiologiques au repos nous permettant d'extraire des traits cognitifs et physiologiques. Nous supposons que cette démarche nous permettra d'identifier les facteurs cognitifs et neuraux de la conscience corporelle chez l'individu lambda, et de comprendre le rôle des SPS dans cette dernière.

ACTE I. L'ORIGINE

Les sensations spontanées, un phénomène périphérique ou central ?

Tableau 1. La sensibilité tactile

D'où proviennent les SPS ? L'explication la plus simple est généralement la bonne : si nous percevons les SPS sur la peau, alors c'est que leur origine s'y trouve.

O'Shaughnessy (1986, 2003) et Gallace & Spence (2008, 2009, 2010) s'accordent sur le rôle des afférences cutanées dans la conscience corporelle. La peau, plus grand organe sensoriel et constamment sollicité, maintiendrait l'intégrité de la conscience corporelle en informant continuellement le système nerveux central sur la position du corps et ses interactions avec l'environnement. Il serait cohérent qu'en l'absence de tels événements, l'activité physiologique spontanée soit perceptible afin de maintenir cette conscience corporelle. Si tel était le cas, la perception de SPS reposerait sur les mêmes mécanismes périphériques que la perception somatosensorielle. Or, la distribution des SPS suit un gradient proximo-distal identique à celui mis en exergue dans l'organisation des cellules sensorielles cutanées (Johansson & Vallbo, 1979a; Vallbo & Johansson, 1984). Leur fréquence est particulièrement élevée sur les phalanges distales où nous possédons une acuité tactile fine, et plus modérée sur la région palmaire à la sensibilité tactile plus émoussée (voir Prologue, partie I-A). Serait-ce une preuve de l'origine physiologique des SPS ?

Eh bien il n'est pas si facile de trancher. Les travaux de Vallbo et Johansson (Vallbo et al., 1979; Vallbo & Johansson, 1976) distinguent la perception tactile sur les doigts et la paume, déterminée par les paramètres physiologiques aux extrémités de la main et par des processus centraux au centre de la paume. Du côté des SPS, on relève aussi l'existence d'une dissociation entre doigts et paume en étudiant l'effet du mouvement (Beaudoin & Michael, 2014), les interactions vision-attention (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015) et l'intéroception (Beaudoin & Michael, 2014). Il serait ainsi possible que des mécanismes tactiles périphériques et centraux contribuent différemment à la perception des SPS en fonction de leur localisation. Par ailleurs, les SPS exhibent un biais vers la main gauche chez les droitiers (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015), ce qui peut être lié à la sensibilité tactile plus fine sur la main non-dominante en raison d'une peau moins calleuse (Boles & Givens, 2011; Weinstein & Sersen, 1961) mais également à la spécialisation de l'hémisphère droit pour les processus tactiles (Genetta-Wadley & Swirsky-Sacchetti, 1990; Tomlinson et al., 2011). En

somme, si les SPS dépendent effectivement de mécanismes tactiles, il y a beaucoup d'incertitudes quant à leur nature.

L'article suivant aborde la question de l'origine des SPS, en investiguant leur dépendance à la sensibilité tactile. Un premier objectif concerne la relation entre le gradient proximo-distal des SPS et celui de la sensibilité tactile. Si la fréquence et l'intensité topographique des SPS augmentent avec une meilleure acuité tactile, cela conforterait l'hypothèse d'une distribution déterminée par des facteurs périphériques. Un second objectif est d'explorer la part des mécanismes centraux communs à la perception tactile et aux SPS. Ces mécanismes devraient induire une différence de traitement entre les doigts et la paume de la main, mais également entre la main gauche et la main droite. En ciblant la sensibilité tactile sur la main glabre comme trait psychophysique, nous espérons donc pouvoir faire la part entre mécanismes périphériques et centraux à l'œuvre dans la perception des SPS.

Article 1 : Salgues, S., Plancher, G. & Michael, G.A., (in Preparation). Is it on my hand? Tactile sensitivity does not explain the perception of spontaneous sensations on the glabrous hand.

Is it on my hand? Tactile sensitivity does not explain the perception of spontaneous sensations on the glabrous hand

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Abstract

The perception of sensations on the skin surface would depend on the peripheral physiological activity and on neural factors. Yet, some sensations can be felt on the skin even though no cutaneous events trigger their perception and are sensitive to the same factors affecting tactile perception. These spontaneous sensations follow a proximal-to-distal gradient that is typically evidenced in the distribution of cutaneous units underlying tactile sensitivity. This study thus aimed to unravel the peripheral underpinnings of the SPS phenomena. The topographical frequency and intensity of SPS perceived on the glabrous hand were confronted to the perceptual threshold extracted from the corresponding hand segment. The tactile sensitivity was associated to a decrease in the frequency and intensity of SPS. These associations differed between the left and right hands and between the digits and palm. We demonstrate that tactile sensitivity is deleterious to SPS perception and discuss about the heavy involvement of hemispheric-dependent tactual processes. This contradicts the hypothesis of physiological determinants underlying SPS.

Keywords: Spontaneous Sensations; Tactile sensitivity; Attention; Hemispheric specialization; Somatosensory distortions

1. Introduction

Tactile awareness is a major component of body awareness, shaping the spatial frontier of the body, bringing information about its interactions with and its location in the environment, and contributing to the feeling of ownership, agency and continuity in time (Gallace & Spence, 2008; Kinsbourne, 1998; Lenggenhager et al., 2009; Tsakiris et al., 2007; Zopf et al., 2011). The sense of touch would be generated from cutaneous pression or motion (Gallace & Spence, 2008, 2010; Vallbo, 1981), but some bodily sensations would be perceived on the surface of the skin in the absence of such deformation (Michael et al., 2012; Michael & Naveteur, 2011). We thus aimed to investigate whether awareness of those spontaneous sensations (SPS) would rely at least partly on tactile sensitivity.

1.1. Tactile perception

The touch is a complex sensory modality, for it relies on the largest sensory organ and encompasses the perception of pressure exerted on the skin surface as well as resulting from limb motion, the identification of warm and cold changes in temperature, and the detection of painful contacts (Burke et al., 1988; Gallace & Spence, 2008, 2010; Kozłowska, 1998; Vallbo, 1981). Surface tactile acuity relies on peripheral units consisting mainly of myelinated afferents mechanoreceptive units, that respond selectively and distinctly to motion and pressure exerted on the glabrous skin (Johnson, 2001). Their innervation of the glabrous skin determines the spatial and topographic dimensions of tactile perception. Narrow receptive fields units with defined border are distributed along a proximo-distal gradient on the glabrous skin: on the hand, they are more densely found on distal phalanges than on palmar area, enabling an acute spatial and numerosity judgement of tactile inputs on the more peripheral body parts (Johansson & Vallbo, 1979a; Kozłowska, 1998; Vallbo & Johansson, 1984; Weinstein, 1962). Tactile sensitivity is also supported by large receptive fields units with undefined borders that are uniformly distributed on the glabrous skin and apprehend the directions of tactile stimulations and cutaneous vibrations, but with less spatial accuracy (Johansson & Vallbo, 1979b; Vallbo & Johansson, 1984). Along with the spatial acuity, the perceptual threshold is lower on more peripheral body segments than proximal ones (Hulliger et al., 1979; Johansson & Vallbo, 1979a, 1979b; Kozłowska, 1998; Olausson et al., 2010; Weinstein, 1962), and on the hands, tactile perception would be determined by physiological parameters of

peripheral segments such as fingers and palm borders, but would involve central factors on the palm (Johansson & Vallbo, 1979a, 1979b; Vallbo & Johansson, 1976).

Variability in tactile sensitivity emerges as well as a function of peripheral and neural factors. Fingertips size explains the tactile acuity discrepancy between men and women (Boles & Givens, 2011; Genetta-Wadley & Swirsky-Sacchetti, 1990; Herren, 1933; Kozłowska, 1998; Woodward, 1993), and the non-dominant hand displays an acuter tactile sensitivity (Genetta-Wadley & Swirsky-Sacchetti, 1990; Tomlinson et al., 2011; Weinstein & Sersen, 1961). Lateral differences arise as well in favor of the left body part due to the right hemisphere lateralization of tactual processes (Coghill et al., 2001; Schwartz et al., 1979; Weinstein & Sersen, 1961), and in relation to hemisphere specialization in local and global processing of tactile inputs (Tomlinson et al., 2011). Some tactile characteristics such as the perceived intensity of the stimulation seems not to depend much on the amplitude of the cutaneous units activity but would relate to neural traits (Vallbo & Johansson, 1984) and integrative mechanisms (Moayedi & Weissman-Fogel, 2009). Tactile perception is a physiological (Peters et al., 2009) and cognitive construct (Aspell et al., 2013; Kennett et al., 2001; van Ede et al., 2014), as such it might support some aspects of illusory tactile perception.

1.2. Perceiving sensations on the skin in the absence of tactile stimulation

Perceptual somatosensory distortions are usually accounted by neural mechanisms in cortical somatosensory and insular cortices (Andoh et al., 2017; Flor, 2003; Haggard & Wolpert, 2005; Halligan, 2002; Ramachandran, 1998; Razmus et al., 2017). Yet many phenomena of tactile hallucinations (Bär et al., 2002; Berrios, 1982; Freudenmann et al., 2010; Kataoka & Ueno, 2017; Shergill, 2001) and somatosensory amplifications (Borg et al., 2018; Colagiuri & Quinn, 2018; Garcia-Larrea & Mauguière, 2018; Gibson et al., 1994; Jensen et al., 2009; Marinus et al., 2011; Schwoebel et al., 2001) are seemingly unrelated to body damage and are associated to distortions of tactile sensitivity (Berrios, 1982; Echalièr et al., 2020; Liu et al., 2020; Riquelme et al., 2016). Besides, there are accumulating evidence that similar phenomena could be exhibited in the general population. A lineage of studies demonstrated that subjective sensations could be reported on the surface of the glabrous skin, with no cutaneous stimulations and the only instruction to attend to their hand (Michael et al., 2012, 2015, 2017; Michael, Guyot, et al., 2020; Michael & Naveteur,

2011; Naveteur et al., 2005, 2015; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021). These spontaneous sensations (SPS) were proposed to be the normal counterpart of distorted somatosensory perception (Borg et al., 2015; Echalié et al., 2020; Michael et al., n.d.; Salgues, Plancher, Jacquot, et al., 2021; Tihanyi, 2019; Tihanyi & Köteles, 2017). They are tingling, tickle, or warming sensations closely resembling elicited tactile sensations and following an identical proximal-to-distal gradient, as SPS are more frequent and intense on distal phalanges than on the palm (Echalié et al., 2020; Michael et al., 2012, 2015, 2017; Michael & Naveteur, 2011; Naveteur et al., 2015). Similarly to tactile perception, SPS are sensitive to vision and attention interactions (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015), and are modulated by gating (Beaudoin & Michael, 2014), a perceptual suppression phenomenon caused by the motion of a limb (Cohen & Starr, 1987; Malinen et al., 2006). Besides, inter-individual factors influencing tactile perception were evidenced as well in the SPS phenomenon, such as age, gender and body mass index (BMI; Naveteur et al., 2015), right-hemisphere cognitive abilities (Michael et al., 2012, 2015, 2017; Michael, Guyot, et al., 2020; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues et al., n.d.; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021), schizotypal traits (Michael, Guyot, et al., 2020) and abnormal somatosensory awareness (Borg et al., 2015; Echalié et al., 2020). Concerns remain whether SPS perception belongs to the tactile sense. And while some evidence were brought regarding the involvement of neural somatosensory mechanisms in their perception (Michael et al., n.d.; Salgues, Plancher, Jacquot, et al., 2021), none eluded the question of peripheral cutaneous factors and tactual processes.

1.3. The present study

This gathering emphasizes the many similarities between tactile and SPS perception and the lack of evidence regarding the involvement of tactual peripheral and central mechanisms in perceiving SPS. The most prominent feature of SPS, their topographical distribution on the glabrous hand (Michael et al., 2012, 2017; Michael & Naveteur, 2011), resembles the proximal-to-distal gradient underlying touch (Johansson & Vallbo, 1979a; Vallbo & Johansson, 1984), raising the question of whether their frequency and intensity might be linked to tactile sensitivity and, hence, to the distribution of receptive units over the glabrous surface of the skin (Michael et al., 2012; Michael & Naveteur, 2011). Besides, there is congruent evidence of cognitive processes distinctly involved

in the perception of SPS on the digits and palm (Michael et al., 2012, 2015; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues, Plancher, & Michael, 2021), and of cutaneous modulation selectively affecting SPS on the digits (Beaudoin & Michael, 2014), meaning SPS might be distinctly associated to the tactile sensitivity of these segments. Finally, with the involvement of right-hemisphere processes both in tactile (Boles & Givens, 2011; Genetta-Wadley & Swirsky-Sacchetti, 1990; Lechelt & Tanne, 1976; Minami et al., 1994; Tomlinson et al., 2011; Weinstein & Sersen, 1961) and SPS perception (Michael et al., 2012, 2015; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues, Plancher, & Michael, 2021), different effects might arise depending on the attended hand. These concerns will be addressed by investigating the relationship between the perception of SPS and the perceptual thresholds as assessed through the two-point discrimination test on the glabrous hands. We are assuming that tactile sensitivity might be associated to either or both the frequency and intensity of SPS, thus leading to the separate investigation of their topographical distribution. If tactile sensitivity is a major source of SPS, then the lower the sensitivity threshold, the more enhanced the perception of SPS, giving rise to a fully negative correlation pattern between them.

2. Method

2.1. Participants

The study was carried out in accordance with the Helsinki Declaration. It was approved by the local ethics committee (reference number IRB 00009118). Forty-one volunteers, that were undergraduate students from Lumière University (Lyon, Eastern France), participated to the study. As a first step, they were required to fill out a form containing questions on sociodemographic and health characteristics. Items consisted of age, gender, height, weight, use of psychotropic medication (antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc., and if so, the reason why), use of other psychoactive substances (alcohol, marijuana, etc., and if so, the frequency and last consumption), and history of cardiovascular disease or type 1 diabetes. They were free to report any information they considered to be of importance to the study. Participants were not included in they mentioned any of the above-mentioned diseases, or if they had frequently or occasionally consumed any psychoactive substance in the three months prior to the experiment. Luckily, only one participant was excluded based on these criteria. Four participants ranked under 50% in the Edinburgh laterality inventory and were not included. In fine, 32 participants (18 female, 14 male), with a mean age of 20.56 ± 2.30 years (ranging from 18 to 28), a laterality score of $79.56\% \pm 16.49$ (ranging from 50% to 100%) and a mean BMI of 22.14 ± 4.12 kg/m² (ranging from 11.29 to 32.05) were included. All participants realized the SPS task for the first time.

Power analyses were conducted on the effect size of the proximo-to-distal gradient in the topography of SPS, which is their most prominent characteristics. Based on seven published studies (Beaudoin & Michael, 2014; Borg et al., 2015; Echalié et al., 2020; Michael et al., 2012, 2015, 2017; Michael & Naveteur, 2011), accounting for nine experiments, 314 participants and 26 hand maps (2 or 4 per study, as a function of the conditions tested), the weighted mean effect size expressed as Cohen's w is .38 (i.e., medium to large) and expressed as Cramér's V is .22 (i.e., medium to large). To provide a power of 70% to detect a similar medium effect size and considering that the frequency map derives from individual hand maps, the number of hand maps needed was 61. In the present study, two hand maps (one per hand) were collected for each participant, thus the sample of 32 participants (i.e., 64 hand maps) provided enough power (72%) to avoid type II errors.

2.2. Materials and Procedure

2.2.1. SPS task

Participants performed the task alone in a quiet, normally lit room at a temperature of 20 to 23°C. They were seated on a chair with a backrest, in front of a table. The experimenter introduced SPS to the participants, emphasizing that they are a normal phenomenon and that can be perceived by everybody. A list of the 11 sensations most likely to be felt (i.e., beat/pulse, itch, tickle, numbness, skin stretch, tingling, warming, cooling, muscle stiffness, flutter, and vibration) was provided to the participants so that they had some expectations of what SPS could be perceived. This list is based on original papers studying micro stimulation-evoked sensations (Macefield et al., 1990; Ochoa & Torebjörk, 1983), and was developed by (Naveteur et al., 2005) as a means of studying SPS. It was specified that participants may encounter SPS that were not on the list. When ready, participants had to remove all jewelry from their hands and roll up their sleeves as far from their wrists as possible. They were asked to cleanse their hands for 15s with an antiseptic gel (Aniosgel[®] 85 NPC, ≈3ml per participant). This step ensures there is no external agents that might interfere with the task and homogenizes the skin surface across all participants. A latency of 15s between the cleansing operation and the start of the task was observed, so that no sensations caused by rubbing hands or applying antiseptic gel would be perceived during the task. The protocol, a pencil and a 25 × 25cm piece of smooth white fabric were distributed to each participant. The protocol contained the standardized reduced maps of each hand shown palm-up (11.2cm between the tip of the middle finger and the palm/wrist boundary), the list of 11 descriptors, and two visual analogue scales (i.e., two 10cm continuous horizontal lines without markers at each end) below each map required for the confidence rating. Once participants were familiar with the material, the start of the session was announced, and the protocol was placed away from the participants on the desk to prevent any visual interference. Participants were asked to sit with their back supported by the backrest of their chair. Each hand was tested in a balanced order across participants. For each hand, the ipsilateral leg was turned outward by 60 degrees from the midline, and the white cotton fabric was placed on the thigh. The tested hand rested on it with the palm up and the fingers spaced slightly apart, so that only a dorsal part of the hand was in contact with the fabric. The hand not being tested hung down on the outer side of the chair contralateral to the tested hand. The beginning of each trial was marked by a 'start' signal given verbally by the experimenter: participants

focused on the tested hand with a direct gaze for 10s and had to retain the characteristics of any sensations occurring. The 'stop' signal given by the experimenter announced the end of the 10s test. Participants immediately reported on the protocol whether they had detected any sensations on the tested hand. If so, they had to (a) map their extent and location by shading the corresponding areas the map of the tested hand; (b) rate the perceived intensity of each sensation according to a 10 point scale (1 = just perceptible; 10 = very intense but not painful); (c) indicate their degree of confidence in the location and the extent of the perceived sensations using the two visual analogue scales (ranging from 'not confident' to 'very confident'), and (d) identify the sensations using the list of descriptors. For this final step, participants could choose more than one descriptor and could add descriptors to the list according to what they had felt. The task lasted approximately 10 min.

2.2.2. The two-point discrimination test

The two-point discrimination test was performed right after the SPS task. This prevented the risk of tactile stimulations interfering with the SPS task, since both tasks involved the glabrous surface of both hands. Participants were seated in front of the experimenter, with a narrow desk placed between them. The experimenter presented the material, two discriminatory disks with 8 distinct fixtures each. All fixtures consisted of 2 metal tips of 5mm long and 0.5mm diameter with rounded extremities, except for one that consisted of a single tip. Each of the other 15 fixtures had a specific distance between the two points, that ranged from 1 to 15 mm and went by steps of 1mm. The experimenter demonstrated on the arm of the participant the pressure at which the points would be applied: sufficient to whiten the skin, with an approximate depth of 1 to 2mm, and maintained for 1second (Yokota et al., 2020). They were instructed that either one or two points would be pressed on the skin, and that for each stimulation they had to immediately report whether they felt one point or distinctly discriminated two points. Participants rested the tested hand upward on the desk, on a thick towel reelevating it, and were seated sideways, contralaterally to the tested hand. This ensured minimal motion and no contractions of the tested arm would happen due to the position. Once comfortably seated, participants were given a blindfold and were asked to keep it on their eyes for the duration of the testing. The order in which hands were tested was balanced across participants and with the order of testing in the SPS task. The glabrous hand was tested on six locations, delimiting the palm and index fingers in proximal, intermediate, and distal segments (see Figure 1). With participants' agreement, the precise locations where the points would be

applied were marked by a cross, using a make-up pen. The initial two points distance was 5mm. The orientation of the two points was always horizontal in respect to the limb (Tong et al., 2013), and each stimulation was spaced by 3 seconds. For a given distance, ten stimulations alternating randomly one and two points were applied. The decision criteria of success established was at least seven correct responses out of the ten stimulations (Moberg, 1990; Yokota et al., 2020). In case of success a lower distance was tested, but in case of failure a greater distance was tested. The two-points distance increased/decreased by step of 1mm. The perceptual threshold was considered as the lower distance at which the participants succeeded in distinctly discriminating two points vs one point, always with the 7/10 criteria. The same procedure was carried out on the six segments, starting on the proximal palm, and following the hand proximo-to-distal direction. The task lasted approximately 20 minutes.

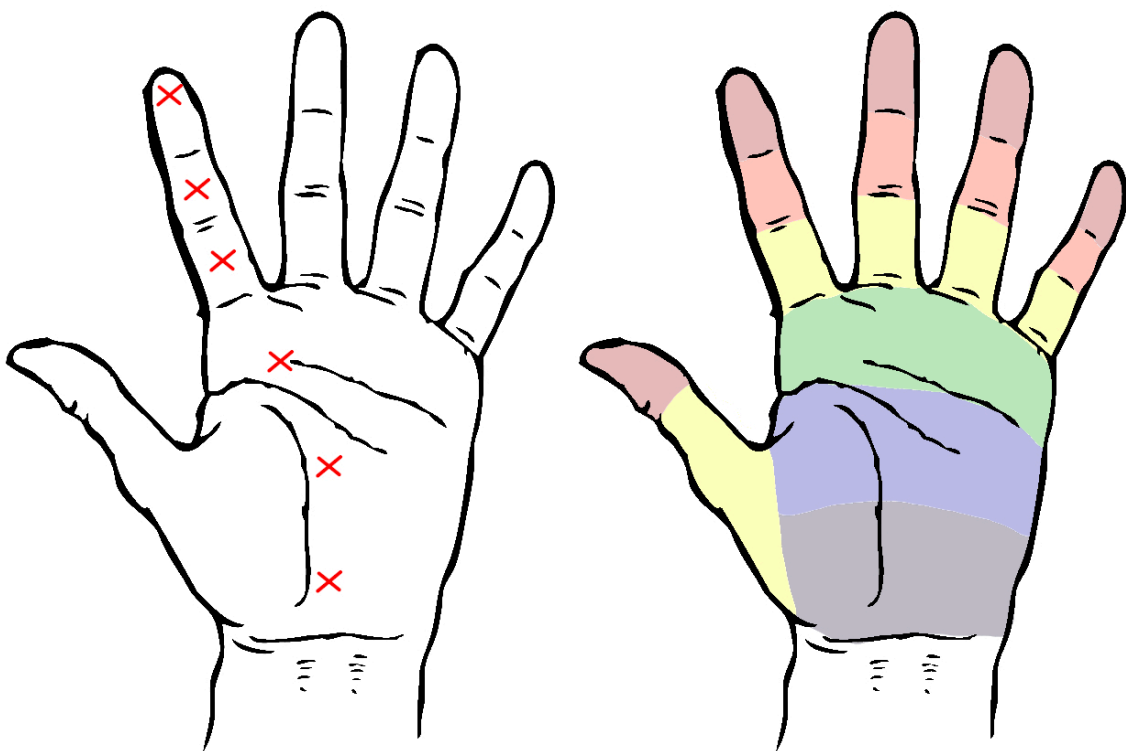


Figure 1 : Depiction of the six stimulated sites on the glabrous hand during the two-point discrimination test, along with a visual representation of the six segments delimited: proximal palm (purple), intermediate palm (blue), distal palm (green), proximal phalanx (yellow), intermediate phalanx (orange), and distal phalanx (red).

3. Results

3.1. The two-points discrimination task performances

The mean perceptual threshold values (mm) for each segment are provided in Table 1. A repeated measure analysis of variance (ANOVA) was carried out with the hand (left and right) and the segments (proximal, intermediate, and distal segments for the palm and the finger) as within-participants factors (Figure 2). Only the main effect of segments was significant ($F(5; 195) = 102.76, p < .001, \eta^2_p = .73$). Post-hoc Newman-Keuls tests revealed significant differences between all segments (all $ps < .05$). The perceptual threshold was the highest on the proximal palm and the lowest on the distal phalanx and decreased between each adjacent segments from proximal to distal hand areas (see Figure 2 and Table 1). This suggests the two-point discrimination task was successful.

Table 1: Mean (SD), minimal and maximal values (mm) of the perceptual threshold for each segment. Spearman-Brown r^* coefficients obtained from the split-half procedure are provided for all segments.

	Mean (SD)	Min	Max	r^*
Finger				
Distal	2.28 (.92)	1	5	.86
Intermediate	4.02 (1.22)	1	6.5	.70
Proximal	5.06 (1.49)	2	8.5	.74
Palm				
Distal	6.17 (1.95)	1	11.5	.82
Intermediate	7.98 (2.59)	2.5	13.5	.83
Proximal	8.59 (2.76)	3.5	16.5	.81

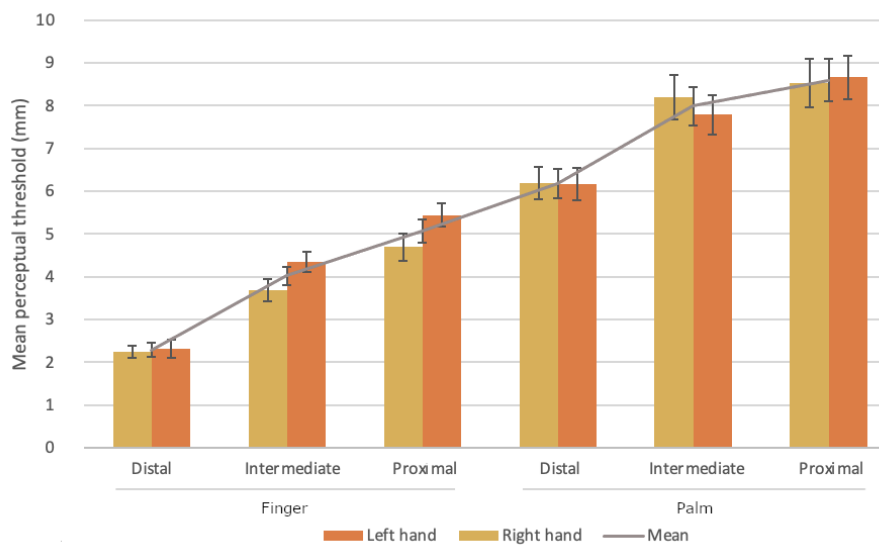


Figure 2 : Mean (mm) perceptual threshold for each segment in left and right hand and averaged between both hands. Error bars depict 1 SEM. The higher the threshold, the less the tactile sensitivity.

The reliability of the measures of perceptual threshold was assessed through a split-half procedure: for each segment, correlations were conducted between the left- and right-hand perceptual thresholds, followed by the application of the Spearman-Brown prophecy formula. Spearman-Brown r^* are displayed in Table 1 and suggest a great reliability for all measures.

3.2. The topography of SPS frequency

The topographical distribution of SPS frequency was computed using the hand maps filled by participants. These maps were projected on a 140×140 mm grid, with a 1mm^2 resolution, and converted to binary code (0=nil, 1=shaded cell). This led to the generation of two binary maps per participant (i.e., right, and left hands), and their superimposition to a frequency map in which each cell represented the percentage of participants having shaded it (left map in Figure 3).

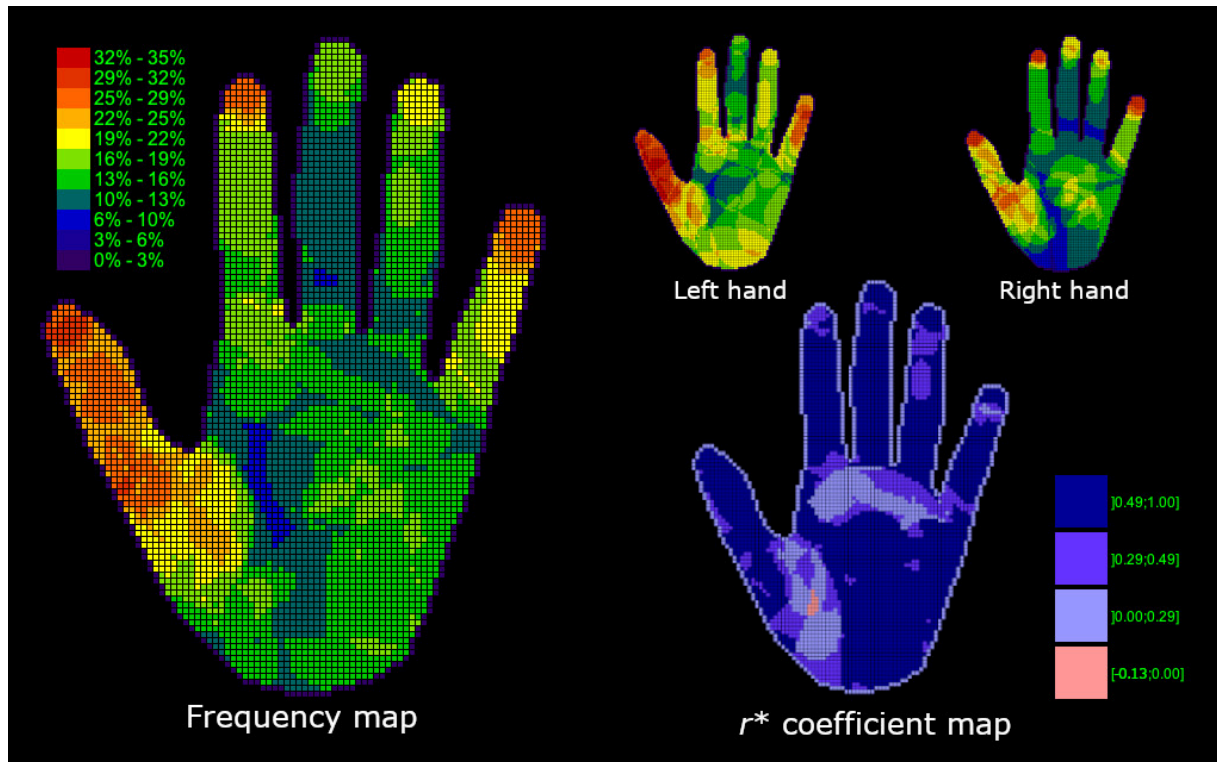


Figure 3 : Topographic maps depicting the SPS frequency (% of participants who had shaded a cell) on the left side, the SPS frequency for each hand on the top right, and the Spearman-Brown r^* coefficients between left- and right-hand frequency maps on the right-side. For the frequency maps, cool/blue colors represent the least frequently shaded areas and warm/red colors represent the most frequently shaded areas. For the coefficient map, bluish colors represent positive r^* coefficients and reddish colors represent negative r^* coefficients. The color intensity denotes the effect size.

SPS were reported over the whole hand but were distributed unequally. The examination of the proximo-to-distal gradient was conducted to assess the validity of SPS (Beaudoin & Michael, 2014; Michael et al., 2012, 2015; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues, Plancher, Jacquot, et al., 2021). This analysis is based on the receptor density dispersion on the glabrous surface of the hand (Johansson & Vallbo, 1979b): a computation of the relative spatial extent of sensations, i.e., the percentage of shaded cells within a segment (distal, intermediate, proximal phalanges, and palm) in comparison to the surface of the whole hand was carried out. Relative surfaces were entered into a proportion specific analysis (Michael, 2007), that revealed the presence of a gradient in the distribution of SPS ($Q(3) = 1098.59$, $p < .0001$; Cramer's $V = .09$). SPS covered a greater surface in the distal phalanx (21.62%) than in the intermediate (14.64%), proximal phalanges (15.66%), and palm (13.46%).

The reliability of the topographical measure of SPS was assessed by conducting a split-half procedure (see maps in the right side of Figure 3). Spearman-Brown coefficients ranged from $r^* = -.13$ to $r^* = 1$. Large size effect coefficients covered 69.85% of the surface, and medium size effect coefficients 18.17% of the surface. Small size effect positive coefficients covered 11.68% of the surface and negative only 0.32% of the surface. This suggests the topographical SPS frequency measure is reliable.

3.3. The topography of SPS intensity

The topographical distribution of SPS intensity was computed using the same procedure carried out for the SPS frequency, with the difference that each shaded cell was filled with the intensity of the sensation. This led to the generation of two maps per participant (i.e., right, and left hands), and their superimposition to an intensity map in which each cell represented the mean intensity of SPS perceived (left map in Figure 4). The split-half procedure between left- and right-hand intensity maps (see maps in the right side of Figure 4) revealed Spearman-Brown coefficients ranging from $r^* = -.07$ to $r^* = .99$. Large size effect coefficients covered 48.77% of the surface, medium size effect coefficients covered 23.55% of the surface, and small size effects positive coefficients covered 27.61% of the surface. Small size effects negative coefficients only covered 0.07% of the surface. This suggests the topographical SPS intensity measure is reliable.

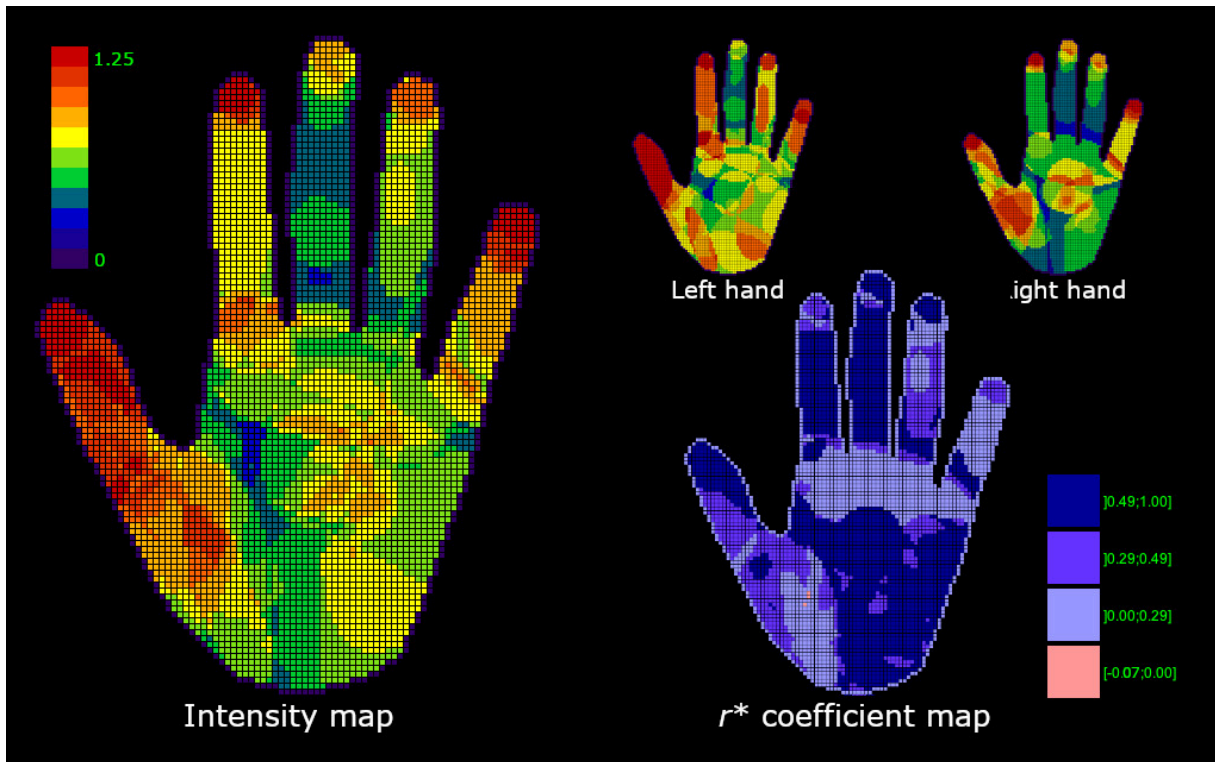


Figure 4 : Topographic maps depicting the SPS intensity (mean intensity of SPS perceived) on the left side, the SPS intensity for each hand on the top right, and the Spearman-Brown r^* coefficients between left- and right-hand intensity maps on the right-side. For the intensity maps, cool/blue colors represent the areas with highest mean intensity and warm/red colors represent the areas with lowest mean intensity. For the coefficient map, bluish colors represent positive r^* coefficients. The color intensity denotes the effect size.

3.4. The relationship between SPS and the perceptual threshold

To achieve a cell-by-cell analysis, the perceptual threshold raw values were used to fill two hand maps (right and left) per participants. But because the perceptual threshold varies according to the hand segments, a special computation was carried out: the areas of the hand maps previously depicted in the right side of Figure 1 were entirely filled with the value extracted in the corresponding segment. To this effect, we used a template elaborated in a previous study (Michael et al., 2012) in which the hand segments as delimited in Vallbo and Johansson's work (Johansson & Vallbo, 1979a) were adapted to the hand map used in the investigation of SPS. In relation with our measures, we discriminated three segments in the palm and each finger (i.e., distal, intermediate, and proximal), except for the thumb in which we only discriminated the distal and proximal segments. This was done so that the perceptual threshold would be correlated to SPS

topographical measures in respect to the segments. Correlations were computed between the 64 hand maps reflecting the SPS topographical measure and the 64 hand maps depicting the raw perceptual threshold. In this processes, perceptual thresholds of the left hand were correlated to the SPS measures of the left hand, and conversely for the right hand. This was done separately for the frequency and the intensity of SPS. The three resulting correlation maps (i.e., total, left hand and right hand) were converted into binary maps (0 = non-significant, 1 = significant), so that a spatial scan procedure for binary data (Kulldorff, 1997) could be applied: it consists of a circular window that scans, detects and localizes significant clusters in a step-wise fashion. A radius of 6 cells was chosen, and 999 runs of the Bernoulli (binomial) model were computed. Only significant clusters of correlations at $p < .001$ were considered. This procedure makes it possible to reduce Type I errors. The corrected probability maps are displayed in Figure 5.

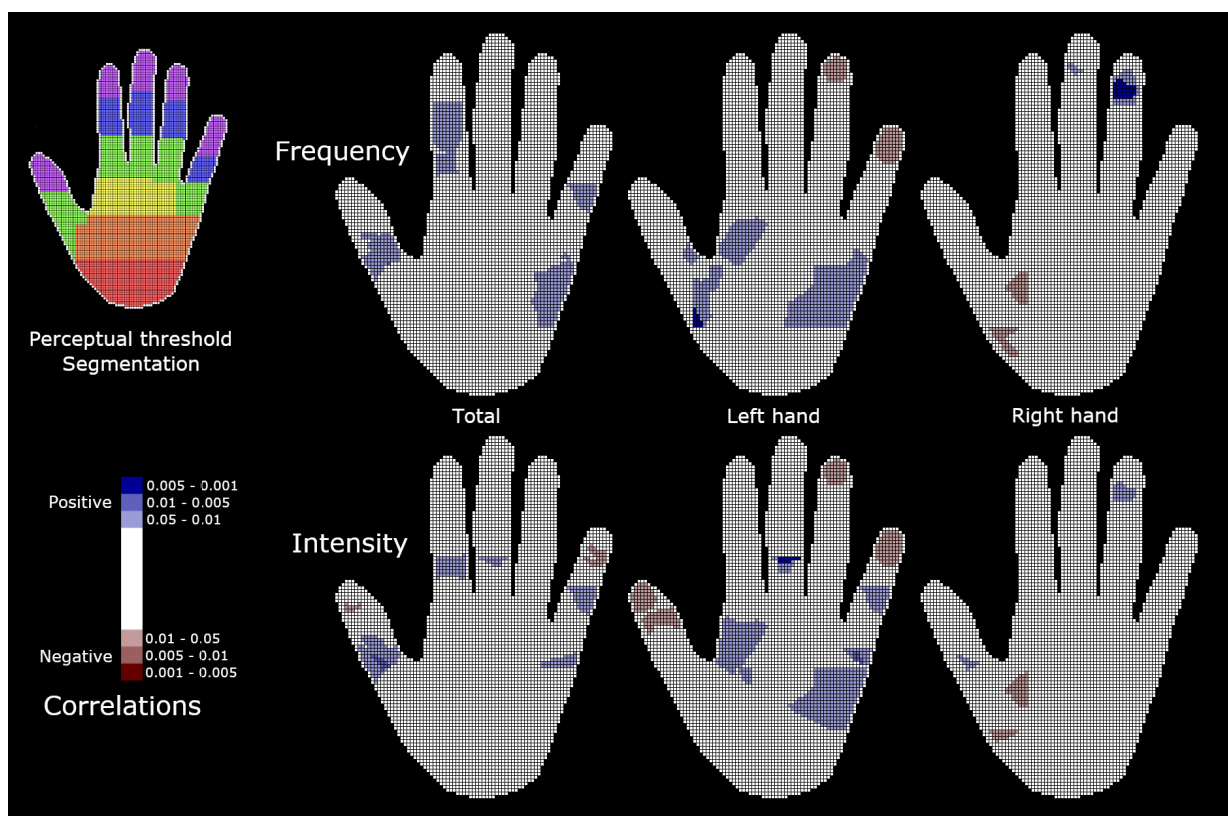


Figure 5 : Topographic probability maps of the correlations between the perceptual threshold and the SPS frequency on the top row, and SPS intensity on the bottom row, computed with both hand and separately for left and right hand. Bluish colors represent significant positive correlations, and reddish colors represent significant negative correlations. The color intensity denotes the significance level. The depiction of the hand segmentation for the perceptual threshold is provided on the top left.

Regarding the frequency of SPS, only positive correlations were found with the perceptual threshold regardless of the hand, on a surface of 11.34% (95% Wilson Confidence Interval [10.43%, 12.32%]). Positive correlations were mainly found on the left hand, on 13.86% (95% CI [12.87%, 14.92%]) of the hand, whereas few negative correlations were found on a surface of 2.75% (95% CI [2.30%, 3.28%]). On the right hand, positive correlations covered 1.90% (95% CI [1.54%, 2.35%]) of the surface, and few negative correlations were found on a surface of 2.06% (95% CI [1.68%, 2.53%]).

For the intensity of SPS, positive correlations with the perceptual threshold regardless of the hand covered 6.76% (95% CI [6.05%, 7.54%]) of the surface. Few negative correlations were found as well on 0.23% (95% CI [0.12%, 0.42%]) of the surface. On the left hand, positive correlations covered 13.24% (95% CI [12.27%, 14.28%]) of the surface and negative correlations 5.25% (95% CI [4.62%, 5.95%]) of the surface. Then, on the right hand, positive correlations covered 1.08% (95% CI [0.81%, 1.43%]) of the surface and negative correlations 1.65% (95% CI [1.31%, 2.07%]) of the surface.

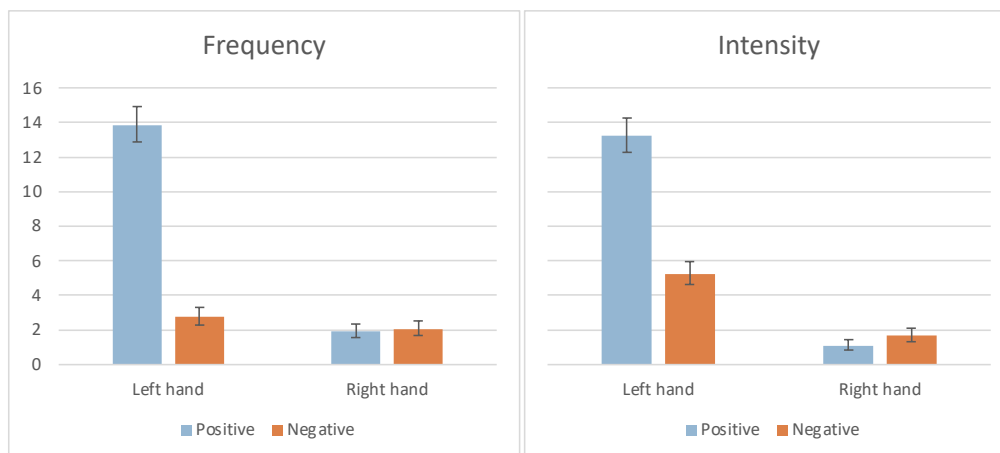


Figure 6: Graphics of the correlated surfaces (%) for the frequency and intensity of SPS and for each hand. Positive correlations are depicted in blue and negative in orange. Error bars represent the 95% Wilson confidence interval.

Similar patterns of correlations were found with the frequency and the intensity of SPS. On the left hand, positive correlations were dispersed on the palm and intermediate phalanges, whereas negative correlations were restricted to distal phalanges. An opposite effect appeared on the right hand, but less pronounced, with positive correlations restricted to distal phalanges and negative correlations to the palm.

3.5. Other parameters

To investigate the relationship between the tactile sensitivity and the other SPS parameters, two composite scores of perceptual thresholds were extracted, one being the mean across all segments and both hands (Mean PT), and the other the α regression slope¹ of the mean perceptual thresholds across both hands (α Slope). This value was positive as it reflected the perceptual threshold increment from distal phalanges toward the proximal palm, hence the greater the slope, the acuter tactile sensitivity on phalanges in contrast to the palm. These scores were entered into multiple regression analyses as predictors, along with participants' gender, age and body mass index (BMI) (Kozłowska, 1998; Naveteur et al., 2015). The non-topographical SPS parameters, consisting of spatial extent, spatial extent per SPS, intensity, variety, number of disjointed areas, and participants' confidence in SPS location and extent, were entered as dependent variables. All variables were z -transformed prior to the analysis. The results (not Bonferroni corrected (Cabin et al., 2000; Perneger, 1998)) are presented in Table 2.

¹ $\alpha = \text{covariance}(x,y)/\text{variance}(x)$, where x is the segment (1 to 6, each indicating a segment from the distal phalanx to the proximal palm) and y the perceptual threshold.

Table 2 : Standardized β coefficients (± 1 SEM) and adjusted R^2 coefficients from the multiple regression analysis carried out on each of the 7 collected dependent variables with age, gender, body mass index, the mean perceptual threshold (Mean PT) and the α regression slope of the perceptual threshold (α Slope) as predictors. Predictions significant at $p < .05$ are noted with an asterisk (*).

	Spatial extent	Spatial extent per SPS	Intensity	Variety	Number of disjointed areas	Confidence in location	Confidence in extent
Gender	.08 (.22)	.24 (.21)	-.03 (.22)	-.06 (.20)	-.15 (.19)	.00 (.22)	-.02 (.22)
Age	.10 (.21)	-.29 (.21)	.14 (.22)	.46 (.20)*	.52 (.19)*	.04 (.22)	-.02 (.22)
BMI	-.26 (.20)	-.16 (.19)	-.26 (.20)	-.27 (.18)	-.16 (.18)	-.08 (.20)	-.07 (.20)
Mean PT	.11 (.20)	.17 (.20)	-.15 (.20)	-.31 (.18)	-.24 (.18)	-.24 (.20)	-.19 (.20)
αSlope	.04 (.19)	.07 (.19)	.05 (.20)	.02 (.18)	-.18 (.17)	-.03 (.20)	-.10 (.20)
Adj. R2	-.069	-.039	-.106	.100	.144	-.125	-.134

Participants' age predicted the variety ($\beta = .46$, SEM = .20, $t(26) = 2.32$, $p = .03$, Adj. $R^2 = .10$) and the number of disjointed areas ($\beta = .52$, SEM = .19, $t(26) = 2.74$, $p = .01$, Adj. $R^2 = .14$). No other significant predictions were found.

3.6. SPS types

All 11 sensations were reported at least once, except for itching. Cracking, draught, and spasm were added to the list by three participants. Based on previous studies (Michael, Guyot, et al., 2020; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021), sensations were clustered into five categories: (i) thermal: warming and cooling; (ii) deep: beat/pulse, muscle tension, and spasm; (iii) surface: tickling, stretching, tingling, trembling, vibration, and draught; (iv) paresis-like: numbness; (v) pain-like: snapping. SPS were not evenly distributed across these categories ($X^2(4) = 74.76$, $p < .001$, Cramer's $V = .36$): surface sensations were the most frequently perceived and reported (44.37%), followed by deep (25.35%), paresis-like (16.20%) and thermal sensations (13.38%). Pain-like sensations were the least frequently perceived (0.70%).

Exactly like non-topographic SPS parameters, the five SPS types and the sum were entered into multiple regression analyses as dependent variables with the same predictors. The results (not Bonferroni corrected (Cabin et al., 2000; Perneger, 1998)) are presented in Table 3.

Table 3 : Standardized β coefficients (± 1 SEM) and adjusted R^2 coefficients from the multiple regression analysis carried out on each of the 5 collected dependent variables with age, gender, body mass index, the mean perceptual threshold (Mean PT) and the α regression slope of the perceptual threshold (α Slope) as predictors. Predictions significant at $p < .05$ are noted with an asterisk (*).

	Thermal	Deep	Surface	Paresis-like	Pain-like	Total
Gender	-.17 (.20)	.15 (.21)	-.13 (.20)	-.23 (.20)	.27 (.21)	-.13 (.19)
Age	.25 (.20)	.21 (.21)	.44 (.20)*	.30 (.20)	-.13 (.21)	.52 (.19)*
BMI	-.01 (.18)	.01 (.19)	-.27 (.19)	.01 (.18)	-.01 (.20)	-.14 (.18)
Mean PT	-.02 (.18)	-.15 (.20)	-.15 (.19)	-.13 (.19)	-.20 (.20)	-.22 (.18)
αSlope	-.45 (.18)*	.19 (.19)	-.03 (.18)	-.38 (.18)*	.14 (.19)	-.19 (.17)
Adj. R2	.097	-.039	.040	.058	-.053	.141

Participants' age predicted surface sensations ($\beta = .44$, SEM = .20, $t(26) = 2.16$, $p = .04$, Adj. $R^2 = .09$) and the total ($\beta = .52$, SEM = .19, $t(26) = 2.71$, $p = .01$, Adj. $R^2 = .14$). The α regression slope of the perceptual threshold negatively predicted thermal ($\beta = -.45$, SEM = .18, $t(26) = -2.55$, $p = .02$, Adj. $R^2 = .10$) and paresis-like sensations ($\beta = -.38$, SEM = .18, $t(26) = -2.10$, $p < .05$, Adj. $R^2 = .14$).

4. Discussion

Some sensations would be perceived on the skin in the absence of cutaneous stimulation (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015), and would display similar characteristics to tactile sensations (Beaudoin & Michael, 2014; Michael et al., 2012; Naveteur et al., 2015). However, whether peripheral factors such as skin receptors that confer tactile sensitivity play a role in SPS is unknown. We thus wondered whether tactile sensitivity would be involved in the perception of SPS on the glabrous hand. If this were the case, then it could be suggested that peripheral factors do determine the perception of SPS. Several patterns were found: (i) contrary to what was expected, a greater tactile sensitivity on the hand was associated to an overall decrease in the frequency and in the intensity of SPS; (ii) yet, a double dissociation was found between the left and right hand, and between the fingers and the palm. On the left hand, on which effects were more prominent, high tactile sensitivity was associated to an increase in the frequency and intensity of SPS on the distal phalanges, but to a decrease on the palm. An inverse pattern was found on the right hand; (iii) finally, a steeper gradient in the perceptual threshold from the proximal palm toward the distal phalanx negatively predicted thermal and paresis-like SPS. We will discuss the mechanisms underpinning such modulations.

4.1. Some peripheral determinants to spontaneous sensations?

This study was conducted with two goals, one being investigating the peripheral underpinnings common to tactile sensitivity and SPS perception. The perceptual threshold on the glabrous hand surface followed the typical proximo-to-distal gradient (Johansson & Vallbo, 1976, 1979b; Vallbo & Johansson, 1976), but no differences in tactile sensitivity were revealed between the left and right hands. This impedes any interpretation of physiological parameters, such as callous skin (Weinstein & Sersen, 1961), accounting for the dissociation between hands in the perception of SPS. Regardless of the hand, SPS were impaired in their frequency and intensity with an acuter tactile sensitivity, which is the opposite of what was announced. This may hint toward a suppression of peripheral tactile mechanisms so that SPS would be better perceived, in the same way that motion of a limb suppress SPS and tactile perception on adjacent areas (Beaudoin & Michael, 2014; R. F. Schmidt, Schady, et al., 1990; R. F. Schmidt, Torebjörk, et al., 1990). This

would be rather consistent with the reduction of tactile sensitivity that accompanies tactile hallucinations and somatosensory distortions (Berrios, 1982; Echalié et al., 2020; Liu et al., 2020), and would highlight the central origin of SPS.

Yet some findings suggest that there may be more to the question of SPS peripheral underpinnings. Indeed, we found that the steeper the proximo-to-distal gradient in the perceptual threshold, the less thermal and paresis-like SPS were reported. Whereas, in a previous study, these specific type of SPS were the only affected by interoception abilities (Michael et al., 2015). The SPS phenomenon might thus have distinct underpinnings according to their type, and some could be peripheral and related to other perceptual dimensions. For instance, studies on thermoception demonstrated that the thermal sensitivity follows an inverse proximo-to-distal gradient on the glabrous hand, in such a way that it increases on the palm and decreases on fingers (Li et al., 2008; Luo et al., 2020; D. Schmidt et al., 2020; Wakolbinger et al., 2014). In addition, thermal sensitivity relies mainly on C-myelinated fibers, that innervate more sparsely the glabrous hand surface than mechanoreceptive units (Granovsky et al., 2005; Green, 2004; Watkins et al., 2021), but contribute as well to tactile perception (Liljencrantz & Olausson, 2014; Riquelme et al., 2016; Schmelz et al., 2003) and respond to surface elicitation such as those provided in the two-point discrimination test (Olausson et al., 2010; Torebjörk & Hallin, 1976). The inverse relationship between the proximo-to-distal gradient in the tactile sensitivity and the occurrence of thermal SPS might be a consequence of this physiological organization. Thus, perceiving some SPS might be as well related to high perceptual threshold senses, such as interoception and viscerosensation (Ferentzi et al., 2017; Michael et al., 2015), and this could hint to their contribution to unconscious body-related processes such as homeostasis (Barrett & Simmons, 2015; Sakson-Obada et al., 2018; Tsakiris & De Preester, 2019).

4.2. Central processes in the detection of SPS

We described a double dissociation between the fingers and the palm, and between the right and left hand. This pattern of correlations seen in both the frequency and the intensity of SPS stands out since no differences were found in the perceptual threshold of the two hands. Consistently, the digit/palm pattern was repeatedly associated to visual attention, through amplification and suppression of SPS and tactile perception (Gálvez-García et al., 2012; Michael et al., n.d., 2012, 2015; Naveteur et al., 2015; Salgues, Plancher, & Michael, 2021). Enhancement operated on the

left distal phalanges and on the right palm, a pattern similar to the one induced by visual attention on SPS in regards to the attended hand (Michael & Naveteur, 2011), which is consistent with evidences of visual attention lowering the perceptual threshold and increasing the spatial acuity (Cardini et al., 2011; Forster & Eimer, 2005; Kennett et al., 2001; Press et al., 2004; Serino et al., 2007; Taylor-Clarke et al., 2002, 2004). But similar observations were made when investigating factors involving motion and deformation of the skin, as decrement and increment of SPS due to thumb motion and cutaneous pressure were restricted to the digits (Beaudoin & Michael, 2014). The tactile suppression mechanisms that operate to enhance the perception of SPS could thus be elicited by inhibition through somatosensory attention (M. Bauer, 2006; Cardini et al., 2011; J. C. Craig & Evans, 1995; Hlushchuk & Hari, 2006), suppression by sympathetic afferents (Johansson & Vallbo, 1979b; Kissin et al., 1987) or both.

Yet, hemispheric specialization in global and local processing (Fink et al., 1997; Tomlinson et al., 2011) seemed to determine the locus of decrement on each hemi-body, as it was restricted to low spatial acuity areas for the left hand, and high spatial acuity areas for the right hand. These findings suggest that there may exist two competitions in the perception of SPS : (i) one that would require the suppression of interfering tactile inputs, which is the best candidate for the engagement of peripheral mechanisms (Kissin et al., 1987), and (ii) one that opposes structural body part representations such as those of the fingers and palm (Gálvez-García et al., 2012), and those between each hemi-body, similar to the one exhibited in tactile extinction (Sarri et al., 2006). This might be a clue indicating the involvement of the primary somatosensory cortex in the perception of SPS, notably because its activations are lateralized in respect to the stimulated body part, whereas activations in the secondary somatosensory cortex respond to both hemi-bodies (Gallace & Spence, 2008, 2009, 2010). All the more so since cortical reorganization of the primary somatosensory cortex in the context of the phantom limb syndrome was associated to peripheral changes, including loss of cutaneous unmyelinated fibers underpinning tactile, thermal and pain perception (Flor et al., 2006).

4.3. Limitations and future considerations

Some remarks may be made regarding the assessment of tactile sensitivity, as the two-point discrimination test is frequently decried for inducing variability among experimenters and displaying a low reliability (Lundborg & Rosén, 2004). As prescribed by Lundborg and Rosén, we

provided references accounting for the choice of each experimental parameter. One could argue that the perceptual threshold values extracted are not consistent with the literature, especially on the distal phalanges where the mean is above 2mm (Johansson & Vallbo, 1979a, 1979b; Moberg, 1990), but the finding of a linear decrement in the perceptual threshold from more proximal segments of the hand toward the most peripheral ones is consistent with the gradation in tactile sensitivity (Johansson & Vallbo, 1979a, 1979b).

Several leads were advanced regarding the findings presented in this study. Tactile sensitivity is rather deleterious the frequency and intensity of SPS, and effects were lateralized in respect with hemispheric specialization (Tomlinson et al., 2011), and restricted to body segments that are underpinned by separate cortical representations (Blankenburg et al., 2003; Gálvez-García et al., 2012; Overduin & Servos, 2004). This suggests a suppression of tactile inputs operating so that central somatosensory mechanisms could elaborate their percept. Yet doubts remain regarding the nature of the suppression mechanisms described here. Besides, we also discussed the idea of different underpinnings for different SPS and argued that perceiving thermal and paresis-like SPS would be more a matter of interoception than hallucinations. Thus, even though these findings suggest of a major involvement of central mechanisms, the evidence we presented here has a limited validity to completely invalidate the hypothesis of a peripheral SPS origin. Further support could be brought in the future, by recording the myelinated afferents conduction during the perception of SPS, by investigating the phenomenon on patients with deafferented limbs, or through the investigation of SPS underpinnings according to their type.

5. Conclusions

The similarities between the tactile perception and the SPS phenomena led us to investigate their relationship. We found that increased tactile sensitivity of the glabrous surface of the hand decreased the perception of SPS and their perceived intensity, suggesting that peripheral factors are unlikely to be a major determinant of SPS. Yet we observed that the perceptual threshold gradient determined the occurrence of thermal and paresis-like SPS specifically. This raised the question of multiple determinants behind the phenomenon and motivate the investigation of SPS phenomenology and underpinnings according to their type. The frequency and intensity of SPS were differently affected on the left and right hand, and on the digits and palm, implying that attention would interact with hemisphere-dependent processes. Future studies might bring more insight toward the origin of SPS by investigating their relationship with the cortical somatotopy.

Tableau 2. Les cortex somatosensoriels

Le Tableau 1 fut l'occasion d'envisager une origine périphérique aux SPS. Au contraire, l'étude que nous y présentons met en exergue un effet délétère de la sensibilité tactile sur leur perception des SPS. Les résultats décrits suggèrent la prééminence de mécanismes centraux dans le phénomène des SPS. Non sans invalider complètement l'hypothèse de soubassements périphériques aux SPS, les éléments que nous avançons ne sont pas cohérents avec l'idée d'une dépendance aux paramètres périphériques. Ces considérations nous ramènent à Kinsbourne (1998) qui suppose un *background* de sensations corporelles ne reposant pas seulement sur la perception sensorielle : les traces sensorielles des représentations corporelles contribueraient à l'expérience subjective du corps. Une seconde hypothèse est donc à envisager : les SPS émergent-elles de mécanismes corticaux ? Cette hypothèse a été déjà avancée dans les premières études portant sur les SPS.

Cette hypothèse motive l'intérêt vers les corrélats neuraux de la perception somatosensorielle en l'absence de source périphérique. Autrement dit, les hallucinations tactiles. L'étude de ces phénomènes pathologiques pointe du doigt des dysfonctionnements au niveau des cortex somatosensoriels (Berrios, 1982; Flor, 2003; Kinsbourne, 1998; Moseley & Flor, 2012), des régions qui élaborent l'expérience subjective du corps (Gallace & Spence, 2008, 2009, 2010). L'organisation somatotopique corticale, particulièrement fine en SI, serait définie à partir des paramètres physiologiques cutanés (Schady et al., 1983) de telle sorte qu'un codage topographique précis aurait lieu au niveau cortical (voir Prologue, partie I-B-1). Ainsi les hallucinations tactiles et syndromes du membre fantôme sont contraints par ce même gradient (Geoffroy et al., 2014). Serait-il possible que ces mêmes mécanismes corticaux soient à l'origine des SPS ?

L'étude suivante vise à apporter des éléments de réponse à cette question par le biais de l'enregistrement EEG au repos. En ciblant l'activité oscillatoire spontanée des corrélats des doigts et paume en SI et SII, nous cherchons à mettre en évidence leur rôle spécifique dans la topographie des SPS. A travers une approche spectrale, nous espérons également pouvoir identifier les mécanismes somatosensoriels requis par la perception de SPS.

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ORIGINAL ARTICLE

Cues to body-related distortions and hallucinations? Spontaneous sensations correlate with EEG oscillatory activity recorded at rest in the somatosensory cortices

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Running Head: Possible mechanisms of bodily perceptual distortions and hallucinations.

ABSTRACT

Body awareness may arise in the total absence of sensory input, as suggested by the spontaneous occurrence of normal and pathological (i.e., hallucinatory) bodily sensations. These phenomena may arise due to back-projections from higher-order cortical areas to the primary (SI) and secondary (SII) somatosensory cortices, and would appear to be reflected in cortical oscillatory activity in both SI and SII. Here, we set to investigate the relationship of SI and SII in SPS. Healthy participants underwent an EEG recording session at rest, and then completed an experiment on the perception of spontaneous sensations occurring on the hands. Cortical oscillatory activity was extracted from specified ROIs in the somatosensory cortices. The findings showed that (i) SPS perceived in the fingers correlated positively with alpha-band oscillations recorded in SI, and that (ii) SPS perceived in the palm correlated positively with gamma-band oscillations and negatively with beta-band oscillations recorded in SII. Apart from supporting the idea that the somatosensory cortices are involved in bodily awareness even in the absence of sensory input, these findings also suggest that default oscillatory activity in the somatosensory cortices reflects individual differences in bodily awareness. The results are interpreted in terms of neural and cognitive processes that may give rise to bodily awareness and modulate it, and their importance in understanding body perception distortions and bodily delusions and hallucinations is discussed.

Keywords: Spontaneous sensations; Resting EEG; Somatosensory Cortex; Brain oscillations; Bodily hallucinations; Tactile hallucinations.

1. INTRODUCTION

Bodily awareness arises from the interplay of multiple interconnected cortical areas, some specialized in solely processing tactile information, such as the primary (SI) and secondary (SII) somatosensory cortices, and others involved in multimodal integration, attention, and interoception, such as the insula and the temporoparietal junction. However, body awareness may arise in the total absence of external triggers, as suggested by the spontaneous occurrence of bodily sensations. Here, we set to investigate the role in spontaneous sensations of oscillations recorded by EEG on SI and SII at rest.

1.1. Perception and awareness

The initial connections supporting the processing of tactile information appear to be based on a serial/hierarchical architecture, such that tactile stimuli that are delivered to the body are first transmitted to the SI *via* thalamocortical connections, and then to SII. Interestingly, SII is reciprocally and somatotopically connected to SI (Barba et al., 2002), but the somatotopy in SII is less refined and less straightforward than in SI. The existence of ambiguous somatotopic representations suggests that information processed in SII is probably loosely connected to bodily structures and that it may be involved in processes that go beyond somatosensation, such as processing and storing tactile memories (Gallace & Spence, 2010), and possibly body-ownership and the conscious perception of the self and its relationship with the environment (Bretas et al., 2020). Beyond neural transmission and integration of sensory signals, awareness of touch would involve higher-order brain areas. Gallace and Spence (Gallace & Spence, 2010) suggested that back-projections from the temporoparietal junction and the posterior insula to SI and SII would lead to the awareness of touch. These back-projections would selectively activate information about texture, shape, location and other tactile qualities in SI, and more complex tactile memories and body representations in SII.

Furthermore, they would probably direct attention in order to modulate the activity of SI and SII (Graziano, 2018; Iguchi et al., 2002; Mima et al., 1998). From a functional point of view, the dynamics of the accumulation and processing of signals leading to the awareness and the decision that something has been perceived is seemingly mediated by alpha- (7.5-12Hz) and beta-band (13-34Hz) cortical oscillations recorded on the somatosensory cortices (Haegens et al., 2011; Kilavik et al., 2013; Palva, 2005).

1.2. Awareness without sensory input

The existence of body-related delusions and hallucinations in psychiatric and neurologic populations, ranging from sensing a gentle touch or a nearby presence, to the pervasive conviction that insects are crawling beneath the skin (i.e., infestation delusion), shows that body awareness does not exclusively arise from stimuli that are delivered physically on peripheral receptors. They are due to spontaneous activity in SI and SII, and their phenomenology (i.e., their content and characteristics) is related to the cortical somatotopic organization of the somatosensory cortices (Bär et al., 2002; Geoffroy et al., 2013, 2014; Jardri et al., 2008; Shergill, 2001). Transient cortical oscillations in the gamma band centered on the parietal lobes have been registered during bodily hallucinations (Baldeweg et al., 1998), suggesting that high frequencies may be related to somatic perceptions in the absence of any stimulation. Such tactile phenomena may thus rely on specific neural activity in cortical areas normally involved in sensory processing of touch, which is expressed in the content of the experience (Allen et al., 2008). Everyday experience of subtle bodily sensations such as itching or flutter in the absence of any evident external trigger (i.e., spontaneous sensations or SPS) may be the normal counterpart, or even the basis, of extreme conditions such as bodily delusions and hallucinations. These phenomena may also be related to the (normal spontaneous) activity of SI and SII, and precipitated by factors such as attention and

visual input (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015), or adjusted by some individual characteristics and pathological conditions (Borg et al., 2015; Echalié et al., 2020; Michael et al., 2015, 2017; Tihanyi & Köteles, 2017). The fact that individual differences determine the perception of SPS (Michael et al., 2017; Tihanyi & Köteles, 2017) might be a sign of a general proneness to perceive SPS. There are some isolated neuroimaging findings suggesting that attending to well-circumscribed and localized SPS results at least in SI activation (C. C. C. Bauer, Díaz, et al., 2014; C. C. C. Bauer, Barrios, et al., 2014). There is however strong behavioral evidence of the involvement of the somatosensory cortices in the perception of SPS. First, SPS perceived in the hands observe a specific graded distribution, a proximodistal gradient. Imprecise and less frequent perception of SPS is reported in the palm, which progressively increases toward the fingers. This omnipresent pattern strikingly resembles traces of peripheral receptor distribution in the somatosensory cortex (Schady et al., 1983). Second, this proximodistal gradient shows an impressive abatement during active movement of a segment of the hand (i.e., gating; (Beaudoin & Michael, 2014)). This phenomenon is known to result from suppression of processing in the somatosensory cortex (L. G. Cohen & Starr, 1987). Activity in SI and SII thus probably contributes to tactile perception regardless of the actual physical presence of tactile stimulation, and this activity might be amplified by attention in order to reach consciousness (C. C. C. Bauer, Díaz, et al., 2014; Mima et al., 1998). The relationship between activity in the somatosensory cortices and SPS would probably be mediated by alpha-band (7.5-12Hz) and gamma-band (35-45Hz) cortical oscillations given that they mostly reflect attentional processes (Benedek et al., 2014; Çiçek & Nalçacı, 2001; Keune et al., 2017; Laufs et al., 2003). The involvement of gamma-band oscillations in SPS is all the more expected since they have been observed during tactile hallucinations (Baldeweg et al., 1998). Yet, on its own, the activation of SI seems insufficient to sustain an awareness of

sensations (Blakemore et al., 2002; Blankenburg et al., 2006; Schubert et al., 2006). On the other hand, it has been suggested that bodily hallucinations and delusions might be caused by the faulty activation of SII (Gallace & Spence, 2009, 2010).

1.3. The present study

Overall, these findings suggest that both SI and SII are necessary for bodily awareness, which would arise through their reciprocal interactions with higher-order areas. Yet, the respective contributions of SI and SII would appear to differ: the former would contribute due to its precise somatotopy, the latter through processing and storing tactile memories. These contributions would be expressed through the alpha-, beta- and gamma-band oscillations that are within the range of the electrical brain activity considered to be a feature of consciousness (Seth et al., 2006), that relate to processes going beyond somatosensation, and are necessary for bodily awareness. It would thus be expected for resting-state activity in SI and SII to determine individual differences in the perception of SPS, particularly through the three above-mentioned frequencies. We therefore set to investigate this issue by EEG, focusing on resting-state current source density in specific ROIs that correspond to the digits and the palm within SI and SII. The distinction between the digits and the palm is justified by the observation that different processes seem to influence the perception of SPS in these two areas of the hand, even though the reason for this is still poorly elucidated.

2. METHODS

2.1. Participants

The study was carried out in accordance with the Helsinki Declaration. Participants were students at the Lumière University in Lyon, France. During the first stages of the

experimental procedure, they were required to complete a form containing questions on sociodemographic and health characteristics. Items included age, gender, height, weight, use of psychotropic medication (and if so, the reason why; antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc.), regular use of other psychoactive substances (alcohol, marijuana, etc.), and history of cardiovascular disease or diabetes mellitus. In addition, participants could report any other information they considered to be of importance for the study. They were excluded if they reported any history of neurological or psychiatric illness, had any history of psychoactive substance abuse, had an abnormal body mass index (BMI) or reported any disease that could affect tactile perception, such as diabetes mellitus or cardiovascular disease. Thirty-eight volunteers participated in the study, ten were excluded on the basis of the above-mentioned criteria, and one because of recording issues compromising their EEG data. Twenty-seven participants (14 female and 13 male), all right-handers, with a mean age of 22.1 ± 2.77 (age range: 19 to 28) and a mean BMI of $21.2 \pm 1.33\text{kg/m}^2$ (range: 19.26 to 23.89 kg/m^2) were therefore included in the study. Power analyses were conducted on the effect size of the proximo-distal gradient in frequency of SPS, which is the most prominent characteristic of these phenomena. Based on published studies (Borg et al., 2015; Michael & Naveteur, 2011), the weighted mean effect size expressed as Cohen's w is .52 (i.e., large) and expressed as Cramér's V is .26 (i.e., medium to large). Provided a power of 90% to detect a similar medium effect size, the number of hand maps needed is 53. Given that, in the present study, two hand maps per participants are collected (one per hand), the sample size needed is 27 participants. With a sample of 27 participants (i.e., 54 hand maps) there is enough power (91%) to diminish Type II errors. All participants gave their written informed consent for their participation prior to the test. The protocol was approved by the local ethics committee (reference number IRB 00009118).

2.2. Materials

2.2.1. Resting-State EEG recordings

A resting-state EEG recording was completed immediately after the completion of the questionnaire. An actiCHamp EEG system with active electrodes was used for this experiment. All participants were comfortably seated in a sound- and light-attenuated room. An investigator ensured that the participants remained calm during recording. Participants were not otherwise engaged during recording. Continuous EEG data were acquired for 3 minutes. Data were collected using a 64-channel BrainVision Recorder Software (Brainproducts, Munich, Germany) arranged based the revised 10/20 system (Jurcak et al., 2007), and 5 EOGs were used. A monopolar montage was chosen, with a reference EOG on the nose bridge. Prior to acquisition, impedances were checked to be below 20k Ω (within recommended guidelines given high-input impedance capabilities of the amplifier)(Berkovich-Ohana et al., 2014). The data were sampled at 1000Hz, filtered, amplified, and referenced to the vertex (electrode EOG5). Once the EEG equipment had been set up, the signal quality was tested by asking participants to move their eyes from left to right, to blink, and to clench their jaw muscles. Instructions advised the participants to relax their jaw and shoulders, to try not to move, to fully relax, to close their eyes, and to resist drowsiness. The session began once the participants stated that they were ready, and the end was announced by the investigator. At the end of the recording session, participants were asked whether they had fallen asleep. No participants reported having fallen asleep during the resting session.

2.2.2. SPS task

Participants completed the SPS task 45 minutes after the resting-state EEG recording. In the meantime, participants performed a distractive visuospatial task. This delay allowed a clear separation between the resting-state and the SPS task. Electrodes and EOGs were removed from the participant's head. They were then seated in a quiet and normally lit room with an ambient temperature of 20-23°C, in front of a desk. Once they were ready, SPS were introduced as normal phenomena, and to give participants some idea of what they could associate with SPS, a list of 11 sensations most likely to be felt was presented (beat/pulse, itch, tickle, numbness, skin stretch, tingling, warming, cooling, muscle stiffness, flutter, and vibration). The list used in the SPS protocol is based on that originally used by (Macefield et al., 1990; Ochoa & Torebjörk, 1983) to study microstimulation-evoked sensations, and subsequently adapted by (Michael & Naveteur, 2011; Naveteur et al., 2005) to study SPS. Participants were then instructed to remove any jewelry from their hands and wrists, and to roll up their sleeves if they were long enough to cover the wrist. They were instructed to cleanse their hands with an antiseptic gel (Aniosgel[®] 85 NPC, ≈3ml per participant) for 15s, in order to remove any external surface agents that could interfere with the task, and to ensure a homogenous glabrous skin surface across all participants. A 15s latency was observed between the cleansing operation and the start of the test. A protocol containing the standardized reduced maps of each hand shown palm up (with a distance of 11.2cm between the tip of the middle finger and the palm/wrist boundary), and below each map, the list of 11 SPS and two visual analogue scales (i.e. two 10cm continuous horizontal lines without markers at each ends) for confidence ratings were given to each participant, along with a pencil and a 25 × 25cm piece of smooth white fabric. Once participants were familiarized with the material, the beginning of the test session was announced. The protocol and the pencil were placed away from the participants on the desk to prevent any interference from visual stimuli. Each hand was tested once in a balanced order across participants. They were

instructed to sit with their back supported by the backrest of their chair. The leg ipsilateral to the tested hand was turned outward by about 60 degrees from the midline. Participants placed the white cotton fabric on their thigh, with the tested hand resting on it, palm up, with fingers spaced slightly apart. Only a dorsal part of the hand was in contact with the fabric, apart from the fingers. The hand not being tested was hung down on the outer side of the chair contralateral to the tested hand. When the “start” signal was given verbally by the investigator, marking the beginning of each trial, participants gazed at their tested hand for 10s, focusing their attention on the hand so that they could detect any sensations that might occur. They were informed beforehand that there was a possibility that they would perceive no sensation. A “stop” signal given by the investigator marked the end of the 10s period. Participants were immediately asked to report in the protocol whether they had detected any sensations on the tested hand or not, and if they had, to (a) map the extent and location of the sensations by shading the areas where they perceived sensations on the map of the tested hands; (b) estimate the perceived intensity of each sensation according to a 10-point scale (1 = just perceptible; 10 = very intense but not painful); (c) indicate their degree of confidence in the location and extent of the perceived sensations according to the two visual analogue scales (ranging from “not confident” to “very confident”); and (d) identify the sensations with the list of descriptors. They had the option to choose more than one descriptor and to add descriptors to the list according to what they had sensed. The task lasted approximately 15 min.

2.3. Data Processing

2.3.1. EEG Preprocessing

The EEG data preprocessing was conducted with BrainVision Analyzer 2.1. To ensure a quality signal was processed, a passband of 0.2-120Hz was first applied, with a 50Hz notch,

and poor electrode signals were removed and replaced by the mean signal of the three nearest electrodes (M. X. Cohen, 2014). On average, 2.37 ± 0.47 electrode signals were replaced (up to 8 electrodes) and those most removed from the signal were FP1, FP2 (11 participants), FT9, TP10 (9 participants), FT10 (8 participants), and TP9 (7 participants). Those least removed were F2, POz, T8 (only one participant per electrode), and T7 (4 participants). An ocular correction with the Gratton & Coles algorithm (Gratton et al., 1983), based on the left horizontal EOG and the under-eye vertical EOG, was applied, subtracting the ocular movement from the signal. For each participant, the 3-minute recording was divided in 90 epochs of 2s, as per the processing used by (Barry et al., 2011) and (Chen et al., 2008) when studying resting-state EEG data. To ensure no evoked response was triggered by the instruction to close the eye, the first 5 epochs were removed (Barry et al., 2011). Artifact rejection, with a maximum amplitude of $80\mu\text{V}$ (Chen et al., 2008), was carried out on these epochs, resulting in a rejection rate of 12.5% epochs. A mean of 74.41 ± 12.45 epochs, ranging from 38 to 85 per participant, was obtained.

2.3.2. ROI current source density analysis using *sLORETA*

3D source localization in the frequency domain was performed by computing the cross-spectra of EEG segments for each participant. The frequency bands in the EEG were classified as delta (0.5-4 Hz), theta (4.5-7.5 Hz), alpha (8-12 Hz), beta (13-30 Hz), gamma (30.5-60 Hz). The *sLORETA* algorithm (LORETA-KEY; KEY Institute for Brain-Mind Research Switzerland) was used to compute the current density (intensity of the current/area, measured in A/m^2) in a cross-spectral analysis. *sLORETA* estimates the standardized current source density using a realistic three-shell head model based on the MNI 152 template provided by Brain Imaging Center of MNI (Fuchs et al., 2002). *sLORETA* was developed on the assumption that the activity of any single neuron should be highly synchronized with the

activity of its closest neighbors. *sLORETA* is a method to localize multiple distributed cortical sources of bioelectric activity in the three-dimensional space. In other words, *sLORETA* demonstrates the synchronously activated neuronal populations underlying EEG activity by computing their cortical localization from the scalp distribution of the electric field. The *sLORETA* inverse solution is based on existing neuroanatomical and physiological knowledge and a mathematical constraint called the smoothness assumption (Pascual-Marqui, 2002). The principles of *sLORETA* and the mathematical tools have been described in detail at <http://www.uzh.ch/keyinst/NewLORETA/Software/Software.htm>. In order to mathematically mitigate the disturbing effects of the electrically conducting layers between the cortical surface and the electrodes, *sLORETA* computes the inverse solution within a three-shell spherical head model including scalp, skull, and brain. The brain compartment of this model was restricted to the cortical gray matter and hippocampus, according to the Talairach Brain Atlas digitized at the Montreal Neurological Institute (Talairach & Tournoux, 1988). The gray matter compartment was subdivided in 6239 voxels, which allows a spatial resolution of 5mm. Cross-modal validation studies disclosed that *sLORETA* and other functional neuroimaging methods showed the same cortical localization of neuropsychiatric dysfunctions (Pascual-Marqui, 2002). Finally, the *sLORETA* is adapted to the purposes of the present study since it can localize to 5mm³. This is comparable with the findings in fMRI (Pascual-Marqui, 2002; Pascual-Montano et al., 2002) where the spatial resolution (1.5T) is 4mm³ under optimal conditions (Özcan et al., 2005; Yoo et al., 2004).

In order to obtain current source density in specific ROIs, an ROI file was constructed with the MNI coordinates for 4 seed mid-points (digits and palm in SI and SII) from a total of 149 coordinates reported in the literature (35 studies) on cortical somatosensory responses to tactile stimulation of the right hand (see Supplementary material). In the left hemisphere, the

mid-point coordinates of the digits ($x = -46$, $y = -29$, $z = 56$) and those of the palm ($x = -51$, $y = -33$, $z = 50$) in SI were used. The Euclidean distance between the two points was 8.77mm. In SII, the mid-point coordinates of the digits ($x = -50$, $y = -23$, $z = 18$) and those of the palm ($x = -53$, $y = -20$, $z = 23$) were used. The Euclidean distance between the two points was 6.56mm (Figure 1). The primary auditory cortex ($x = -52$, $y = -19$, $z = -7$) was used as a control seed. If findings are specific for the somatosensory cortices, then no correlations would be expected between SPS and the activity extracted from the control area. Positive values of the x -axis were used for the right hemisphere. Current source density levels were extracted from each of the ROI seeds (5mm^3). The resulting file produced log-transformed average current source density across multiple EEG segments for all participants for each seed. In order to make all data comparable, log values were z -transformed before any further analysis.

INSERT FIGURE 1 HERE, PLEASE

3. RESULTS

3.1. Topography of SPS frequency

This analysis was carried out to detect any significant effects in the spatial distribution of SPS as a function of SI and SII activity for each of the five frequency bands. Maps filled by participants with shaded areas were projected on a $140 \times 140\text{mm}$ grid, with a 1mm^2 resolution, and converted into binary code (0 = nil, 1 = shaded cell). As a result, two binary maps per participant (i.e. right and left hand) were generated. By superimposing these maps, a

frequency map was obtained, in which each cell value represented the percentage of participants who had shaded it. The presence of a distal-to-proximal gradient in frequency was observed (Figure 2), with the surface of reported SPS relative to the surface of each anatomical segment of the hand being, respectively, 29.3% for the distal phalanx, 22.0% for the intermediate phalanx, 17.5% for the proximal phalanx, and 18.02% for the palm. This suggests that the SPS task was successful.

Insert Figure 2 here please

3.1.2. The relationship between SPS frequency topography and current densities for each frequency band

In order to achieve a cell-by-cell analysis, z -transformed current densities were used to fill two maps (right and left hand) *per* participant. The current densities of the left hemisphere were used to fill the map of the right hand, and the current densities of the right hemisphere were used to fill the map of the left hand. In this way, 54 maps reflecting the SPS frequency were correlated to 54 maps filled with z -transformed current densities. This was performed separately for digit and palm SI ROIs, and likewise for SII, and was performed for each frequency band separately. A point biserial cell-wise correlation between the presence of SPS and the z -transformed current densities was then conducted, and the probability threshold was set at 0.05 bicaudal. This is a special case of Pearson product moment correlation that follows the t -distribution and in which one variable is dichotomous (here, 0 = unshaded cell; 1 = shaded cell) and the other variable is continuous (here, the z -transformed current densities). Only significant correlations that were found in hand segments that were compatible with the

ROIs (i.e. correlations between SPS in the fingers with finger ROIs, and correlations between SPS in the palm with palm ROIs) were considered for further analysis. During a second step, the correlation maps obtained were converted into binary maps (0 = non-significant, 1 = significant), for the application of a spatial scan procedure for binary data (Kulldorff, 1997) consisting of a circular window that scans, detects and localizes significant clusters in a step-wise fashion. Based on previous studies, a radius of 6 cells was chosen, containing 113 cells, and corresponding to a surface area of 1cm^2 on an actual hand (Michael et al., 2012, 2015). After 999 runs of the Bernoulli (binomial) model, all detected and localized clusters were significant at least at the $p < .001$ level bicaudal. After the spatial scan had detected significant clusters, a final step consisted in posing a threshold of 5% relative to the surface area of the hand (which also corresponds to clusters formed of less than 113 cells), below which the total percentage of hand surface area that correlated with a frequency band was considered as an artifact. Finally, the 95% two-sided asymmetric confidence interval was also computed (Altman et al., 2000) for the significance of the overall percentage of area of the hand covered by previously detected reliable clusters. The combination of these procedures makes it possible to reduce Type I errors.

3.1.2.1. SPS frequency and the SI

For the relationship between the SPS frequency and the SI (left side of Figure 3), a positive significant correlation was found covering a surface area of 7.1% (95% asymmetric confidence intervals 6.0 to 8.2) in the alpha band, which was located in the fingers. A second, negative cluster was also detected in the fingers in the gamma band, but it failed to reach the 5% threshold (4.8% with the 95% asymmetric confidence intervals including the 5% value: 3.8 to 5.7). No reliable clusters were detected in the palm.

3.1.2.2. *SPS frequency and the SII*

For the relationship between the SPS frequency and the SII (right side of Figure 3), a positive significant correlation was found with the gamma band covering a surface area of 8.85% (95% asymmetric confidence intervals 7.8 to 10.0) and it was located in the palm. A second, negative, cluster was also detected in the palm in the beta band, and it subtended a surface of 6.82% (95% asymmetric confidence intervals 5.7 to 7.8). Interestingly, the area with which correlations were found between SPS and the gamma band was approximately the same as the area where correlations were found with the beta band. No reliable clusters were detected in the fingers.

3.1.2.3. *SPS frequency and the primary auditory cortex*

Resting state activity of the primary auditory cortex was used as a control condition. Small clusters of correlations were found in all frequency bands, except in the gamma band. However, all those clusters failed to reach the 5% threshold (delta = 1.4%, 95% asymmetric confidence intervals 1.1 to 1.8; theta = 1.1%, 95% asymmetric confidence intervals 0.8 to 1.4; alpha = 1.8%, 95% asymmetric confidence intervals 1.4 to 2.2; beta = 2.0%, 95% asymmetric confidence intervals 1.6 to 2.4; gamma = 0%, 95% asymmetric confidence intervals 0.0 to 0.1).

 Insert Figure 3 here please

3.2. *Other parameters*

Internal validity of all other parameters of SPS was inspected through Spearman-Brown coefficients (*SPr*) between the left and the right hand. Good validity was found for mean perceived intensity (*SPr* = .65), confidence in location (*SPr* = .33) and in extent (*SPr* = .37), the number of disjointed areas reported (*SPr* = .66), and variety of SPS (*SPr* = .57). The relationship between the mean *z*-transformed current densities for SI digits, SI palm, SII digits, SII palm and primary auditory cortex ROIs with each of these parameters of SPS was examined by means of correlation analyses, with the significance threshold being corrected for the number of correlations carried out. No correlations were found (Table 1), and this was already the case without multiple analysis correction.

3.3. *Types of sensations*

All SPS types were reported at least once and some participants even reported other types of sensations, such as pins and needles, weightiness, and compression. Types of reported SPS were clustered into five categories based on previous studies (Beaudoin & Michael, 2014): thermal (warming and cooling), deep (beat/pulse and muscle tension), paresis-like (numbness and weightiness), surface (tickle, stretch, tingling, flutter, vibration, and compression), and pain-like (pins and needles and itch). SPS types were not clustered uniformly among these five categories ($\chi^2(4) = 84.95, p < .001$, Cramér's $V = .43$). Surface types of SPS were most likely to be perceived and reported (51.72%), followed by deep (20.69%), thermal (14.66%), paresis-like (12.07%), and then pain-like sensations (0.86%). Each of the five categories of sensations as well as the sum of SPS reported underwent a correlation analysis. No significant link was observed between these categories and mean *z*-transformed current densities for the four somatosensory cortex ROIs, and the primary auditory cortex ROI (Table 1) without multiple analysis correction.

Insert Table 1 here please

4. DISCUSSION

Previous investigations demonstrated that the somatosensory cortices are involved in the conscious perception of non-triggered spontaneous bodily sensations, whether normal or related to pathological conditions. The variability with which such sensations are reported and the fact that some individual characteristics modulate their perception suggest that there might be a proneness to perceive spontaneous bodily sensations. This trait could be related to spontaneous neural activity in the somatosensory cortices and probably expressed through alpha, beta, and gamma oscillations (7.5 to 45Hz). We therefore asked whether EEG oscillatory activity recorded in the SI and SII at rest was related to spontaneous sensations perceived in the hands. The results confirmed this. Specifically, (i) SPS perceived in the fingers correlated positively with alpha-band oscillations recorded in SI, (ii) SPS perceived in the palm correlated positively with gamma-band oscillations, and negatively with beta-band oscillations, both recorded in SII, (iii) the perception of SPS did not correlate with the oscillatory activity of a non-somatosensory cortical area - that is the primary auditory cortex - suggesting that they are related to the somatosensory system only.

4.1. A physiological trait

These results extend previous findings and constitute a bridge between two different aspects of the literature. The relationship between bodily perceptions without external triggers and activity in the somatosensory cortices is one aspect. The findings are in agreement with extant literature that has shown that focusing on SPS activates the somatosensory cortices (C. C. C.

Bauer, Díaz, et al., 2014; C. C. C. Bauer, Barrios, et al., 2014), and that bodily hallucinations are related to spontaneous faulty activity on the somatosensory cortices (Baldeweg et al., 1998; Bär et al., 2002; Garrison et al., 2017; Geoffroy et al., 2013; Jardri et al., 2008; Shergill, 2001). Second, the results confirm that individual characteristics may determine proneness to perceive SPS (Michael et al., 2015, 2017; Tihanyi & Köteles, 2017). The incremental value of the present study is that default oscillatory activity in the somatosensory cortices may constitute a signature physiological trait of proneness to perceive SPS, in a similar way as interoceptive accuracy does, and the tendency to turn attention toward self-referential processes. Perception of SPS is at least partly related to the electrical oscillatory activity of the somatosensory cortices.

4.2. Dissociable patterns

However, the pattern of correlations between somatosensory cortical oscillatory activity and the frequency of SPS was not homogenous. In fact, when combined, the results reveal some dissociation that may unravel some of the mechanisms underlying the perception of SPS. The frequency band that correlated with SPS perceived in the fingers (i.e., the alpha band) was not the same as those frequency bands that correlated with the palm (i.e., beta and gamma bands). The exact same dissociation was also found between SI and SII, leading to the conclusion that SI alpha oscillations mainly underlie the perception of SPS on the most sensitive segments of the hand (i.e., the fingers), while SII beta and gamma oscillations mostly underlie the perception of SPS on the least sensitive segment of the hand (i.e., the palm). Patterns of dissociation between the fingers and the palm are commonly observed in the behavioral literature on SPS (Beaudoin & Michael, 2014; Michael et al., 2015; Naveteur et al., 2015). The results of the present investigation suggest that this dissociation has a neural basis. Another observation is that the SII beta and gamma bands have an opposite relationship with

palmar SPS even though they are expressed in the same area, suggesting that their contribution is different, or may be complementary. They may therefore convey the involvement of different or complementary mechanisms. The rough segmentation of the glabrous surface of human hand into two areas, the fingers, and the palm, is not a new one. Already, in an effort to summarize their pioneering studies in the late '70s and early '80s, Vallbo and Johansson (Vallbo & Johansson, 1984) suggested that perceptual precision in the fingers is set by different mechanisms to those conferring perceptual precision in the palm. Similarly, Gálvez-García and colleagues (Gálvez-García et al., 2012) found different effects of tactile attentional cueing in the fingers and the palm, and suggested that these two areas do not share the same mental representation. Such distinctions have also been found in studies of SPS. For instance, attention seems to enhance perception of SPS mostly in the digits and suppresses it in the palm (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015); tactile stimulation increases SPS perception in the fingers (Beaudoin & Michael, 2014); movement produces widespread gating effects that are confined to the fingers (Beaudoin & Michael, 2014); ageing produces a shift of sensitive zones toward the palm (Naveteur et al., 2015); the availability of visual input (Michael et al., 2012) and interoceptive accuracy (Michael et al., 2015) mostly increase SPS perception in the palm; and finally resting-state physiological arousal correlates more strongly with decreased SPS perception in the palm than in the fingers (Salgues et al., 2021).

The reasons why different sets of factors have different effects on SPS perception in the fingers and in the palm are not clear yet, but elucidating such a puzzle would also help capture the fingers-alpha-SI / palm-beta & gamma-SII dissociation found in the present study. Rather than assuming that each factor has a specific effect, one hypothesis is that all the above-mentioned effects would result from a single general and omnibus process. This process

would confer different sensitivities in the two hand segments because they have distinct representations (Gálvez-García et al., 2012). One plausible candidate is attention and its effects on neural signal-to-noise ratio (Briggs et al., 2013; Buschman, 2015; Schmitz & Duncan, 2018). Research suggests that substantial neural noise is present in those parts of the somatosensory system that process information from the fingers and the palm, and that this noise is greater for the palm than the fingers (Vallbo & Johansson, 1976). Attention would intervene to change this ratio and shape perceptual experiences (Gomez-Ramirez et al., 2016). There is also evidence that attention has a push-pull effect on somatosensory oscillatory activity. Gamma-band amplitude increases when attention is focused on a body part (M. Bauer, 2006), and the amplitude of both alpha and beta bands increases on the unattended body location (Jones et al., 2010; F. van Ede et al., 2011; Freek van Ede et al., 2014). Since alpha-band oscillations are usually negatively related to attention and perception, the positive correlation observed here between alpha-band oscillations and SPS may thus reflect a noise-suppression effect. The positive gamma/SPS correlation may reflect a signal-amplification effect, reinforced by a release of suppression reflected through the negative beta/SPS correlation. Taken altogether, this suggests that the patterns defining the fingers-alpha-SI / palm-beta & gamma-SII dissociation reflect how the default functioning of the somatosensory cortices induces suppression of perceptual experiences in the fingers that arise from the spontaneous activity in SI, and facilitation of perceptual experiences in the palm expressing spontaneous activity in SII.

Interestingly enough, while attention has an effect on the neuronal activity of both SI and SII, the effects on SII activity are greater (for a review, see (Gomez-Ramirez et al., 2016)). Transposed to our findings, this may suggest that default attentional processes related to the somatosensory oscillatory activity would mostly act to facilitate SII-dependent perceptual

experiences, such as tactile memories (Gallace & Spence, 2010), and body-ownership (Bretas et al., 2020). Shifting the focus of attention intentionally would produce shifts in this pattern and result in all the dissociable patterns between the fingers and the palm mentioned earlier. However, several authors cast doubts as to whether activity in SI and SII is sufficient for bodily awareness to take place (e.g., (Gallace & Spence, 2010)), and suggest that awareness would result from back-projections from higher-order brain areas such as the temporoparietal junction and the insula. It is interesting to note that both these areas are involved in body-related processes and attention (Igelstrom et al., 2015; Kurth et al., 2010), suggesting that oscillatory activity in the somatosensory cortices would be modulated by their own activity to shape the perception of SPS. Further investigation of this issue is required, especially the functional connectivity between SII and the temporoparietal junction.

4.3. Cues to body perception distortions and bodily hallucinations

The finding that intrinsic oscillatory activity of the somatosensory cortices is related to the perception of SPS supports and confirms the idea that proneness to perceive bodily sensations may constitute a normal counterpart of extreme and pathological body-related perceptual phenomena. Specific normal and healthy spontaneous somatosensory neural activity is expressed in the content of perceptual experiences, and disorder would result in disturbances of bodily perceptual experiences. This is reflected in several syndromes. For instance, distortions of body perception are observed in chronic pain syndromes (Schwoebel, 2001), fluctuate with the intensity of pain and range from feelings of disownership and foreignness of the affected limb, to distortions in the perception of its size, shape and location (Lewis et al., 2007). Their occurrence coincides with changes and neuronal reorganization taking place within the somatosensory cortices, and other areas with which they are connected (Flor, 2003; Kim et al., 2017; Moseley & Flor, 2012). The fact that previous research showed that chronic

pain is associated with misperceptions of SPS (Borg et al., 2015; Echalié et al., 2020) reinforces the idea that it is modified somatosensory cortical activity that relates to spontaneous and untriggered misperceptions. Similarly, cortical reorganization of the somatosensory cortices also coincides with phantom limb sensations (Flor, 2003), which are also considered as disturbances of body perception (Rasmus et al., 2017). It would be of outstanding interest to investigate SPS in phantom limb patients especially as the nature of SPS and the methodology whereby they are assessed make such an investigation possible and plausible, even in the absence of a limb.

However, bodily perceptual disturbances are not only encountered in chronic pain syndromes. Individuals across the schizophrenia spectrum, ranging from schizotypal individuals from the general healthy population to schizophrenia, have been reported to suffer from perceptual bodily aberrations and disturbances of the self (Berrios, 1982; Ettinger et al., 2015; Franck et al., 2002). We believe that the present study mostly contributes towards understanding these phenomena. Several imaging investigations have reported activity in the somatosensory cortices during tactile and bodily hallucinations (Baldeweg et al., 1998; Bär et al., 2002; Geoffroy et al., 2013, 2014; Jardri et al., 2008; Shergill, 2001), and psychophysical sensory evidence suggests modified somatosensory cortical processing in schizotypy (Lenzenweger, 2000) that may be at least partly responsible for bodily perceptual aberrations. Some theoretical models assume that hallucinatory experiences in psychiatric populations and in healthy individuals with proneness to delusion-like and hallucination-like phenomena arise from failures in mechanisms responsible for distinguishing whether the source of an experience is internal or external (Allen et al., 2008; Blakemore et al., 2002), even though some doubts persist (Garrison et al., 2017). It is suggested that internal thoughts are not experienced as being one's own and are attributed to someone else, giving rise to an auditory

hallucination. A similar mechanism may apply to bodily hallucinations. For instance, combined sensations of tingling and movement due to the spontaneous activity of the somatosensory cortices can be easily mistaken for insects crawling on the skin, and a combination of tingling and itching may even give the impression of an insect bite. Faulty monitoring of the source of such experiences may give rise to the belief that insects are crawling beneath the skin and entering the body (i.e., infestation delusion), which is only one of the bodily hallucinations reported in psychiatric and neurologic populations (Berrios, 1982; Kataoka & Ueno, 2017).

It is encouraging that imaging studies have shown that complex bodily hallucinations, such as skin infestation sensations, and perceptual aberrations are related to dysfunction in both the somatosensory cortex and the higher-order areas - the insula and the temporoparietal junction - that back-project to the somatosensory cortex and are thought to play an important role in bodily awareness (Blanke, 2008; Brosey & Woodward, 2017; Eccles et al., 2015; Freudenmann et al., 2010). However, they have also shown that tactile hallucinations (Bär et al., 2002; Geoffroy et al., 2013, 2014; Jardri et al., 2008; Shergill, 2001) are accompanied by transient gamma-band oscillations (Baldegweg et al., 1998). In a provocative paper, Behrendt (Behrendt, 2006) suggested that synchronization of gamma oscillations in thalamocortical networks is at the origin of normal perceptual experiences, with oscillatory activity being constrained by sensory input and attention. In psychiatric diseases such as schizophrenia, modulation of thalamocortical gamma activity by sensory input is impaired, allowing attentional mechanisms to play a predominant role in the absence of sensory input. This may lead to hallucinations. Interestingly, the suggested role of attention in awareness in the absence of any external triggers (Behrendt, 2006) is similar to that advocated by us in this paper and supported by several empirical findings about the modulation of spontaneous

experiences by attention (C. C. C. Bauer, Díaz, et al., 2014; Borg et al., 2015; Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015; Tihanyi & Köteles, 2017). We therefore believe that the present study makes a significant contribution to the field of tactile and bodily hallucinations. Proneness to perceive normal phenomena that are associated with spontaneous intrinsic activity of the somatosensory cortices, and alterations of the source monitoring mechanism that makes an individual attribute those sensations to external events may constitute a basis for bodily hallucinations and other perceptual aberrations. Dysfunction in other brain regions and aberrant connectivity between the somatosensory cortices and those regions may account for other characteristics of the experiences, such as emotional content (Allen et al., 2008). This precise hypothesis should receive more attention and be further investigated in the near future, both in clinical populations and in healthy populations with schizotypal traits and hallucination-like and delusion-like proneness.

4.4. Limitations

Several limitations may restrict the significance of the present study and should be acknowledged. The first one is related to the relatively small sample size. However, most research using EEG techniques use samples of a size that is either similar or smaller to the sample used here. Furthermore, the use of a relatively high number of 2-second EEG epochs *per* participant, the use of two SPS hand maps *per* participant, and the step-wise and adapted statistical methods used to limit errors may mitigate this limitation. The second limitation is the use of defined ROIs while EEG techniques have a poor spatial resolution. As in can be seen in figure 1, the ROIs of the digit cortical representation is in spatial proximity to the ROI of the palm representation and current densities may exhibit substantial overlap. However, *a posteriori*, the results cannot account for such an overlap, as dissociable patterns were found. Furthermore, the results are difficult to interpret in other terms than the specific involvement

of the somatosensory cortices in the perception of SPS since no relationship was found between SPS and activity of the primary auditory cortex. Finally, only the spatial distribution was found to relate to cortical oscillatory activity, the remaining SPS parameters did not. Previous research has suggested that these parameters are indeed less sensitive than the spatial distribution frequency of SPS probably, due to great between-subject variability, and this may be the reason why no reliable results were observed.

5. CONCLUSIONS

In this paper, it is demonstrated that resting-state EEG activity in the alpha-, beta-, and gamma-band frequencies recorded in SI and SII, but not in the primary auditory cortex, is related to individual differences in the perception of bodily SPS. However, the results also show a fingers-alpha-SI / palm-beta & gamma-SII dissociation, suggesting differences in the neurocognitive mechanisms underlying the perception of SPS. It is suggested that a general process such as attention acts to modulate the signal-to-noise ratio and this would result in the dissociable patterns observed. We believe that the results help understand normal and disordered bodily awareness as expressed through body perception distortions in chronic pain syndromes and through tactile and bodily hallucinations in psychiatric and neurologic diseases. The role of attention processes in misattributing noisy internal activity, which occurs within the somatosensory cortices, as the origin of psychiatric symptoms, seems important to investigate and specify in future research.

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Data linking:

<https://recherche.univ-lyon2.fr/etmeco/data/Michael-et-al-SPS-SomatosensoryCortex.xlsx.zip>

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FIGURE LEGENDS

Figure 1. Spatial MNI coordinates obtained from studies on tactile stimulation and used to localize the mid-point ROIs in SI and SII. Green dots represent the coordinates of the cortical representation of the digits, and the red dot represents their mid-point. Yellow dots represent the coordinates of the cortical representation of the palm, and the dark blue dot represents their mid-point. The light blue dot represents the center of the primary auditory cortex.

Figure 2. Frequency of spontaneous sensations. The colored scale represents the percentage of participants who reported sensations.

Figure 3. Percentages of areas where correlations were found between SPS and cortical oscillatory activity in SI (left side of the graph), and SII (right side of the graph) recorded in ROIs of the cortical representation of the digits (grey histograms), and the palm (white histograms). The top portion of the graph shows positive correlations, while the bottom portion depicts negative correlations. Shadowed areas of the hands depict the areas where significant correlations were observed. Only $p < .001$ clusters are shown, with the requirement that their total surface would cover an area greater than or equal to 5% of the hand. The dashed line marks this 5% threshold. Asterisks denote those clusters that went above this threshold. Error bars represent 95% asymmetric confidence intervals for percentages.

Figure 1

[Click here to access/download;Figure;Figure1.tif](#)

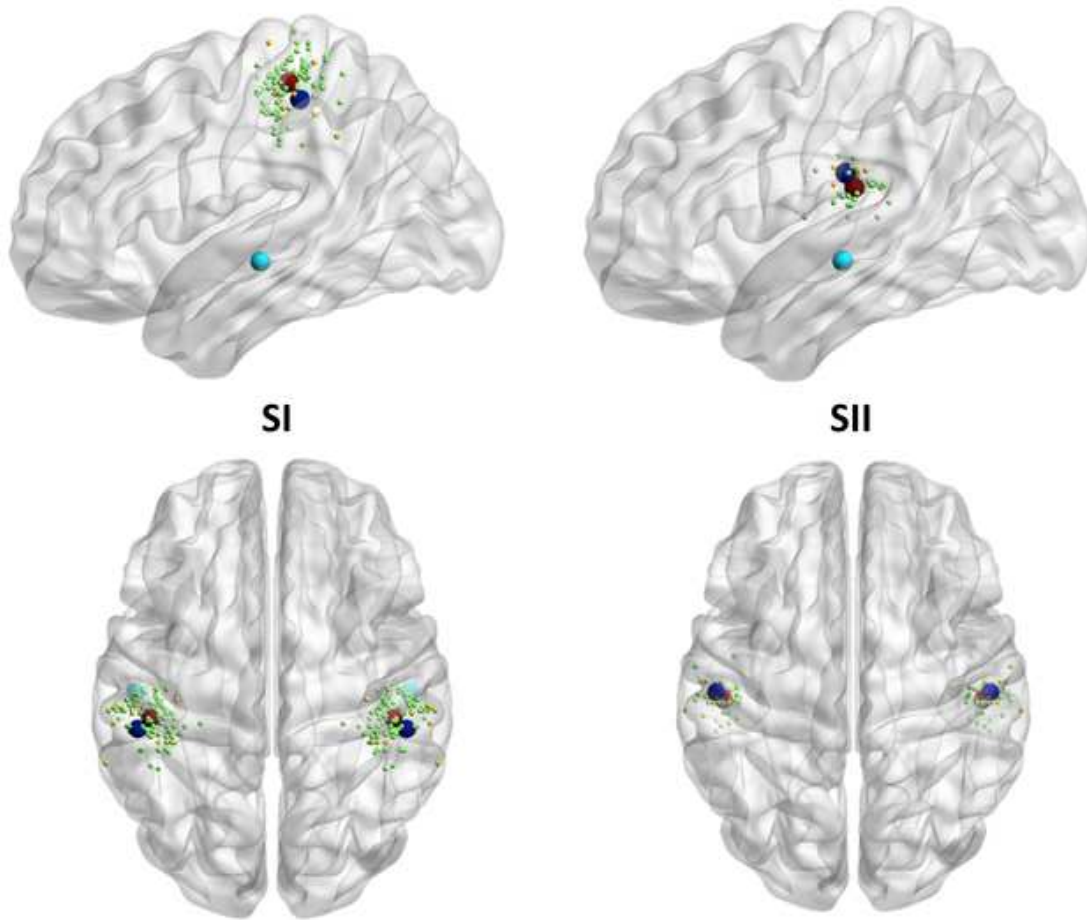


Figure 2

[Click here to access/download;Figure;Figure2.tif](#)

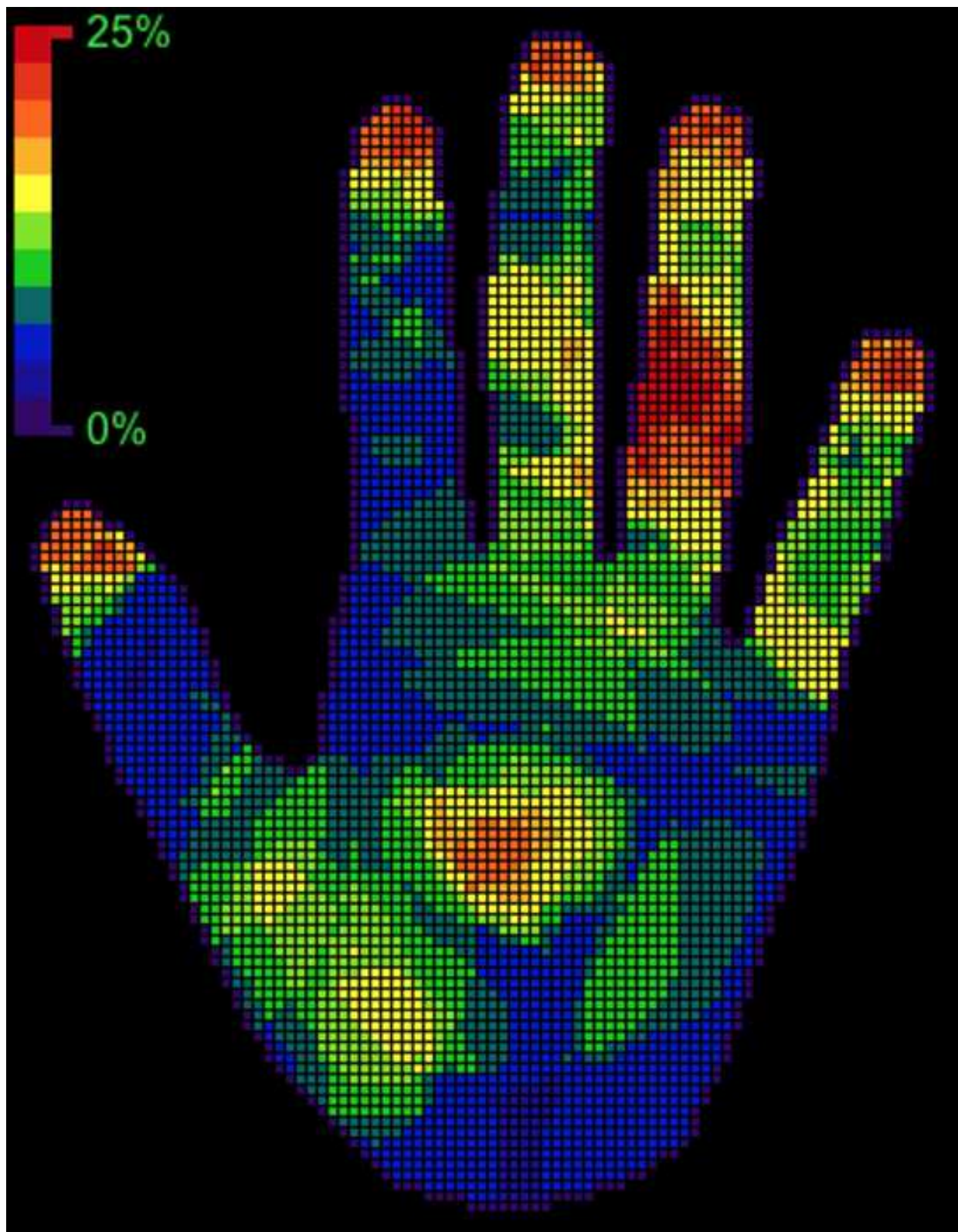


Figure 3

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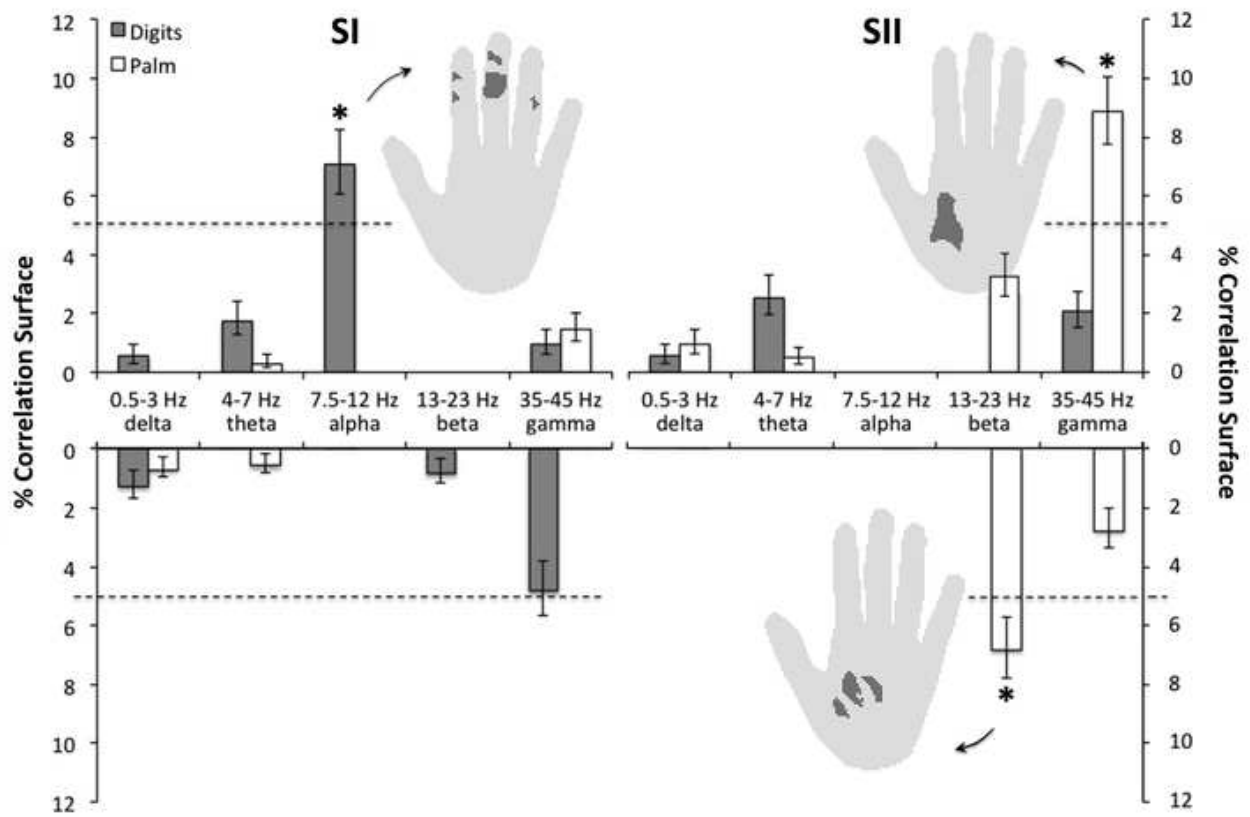


Table 1

[Click here to access/download;Table;Table 1.docx](#)**Table 1.** Pearson correlation coefficients between the parameters and the categories of Spontaneous Sensations and oscillatory activity in SI, SII and the primary auditory cortex. None of the correlations proved significant.

		Parameters of Spontaneous Sensations					Categories of Spontaneous Sensations					
		Intensity	Confidence in Location	Confidence in Extent	Number of zones	Variety	Thermal Deep	Paresis-like	Surface	Pain-like		
SI	Digits	Delta	0.231	0.287	0.196	0.111	0.098	0.127	-0.095	0.159	0.028	-0.093
		Theta	0.260	0.291	0.331	0.181	0.212	0.194	-0.135	0.147	0.181	-0.108
		Alpha	-0.083	-0.045	-0.112	-0.102	-0.089	-0.092	0.158	-0.124	-0.083	-0.003
		Beta	0.138	0.041	0.013	0.010	-0.029	-0.058	-0.029	0.088	-0.014	-0.074
		Gamma	0.120	0.306	0.222	0.127	0.091	0.226	-0.161	0.133	0.054	-0.044
	Palm	Delta	0.200	0.272	0.189	0.085	0.092	0.126	-0.141	0.156	0.028	-0.056
		Theta	0.167	0.173	0.335	0.164	0.251	0.104	-0.155	0.143	0.258	0.006
		Alpha	-0.148	-0.238	-0.195	-0.098	-0.078	-0.174	0.210	-0.215	-0.006	0.105
		Beta	-0.027	-0.279	-0.180	-0.106	-0.106	-0.246	0.043	-0.048	-0.009	0.030
		Gamma	-0.124	-0.116	-0.062	-0.014	0.001	0.028	-0.014	-0.041	0.005	0.108
SII	Digits	Delta	0.221	0.309	0.217	0.144	0.107	0.129	-0.056	0.182	0.025	-0.078
		Theta	0.248	0.330	0.345	0.211	0.218	0.220	-0.079	0.145	0.162	-0.107
		Alpha	-0.049	-0.049	-0.147	-0.005	-0.138	-0.197	0.269	-0.146	0.034	0.002
		Beta	0.159	0.089	0.044	0.071	-0.004	-0.023	-0.029	0.127	0.029	-0.096
		Gamma	0.081	0.313	0.213	0.129	0.076	0.285	-0.151	0.106	0.037	-0.075
	Palm	Delta	0.211	0.294	0.209	0.114	0.094	0.119	-0.079	0.172	0.011	-0.072
		Theta	0.218	0.277	0.356	0.186	0.239	0.177	-0.116	0.135	0.201	-0.053
		Alpha	-0.118	-0.189	-0.212	-0.079	-0.156	-0.234	0.251	-0.221	0.017	0.079
		Beta	0.102	-0.056	-0.049	0.005	-0.040	-0.126	-0.008	0.047	0.041	-0.046
		Gamma	-0.072	0.071	0.052	0.027	0.018	0.218	-0.108	-0.023	-0.003	0.031
Primary Auditory Cortex	Delta	0.223	0.274	0.184	0.102	0.087	0.150	-0.090	0.149	0.004	-0.099	
	Theta	0.247	0.256	0.337	0.195	0.232	0.139	-0.108	0.139	0.222	-0.052	
	Alpha	-0.090	-0.133	-0.135	-0.033	-0.084	-0.154	0.251	-0.199	0.029	0.075	
	Beta	0.126	-0.042	0.001	0.032	-0.045	-0.091	0.002	0.037	0.058	-0.052	
	Gamma	0.004	0.099	0.138	0.124	0.017	0.094	-0.070	0.017	0.152	0.044	

Supplementary material

Literature search procedure

To locate relevant studies, we conducted computer-based searches on Psychological Abstract, PsycInfo, PsycLit, Communication Abstract, Dissertation Abstract International, Worldcat and Yahoo through September 2019 using the keywords *primary and secondary somatosensory cortex, primary and secondary areas, human finger somatotopy, digit somatotopy, postcentral gyrus areas*. We repeated our search in October of 2019. No other reports were added after that date.

Criteria for Inclusion and Exclusion of studies

We included 35 studies published between 1997 and 2019 in which SI and SII activations based on fMRI and PET were reported. The inclusion was restricted to activation of the specified hand region, i.e., digits and palm. All foci labeled as SI, BA1, BA2, BA3, SII, Parietal Operculum were included since these terms are often used as equivalents in the literature. Overall, a total of 94 coordinates for digits and 8 coordinates for the palm in SI were obtained and analyzed, and 40 coordinates for digits and 7 for the palm in SII. Experimental conditions included pain, touch, tactile discrimination, object manipulation and electrical stimulation. Coordinates reported in Talairach space were adjusted by an affine transformation of the Talairach reference brain to the MNI single-subject template (in anatomical MNI space), and are presented in Tables 1 and 2.

Table 1: Studies included in literature search for Digits and Palm in SI

Authors	MNI coordinates		
	x	y	z
Digits			

Blankenburg et al, 2003	-41	-29	60
	-43	-28	63
	-46	-30	65
	-45	-32	67
	-47	-34	58
	-47	-34	60
	-46	-34	61
	-54	-32	67
<hr/>			
Blatow et al, 2011	-50	-27	52
<hr/>			
Brodoehl et al, 2013	-42	-28	61
	-48	-25	49
<hr/>			
Brodoehl et al, 2016	-45	-25	46
	-39	-34	64
	-48	-25	43
	-42	-22	46
<hr/>			
Carey et al, 2008	-44	-26	50
	-44	-26	52
	-42	-24	54
	-52	-20	46
	-52	-24	38
	-44	-18	62
<hr/>			
Chung et al, 2014	-51	-20	49
<hr/>			
Deuchert et al, 2002	-40	-35	52
	-40	-38	55
	-49	-32	55
	-37	-29	58
	-43	-35	60
	-39	-42	64
	-55	-32	54
	-27	-31	74
	-43	-48	59
	-50	-41	54
	-46	-47	49
	-37	-38	51
	-40	-41	58
	-43	-41	58
	-33	-32	57
	-43	-29	60
	-39	-42	65
	-27	-31	74
-43	-48	59	
-49	-41	55	
<hr/>			
Dresel et al, 2008	-38	-36	70

	-52	-22	58
	-40	-36	68
	-62	-26	52
	-56	-26	56
	-52	-24	58
Gelnar et al, 1999	-37	-32	70
	-44	-29	47
	-53	-26	44
Hlushchuk & Hari, 2006	-49	-28	54
	-43	-27	54
Hlushchuk et al, 2015	-49	-18	53
Kitada et al, 2003	-40	-18	58
Martuzzi et al, 2014	-48	-18	52
	-44	-20	54
	-43	-22	58
	-40	-26	59
	-40	-27	61
	-55	-22	54
	-52	-23	58
	-49	-25	61
	-47	-29	64
	-47	-30	64
	-46	-36	58
	-48	-33	59
	-47	-35	61
	-46	-36	62
	-45	-34	62
	-48	-19	53
	-44	-21	56
	-43	-23	59
	-41	-25	60
	-38	-27	62
Nebel et al, 2010	-54	-24	56
Overdouin & Servos, 2004	-46	-23	45
	-35	-35	57
	-41	-29	59
Summers et al, 2009	-57	-25	49
	-59	-24	45
Tsakiris et al, 2007	-42	-24	40
Weibull et al, 2008	-53	-21	45
	-44	-28	53
	-40	-32	55
	-51	-21	47

	-45	-29	55
	-40	-32	58
	-51	-22	58
	-44	-24	52
	-42	-31	60
Yoo et al, 2003	-58	-29	40
	-59	-26	34
	-57	-26	36
Palm			
Bjornsdotter et al, 2014	-43	-38	45
Blankenburg et al, 2003	-38	-38	63
Lee et al, 2017	-60	-31	52
	-36	-22	70
	-60	-25	52
	-63	-46	37
	-54	-34	34
McGlone et al, 2012	-53	-27	47

Table 2: Studies included in literature search for Digits and Palm in SII

	x	y	z
Digits			
Borstad et al, 2012	-56	-24	16
Boakye et al, 2000	-55	-22	12
Bodegard et al, 2000	-53	-35	13
Brodoehl et al, 2016	-57	-22	25
Burton et al, 1997	-45	-21	19
	-45	-23	19
Burton et al, 1999	-56	-21	15
Carey et al, 2008	-48	-32	18
Deuchert et al, 2002	-51	-23	14
	-47	-23	14
	-48	-26	17
	-48	-23	17
	-51	-24	23
	-45	-30	20
	-52	-24	24
	-46	-23	16
	-48	-26	18
	-50	-24	18
	-50	-24	24
	-51	-33	19

Gelnar et al, 1999	-61	-10	24
	-48	-24	24
Grefkes et al, 2002	-59	-16	13
Hlushchuk & Hari, 2006	-45	-22	17
Kitada et al, 2003	-44	-24	22
Malinen et al, 2006	-38	-18	16
Nebel et al, 2010	-50	-28	20
	-46	-6	8
Nelson et al, 2004	-60	-21	23
	-61	-23	28
Ozcan et al, 2005	-55	-21	8
Pleger et al, 2003	-48	-28	20
Ruben et al, 2001	-47	-19	15
	-44	-22	16
Schurmann et al, 2006	-51	-21	16
Summers et al, 2009	-48	-22	16
	-50	-21	12
Yoo et al, 2003	-58	-29	19
	-53	-31	8
Hochsetter et al, 2001	-45	-18	29
Palm			
Björnsdotter et al, 2014	-65	-27	24
Lee et al, 2017	-48	-19	22
	-48	-19	22
	-51	-16	19
	-51	-22	22
	-57	-16	25
McGlone et al, 2012	-54	-24	24

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Entracte

Depuis les premières publications sur les SPS, la même remarque revient : « Oui mais ». Oui, il est vrai que nous ressentons spontanément des sensations sur la peau même si rien ne semble les provoquer. Ne seraient-elles pas pour autant causées par des micromouvements, des contractions musculaires, ou autres événements internes, qui solliciteraient les afférents tactiles ? L'origine des SPS n'est pas source de débat ou de dissension, elle est inconnue (Ferentzi et al., 2017; Tihanyi, 2019; Tihanyi et al., 2018), et tant que nous manquons d'arguments pour définir leur nature nous pouvons difficilement juger de leur rôle dans la conscience corporelle. Dans ce premier axe, nous avons ainsi investigué les deux possibles origines des SPS.

Nous avons d'abord envisagé l'hypothèse selon laquelle les SPS seraient générées par l'activité physiologique spontanée des afférents tactiles. Si tel est le cas, il existerait un parallèle entre la sensibilité tactile des individus et leur capacité à percevoir des SPS. Les résultats que nous présentons en Tableau 1 ne confortent pas cette hypothèse. Nous y montrons que nous percevons mieux les SPS lorsque nous avons une mauvaise sensibilité tactile, et également que les effets de facilitation dans leur perception relèvent de processus centraux latéralisés. Ces effets nous amènent naturellement à considérer l'hypothèse d'une origine centrale aux SPS. Cette seconde hypothèse suppose des mécanismes communs aux hallucinations tactiles et aux SPS, que l'on retrouve au niveau des cortex somatosensoriels. L'étude que nous présentons dans ce premier article est encourageante. D'une part car nous y mettons en évidence une relation entre la somatotopie en SI et SII et la topographie des SPS. D'autre part car nous observons des phénomènes d'amplification et de suppression susceptibles de refléter des processus attentionnels à l'œuvre dans la modulation de l'expérience perceptuelle.

Ainsi, avant de discuter de ces études et de ce que leurs résultats infèrent sur la nature des SPS, nous allons aborder la question des processus cognitifs qui contribuent à leur perception.

ACTE II. LES DETERMINANTS COGNITIFS

La cognition derrière l'expérience subjective du corps

Tableau 1. La sélection attentionnelle

L'Acte I fut l'occasion d'explorer la nature des SPS. Les résultats que nous y avons présentés suggèrent l'implication de processus attentionnels dédiés à moduler leur perception. Nous en venons ainsi à aborder notre second objectif : comment prenons-nous conscience des SPS ? Quels sont ces mécanismes attentionnels, et comment ces modulations nous permettent-elles de prendre conscience de notre corps ?

Des effets similaires d'amplification et de suppression des SPS causés par le focus visuel ont été rigoureusement documentés (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015). On associe ces phénomènes à la sélection attentionnelle des sensations pouvant accéder en conscience parmi la multitude de signaux corporels (Kinsbourne, 1998), mais on n'identifie pas pour autant les processus responsables de ces modulations. Pourtant, ces phénomènes suggèrent que la suppression opère de façon à ce que d'autres sensations soient mieux perçues, et qu'en l'absence de mécanismes supprimeurs la conscience du corps serait perturbée car nous le percevons trop (Borg et al., 2015). Ce qui nous amène assez naturellement à considérer les processus d'inhibition et les unités de régulation des ressources cognitives, dont les interactions déterminent la sélectivité de l'attention (voir Prologue, partie II-A; Egeth & Kahneman, 1975; Michael et al., 2006, 2007; Michael, Dorey, et al., 2020; Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014). En effet, l'inhibition de signaux externes et internes distrayeurs serait bénéfique à la perception des SPS, qui sont si discrètes sur la peau. Au contraire, la distribution des ressources cognitives entre tous ces signaux équivaldrait à tous les prendre en compte indistinctement, rendant plus difficile la perception de signaux peu saillants. Malheureusement, au-delà du focus, la littérature n'apporte aucune précision sur les rôles spécifiques des processus attentionnels dans la conscience corporelle, et le plus souvent seule la notion d'attention, vague et imprécise, est évoquée. C'est donc le point d'ombre que cherche à éclaircir l'étude suivante, où nous nous intéressons aux compétences à inhiber des distrayeurs et à partager les ressources entre plusieurs tâches, et de comment elles affectent la perception des SPS.

Article 3 : Salgues, S., Plancher, G., & Michael, G. A. (Submitted). Attention and body awareness: the role of inhibition and the management of cognitive resources in the perception of SPS. *Cognitive Psychology*

1 **Running head:** *Attention and body awareness: the role of inhibition and the management of cognitive*
2 *resources in the perception of spontaneous sensations*

3

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Abstract

Abstract

When the body is attended to and viewed, it appears that only a subset of bodily sensations enters awareness. Some of these sensations can be felt on the skin even though no stimulation triggers their perception: they are commonly referred to as spontaneous sensations (SPS). It is thought that inhibition and the management of cognitive resources are involved in their perception through phenomena of amplification and suppression. However, the involvement of these processes in body awareness remains poorly understood. We investigated the relationship between attentional abilities and the perception of SPS in order to provide further information regarding this matter. A dual-task paradigm involving visual search and auditory detection was used to assess attentional abilities prior to the investigation of SPS perceived when attending to the glabrous and visible surface of the hand. We found that difficulties in inhibiting distractors were associated with a lower perception of SPS, while difficulties in managing cognitive resources were associated with an increase in the frequency of SPS and a decrease in the perception of paresthesia-like SPS. This suggests that these attentional processes are involved separately in body awareness and allows us to discuss how attention contributes to the conscious awareness of the body.

Keywords: Attention; Inhibition; Cognitive resources; Focusing; Divided attention; Spontaneous sensations; Body awareness.

1 **1. Introduction**

2 Body awareness is the result of the attention paid to the body and the many signals it conveys (A. D.
3 Craig, 2009; Gallace & Spence, 2010; Kinsbourne, 1998). The attentional theory of body awareness
4 (Kinsbourne, 1998) holds that body awareness is constructed from an ever-present background of bodily
5 sensations, i.e. tactile, interoceptive and somatosensory sensations (Gallace & Spence, 2010). This
6 background provides knowledge about the spatial boundaries of the body, generates a sense of
7 ownership, and allows the feeling of continuity in time, even though the body is not permanently the
8 subject of awareness (Gallace & Spence, 2010; Kinsbourne, 1998). Attending to and seeing the body
9 would bring to awareness some of these bodily sensations and, consequently, permit conscious
10 awareness of the body (Kinsbourne, 1998). Some bodily sensations such as warming, tingling, or
11 heartbeats can be perceived on the surface of the skin even though no external triggers (i.e. tactile
12 stimulation or movement) provoke them (Michael et al., 2012; Michael & Naveteur, 2011). These are
13 called spontaneous sensations (SPS) and appear to be better perceived at rest when attending to one's
14 own body. In the past, it has been assumed that perceiving, localizing, identifying, and retaining in
15 working memory the characteristics of SPS and their location on the body depends on attention (Bauer,
16 Barrios, et al., 2014; Bauer, Díaz, et al., 2014; Ferentzi et al., 2017; Michael et al., 2012; Michael &
17 Naveteur, 2011; Naveteur et al., 2015; Salgues et al., 2021; Tihanyi, 2019; Tihanyi et al., 2018).

18 Tihanyi and collaborators proposed three hypothetical causes of the perception of SPS, all of
19 which emphasized the involvement of attention. Their first hypothesis was that SPS arise when attention
20 fails to suppress signals resulting from spontaneous physiological activity, since cognitive resources
21 would be allocated to their processing (Tihanyi, 2019; Tihanyi & Köteles, 2017). In a sense, SPS might
22 be due to the same attentional mechanisms that give rise to the false detection of undelivered
23 electrocutaneous shocks which are expected to be received on the attended body part (Naveteur et al.,
24 2005). According to these authors, another potential explanation is that the perception of interoceptive
25 and other relevant bodily signals initiates self-regulatory processes (Barrett & Simmons, 2015; Fiacconi
26 et al., 2017; Tsakiris, 2010), and that the resulting peripheral changes cause awareness of SPS (Tihanyi,
27 2019; Tihanyi & Köteles, 2017). Indeed, the perception of SPS is related to functions associated with
28 body awareness which require attention to be turned inwards, such as interoception, i.e. the sense of the

1 physiological state of the body (A. D. Craig, 2003; Michael et al., 2015), embodiment, i.e. localizing
2 the self within the body's boundaries (Lopez et al., 2008; Michael, Guyot, et al., 2020), and self-
3 processing through inner speech and the propensity to mind-wandering (Michael et al., 2017; Salgues
4 et al., 2021). The final hypothesis was that perception of SPS might result from the top-down modulation
5 of the somatosensory cortices (Tihanyi, 2019; Tihanyi & Köteles, 2017), meaning that SPS might be
6 the normal manifestation of the somatosensory mechanisms responsible for experiences like phantom
7 limb sensations (Andoh et al., 2017; Flor, 2003; Ramachandran, 1998) or tactile hallucinations (Bär et
8 al., 2002; Freudenmann et al., 2010; Gallace & Spence, 2010; Shergill, 2001)(Michael et al., submitted).
9 Scientific evidence supports the idea that attention, and especially visuo-spatial attention, may provoke
10 top-down modulation of the somatosensory cortex in the form of suppressions/amplifications (Bauer,
11 Díaz, et al., 2014; Cardini et al., 2011; Gallace & Spence, 2008, 2009, 2010; Taylor-Clarke et al., 2002).
12 Furthermore, previous studies have also suggested the involvement of visual attention in the perception
13 of SPS (Bauer, Barrios, et al., 2014; Bauer, Díaz, et al., 2014; Michael et al., 2012; Michael & Naveteur,
14 2011). Michael and Naveteur (Michael & Naveteur, 2011; Naveteur et al., 2015) showed that viewing
15 the attended hand provoked suppression of some SPS and amplification of others, and found that this
16 effect increased when it was not possible to see the attended hand (Michael et al., 2012). Conversely,
17 only suppression was found when vision was diverted to another object (Michael et al., 2012; Michael
18 & Naveteur, 2011; Naveteur et al., 2015). These phenomena, which are well known in many sensory
19 modalities such as vision (Chelazzi et al., 1993; Watson & Humphreys, 1997), audition (Schwartz &
20 David, 2018), and touch (J. C. Craig & Evans, 1995), suggest the involvement of supramodal attention.

21 Visual and somatosensory attention are thought to involve common attentional processes, and
22 this accounts for their interactions in tactile perception. Visual perception of the body would lower the
23 tactile perceptual threshold (Kennett et al., 2001; Taylor-Clarke et al., 2004) and enhance spatial tactile
24 processing (Press et al., 2004). This is beneficial for patients with low tactile acuity (Serino et al., 2007)
25 or impaired body awareness (Haggard & Wolpert, 2005; Wolpert et al., 1998). Distractors appearing in
26 the visual or tactile modality would alter the detection of targets in the other modality (Amlôt et al.,
27 2003), with the result that visual and somatosensory attention modulate each other's perceptual cortical
28 activity (Doricchi et al., 2010; Gomez-Ramirez et al., 2016; Macaluso & Driver, 2005; Taylor-Clarke

1 et al., 2002). It has thus been suggested that the similarities between their anatomical structures reflect
2 similar modes of functioning in the conscious processing of tactile and visual stimuli (Gallace & Spence,
3 2008, 2009, 2010). These interactions are also observed in the perception of SPS (Michael et al., 2012;
4 Michael & Naveteur, 2011; Naveteur et al., 2015). However, the question of which attentional processes
5 cause these amplification and suppression phenomena is poorly understood.

6 Kinsbourne posits that there are links between body awareness and attention (Kinsbourne,
7 1998). The ever-present background of bodily sensations which constantly underpins body awareness
8 would induce only a marginal level of awareness. This may be due to the limited nature of the available
9 cognitive resources, which have to be split across all ongoing activities (Egeth & Kahneman, 1975;
10 Gopher, 1986; Moray, 1967). However, when individuals focus on their bodies, they need to select the
11 subset of these sensations that will enter awareness (Kinsbourne, 1998). This strongly suggests that
12 inhibitory processes (Kane et al., 2001; Michael et al., 2006, 2007; Watson & Humphreys, 1997) may
13 also operate to suppress irrelevant signals so that more relevant signals are prioritized and better
14 processed (Michael et al., 2007; Watson & Humphreys, 1997). This kind of functioning would optimize
15 the processing of selected signals at the expense of others. Conversely, dividing and distributing
16 attention would allow cognitive resources to be allocated to the processing of multiple signals without
17 prioritizing certain of these over the others (Couffe & Michael, 2017; Egeth & Kahneman, 1975;
18 Michael et al., 2007). Dividing attention leads to the less optimal processing of a larger number of
19 signals. Thus transposed to the domain of the perception of bodily signals, inhibition may consequently
20 result in the suppression of some bodily signals, thereby accounting for the selective amplification of
21 SPS when focusing on a body part (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al.,
22 2015). This would eventually lead to conscious awareness of the body (Kinsbourne, 1998). In contrast,
23 distributing cognitive resources among many bodily signals might account for the abnormal
24 amplification of SPS in patients with hypervigilance and pathological body awareness (Borg et al.,
25 2015). Similarly, these processes make distinct contributions to the selectivity of attention, and
26 inhibition and the management of cognitive resources might make opposing contributions to body
27 awareness.

1 In sum, attentional processes, and more specifically inhibition and the management of cognitive
2 resources, appear to make distinct contributions to body awareness. However, their involvement in body
3 awareness, especially through the perception of SPS, has only ever been the subject of speculation and
4 has never truly been investigated. This was the motivation for the present study, in which we
5 investigated how inhibition might be related to a better perception of bodily signals and how the
6 distribution of cognitive resources might be related to a weaker perception of bodily signals. Given that
7 they are modulated by visual and somatosensory attention, these processes would be supramodal (Amlôt
8 et al., 2003; Doricchi et al., 2010; Forster & Eimer, 2005; Kennett et al., 2001; Macaluso & Driver,
9 2005; Naveteur, 2007; Press et al., 2004; Serino et al., 2007; Taylor-Clarke et al., 2002). In the same
10 way as previous studies investigating the involvement of attention in body awareness (Gregory et al.,
11 2003; Matthias et al., 2009; Pollatos et al., 2007), we thus assumed that performance in a body-unrelated
12 attention paradigm should be associated with inter-individual differences in the perception of SPS.
13 Consequently, participants' attentional abilities were assessed using a dual-task approach (Michael et
14 al., 2007; Michael, Dorey, et al., 2020; Michael, Pannetier, et al., 2014). The primary task, a visual
15 search task, involved inhibition in order to suppress visual distractors, while the secondary ongoing task,
16 an auditory detection task, required the management of cognitive resources between the two tasks. The
17 difficulty of the auditory detection task was also varied in order to add further complexity by forcing
18 cognitive resources to be withdrawn from the visual search task. The standard SPS task, which required
19 the detection, localization on the glabrous surface of the hands, and identification of SPS (Michael et
20 al., 2015; Salgues et al., n.d., 2021), was then administered. We hypothesized that difficulties in
21 inhibiting distractors would be negatively related to the perception of SPS. In contrast, difficulties in
22 distributing cognitive resources would be positively related to the perception of SPS. Following the
23 approach adopted in previous studies investigating the involvement of cognitive factors in the perception
24 of SPS (Echalier et al., 2020; Michael et al., 2015, 2017; Salgues et al., n.d., 2021), we compared the
25 measures of attentional difficulties with topographical and non-topographical SPS characteristics. We
26 expected the relationship between attentional difficulties and the perception of SPS to be revealed by
27 the frequency of SPS and their non-topographical characteristics.

28

1 **2. Experiment**

2 *2.1. Participants*

3 The participants were students from Lumière University (Lyon, Eastern France). They were asked to
4 fill out a form containing sociodemographic and health-related questions regarding their age, gender,
5 height, weight, use of psychotropic medication (and if so, the reason why: antidepressants, anxiolytics,
6 neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc.), regular use of other psychoactive
7 substances (alcohol, marijuana, etc.) and any history of cardiovascular disease or diabetes mellitus. They
8 were free to report any information they considered to be of importance for the study. Participants were
9 not included if they mentioned any of the above diseases. Forty-four participants volunteered for the
10 study. Among them, three were excluded based on the above-mentioned criteria, and six were not
11 included as they reported no SPS at all. Thus, 35 participants (28 women and 7 men), with a mean age
12 of 21 ± 2.58 years (ranging from 18 to 29) and a mean body mass index (BMI) of 22.12 ± 4.64 kg/m²
13 (ranging from 16.14 to 39.87), were included in the study. All participants reported normal or corrected-
14 to-normal vision and audition. None had ever completed the attention task or the SPS task before the
15 experiment.

16 Power analyses were conducted on the effect size of the proximo-distal gradient in the frequency
17 of SPS, which is the most prominent characteristic of these phenomena. Based on 10 published studies
18 (Beaudoin & Michael, 2014; Borg et al., 2015; Echalié et al., 2020; Michael et al., 2012, 2015, 2017;
19 Michael, Guyot, et al., 2020; Michael & Naveteur, 2011; Salgues et al., n.d., 2021), the weighted average
20 effect size expressed as Cohen's w was .35 (i.e., medium to large) and as Cramer's V , it was .19 (i.e.
21 medium to large). Given that a power of 70% is required to detect a similar medium to large effect size
22 and alpha at .05, the number of hand maps needed is 70. Since two hand maps per participant were
23 collected in the present study (one per hand), the required sample size was 35 participants (i.e., 70 hand
24 maps) on order to provide enough power (70%) to reduce Type II errors.

25 All participants gave their written informed consent before the experiment. The study was conducted in
26 compliance with the Helsinki Declaration, and the protocol was approved by the local ethics committee
27 (reference number IRB 00,009, 118).

28

1 2.2. *Material & Procedure*

2 The participants first performed the MAM task and then the SPS task in one and the same session.

3

4 2.2.1. *MAM task*

5 The task was the same as that reported by Michael et al. (2020).

6

7 2.2.1.1. *Primary visual search task*

8 The stimuli were outlined white squares (luminance 37.37 cd/m²) presented on a black background
9 (luminance 0.034 cd/m²). At a viewing distance of 30 cm, the angular size of each square was 0.5° ×
10 0.5°. Each square had a gap in it and was rotated clockwise through 0°, 90°, 180° or 270°. The target
11 orientations were 90° or 270°, while that of non-targets was 0° or 180°. To make the target salient, it
12 was placed inside an outlined white 1° × 1° diamond (luminance 37.37 cd/m²). To make a non-target
13 (i.e., the critical distractor) salient, it was placed inside an outlined white circle (luminance 37.37 cd/m²)
14 with a radius of 1°. The stimuli were displayed on a Dell Latitude computer equipped with a Pentium II
15 200-Mhz processor.

16

17 2.2.1.2. *Concurrent auditory task*

18 The stimuli used in the auditory task were the numbers 0 to 9. They were recorded as an mp3 file and
19 played back using speakers at a rate of 1 per second. The stimuli were arranged in a series of 10 numbers,
20 with all the numbers being presented randomly and once only within each series. Each new series started
21 only when the previous series had ended, but there was no indication in the mp3 file to signal the end of
22 one series and the beginning of the next. Instead, a continuous flow was perceived. This arrangement
23 prevented participants from developing detection and response strategies. The mp3 file was played
24 through two speakers connected to an iPad device.

25

26 2.2.1.3. *Procedure*

27 The visual stimuli were randomly distributed inside an imaginary 7.8° × 7.8° square and the search
28 display remained visible until a response was given. The session started with 10 training trials showing

1 all possible conditions. A trial started with the appearance of a central fixation point displayed for 1000
2 ms. Then, the search display was presented. Two conditions were manipulated throughout the study,
3 each occurring with equal probability: (a) in the baseline condition, only the target was placed in the
4 center of the salient surround (diamond); (b) in the distractor condition, in addition to the salient
5 distractor, one of the non-target items was placed in the center of the salient surround (circle) to indicate
6 a critical distractor to be avoided. The display consisted of either 6 or 10 items, including the target (and
7 the distractor, in the corresponding condition). The presence of the distractor (present vs. absent) and
8 the display size (6 vs. 10 items) varied randomly from trial to trial. The participants were asked to
9 indicate the location of the gap in the target (right or left) by pressing one of two pre-defined response
10 keys on the computer keyboard as quickly as possible. The next trial started 500 ms after a response had
11 been given. RTs and errors were recorded by the computer. Overall, the visual task consisted of 240
12 trials (3 identical blocks of 20 trials per condition and display size). The subdivision into 3 blocks was
13 related to the concurrent auditory task.

14 Simultaneously, the participants had to complete a concurrent auditory task, the difficulty of
15 which varied: (a) they had to listen to the auditory list but without responding to it (i.e., 0 auditory
16 targets); (b) they had to detect a single target (the number 2) and make a verbal response ("stop"
17 response; i.e., 1 auditory target condition); (c) they had to detect three targets (numbers 2, 4 and 6) and
18 make the same verbal response (i.e., 3 auditory targets condition). The auditory target(s) was (were)
19 presented in a completely random and unpredictable order. The three degrees of difficulty were
20 presented in three separate blocks during which the participants performed the same visual task (i.e., the
21 visual task remained constant since the aim was to assess the effects of a secondary task). The three
22 blocks were balanced in a Latin-square design across participants. To optimize time-sharing between
23 the visual and auditory tasks, the auditory items were played continuously from the beginning of the
24 block right through to the end, without interruption. Furthermore, the high presentation rate of the
25 auditory items (1 per second) was intended to make the task demanding in terms of resources, because
26 it has been shown that if one stream of stimuli is presented at a high rate, another stream cannot be
27 handled efficiently at the same time. This procedure (Michael, Dorey, et al., 2020; Michael, Mizzi, et
28 al., 2014) was therefore a straightforward way of drawing resources away from the visual task and

1 observing the effects of reduced resource availability. The participants were informed that the two tasks
2 (visual and auditory) were equally important and that one should not be favored over the other. Their
3 responses were recorded by the experimenter, who was sitting at some distance from the participant and
4 had the full list of auditory stimuli. Based on the results of a pilot study as well as on previous research
5 (Michael, Mizzi, et al., 2014), target detections were considered correct if the response was given within
6 2 s. The participants were fully informed of these criteria.

7

8 2.2.2. SPS task

9 Participants performed the task alone in a quiet and brightly lit room heated to 20 to 23°C. They were
10 seated in front of a table on a chair with a backrest. The concept of SPS was introduced to the participants
11 by the investigator, who explained that they were a normal phenomenon that could be perceived by
12 everybody and presented a list of the 11 sensations most likely to be felt (i.e., beat/pulse, itch, tickle,
13 numbness, skin stretch, tingling, warming, cooling, muscle stiffness, flutter, and vibration) so that
14 participants had some idea of what SPS felt like. This list was designed based on the original study of
15 microstimulation-evoked sensations (Macefield et al., 1990; Ochoa & Torebjörk, 1983), and was further
16 developed by (Naveteur et al., 2005) to study SPS. Participants first had to remove all jewelry from their
17 hands and roll up their sleeves as far away from their wrists as possible. They were then given antiseptic
18 gel (Aniosgel® 85 NPC, ≈3ml per participant) and were asked to clean their hands for 15s. This cleansing
19 removes any external agents that may interfere with the task and homogenizes the skin surface across
20 all participants. To ensure no sensations caused by rubbing hands or applying antiseptic gel would be
21 perceived during the SPS task there was a 15-s interval between hand-cleaning and the start of the task.
22 Each participant was given a response booklet containing the standardized reduced maps of each hand
23 shown palm-up (with a distance of 11.2cm between the tip of the middle finger and the palm/wrist
24 boundary), the list of 11 SPS, and two visual analog scales (i.e., two continuous 10-cm horizontal lines
25 without markers at each end) below each map required for the confidence rating. A pencil and a 25 x
26 25-cm piece of smooth white fabric were also distributed to each participant. The start of the session
27 was announced once the participants were familiar with the material and the protocol was placed away
28 from the participants on the desk to prevent any visual interference. Participants were asked to sit with

1 their backs supported by the backrest of their chair. Each hand was tested in a balanced order across
2 participants. For each hand, the ipsilateral leg was turned outward by 60 degrees from the midline. The
3 white cotton fabric was placed on the thigh, and the tested hand rested on it with the palm up and the
4 fingers slightly spaced apart. In this way, only a dorsal part of the hand was in contact with the fabric.
5 The hand not being tested hung down on the outer side of the chair contralateral to the tested hand. The
6 “start” signal given verbally by the investigator marked the beginning of each trial: participants focused
7 on the tested hand by gazing directly at it for 10s so that they could detect any sensations that might
8 occur. The "stop" signal given by the investigator announced the end of the 10-s test. Participants had
9 to immediately report in the protocol whether they had detected any sensations on the tested hand. If
10 they had, they were asked to (a) map the extent and location of the sensations by shading the areas where
11 they perceived these sensations on the map corresponding to the tested hand; (b) specify directly on the
12 map the perceived intensity of each sensation on a 10-point scale (1 = just perceptible; 10 = very intense
13 but not painful); (c) indicate their degree of confidence in the location and the extent of the perceived
14 sensations using the two visual analog scales (ranging from "not confident" to "very confident"), and
15 (d) identify the sensations using the list of descriptors. For this final step, participants could choose more
16 than one descriptor and could add descriptors to the list according to what they had sensed. The task
17 lasted approximately 5 min.

18

19 **3. Results**

20 *3.1. MAM task*

21 Performances on the MAM task for each condition are presented in Table 1.

22

23

INSERT TABLE 1 PLEASE

24

25

26 *3.1.1. Performance on the visual search task*

27 The number of errors and medians of correct RTs were analyzed. The Greenhouse-Geisser correction
28 was applied whenever the assumption of sphericity was not met.

1 The mean percentage of errors was 3%. The percentage of correct responses was subjected to a repeated-
 2 measures analysis of variance (ANOVA), with the auditory task difficulty (0, 1, or 3 auditory targets for
 3 detection), the distractor condition (absent vs present), and display size (6 vs 10 items) as within-
 4 participants factors. No significant result was found.

5 Response times shorter than 200 ms and longer than 2000 ms were discarded. Discarded trials
 6 accounted for less than 0.5% of the total number of trials. A repeated-measures ANOVA was carried
 7 out on RT, with auditory task difficulty (0, 1 or 3 auditory targets for detection), distractor condition
 8 (absent vs present), and display size (6 vs 10 items) as within-participants factors. The main effect of
 9 auditory task difficulty was significant ($F(1.76, 59.92) = 12.06, p < .001, \eta^2p = .26$). Newman-Keuls
 10 post hoc tests revealed that RT were significantly slower in the 3 auditory targets (Mean = 717, SD =
 11 87) than in the 0 target (Mean = 669, SD = 75; $p < .001$) and 1 target conditions (Mean = 681, SD = 85;
 12 $p < .001$). The main effect of distractor condition was also significant ($F(1, 34) = 475.95, p < .001, \eta^2p$
 13 $= .93$), with RT being longer when a distractor was present (Mean = 763, SD = 99) than when it was
 14 absent (Mean = 614, SD = 65). The main effect of display size was also significant ($F(1, 34) = 7.29, p$
 15 $= .011, \eta^2p = .18$), with longer RT for 10-item (Mean = 694, SD = 87) than for 6-item trials (Mean =
 16 683, SD = 78). Finally, the auditory task difficulty \times distractor condition interaction was significant
 17 ($F(1.80, 61.18) = 3.34, p = .05, \eta^2p = .09$). The Newman-Keul post-hoc tests revealed a significant effect
 18 of distractors for 0 targets (Difference = 146 ms, SD = 69; $p < .001$), for 1 target (Difference = 137 ms,
 19 SD = 58; $p < .001$) and for 3 targets (Difference = 165, SD = 70; $p < .001$). The interaction results from
 20 the fact that the distractor effect was much greater with 3 auditory targets than with 0 or 1 target (see
 21 Figure 1).

22 -----
 23 INSERT FIGURE 1 PLEASE
 24 -----

26 3.1.2. Performance on the auditory task

27 A detection accuracy score was computed by subtracting the percentage of false positives (erroneous
 28 detections) from the percentage of hits (correctly detected targets). A paired *Student's* test revealed

1 significant differences in the accuracy detection score, as participants performed better when detecting
 2 1 target (Mean = 97.27, SD = 5.41, Mean = 84.21, Max = 100) than when detecting 3 targets (Mean =
 3 84.16, SD = 9.92, Mean = 60, Max = 100, $t(34) = 7.30$; $p < .001$, Cohen's $d = 1.23$).

4
 5 These results indicate that the MAM task successfully highlighted differences in RT in the visual task
 6 caused by the presence of a distractor and the increasing difficulty of the secondary task, as well as
 7 differences in the detection accuracy in the auditory task caused by the number of auditory targets to
 8 process. The MAM task is extremely reliable, with a Cronbach's α of .95 and a split-half r^* coefficient
 9 (obtained through a split-half correlation between odd and even-numbered trials followed by the
 10 application of the Spearman-Brown prophecy procedure) of .97.

11

12 3.1.3. MAM indices

13 Indices for inhibition and management of cognitive resources were extracted so that further analyses
 14 regarding their relationship with SPS could be conducted.

15 The Inhibition Difficulty index (hereafter: ID) was obtained by computing the effect of
 16 distractor presence (i.e., the difference between trials with and without distractor) on RTs and proportion
 17 of errors and then z -transforming and averaging these scores to obtain a single value. The Resources
 18 Difficulty index (hereafter: RD) was extracted by computing the effect of auditory targets on RTs and
 19 the proportion of errors in the visual task and the auditory task. The α regression slope¹ was used to
 20 obtain a single value for each of these dependent variables, which were then z -transformed and averaged
 21 to obtain a single value. The ID and RD reflect difficulties in, respectively, inhibiting distractors and
 22 sharing resources in a dual-task (Michael, Dorey, et al., 2020).

23 The indices showed acceptable to good reliability, with a Cronbach's α of .76 and a split-half r^*
 24 coefficient of .77 for ID, and a Cronbach's α of .80 and a r^* coefficient of .81 for RD. No significant

¹ $\alpha = \text{covariance}(x,y)/\text{variance}(x)$, where x is the number of auditory targets to be detected (0,1, or 3) and y the dependent variable.

1 correlation was found between them ($r = -.04, p = .83$), thus suggesting that ID and RD do reflect distinct
 2 processes (Michael et al., 2007; Michael, Dorey, et al., 2020; Michael, Mizzi, et al., 2014).

3

4 3.2. SPS task

5 3.2.1. The topography of SPS frequency

6 An examination of the spatial distribution of the SPS on the hand was performed. Hand maps filled with
 7 shaded areas representing SPS perceived by participants were projected onto a 140×140 -mm grid, with
 8 a 1-mm^2 resolution and were converted to binary code (0=nil; 1=shaded cell). This process produced
 9 two binary maps per participant (i.e., left hand and right hand). A frequency map (see Figure 2) was
 10 obtained by summing these maps, with each cell value corresponding to the percentage of participants
 11 who shaded it.

12

13

 INSERT FIGURE 2 PLEASE

14

15

16 Spontaneous sensations were reported at least once in each cell, but they were not evenly distributed
 17 over the entire hand. A proximal-to-distal gradient can be observed in the frequency of SPS, as depicted
 18 in the map presented in Figure 2. An examination of the gradient was conducted based on the relative
 19 receptor density logic (Johansson & Vallbo, 1979): the percentage of shaded surface area within a
 20 segment (i.e. distal phalanx, intermediate phalanx, proximal phalanx, and palm) was compared to the
 21 surface area of the whole segment. This comparison revealed significant differences in relative spatial
 22 extent ($Q(3) = 3633.07, p < .0001$, Cramer's $V = .18$), with a greater relative surface area of SPS in the
 23 distal phalanx (29.60%) than in the intermediate (21.75%) and proximal (20.87%) phalanges or in the
 24 palm (14.85%). The finding of this typical gradient, which has been repeatedly observed in the
 25 distribution of SPS (Michael et al., 2012, 2015; Michael & Naveteur, 2011), implies that the SPS task
 26 was performed successfully.

27

28

Further analyses were conducted to assess the reliability of the frequency map by means of a
 split-half correlation followed by the application of the Spearman-Brown prophecy formula between the

1 left and right-hand frequency maps (See Figure 2). Coefficients ranged from $r^* = .07$ to $r^* = .95$. Large
 2 size coefficients ($r^* > .50$) predominated, as they covered 77.8% of the surface of the hand, accompanied
 3 by medium size coefficients (r^* from .30 to .49), which covered 21.51% of the surface of the hand.
 4 Small size coefficients ($r^* < .29$) were the least frequent and were found on 0.69% of the hand. This
 5 suggests that the measure of SPS frequency is reliable.

6

7 3.2.2. *Non-topographic SPS parameters*

8 Seven non-topographic SPS parameters, i.e., spatial extent, spatial extent per area, intensity, variety,
 9 number of disjointed areas, and participants' confidence in the extent and the location of SPS, were
 10 extracted from the SPS task and analyzed. Their reliability was assessed using the same split-half
 11 procedure as that mentioned above. This revealed that reliability for all parameters ranged from $r^* = .29$
 12 to $r^* = .78$ (See Table 2).

13

14

 INSERT TABLE 2 PLEASE

15

16

17 Regarding the variety of sensations, all types of sensations were reported at least once, and participants
 18 also reported other types of sensations not presented in the list, such as contraction, pressure, lightness,
 19 blood circulation, pins-and-needles, and pain. Based on previous studies (Beaudoin & Michael, 2014;
 20 Michael, Guyot, et al., 2020; Salgues et al., 2021; Vallbo, 1981), the reported sensations were clustered
 21 into five categories: (i) thermal: warming and cooling; (ii) deep: beat/pulse, bloodstream, muscle
 22 tension, and contraction; (iii) surface: tickling, stretching, tingling, trembling, vibration, floating and
 23 pressure; (iv) paresis-like: numbness; (v) pain-like: itching, pins-and-needles, and pain. SPS were not
 24 evenly distributed across these categories ($X^2(4) = 206.11$, $p < .001$, Cramer's $V = .49$): surface
 25 sensations were the most frequently perceived and reported (57.14%), followed by deep (20.74%),
 26 thermal (11.06%) and paresis-like sensations (8.76%). Pain-like sensations were the least frequently
 27 perceived (2.3%).

28

1 3.3. *The relationship between SPS and MAM indices*

2 3.3.1. *SPS frequency and MAM indices*

3 The relationship between the distribution of SPS and the attentional indices was investigated by means
4 of topographical analyses. A 140 x 140-mm grid identical to the one used for the computation of SPS
5 frequency was filled with ID and RD indices separately for each participant and each hand. In this way,
6 it was possible to compute point-biserial cell-wise correlations between the 70 individual maps
7 reflecting the frequency of SPS and the 70 individual maps filled with each investigated index.
8 Corrections were applied to the resulting probability maps by converting them to binary maps (0 = non-
9 significant cell; 1 = significant cell) and running a spatial scan procedure (Kulldorff, 1997). This took
10 the form of a circular window scanning the map in a stepwise fashion in order to highlight significant
11 clusters of correlated cells. A maximum radius of 6 cells was chosen, and 999 iterations of the Bernoulli
12 (binary) model were computed. Only clusters significant at $p < .001$ were retained. The resulting maps
13 are presented in Figure 3.

14

INSERT FIGURE 3 PLEASE

15

16

17
18 Significant correlations between the MAM indices and the SPS frequency were found, with opposite
19 signs between ID and RD. The ID index exhibited negative correlations covering 23.99% (95% Wilson
20 Confidence Interval [22.74%, 25.28%]) of the surface of the hand, while the RD index revealed mainly
21 positive correlations covering 9.97% (95% IC [9.11%, 10.89%]) of the surface of the hand. Although a
22 few significant negative correlations were also found with RD, these accounted for only 0.44% (95%
23 IC [0.28%, 0.68%]) of the overall surface and may be considered as an artifact.

24

25 3.3.2. *Non-topographic SPS parameters and MAM indices*

26 Multiple regression analyses were carried out to investigate whether the seven non-topographical SPS
27 parameters and the five types of SPS would be predicted by the ID and RD indices. Gender, age, and
28 body mass index (BMI) were also added as predictors as they are factors known to modulate SPS and

1 tactual sensitivity (Kozłowska, 1998; Naveteur et al., 2015). All variables were *z*-transformed prior to
 2 the analysis. The results (not Bonferroni corrected (Cabin et al., 2000; Perneger, 1998)) are presented
 3 in Table 3 for the seven non-topographic parameters, and in Table 4 for the types of sensations.

4 Intensity was negatively predicted by participants' age ($\beta = -.41$, SEM = .18, $t(34) = -2.26$, $p =$
 5 .03, Adj. $R^2 = .10$) and positively predicted by participants' gender ($\beta = .37$, SEM = .17, $t(34) = 2.11$, p
 6 = .04, Adj. $R^2 = .10$). Gender also significantly predicted participants' confidence in location ($\beta = .46$,
 7 SEM = .17, $t(34) = 2.65$, $p = .01$, Adj. $R^2 = .13$) and extent ($\beta = .55$, SEM = .17, $t(34) = 3.27$, $p = .00$,
 8 Adj. $R^2 = .16$). This suggests that high-intensity SPS were more frequently reported by young individuals
 9 and men, and that men were also more confident in the location and extent of perceived SPS than
 10 women.

11 -----
 12 INSERT TABLE 3 PLEASE
 13 -----

14
 15 Pain-like SPS were significantly predicted by participants' BMI ($\beta = .39$, SEM = .17, $t(34) = 2.23$, $p =$
 16 .03, Adj. $R^2 = .13$), meaning that participants with a higher BMI perceived more pain-like SPS than
 17 participants with lower BMI. Interestingly, the RD index negatively predicted the perception of paresis-
 18 like SPS ($\beta = -.37$, SEM = .17, $t(34) = -2.23$, $p = .03$, Adj. $R^2 = .12$), suggesting that participants with
 19 difficulties in managing cognitive resources in a dual-task setting report less paresis-like SPS.

20 -----
 21 INSERT TABLE 4 PLEASE
 22 -----

24 4. Discussion

25 Given the amount of evidence indicating the high prevalence of interactions between visual and
 26 somatosensory attention (Amlôt et al., 2003; Cardini et al., 2011; Doricchi et al., 2010; Forster & Eimer,
 27 2005; Kennett et al., 2001; Macaluso & Driver, 2005; Naveteur, 2007; Naveteur et al., 2005; Press et
 28 al., 2004; Serino et al., 2007; Spence, 2002; Taylor-Clarke et al., 2002, 2004), many studies have also

1 raised the question of whether attentional processes mobilized in unrelated paradigms are associated
2 with body awareness (Gregory et al., 2003; Matthias et al., 2009; Pollatos et al., 2007; Salgues et al.,
3 n.d.). Previous studies have suggested that attentional processes like inhibition (Michael et al., 2012;
4 Michael & Naveteur, 2011; Naveteur et al., 2015) and the management of cognitive resources (Matthias
5 et al., 2009) are those most likely to contribute to body awareness. Inhibition would prevent distracting
6 bodily signals and distracting external stimuli from interfering with the processing of the attended body
7 part, thereby permitting better processing of the body part that is currently being focused on. At the
8 same time, the distribution of cognitive resources would cause multiple signals to be taken into account
9 concomitantly, thus impeding the prioritization of any specific signal over another. If these attentional
10 processes are involved in the conscious awareness of the body, then this would be manifested through
11 the relationship between SPS and attentional abilities. Indeed, we found that attention determined the
12 proneness to perceive and report SPS: inhibition difficulties correlated negatively with the topographical
13 frequency of SPS, while difficulties in distributing and managing cognitive resources correlated
14 positively with SPS frequency and were related to a decrease in paresis-like sensations. On the one hand,
15 these findings argue for a central role of attentional processes in body awareness, at least as it is assessed
16 through the perception of SPS. On the other, they contribute to our understanding of how distinct
17 attentional processes modulate the conscious awareness of the body. We will therefore discuss the role
18 of inhibitory processes and the management of cognitive resources in the perception of SPS.

19

20 *4.1. Inhibition, focusing, and conscious body awareness*

21 Inhibition suppresses irrelevant and low-priority inputs so that cognitive resources are fully allocated to
22 the processing of priority stimuli (Michael et al., 2007; Michael, Mizzi, et al., 2014; Treisman & Gelade,
23 1980). This promotes focusing as it reduces the detrimental effect of salient irrelevant bodily and
24 external stimuli (Couffe & Michael, 2017; Michael et al., 2015) and enhances the processing of relevant
25 ones. In our study, we found that difficulties in inhibiting distractors were inversely related to the
26 perception of SPS, implying that attentional processes are involved in perceiving SPS. This is consistent
27 with the attentional theory of body awareness (Kinsbourne, 1998) and suggests that inhibition operates
28 to suppress sensations within the background of bodily sensations, with the result that only a subset of

1 them actually enter awareness. This would be manifested through the inhibition of low-priority SPS on
2 the palm, thus promoting the processing of high-priority SPS occurring on the fingers (Michael et al.,
3 2012; Michael & Naveteur, 2011; Naveteur et al., 2015). Such an observation is consistent with the idea
4 that bodily sensations such as SPS contribute to defining body frontiers (Kinsbourne, 1998; Michael et
5 al., 2012; Michael & Naveteur, 2011). Inhibition would also promote exploration of the body, and this
6 might account for the better perception of the palm to the detriment of the fingers in individuals with
7 good visuospatial working memory abilities (Salgues et al., n.d.) or a high level of interoception
8 (Michael et al., 2015), given that these cognitive abilities also rely on attention (Kane et al., 2001, 2016;
9 Kane & Engle, 2003; Matthias et al., 2009; Pollatos et al., 2007). Interestingly, the phantom limb
10 phenomenon might then result from focusing on the representation of the missing limb, meaning that
11 currently available bodily sensations might be inhibited so that signals from the former representation
12 present within the background of bodily sensations can be prioritized (Kinsbourne, 1998).
13 Consequently, these bodily sensations would not enter awareness and would not be taken into account
14 when updating the body-part representation (Kinsbourne, 1998), ultimately resulting in a
15 misrepresentation of the current body state (Haggard & Wolpert, 2005; Kinsbourne, 1998). This further
16 supports the idea that inhibitory processes make it possible to focus on the body by suppressing low-
17 priority signals and permitting the prioritization of certain bodily sensations such as SPS. This would
18 contribute to body awareness as it permits the exploration of the body and leads to the maintenance of
19 the current body state in memory.

20

21 *4.2. Management of cognitive resources, dividing attention and body awareness alterations*

22 Managing cognitive resources between multiple signals leads to attention being distributed in such a
23 way that multiple stimuli are processed simultaneously (Couffe & Michael, 2017; Egeth & Kahneman,
24 1975). Focusing on bodily sensations would permit conscious awareness and would update the
25 underlying body representations (Kinsbourne, 1998). Consequently, attending to multiple bodily
26 sensations can be assumed to impede the emergence of body awareness and create distortions in body
27 awareness. Indeed, we observed that individuals who experienced difficulty managing cognitive
28 resources not only reported more SPS, but also had a lower perception of paresis-like SPS, i.e. SPS that

1 are among the least frequently reported type (Michael et al., 2012, 2017; Michael, Guyot, et al., 2020;
2 Salgues et al., 2021). This distortion in the type of SPS suggests that sharing cognitive resources among
3 bodily sensations might enhance the processing of low-priority SPS. The finding of such distortions in
4 the variety of SPS in previous studies which have assessed attentional factors (Salgues et al., 2021), and
5 more specifically one study involving the distribution of cognitive resources in visuospatial working
6 memory (Salgues et al., n.d.), further supports this assumption.

7 Meanwhile, there are many cases of distorted body awareness in patients exhibiting abnormal
8 attentional processing (Borg et al., 2015; Echalier et al., 2020; Herman et al., 2021; Tsakiris & De
9 Preester, 2019). This is the case of fibromyalgia, a pathology characterized by hypervigilance toward
10 the body, which is associated with a major and non-selective amplification of SPS (Borg et al., 2015).
11 Many models argue that bodily signals guide behavior (Apps & Tsakiris, 2014; Tsakiris, 2010; Tsakiris
12 et al., 2007; Tsakiris & De Preester, 2019) and that distortions at the perceptual level lead to inadequate
13 behavioral and emotional reaction regarding the body (Hoehn-Saric & McLeod, 2000; Sakson-Obada
14 et al., 2018). This is all the more true as patients with fibromyalgia suffer greatly from body-directed
15 anxiety (Borg et al., 2018). Another example is Complex Regional Pain Syndrome, a pathology
16 associated with distorted body perception and a distortion in the topographical distribution of SPS,
17 which occur mainly on the same side as the affected lower limb (Echalier et al., 2020): pain appears to
18 cause an overly constant focus on the body (Borg et al., 2018; Marinus et al., 2011; Ramachandran,
19 1998) in such a way that bodily sensations involuntarily attract cognitive resources. Overall, this
20 supports the idea that attention is involved in conscious awareness of the body and that attending to
21 multiple bodily signals present in the background of bodily sensations may prevent or alter the body
22 representation (Kinsbourne, 1998).

23 Unlike us, Matthias and collaborators concluded that attentional abilities in divided attention
24 contribute to body awareness as they are associated with better interoception (Matthias et al., 2009),
25 suggesting that good resource management might be necessary for the perception of bodily signals. This
26 discrepancy may arise from many differences in the way attention has been assessed. Indeed, Matthias
27 and colleagues used a neuropsychological task assessing divided attention without comparing
28 performance between single and dual-task conditions. Such an approach does not permit the

1 investigation of the resource-sharing effect. Here, we used a task where not only was a single task
2 compared to a dual-task, but the difficulty of the dual-task also varied. This therefore made possible a
3 fine-grained analysis of resource management. Another discrepancy can be observed compared to a
4 previous study (Salgues et al., n.d.) in which we found that difficulties in performing a memoranda-
5 recall task alongside a number processing task were associated with a fall in SPS frequency as the
6 difficulty of the latter task increased. If the management of cognitive resources between two ongoing
7 tasks is involved here, then this should reflect the same process as that addressed in the present study,
8 and the discrepancy might therefore not be due solely to the use of the visuospatial working memory
9 paradigm. Hence, the above-mentioned study focused on the difficulties experienced in maintaining
10 representations in working memory, regardless of whether the number processing task was efficiently
11 processed, meaning that this does not provide us with any information concerning whether cognitive
12 resources were distributed efficiently between the two tasks or whether one was favored over the other.
13 Such findings might, ultimately, be complementary to our own: the perception – and retention in
14 working memory – of SPS would require the allocation of a substantial quantity of cognitive resources
15 and dividing attention would cause resources to be diverted from SPS to other bodily signals, thus
16 impeding their perception. Further investigations might be needed to support this assumption.

17

18 *4.3. Limitations and other considerations*

19 Some limitations of the present investigation have to be pointed out. We found some evidence of gender
20 and age differences in the perception of SPS that could relate to attention. Men were more confident in
21 the location and the extent of their SPS than women. This was not surprising as men seemingly report
22 SPS more frequently than women (Naveteur et al., 2015). Gender differences in attentional processing
23 might account for these findings, as men seem to mobilize inhibitory processes more frequently in the
24 presence of distractors (Bayliss et al., 2005) and suffer less from invalid cues in Posner paradigms
25 (Merritt et al., 2007). We also found that younger participants reported more intense SPS. This finding
26 recalls a previous study in which young people deployed attentional processes more easily when
27 focusing on SPS (Naveteur et al., 2015) and could be linked to the age difference in inhibition efficiency
28 (Madden & Langley, 2003; McLaughlin et al., 2010). The gender imbalance in our sample might raise

1 doubts regarding the interpretation of these specific findings. However, it might be preferable to have a
2 majority of women when studying SPS, given that they are more sensitive (Naveteur et al., 2015) and
3 ceiling effects – such as those observed in the frequency measure at the distal areas of the fingers - might
4 compromise correlational studies. Overall, these findings imply that inter-individual differences in body
5 awareness could be associated with age and gender differences in attentional processing.

6 Other criticisms can be made regarding the SPS task. Firstly, it relies on subjective data and is
7 thus prone to subjectivity biases. Previous studies (Michael et al., 2012; Michael & Naveteur, 2011)
8 have argued that the finding of a proximal-to-distal gradient in the frequency of SPS of which the
9 participants are unaware proves that subjectivity biases do not greatly alter the topographical measure
10 of SPS. There is, in addition, growing evidence that the SPS phenomenon is associated with cognitive
11 (Michael et al., 2017; Michael, Guyot, et al., 2020; Salgues et al., n.d.) and electroencephalographic
12 factors (Salgues et al., 2021), thereby lending greater legitimacy to the study of SPS. In combination
13 with these studies, we hope to bring about a better understanding of the cognitive underpinnings of this
14 subjective experience.

15 Secondly, it could be argued that the SPS task assesses the memory of SPS and not only their
16 perception (Salgues et al., n.d.). If we consider that perceptual and memory processes are embedded
17 (Slotnick, 2004), it is rather difficult to distinguish mnemonic processes from perception in the SPS
18 task. What is more, since the involvement of cognitive resource management in the encoding and
19 retrieval stage has been extensively documented (Anderson et al., 1998; Craik et al., 1996; Muzzio et
20 al., 2009), we cannot exclude the interpretation that holds that attentional processes are involved not in
21 the perception but in certain other stages of the mnemonic processing of SPS. This idea is consistent
22 with models that argue in favor of the role of memory in conscious experience (Baars, 1997; Calabrò et
23 al., 2015; Soto & Silvanto, 2014; Wolpert et al., 1998) and would further support the idea that focusing
24 on SPS contributes to the updating of stored body-part representations (Kinsbourne, 1998).

25 By investigating the relationship between attentional processes and SPS phenomena, this study
26 has made it possible for us to gain a better understanding of the role played by inhibition and the
27 management of cognitive resources in body awareness. In contrast to previous studies on this issue
28 (Matthias et al., 2009; Michael et al., 2012), we targeted attentional processes other than body awareness

1 and obtained evidence indicating a distinct and opposite involvement of inhibition and distribution of
2 cognitive resources. This was revealed by a dissociation in the topographical frequency of SPS
3 depending on whether we considered inhibition or cognitive resource management, a finding which is
4 congruent with models of attention (Egeth & Kahneman, 1975; Michael et al., 2007; Michael, Dorey,
5 et al., 2020; Michael, Mizzi, et al., 2014). In the light of these remarks, we hope that we have contributed
6 to a better understanding of the involvement of attention in body awareness. Future research will be
7 required to support our claims, in particular by investigating whether inhibition and cognitive resource
8 management are attentional components in certain asomatognosia – such as the phantom limb
9 phenomenon – and other syndromes that disrupt body awareness.

10

11 **5. Conclusions**

12 This study investigated the involvement of inhibition and cognitive resource management in body
13 awareness through the perception of SPS. Inhibition appears to intervene in the conscious awareness of
14 the body, suppressing low-priority bodily sensations so that high-priority ones can be processed.
15 Meanwhile, distributing cognitive resources in order to process multiple bodily sensations appears to
16 impede conscious body awareness and might lead to some form of alteration of body awareness.

17

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24

25 **Competing interest**

26 The authors declare that they have no competing interests.

27

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14

1 **FIGURE LEGENDS**

2

3 **Figure 1:** Graph depicting the difference in the mean median RT (± 1 SEM) between the conditions
4 with and without distractors as a function of the number of auditory targets to be detected.

5

6 **Figure 2:** Topographic maps depicting SPS frequency (% of participants who shaded a cell) on the left,
7 SPS frequency for the left and right hands at the top right, and the Spearman-Brown r^* coefficients
8 between left- and right-hand frequency maps on the right. For the frequency maps, cool/blue colors
9 represent the least frequently shaded areas and warm/red colors represent the most frequently shaded
10 areas. For the probability map, bluish colors represent positive correlations and reddish colors represent
11 negative correlations. The color intensity indicates the effect size.

12

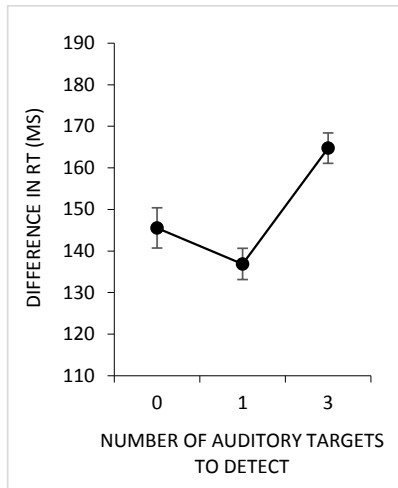
13 **Figure 3:** Topographic probability maps of the correlations between SPS frequency and the attentional
14 indices for inhibition difficulties (ID; left) and distribution of cognitive resources difficulties (RD; right).
15 Bluish colors represent significant positive correlations, and reddish colors represent significant
16 negative correlations. The color intensity denotes the significance level.

17

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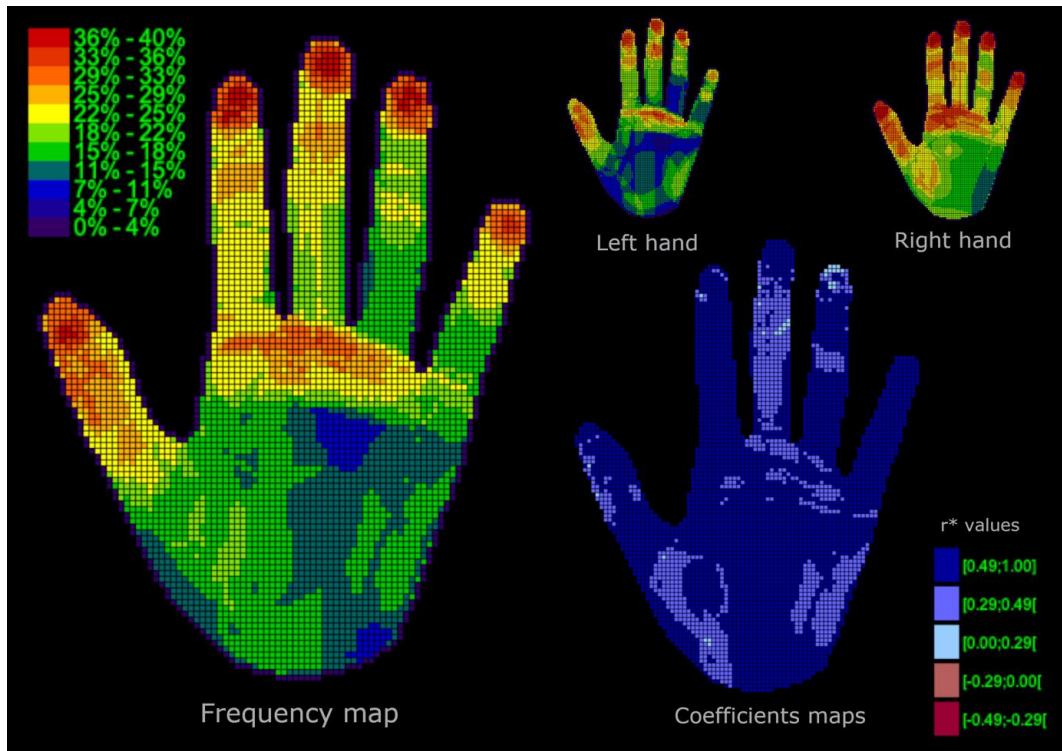
1 **Figure 1**

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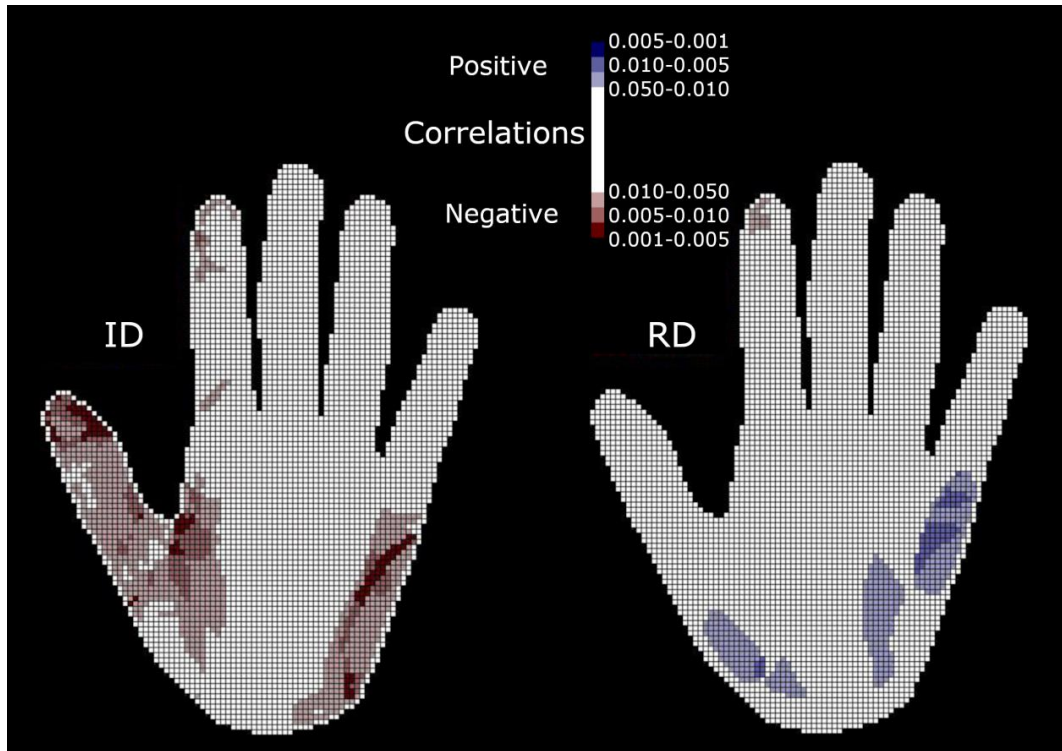
1 **Figure 2**
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1 **Figure 3**

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- 1 **Table 1:** Mean (SD) values for errors and median RT in the MAM visual search task, for hits and false
 2 alarms in the MAM auditory detection task.

Visual search task	Errors (%)	Mean Median RT (ms)
Auditory task difficulty		
0 auditory target	2.75 (4.56)	681 (85)
1 auditory target	3.21 (4.08)	669 (75)
3 auditory targets	3.04 (3.74)	717 (87)
Distractor		
Absent	2.55 (3.71)	614 (65)
Present	3.45 (4.54)	763 (99)
Display size		
6 items	3.26 (4.33)	683 (78)
10 items	2.74 (3.92)	694 (87)
Auditory detection task	Hits (%)	False alarm (%)
Number of auditory targets		
1 auditory target	95.29 (5.40)	0.02 (0.11)
3 auditory targets	84.39 (9.88)	0.23 (0.4)

3
4

1 **Table 2:** Mean (SD) values and Spearman-Brown r^* coefficients of the non-topographic SPS
 2 parameters.

Measures	Mean (SD)	r^*
Spatial extent (%)	18.99 (24.71)	.78
Spatial extent per area (%)	8.29 (13.28)	.37
Intensity (/10)	4.17 (1.99)	.30
Variety	3.23 (1.93)	.54
Number of disjointed areas	5.49 (3.08)	.29
Confidence in location (/10)	6.91 (2.10)	.39
Confidence in extent (/10)	5.95 (2.30)	.30

3

4

1 **Table 3:** Standardized β coefficients (± 1 SEM) and adjusted R^2 coefficient from the multiple regression
 2 analysis carried out on each of the 7 collected dependent variables with age, gender, body mass index,
 3 ID, and RD as predictors. Predictions significant at $p < .05$ are noted with an asterisk (*).

	Spatial extent	Spatial extent per SPS	Intensity	Variety	Number of disjointed areas	Confidence in location	Confidence in extent
Age	-.07 (.20)	-.15 (.20)	-.41 (.18)*	.04 (.20)	.06 (.20)	-.05 (.18)	-.16 (.18)
Gender	.08 (.19)	.02 (.19)	.37 (.17)*	.16 (.19)	.09 (.19)	.46 (.17)*	.55 (.17)*
BMI	.22 (.19)	.13 (.19)	.10 (.18)	.23 (.19)	.01 (.19)	-.12 (.17)	.08 (.17)
ID	-.23 (.18)	-.01 (.18)	-.22 (.17)	-.11 (.18)	-.18 (.18)	-.08 (.16)	-.19 (.16)
RD	.17 (.18)	.30 (.18)	-.15 (.17)	.11 (.18)	-.28 (.18)	-.21 (.16)	-.04 (.16)
Adj. R2	-.047	-.046	.103	-.06	-.019	.132	.161

4

5

1 **Table 4:** Standardized β coefficients (± 1 SEM) and adjusted R^2 coefficient from the multiple regression
 2 analysis carried out on each of the 5 collected dependent variables with age, gender, body mass index,
 3 ID, and RD. Predictions significant at $p .05$ are noted with an asterisk (*).

	Thermal	Deep	Surface	Paresis	Pain-like	Total
Age	.01 (.20)	.15 (.20)	-.07 (.20)	-.14 (.18)	.20 (.18)	-.06 (.20)
Gender	.01 (.21)	.08 (.20)	.13 (.20)	-.23 (.17)	.07 (.17)	.09 (.19)
BMI	-.03 (.20)	-.04 (.20)	.06 (.20)	-.05 (.17)	.39 (.17)*	.06 (.20)
ID	-.06 (.19)	.04 (.18)	-.18 (.18)	.21 (.16)	-.08 (.16)	-.09 (.18)
RD	.06 (.19)	-.09 (.19)	-.05 (.19)	-.37 (.17)*	.18 (.16)	-.19 (.19)
Adj. R2	-.162	-.117	-.122	.116	.127	-.106

4

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Tableau 2. Le maintien en mémoire de travail visuospatiale

Grâce au Tableau 1, nous avons une meilleure compréhension de comment inhibition et régulation des ressources cognitives contribuent distinctement et de façon complémentaire à générer l'expérience subjective du corps. Les résultats que nous y avons discuté confortent l'idée d'une relation étroite entre le traitement attentionnel des représentations du corps et le contenu qui accède à la conscience (Kinsbourne, 1998). D'après Kinsbourne, l'expérience subjective du corps requiert un focus attentionnel ET un maintien en conscience. Et selon Cowan (1999), les représentations au cœur du focus attentionnel sont en conscience tant qu'elles sont maintenues et manipulées en mémoire de travail.

La dimension mnésique de la conscience corporelle est fréquemment abordée dans les conceptions théoriques. On identifie la nécessité d'élaborer et de mettre à jour les représentations du corps, la dualité entre la mémoire corporelle à long terme et à court terme, et le rôle de cette dernière dans sa prise de conscience (Carruthers, 2008; Kinsbourne, 1998; O'Shaughnessy, 1986, 2003; Sirigu et al., 1991). Wolpert décrit par ailleurs un cas particulier où l'individu peut prendre conscience de son corps et de ses sensations, mais échoue à maintenir cette conscience plus de quelques secondes sans garder son corps en focus visuel (Haggard & Wolpert, 2005; Wolpert et al., 1998). Il n'y a pas de consensus sur la nature des mécanismes mnésiques agissant sur les représentations corporelles, mais l'ensemble des éléments que nous avons abordés jusqu'à présent nous font penser que ces processus pourraient être non-spécifique au corps et appartiendraient tout simplement à la mémoire de travail telle qu'elle est définie par Cowan (1999; voir Prologue, partie II-B). Ainsi, le maintien des représentations corporelles en mémoire de travail assurerait l'intégrité et la continuité de l'expérience subjective.

L'article suivant cherche donc à mettre en évidence la contribution de la mémoire de travail à la conscience corporelle. Nous y supposons que si ces mécanismes mnésiques modalité-spécifiques ont un rôle dans la conscience du corps, alors cette expérience subjective est contrainte par les mêmes facteurs qui affectent la mémoire de travail visuospatiale (Vergauwe et al., 2009, 2010). Plus spécifiquement, que la conscience du corps est sujette à un déclin naturel temporel (Barrouillet et al., 2012) et peut être altérée par des facteurs coexistant, comme l'engagement simultanée dans

Acte II - Les déterminants cognitifs

d'autres opérations cognitives et la demande en ressources de ces opérations (Oberauer et al., 2016; voir Prologue, partie II-B). Ainsi nous observons ici comment la perception de SPS est affectée par le déclin des représentations, la gestion d'une tâche secondaire en simultanée, et l'effet de sa difficulté en mémoire de travail visuospatiale.

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Visuospatial working memory abilities and spontaneous sensations perception

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ABSTRACT

Aim: Body awareness arises when attending to and maintaining awareness of visuospatial body representations. By the same token, focussing on representations transfers them to working memory. Body awareness and working memory seemingly rely on similar processes and recruit common parietal areas involved in perception. Therefore, we asked whether visuospatial working memory abilities would define individual differences in the perception of spontaneous sensations (SPS), i.e., bodily sensations perceived in the absence of triggers (e.g., tactile stimulation or movement), when attending to the body.

Method: Participants completed two visuospatial working memory tasks to assess various mechanisms: (i) the decay of representations was assessed through a Brown-Peterson task in which the delay between the memorandum presentation and its recall was manipulated, and (ii) the impact of distractors' interference and cognitive load (i.e., complexity) on recall performances were assessed through a complex span task that required the processing of distractors while maintaining a memorandum. A standard SPS task involving localization and characterization of SPS perceived on the hands was completed afterwards.

Results: Low performance due to decay, distractors' interference and cognitive load in visuospatial working memory was associated with a decrease in the frequency of SPS. Additionally, low performance due to distractors' cognitive load predicted a decrease in the perception of surface-type sensations, and high performance despite distractors' interference led to a better perception of SPS on less sensitive areas of the hand.

Conclusion: We discuss how visuospatial working memory processes might contribute to body awareness and perceptual distortions of the body.

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Introduction

Body awareness would rely on body part representations that are constructed and stored in memory (Kinsbourne 1998; Craig 2009; Berlucchi and Aglioti 2010; Sakson-Obada et al. 2018). Conscious body awareness is achieved, according to some models, by focussing attention on such stored body representations (Kinsbourne 1998; Gallace and Spence 2010). Meanwhile, representations on which attention is focussed would access working memory (Cowan 1999). This would favour the idea that activating, maintaining, and processing body representations in working memory are important for having a bodily experience.

According to Kinsbourne (Kinsbourne 1998), there is an ever-present background of bodily sensations that may be the basis for constructing the continuity of the experiencing self. This background is 'the familiar feeling that one's body exists as a backdrop to whatever one is thinking, experiencing or doing, though its various parts are not being monitored' (p. 217) (Kinsbourne 1998). Hence, this background does not represent the body in detail as an articulated object. Only a portion of these sensations enters

consciousness, through an attentional focus on the representation underlying the body part. Spontaneous sensations (SPS) are regarded as being part of the background of bodily sensations (Michael et al. 2015). These are bodily sensations, such as tingling, warmth, or pulse/heartbeat, that are perceived in the absence of any stimulation, mostly at rest, and when one focuses on one's own body. The perception of these is linked to interoceptive abilities (Michael et al. 2015), i.e., the sense of the physiological condition of the body (Craig 2003), arousal and self-processing propensity through mind-wandering and inner-speech (Michael et al. 2017; Salgues et al. 2021), and embodiment (Michael, Guyot, et al. 2020), i.e., the experience that the self is localized within the body's boundaries (Lopez et al. 2008). Spontaneous sensations have topographic and spatial properties in the sense that they are more frequently perceived on the left hand in right-handers, a pattern that is most evident when interactions with spatial attention are investigated, implying that they could depend on visuospatial abilities (Michael and Naveteur 2011; Michael et al. 2012). As such, SPS could contribute to body awareness, shaping the spatial limits of the body (Michael et al. 2012; Sakson-Obada et al. 2018).

An array of studies investigating SPS on the hands repeatedly highlighted the major involvement of visual attention in their perception, specifically through the phenomena of amplification and suppression of SPS (Michael and Naveteur 2011; Michael et al. 2012; Naveteur et al. 2015). These phenomena could be the result of the top-down impact of attention and vision on the somatosensory cortices (Taylor-Clarke et al. 2002; Gallace and Spence 2008, 2009, 2010; Cardini et al. 2011; Bauer et al. 2014) underlying body representations (Kinsbourne 1998; Nakamura et al. 1998). Hence, when brought to a body part, visual attention would allow selective attending to the corresponding body representation (Chelazzi et al. 1993), resulting in an improvement of perception (Kennett et al. 2001; Press et al. 2004; Naveteur 2007; Serino et al.).

At the same time, visual attention would contribute to the maintenance of such body representations in working memory, as suggested through the recruitment of early sensory parietal areas by maintenance in visual working memory (Mima et al. 1998; Slotnick, 2004; Harrison and Tong 2009; Teng and Kravitz 2019). This is supported by the fact that bringing a body part into visual focus compensates for failures to hold limb awareness due to cortical somatosensory damage (Wolpert et al. 1998; Haggard and Wolpert 2005) in the same way that visual attention improves the maintenance of representations in working memory (Kuo et al. 2012; Williams et al. 2013). Perceiving SPS could be a direct consequence of structural body representations being accessed and processed through visual attention. As those representations are seemingly shaped via the vision of the body (Kinsbourne and Lempert 1980; Kinsbourne 1998) and are mainly visuospatial (Sirigu et al. 1991; Longo et al. 2010), it may be speculated that perceiving SPS requires visuospatial working memory.

There is some evidence that backs this hypothesis, mostly pointing to the fact that limited working memory capacity may also impact body awareness. For instance, cortical somatosensory damage can be responsible for the decay in limb awareness (Wolpert et al. 1998; Haggard and Wolpert 2005), which may indicate the involvement of working memory processes. Indeed, temporal decay of representations is a passive and natural mechanism in working memory, occurring within seconds when representations cannot be kept active, therefore causing forgetting (Peterson and Peterson 1959; Brown 1997; Barrouillet et al. 2012). It was also found that tactile processing is altered when concurrently processing distractors (i.e., concurring inputs) (Bancroft et al. 2011; Blom et al. 2012). Processing distractors while maintaining representations in working memory could induce an attentional shift to these distractors and yield interference (Cowan 1999; Egeth and Kahneman 1975), resulting in altered memory performance. Furthermore, the complexity of distractors requires more complex cognitive processing. This change in the cognitive load results in forgetting as well since it reduces the resources allocated to the maintenance of the representations and increases the level of interference (Egeth and Kahneman 1975; Barrouillet et al. 2004).

In summary, logic dictates that the perception of SPS could suffer from factors that impact visuospatial working memory: abilities in managing decay of representations, distractors' interference and cognitive load in visuospatial working memory might determine individual differences in the perception of SPS. To assess this hypothesis, participants were asked to complete two visuospatial working memory tasks and, afterwards, a standard SPS perception task. The impact of decay was investigated via a Brown-Peterson task (Peterson and Peterson 1959; Brown 1997), which manipulates the delay between the memorandum presentation and its recall. A complex span task, during which the memorandum presentation is interlaced with distractors, was used to assess the impact of distractors' interference and cognitive load on recall performances (Redick et al. 2012; Vergauwe and Cowan 2014). The SPS task required localization of SPS on the hands and characterization of their properties. The hands are easily accessible to vision, which is why these body parts are preferred. But this also allows comparison with previous SPS studies (Naveteur et al. 2005; Michael et al. 2012, 2015, 2017; Beaudoin and Michael 2014; Borg et al. 2015; Echalié et al. 2020; Michael, Guyot, et al. 2020; Salgues et al. 2021). As in previous studies (Michael et al. 2015, 2017; Tihanyi and Köteles, 2017; Michael, Guyot, et al. 2020; Salgues et al. 2021), the relationship between the perception of SPS and the investigated cognitive factors will be assessed through correlational analyses for the topography of SPS frequency and with multiple regression analyses for the non-topographic SPS parameters. It is expected that decay, distractors' interference and cognitive load impact on recall performance will be associated with decreased SPS perception overall.

Method

Participants

The study was conducted following the Helsinki Declaration and the protocol was approved by the local ethics committee (reference number IRB 00009118). Participants were undergraduate students from Lumière University (Lyon, Eastern France). They were first asked to fill out a form containing questions on sociodemographic and health characteristics, such as age, gender, height, weight, use of psychotropic medication (antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc. and if so, the reason why), use of other psychoactive substances (alcohol, marijuana, etc.), and history of cardiovascular disease or type 1 diabetes. They were also free to report any information they considered to be of importance to the study. Participants were not included if they mentioned any of the above-mentioned diseases. Fifty-six people volunteered for the study, five were excluded based on the above-mentioned criteria, and three others were excluded as they reported no SPS. Therefore, 49 participants (44 women and 5 men), with a mean age of 23 ± 5.2 years (ranging from 18 to 44), and a mean body mass index (BMI) of 21.18 ± 3.10 kg/m² (ranging from 16.54 to 31.86) were

included in the study. None of these participants had ever realized the SPS task before.

Power analyses were conducted on the effect size of the proximo-distal gradient in the frequency of SPS, which is the most prominent characteristic of these phenomena. Based on seven published studies (Michael and Naveteur 2011; Michael et al. 2012, 2015, 2017; Beaudoin and Michael, 2014; Borg et al. 2015; Echalié et al. 2020) with a total number of nine experiments, 314 participants and 26 hand maps (2 or 4 per study, as a function of the conditions tested), the weighted mean effect size expressed as Cohen's w is .38 (i.e., medium to large) and expressed as Cramér's V is .22 (i.e., medium to large). To provide a power of 80% to detect a similar medium effect size and given that the frequency map derives from individual hand maps, the number of hand maps needed was 76. In the present study, two hand maps per participant were collected (one per hand), thus the sample of 49 participants (i.e., 98 hand maps) provided enough power (87%) to avoid type II errors.

Materials and procedure

All participants gave their written informed consent before the experiment. Each participant completed the Brown-Peterson and the complex span tasks before completing the standard SPS task.

Visuospatial working memory tasks

A Brown-Peterson (BP; Figure 1(a)) task and a complex span (CS; Figure 1(b)) task were programmed with OpenSesame (Mathôt et al. 2012). The BP task assessed the impact of decay on recall performance, and the CS task the impact of distractors' interference and cognitive load on recall performance. These tasks were performed on a 13-inch display with a 1280 × 800-pixel resolution. A 15-location grid was generated for the main task that was common to the BP and CS tasks, presented as outlined black squares arranged randomly on a white background. At a viewing distance of 40 cm, the angular size of each square was $3.5 \times 3.5^\circ$ and, from centre to centre, squares were separated by an average angular distance of 7.99° (Min = 4.3° ; Max = 10.74°). The grid was displayed across the screen, occupying an angular space of $40.11 \times 25.07^\circ$. The BP secondary task involved the generation of random numbers from 100 to 999, which were displayed in a 40-px mono black font in the centre of the screen. Regarding the CS secondary task, digits from 1 to 10 were displayed in a 50-px mono black font in the centre of a white screen. A larger font was used so that digits would occupy roughly the same space on the screen as the numbers used in the BP task.

Main task. The main task was presented to participants as a first step. A trial started with a fixation cross for 500 ms, followed by the 15-location grid. In each trial, four locations to be remembered were cued. Locations to be remembered were cued by filling the squares in blue at a rate of one square per second. The order in which locations were filled

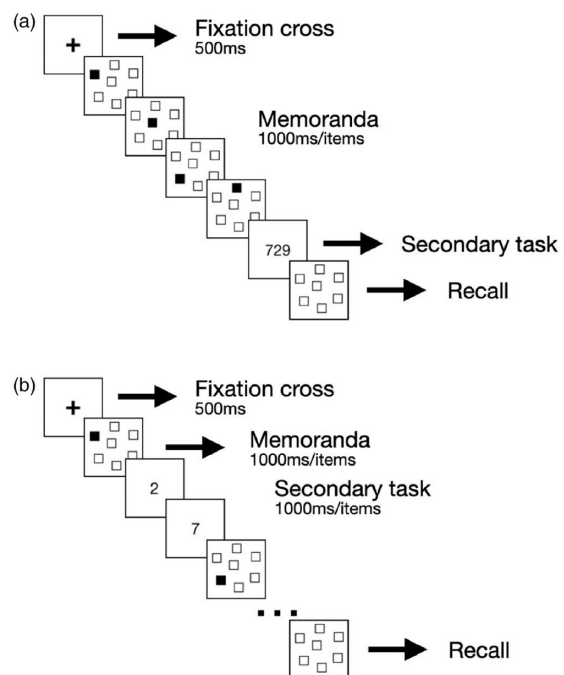


Figure 1. Illustration of the trial sequence for (a) the BP task and (b) the CS task. In both tasks, participants realized a visuospatial working memory task, where they had to recall four locations previously presented. In the BP task, the presentation of a number right after the memorandum presentation and before its recall prompts the beginning of the counting backward task (lasting either 5 ms or 20 s). In the CS task, the memorandum presentation is interleaved with two consecutive screens displaying digits, requiring either no reaction from the participants, a simple reaction (i.e., pressing the space bar), or a complex reaction (i.e., judging the parity and reporting it using two predefined keys).

in blue was randomized so that no identical pattern could be presented twice. After cueing the four locations to be remembered, an empty grid appeared, and participants were required to recall locations in serial order by clicking in the squares with the mouse pointer. The recall screen stayed for as long as needed for participants to retrieve the four locations. If any were forgotten, participants were advised to guess an answer to ensure four locations were reported each time. Each time a location was correctly recalled in the correct order, a point was awarded to the participant. Participants' clear understanding of the main task was checked before further explanation concerning the BP and the CS tasks.

Brown-Peterson task. Each trial of the BP task began with a fixation cross for 500 ms and was followed by the presentation of the memorandum. Then, a number from 100 to 999 was displayed in the centre of the screen. Participants started counting backwards by increments of one from when the number appeared until it was removed. Two experimental conditions were introduced: the presentation of the number lasted either 5 s or 20 s. Numbers were randomized so that no identical number would appear twice. Immediately after the counting task, the recall grid was presented. Each experimental condition (i.e., 5 s or 20 s) counted 12 trials, which

were randomized to counteract any training bias. Participants' clear understanding of the task was checked before it was performed. With 24 trials in total, the BP task lasted five minutes.

Complex span task. Each trial of the CS task began with a fixation cross followed by a memorandum. The presentation of locations alternated with interfering subtasks. Strings of two digits from 1 to 10 were displayed at the centre of the screen at a rate of one per second. Then, after each to-be-remembered location presentation, two digits appeared successively on the screen. Digits were pseudo-randomised so that two successive digits were different. Three interfering subtasks were introduced: (a) No Reaction: participants were asked not to react to the digits; (b) Simple Reaction: participants were asked to react as quickly as possible to the appearance of each digit by pressing the space bar; (c) Choice Reaction: participants indicated whether each digit was odd or even by pressing two predefined keys on the computer keyboard. After four location cue-digit pairs, the recall grid was presented. The three subtasks were carried out in separate blocks of 12 trials each. To avoid any confusion, instructions for each subtask were presented before it was performed. Subtasks were presented in a Latin square order across participants to prevent any training effect. Participants' clear understanding of each subtask was checked before it was performed.

SPS task

Participants performed the task alone in a quiet, brightly lit room at a room temperature of 18–20 °C. They were seated on a chair with a backrest, in front of a table. SPS were introduced to the participants by the experimenter, who stressed that they are a normal phenomenon that can be perceived by everybody. A list of the 11 sensations most likely to be felt (i.e., beat/pulse, itch, tickle, numbness, skin stretch, tingling, warming, cooling, muscle stiffness, flutter, and vibration) was then presented to the participants so that they had some idea of what SPS felt like. This list is based on original papers studying microstimulation-evoked sensations (Ochoa and Torebjörk 1983; Macefield et al. 1990), and was developed by (Naveteur et al. 2005) as a means of studying SPS. When ready, participants had to remove all jewellery from their hands and roll up their sleeves as far from their wrists as possible. They were given antiseptic gel (Aniosgel® 85 NPC, ≈3ml per participant), and were asked to clean their hands for 15 s. Cleansing removes any external agents that might interfere with the task and homogenizes the skin surface across all participants. A latency of 15 s between the cleansing operation and the start of the task was observed, to ensure no sensations caused by rubbing hands or applying antiseptic gel would be perceived during the SPS task. Each participant was given a protocol containing the standardized reduced maps of each hand shown palm-up (with a distance of 11.2 cm between the tip of the middle finger and the palm/wrist boundary), the list of 11 SPS, and two visual analogue scales (i.e., two 10 cm continuous horizontal lines without markers at each end) below each map required for

the confidence rating. A pencil and a 25 × 25 cm piece of smooth white fabric were also distributed to each participant. The start of the session was announced once the participants were familiar with the material, and the protocol was placed away from the participants on the desk to prevent any visual interference. Participants were asked to sit with their back supported by the backrest of their chair. Each hand was tested in a balanced order across participants. For each hand, the ipsilateral leg was turned outward by 60 degrees from the midline. The white cotton fabric was placed on the thigh, and the tested hand rested on it with the palm up and the fingers spaced slightly apart. In this way, only a dorsal part of the hand was in contact with the fabric. The hand not being tested hung down on the outer side of the chair contralateral to the tested hand. The 'start' signal given verbally by the experimenter marked the beginning of each trial: participants focussed on the tested hand with a direct gaze for 10 s so that they could detect any sensations that might occur. The 'stop' signal given by the experimenter announced the end of the 10 s test. Participants had to immediately report in the protocol whether they had detected any sensations on the tested hand. In this case, they were asked to (a) map the extent and location of the sensations by shading the areas where they perceived sensations on the map corresponding to the tested hand; (b) specify directly on the map the perceived intensity of each sensation according to a 10 point scale (1 = just perceptible; 10 = very intense but not painful); (c) indicate their degree of confidence in the location and the extent of the perceived sensations using the two visual analogue scales (ranging from 'not confident' to 'very confident'), and (d) identify the sensations using the list of descriptors. For this final step, participants could choose more than one descriptor and could add descriptors to the list according to what they had sensed. The task lasted approximately 5 min.

Design and statistics

Visuospatial working memory variables

Performance analysis. The total of correctly recalled items for each condition and subtask was converted into percentages. The difference in performances between the conditions of the BP task was assessed using a paired *Student's T*-test. For the CS task, a repeated measure analysis of variance (ANOVA) was carried on with the subtask as the unique within-participant factor (No Reaction, Simple Reaction, and Complex Reaction), followed by *post-hoc* Newman-Keuls tests.

Working memory indices. Since the main aim here was to unravel the relationship between visuospatial working memory and SPS, four indices from the visuospatial working memory tasks were computed. For each of these four indices, the greater the value, the more forgetting occurred: (i) decay rate in the BP task (hereafter DEC index) was obtained through the difference in performance between trials with short (i.e., 5 s) and trials with long (i.e., 20 s) intervals between the memorandum presentation and its recall; (ii)

interference in the CS task (hereafter INT index) was obtained through the difference in performance between the conditions without (i.e., No Reaction) and with the processing of the distractor (i.e., Simple Reaction); (iii) cognitive load in the CS task (hereafter CL index) was computed through the difference in performance between the conditions requiring a simple (i.e., Simple Reaction) and a complex (i.e., Complex Reaction) processing of the distractor. Given that the complex span task presents with three graded levels of complexity (i.e., No Reaction, Simple Reaction and Complex Reaction), a second index of cognitive load, CLslope, was obtained by computing the alpha regression slope of performance decrement¹ as a function of the task complexity (No Reaction, Simple Reaction, and Choice Reaction were respectively defined as complexity levels 0, 1, and 2). To ascertain that the CLslope index was not nil, it was compared to the 0 value through a paired-samples *T*-test.

To assess the validity and reliability of the indices, a split-half correlation procedure was conducted between previously extracted indices for odd and even-numbered trials, followed by the application of the Spearman-Brown prophecy formula. Here, reliability is expressed in r^* . As they were extracted from performances obtained in common tasks, Pearson correlations were also performed between all four indices.

SPS variables

SPS frequency benefitted from special treatment as it is characterized by its topographical distribution. Hand maps filled with shaded areas representing perceived SPS by participants were projected onto a 140×140 mm grid, with a 1mm^2 resolution, and were then converted to binary code (0 = nil; 1 = shaded cell). This process resulted in two binary maps per participant (i.e., left and right hand). A frequency map (Figure 2) was then obtained by summing these maps, with each cell value representing the percentage of participants having shaded it.

Two topographical analyses were conducted as follows: (i) an examination of the spatial distribution depicted in the frequency map was conducted. It asserts that the task was successful and confers validity as regards the spatial characteristics of tactual sensitivity of the hands. The analysis was based on the relative receptor density (Johansson and Vallbo 1979). Percentages of shaded surface area within a segment (i.e., distal phalanx, intermediate phalanx, proximal phalanx, and palm) compared to the surface area of the whole segment were submitted to a Q' test (Michael 2007) for the analysis of proportions. This was done to highlight the differences in proportions of SPS reported between segments; (ii) a secondary analysis, conducted to assess the reliability of the topographical data, consisted in a split-half correlation, followed by the application of the Spearman-Brown prophecy formula between the left and right-hand frequency maps.

The other SPS variables investigated were the mean surface percentage of SPS as referred to the whole hand, surface percentage per SPS, intensity, number of areas, variety, and participants' confidence in location and extent of the

perceived SPS. Their reliability was assessed through the same split-half procedure described above. The frequency of the types of sensations was assessed through chi-squared tests.

Relationship between visuospatial working memory indices and SPS variables

To allow topographical statistics between the topography of SPS frequency and visuospatial working memory indices, 140×140 mm grids, the same as those described above, were each filled with z-transformed indices, for each participant and each hand. This way, cell-wise point biserial correlations were performed between the 98 individual maps reflecting the frequency of SPS and the 98 individual maps filled with the investigated z-transformed indices. This was done separately for each visuospatial working memory index. The resulting probability map was then converted into binary maps (0 = non-significant cell; 1 = significant cell) so that a spatial scan procedure (Kulldorff 1997) could be performed. This consists of a circular window scanning the map in a stepwise fashion to highlight significant clusters of correlated cells. A maximum radius of six cells was chosen, and 999 iterations of the Bernoulli (binary) model were computed. Only significant clusters at $p < .001$ bicaudal were kept. This procedure accounts as a correction, as it eliminates incidental clusters of correlations.

Complementary analyses were computed using a spatial correlation procedure (Sim and Johnson 1998) to assess the differences between the spatial correlation patterns of the indices. This consists of an auto-logistic model for dichotomous spatial data allowing the comparison of two spatial patterns based on their statistical properties. The sum of products of the nearest neighbours was compared between maps with 999 Monte Carlo simulation runs.

Further statistics were conducted to investigate whether visuospatial working memory indices predicted the non-topographic SPS parameters. Multiple regression analyses (not Bonferroni-corrected (Perneger 1998; Cabin et al. 2000)) were conducted with DEC, INT, CL and CLslope indices as predictors, along with age, gender, and BMI since these are factors known to modulate SPS and tactual sensitivity (Kozłowska 1998; Naveteur et al. 2015). This was done for the non-topographic SPS parameters and types of SPS as dependent variables. All variables were z-transformed beforehand.

Results

Reliability and validity analysis

Visuospatial working memory performances

In the BP task, participants performed better under the 5 s condition than the 20 s condition ($t(48)=8.14$, $p < .001$, Cohen's $d = 1.16$, see Table 1 and Figure 3). Two participants completed the 5 s condition without errors, but none completed the 20 s condition without any errors.

In the CS task, the main effect of the subtask was significant ($F(2; 96)=79.5$, $p < .001$, $\eta^2_p=0.62$): participants

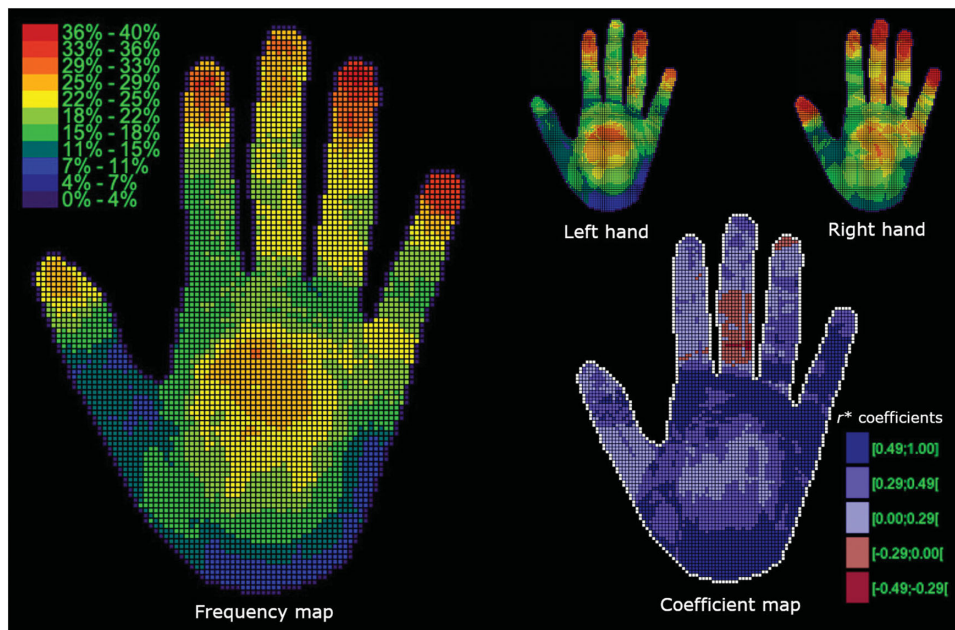


Figure 2. Topographic maps depicting the SPS frequency (% of participants who had shaded a cell) on the left side, the SPS frequency for each hand on the top right, and the Spearman-Brown r^* coefficients between left- and right-hand frequency maps on the right-side. For the frequency maps, cool/blue colours represent the least frequently shaded areas and warm/red colours represent the most frequently shaded areas. For the coefficients map, bluish colours represent positive r^* coefficients and reddish colours represent negative r^* coefficients. The colour intensity denotes the effect size.

Table 1. Mean (SD), minimal and maximal values for performances (%) of the visuospatial working memory tasks, indices extracted from the visuospatial working memory tasks, and non-topographic SPS parameters. The Spearman-Brown r^* coefficient is provided for the visuospatial working memory indices and the non-topographic SPS parameters.

Measures	Mean (SD)	Min	Max	r^*
Visuospatial working memory performances (%)				
Brown-Peterson conditions				
5 seconds	76.49 (14.00)	33.33	100	
20 seconds	63.05 (16.17)	22.92	93.75	
Complex span subtasks				
No reaction	96.94 (3.83)	85.42	100	
Simple reaction	90.9 (8.92)	62.50	100	
Complex reaction	72.28 (19.43)	22.92	100	
Visuospatial working memory indices				
DEC	6.45 (5.55)	-3	22	0.27
INT	2.9 (3.95)	-6	13	0.17
CL	8.94 (7.28)	-5	23	0.52
CLslope	0.09 (0.11)	-0.33	0.43	0.20
Non-topographic SPS parameters				
Spatial extent (%)	19.3 (20.92)	0.29	100	0.76
Spatial extent per area (%)	10.69 (17.28)	0.29	100	0.67
Intensity (/10)	3.52 (2.00)	0.5	7.75	0.69
Variety	2.78 (1.39)	1	7	0.59
Number of areas	4.8 (2.84)	1	11	0.36

performed better in the No Reaction subtask than in the Simple Reaction subtask ($p < .001$; Cohen's $d = 0.73$), and better in the Simple Reaction subtask than in the Choice Reaction subtask ($p < .001$; Cohen's $d = 1.23$, see Table 1 and Figure 3). Twenty-four participants completed the No Reaction subtask without errors (i.e., 48.97% of the sample), while only six completed the Simple Reaction subtask without errors. Two participants completed the Choice Reaction subtask without errors, while also completing the other two subtasks without errors. One of the two subjects also had ceiling performances in the 5 s condition of the BP task.

Visuospatial working memory indices

The means and standard deviations of the visuospatial working memory indices are presented in Table 1. The mean CLslope index was greater than the 0-value ($t(48) = 5.9$; $p < .001$; Cohen's $d = 0.84$).

The Spearman-Brown coefficients obtained for each visuospatial working memory index ranged from $r^* = 0.17$ to $r^* = 0.52$ (see Table 1). Correlations between the indices were low and ranged from $r = -0.13$ to $r = 0.21$, confirming that DEC, INT, CL, and CLslope measured distinct aspects of working memory.

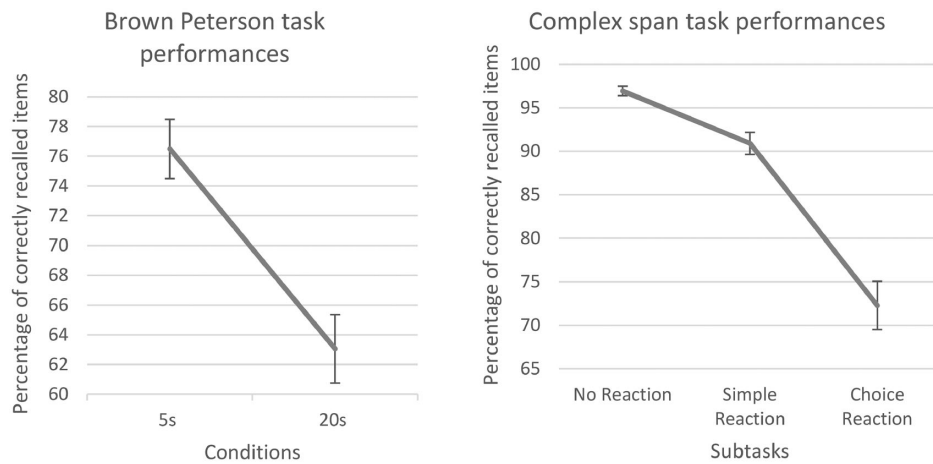


Figure 3. Graphics depicting the mean percentage (\pm 1 SEM) of correctly recalled items in the Brown–Peterson task (left) for each experimental condition, and in the complex span task (right) for each subtask.

Spatial distribution of the SPS frequency

Spontaneous sensations were reported at least once in each cell; however, they were not evenly distributed over the whole hand. The map presented in Figure 2 depicts a proximo-distal gradient in the frequency of SPS. Significant differences were found in the relative spatial extent of SPS ($Q'(3)=2973.4$, $p<.00001$, Cramer's $V=0.11$), as the SPS surface was greater in the distal phalanx (29.3%) than in the intermediate (22%) and the proximal (17.5%) phalanges, as well as in the palm (18%). The finding of the proximo-distal gradient without any contact between the hand and any surface seems related to the traces left by sensory receptors on the skin on the primary somatosensory cortex (Johansson and Vallbo 1979; Gallace and Spence 2010). This replicates previous findings (Michael and Naveteur 2011; Michael et al. 2012, 2015; Borg et al. 2015) and implies that the SPS task was successful. The split-half analysis revealed that Spearman–Brown coefficients ranged from $r^*=-0.39$ to $r^*=0.90$ (Figure 2). Positive correlations were prevalent: large size effect coefficients ($r^*>0.50$) covered 36.61% of the surface of the hand, medium size effect coefficients (r^* from 0.30 to 0.49) covered 32.72% of the surface of the hand, and small size effect coefficients ($r^*<0.29$) covered 24.99% of the surface of the hand. Few negative correlations were found as well: medium size effect r^* coefficients covered only 0.25% of the surface of the hand, and small size effect r^* coefficients covered 4.15% of the surface of the hand. These findings suggest that the measure of SPS frequency is reliable.

Non-topographic SPS parameters

Split-half analyses on the non-topographic SPS parameters revealed acceptable r^* coefficients for all parameters (see Table 1) with the exception of the confidence in location ($r^*=0.004$) and confidence in extent ($r^*=0.097$). Therefore, confidence parameters were not taken into account in subsequent analyses.

All sensations were reported at least once, and several participants added sensations that were not presented in the list, namely contraction, stiffness, pressure, gravity, and airflow.

Based on previous investigations, all reported SPS were classified into five categories: (i) thermal: warming and cooling; (ii) deep: heartbeat, muscle tension, and contraction; (iii) surface: tickle, skin stretch, tingling, flutter, and vibration; (iiii) paretic: numbness and weight; (v) pain-like: itch, and pins and needles. The types of sensation were not equally represented ($\chi^2(5)=172.08$; $p<.000001$; Cramer's $V=0.41$): surface sensations were the most frequently reported (48%), followed by deep (23%), thermal (20%), and paretic (9%) sensations. Pain-like sensations were rarely reported by participants (0.39%).

The relationship between SPS frequency and visuospatial working memory indices

Correlational maps between SPS frequency and visuospatial working memory indices are displayed in Figure 4. Negative correlations indicate a decrease in the frequency of SPS with higher indices, while positive correlations indicate an increase in the frequency of SPS with higher indices. Negative correlations were mostly found between SPS frequency and DEC, covering as little as 1.37% (95% Wilson Confidence Interval [1.1, 1.8%]) of the surface of the hand, INT covering as much as 12.6% (95% CI [11.0%, 13.0%]) of the surface of the hand, CL covering as much as 12.14% (95% CI [11.2%, 13.1%]) of the surface of the hand, and CLslope covering a surface of 11.62% (95% CI [10.7%, 12.6%]) of the hand. Meanwhile, positive correlations were found between SPS frequency and INT, covering 4.3% (95% CI [3.7%, 5.0%]) of the surface of the hand, and CLslope covering 0.62% (95% CI [0.4%, 0.9%]) of the hand.

Differences in the topography of correlations

Negative correlations with DEC were restricted to the intermediate phalanx, and negative correlations with CL were distributed between the distal phalanx and the base of the palm. Meanwhile, differences in the topography of the correlations were observed for INT and CLslope, with negative

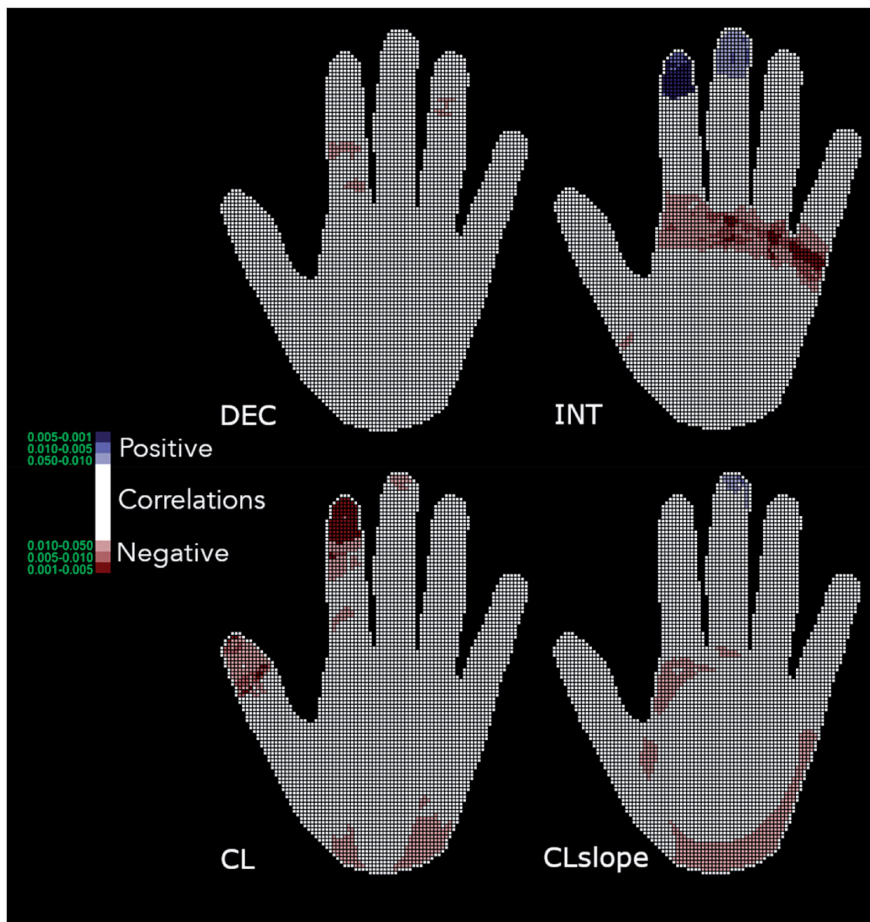


Figure 4. Topographic probability maps of the correlations between SPS frequency and the working memory indices DEC, INT, CL, and CLslope. Bluish colours represent significant positive correlations, and reddish colours represent significant negative correlations. The colour intensity denotes the significance level.

correlations gathered around the palm and positive correlations over the distal phalanx.

The correlation pattern observed with DEC was significantly different from that observed with INT ($p=.001$), CL ($p=.001$) and CLslope ($p=.001$). This was also the case between CL and CLslope correlation patterns ($p=.001$) and between INT and CLslope correlation patterns ($p=.001$). A similarity is evident between INT and CL in that significant clusters were located in the distal segment of the index fingers. However, these are distinct effects on SPS perception as the signs of the correlations are opposite. This supports that each aspect of working memory processes assessed through these indices is differentially involved in the perception of SPS, and also backs the previously reported weak correlations between these indices.

Difference between good and poor interference managers

Distinct and opposite patterns appear to be associated with INT (Figure 4): a low INT score is associated with an increase

of SPS on the palm at the expense of SPS on the fingertips, and conversely, a high INT score is associated with an increase of SPS on the fingertips at the expense of SPS on the palm. Secondary analyses were conducted through a median split procedure based on INT scores, resulting in the creation of two frequency maps (Figure 5), reflecting the frequency of SPS reported by good interference managers (i.e., low INT scores, $N=24$) and by poor interference managers (i.e., high INT score, $N=25$). A cell-by-cell comparison between poor and good interference managers' frequency maps was performed, using the Barnard test (Barnard 1945). The alpha level was set to 0.05 uncausal. The resulting map depicting cells where differences between good and poor interference managers were significant was also submitted to the spatial scan procedure (Kulldorff 1997). As can be seen in Figure 5, good interference managers reported more SPS on the palm than poor interference managers on 5.18% (95% CI [4.56%, 4.39%]) of the hand, while poor interference managers reported more SPS on the fingertips than good interference managers on 4.99% (95% CI [4.39%, 5.68%]) of the

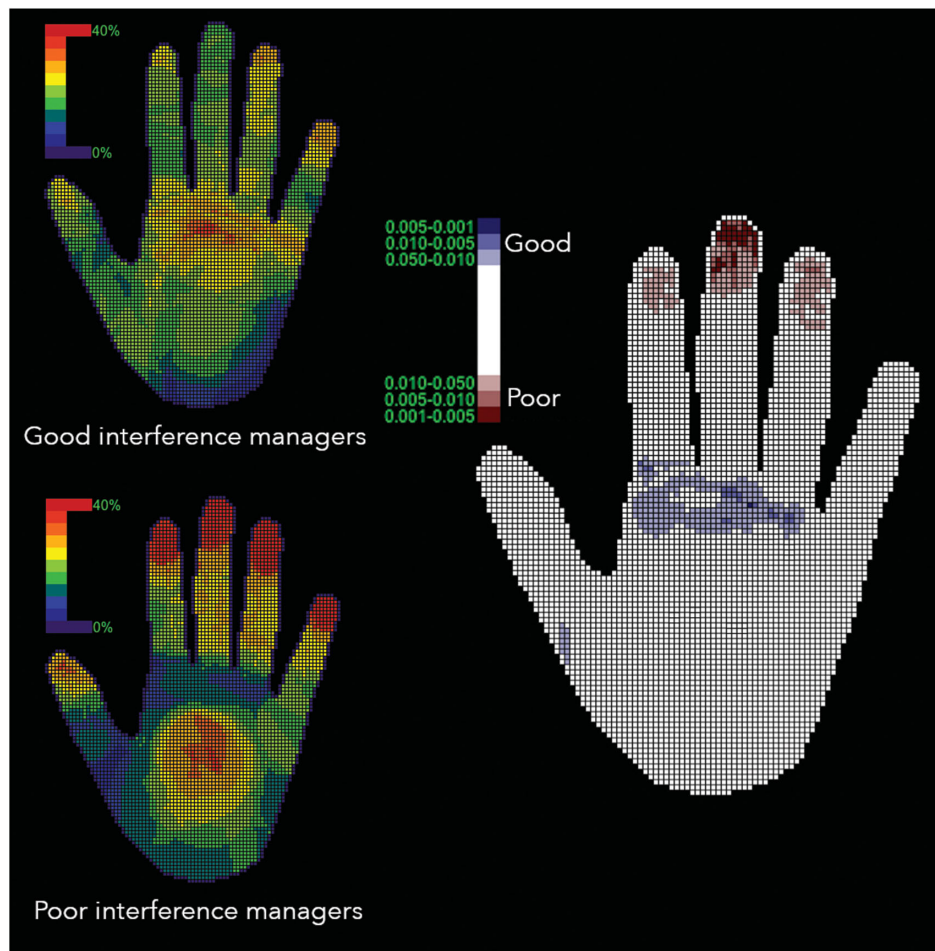


Figure 5. Topographic maps of SPS frequency (% of participants who had shaded a cell) for good interference managers and poor interference managers, using a colour scale: cool/blue colours represent the least frequently shaded areas, and warm/red colours represent the most frequently shaded areas. The topographic map is an exact probability map based on the difference between good and poor interference managers. Only significant clusters ($p < .001$) are presented. Bluish colours denote the supremacy of good interference managers, and reddish colours denote the supremacy of poor interference managers. The colour intensity represents different probabilities.

hand. This suggests that individual differences in managing interference probably determine the locus of sensitivity to SPS.

Visuospatial working memory indices and non-topographic SPS parameters

The age of participants negatively predicted the spatial extent of SPS ($\beta = -0.32$, $SEM = 0.14$, $t(48) = -2.30$, $p = .03$, $R^2 = 0.20$) and INT positively predicted the number of disjointed areas ($\beta = 0.33$, $SEM = 0.14$, $t(48) = 2.41$, $p = .02$, $R^2 = 0.25$) (Table 2). This means that younger participants reported SPS on an overall larger surface, and that participants with higher forgetting due to interference reported more disjointed areas.

The CL index negatively predicted the perception of surface-type sensations ($\beta = -0.37$, $SEM = 0.15$, $t(48) = -2.55$, $p = .02$, $R^2 = 0.20$) (Table 3). This indicates that participants

with higher forgetting due to cognitive load reported less surface-type sensations.

Discussion

We hypothesized that conscious body awareness, as assessed through the perception of SPS, would be modulated by visuospatial working memory abilities. Difficulties in visuospatial working memory resulting from the decay of representations as well as interference and cognitive load induced by distractors were examined in relation to the perception of SPS. This study found that poor performance due to decay and cognitive load was associated with a reduction of SPS frequency. Interestingly, two distinct patterns in the frequency of SPS were found between good and poor interference managers, respectively reporting more SPS on the palm and the fingertips. Regarding non-topographic SPS

Table 2. Standardized β coefficient (+1 SEM) and adjusted R^2 determination coefficients from the multiple regression analysis carried out on the five collected dependent variables with gender, age, body mass index (BMI), DEC, INT, CL, and CLslope as independent variables.

	Spatial extent	Spatial extent/area	Intensity	Variety	Number of areas
Age	-0.33 (0.14)*	-0.25 (0.14)	0.01 (0.15)	-0.25 (0.14)	-0.25 (0.14)
Gender	-0.12 (0.14)	-0.07 (0.14)	-0.18 (0.15)	-0.02 (0.14)	-0.02 (0.14)
BMI	-0.13 (0.14)	-0.17 (0.14)	0.18 (0.15)	0.00 (0.15)	0.05 (0.14)
DEC	0.07 (0.15)	0.03 (0.14)	-0.21 (0.15)	0.23 (0.15)	0.05 (0.14)
INT	-0.03 (0.14)	-0.11 (0.14)	0.20 (0.15)	-0.08 (0.14)	0.33 (0.14)*
CL	-0.25 (0.15)	-0.25 (0.15)	-0.04 (0.15)	-0.26 (0.15)	-0.19 (0.14)
CLslope	-0.09 (0.15)	-0.21 (0.14)	0.01 (0.15)	0.10 (0.15)	0.18 (0.14)
Adjusted R^2	0.059	0.067	-0.026	0.03	0.12

Significant predictors at least at $p < .05$ are marked with an asterisk.

Table 3. Standardized β coefficient (+1 SEM) and adjusted R^2 determination coefficients from the multiple regression analysis carried out on the six collected dependent variables with age, gender, BMI, DEC, INT, CL, and CLslope as independent variables.

	Thermal	Deep	Surface	Paretic	Pain-like	Total
Age	-0.14 (0.15)	0.05 (0.15)	-0.18 (0.14)	-0.09 (0.15)	-0.20 (0.14)	-0.13 (0.15)
Gender	-0.16 (0.15)	0.01 (0.16)	-0.05 (0.14)	-0.06 (0.15)	-0.13 (0.14)	-0.02 (0.15)
BMI	-0.06 (0.15)	-0.04 (0.15)	0.02 (0.14)	0.01 (0.15)	-0.04 (0.14)	-0.24 (0.15)
DEC	-0.03 (0.16)	-0.16 (0.16)	0.13 (0.15)	-0.05 (0.15)	-0.02 (0.15)	0.01 (0.15)
INT	-0.08 (0.15)	0.26 (0.15)	-0.05 (0.14)	0.20 (0.15)	0.12 (0.14)	-0.01 (0.15)
CL	-0.11 (0.16)	0.07 (0.16)	-0.37 (0.15)*	-0.06 (0.15)	-0.29 (0.14)	-0.08 (0.16)
CLslope	0.16 (0.15)	0.01 (0.15)	0.12 (0.15)	0.23 (0.15)	0.24 (0.14)	0.10 (0.16)
Adjusted R^2	-0.062	-0.064	0.067	-0.032	-0.073	0.096

Significant predictors at least at $p < .05$ are marked with an asterisk.

parameters, poor performances due to interference led to an increase in the number of disjointed areas, while poor performances due to cognitive load led to a decrease of surface type SPS. Each of these findings will be described and discussed independently, and a conclusion will be reached by comparing these findings.

Decay

Decay in working memory refers to the passive mechanism responsible for the loss of previously activated and maintained representation. In this study, we observed that forgetting due to decay was associated with lower SPS frequency on the fingers. Hence, fast decay in working memory would also alter body awareness. This would emphasize the time-dependent nature of body awareness – indeed, body awareness *ascends* or *emerges* but never remains indefinitely. This temporary access to body awareness would depend on the individual's decay rate in working memory.

As working memory is quantity-limited (Cowan 1999; Baddeley and Hitch 2010; Barrouillet and Camos 2012), it depends on loss of information to remain efficient (Brown 1958; Peterson and Peterson 1959). The decay of representations would be their natural pathway out of the working memory to their original state of long-term stored representations (Cowan 1999). In the case of body awareness, decay could be explained as body-part representations returning to their original state of “background of bodily sensations” (Kinsbourne 1998). Hence, as time goes by, body representations would fade from awareness, and the perception of SPS would follow. Decay in working memory is prevented when keeping representations active, and this would be achieved by focussing attention on the representation (Kinsbourne 1998; Wolpert et al. 1998; Cowan 1999). An inability to prevent decay could account for deficits where limb awareness

is lost within seconds and can only be held when the body part is brought into visual focus (Wolpert et al. 1998; Haggard and Wolpert 2005). Hence, without attentional focus, body representations would decay. Our findings demonstrate that decay is a mechanism involved in the perception of the body and that individual differences in the managing of decay modulate body awareness through the perception of SPS. Temporal variability in body awareness as proposed by models in neuropsychological research (Kinsbourne 1998; Wolpert et al. 1998; Haggard and Wolpert 2005) could be linked to working memory capability.

Interference

Managing distractors results in a diversion of the focus of attention away from the active content of working memory, causing interference and, thus, forgetting. Increased forgetting due to distractors' interference was associated with both reduced SPS on the upper segment of the palm and increased SPS on the fingertips. The key finding is the finger/palm dissociation that was first observed when investigating tactile sensitivity of the hand (Vallbo and Johansson 1984) and which appears with tactile attention too (Gálvez-García et al. 2012). Spontaneous sensations were reported more on the fingertips by participants who have difficulties managing interference and reported more on the palm by participants who can easily handle interference.

Attention and vision are major factors in the emergence of body awareness, as they enhance and suppress activations in the primary somatosensory cortex (Mima et al. 1998; Gallace and Spence 2008, 2010) and facilitate tactile perception (Naveteur 2007) when brought onto a body part. Meanwhile, when diverted from the active representation in working memory, attention and vision lead to the interference from distractors (Cowan 1999; Barrouillet et al. 2004;

Oberauer et al. 2016). Those enhancing and suppressive effects generated by attention and vision were observed as well on SPS, probably reflecting the inhibition of less salient SPS (i.e., on the palm) to the benefit of SPS arising on more sensitive areas of the hand (i.e., fingers) (Macefield et al. 1990; Michael and Naveteur, 2011; Michael et al. 2012; Naveteur et al. 2015).

But the finger/palm distinction in SPS is also determined by interoceptive abilities, as heightened interoception leads to the perception of SPS on the palm and poor interoception to a greater perception of SPS on fingers (Michael et al. 2015). It seems that perceiving SPS and maintaining representations in working memory despite distractors both rely on inhibition. Indeed, inhibition of SPS arising on the fingers allows the exploration of other areas of the hand, leading to the perception of SPS that are less salient and less frequent (Michael et al. 2012, 2015). The finding that increased interference from distractors predicted a greater number of disjoined areas may be reminiscent of this. Meanwhile, inhibition of distractors places the focus back on the active representation in working memory (Michael et al. 2006). The similarity of the results observed here suggests that the ability to maintain representation in working memory despite distractors may be related to interoception.

Cognitive load

Cognitive load increases as the complexity of distractors increases and may be a further reason for forgetting. Highly complex distractors would alter how representations are maintained in working memory (Barrouillet et al. 2004; Oberauer et al. 2016). We observed that forgetting due to the distractors' cognitive load in visuospatial working memory was associated with a decrease in the frequency of SPS. But we also found that it led to alterations of SPS characteristics, with fewer surface-type SPS perceived.

Working memory efficiency depends on limited attentional resources that need to be shared between keeping representations active and processing interfering information (Barrouillet et al. 2004; Egeth and Kahneman 1975). As the complexity of the interfering information increases, attentional demand would also rise, and as demand exceeds available capacity, performances in one or both tasks suffer since they compete for attentional resources (Egeth and Kahneman 1975; Gopher and Navon 1980; Barrouillet et al. 2004). With performances suffering from increasing complexity, representations that have been kept active might be altered in different ways, referred to as the seven sins of the memory (Schacter and Slotnick 2004). Hence, representations might be prone to various degrees of forgetting (i.e., transience, absent-mindedness, or blocking), but could also be distorted by stored representations (i.e., persistence or bias), altered to incorporate external information (i.e., suggestibility), or be attributed to an incorrect source (i.e., misattribution). As Schacter states, 'human memory is not an exact reproduction of past experiences but instead an imperfect process that is prone to various kinds of errors and distortions' (P467) (Schacter et al. 2011). Body representation in

the case of asomatognosia is subject to similar alterations. For example, brain lesions lead to a distortion of the representation underpinning the hand in a tactile stimulation localization task (Rapp et al. 2002; Haggard and Wolpert 2005; Longo et al. 2010). Mislocalization of body parts is typically observed in autotopagnosia, while fingers seem indissociable in finger agnosia, symptoms that are linked to distorted body representations (Haggard and Wolpert 2005). Autoscopic illusions such as out-of-body experiences demonstrate that body representation can be subject to alteration without massive brain damage (Persinger 2001). Some models posit that alterations of body representations lead to perceptual distortions, resulting in maladaptive behaviour regarding the body state and physical needs (Kinsbourne and Lempert 1980; Kinsbourne 1998; Sakson-Obada et al. 2018). Accordingly, such alterations in body representations may be reflected in the perception of SPS, altering the reporting of their characteristics on the hand. Overall, our findings suggest that – similar to representations in working memory – body awareness could suffer from both forgetting and distortion of body representations.

Interference and cognitive load

Decay, interference, and cognitive load indices were considered to reflect distinct cognitive processes. This was supported by the lack of correlation between the indices, and between the topographical patterns of correlations with the frequency of SPS. However, concerns remain regarding the second distractors cognitive load index (CLSlope). Similar to the interference, it revealed a finger/palm dissociation in the pattern of correlation, only with smaller correlated surfaces and more dispersed correlations on the palm. This could be because CLSlope uses the performances from which the interference (INT) and cognitive load (CL) indices are derived. Consequently, interference and cognitive load – involving inhibition and resource sharing respectively – may both modulate the perception of SPS distinctly. After all, evidence and theoretical models suggest that these two processes are dissociable yet interacting (Michael et al. 2006, 2007, 2014; Michael, Dorey, et al. 2020). However, when assessed together, inhibition processes seem to have a greater impact on SPS than resource sharing. This claim appears to be certainly plausible as inhibition of SPS has been repeatedly documented (Michael and Naveteur 2011; Michael et al. 2012; Naveteur et al. 2015).

Limitations and further considerations

The study presented in this paper suffers from some limitations, the main ones being discussed below. The choice of measures may be subject to debate, as working memory factors are not easily dissociable. On one hand, according to some models, decay results from the presence of distractors, diverting the focus away from the representation activated in working memory (Brown 1958; Cowan 1999; Barrouillet and Camos 2012; Barrouillet et al. 2012). On the other hand, processing distractors while maintaining representations in

working memory adds complexity, and thus increases the cognitive load (Egeth and Kahneman 1975). Moreover, we acknowledge that decay is a controversial topic in working memory literature, with models advocating that there is no timely decay of representations and that loss of information in working memory is due to interference (Oberauer et al. 2016). Therefore, the question arises as to whether the indices of working memory indeed reflect independent processes. However, we contend that the observation of dissimilar effects and spatial distribution of correlations between these factors with SPS is evidence that they are indeed distinct factors within visuospatial working memory and probably contribute differently to body awareness.

The sample may constitute another limitation of our study as it is composed mainly of young women. This disparity is a direct consequence of the male-to-female ratio in the population of undergraduate students who voluntarily participated in the research. Gender and age differences were repeatedly observed in many measures of visuospatial abilities (Halpern and Collaer 2009), as well as in the perception of SPS (Naveteur et al. 2015). However, young women tend to show the most representative result regarding SPS perception, as they report less frequent SPS than men independently of age and demonstrate a stronger attentional effect on SPS frequency. This provides insights into the age differences we observed, with larger areas of SPS reported by younger individuals. Therefore, a sample with a majority of young women has the advantage of avoiding ceiling effects in the perception of SPS, while at the same time providing sufficient data to highlight the involvement of cognitive processes. Finally, the female/male ratio of this present study is very close to that of the previous investigation on SPS, ensuring the comparability of the results through studies.

The SPS task may as well be subject to criticism. First, it depends on subjective reports, meaning that SPS perception is subject to various sources of bias (Michael et al. 2015, 2017). It could also be argued that we focus more on SPS memory than on SPS perception, a concern that cannot be completely ruled out because memory processes are embedded in perceptual systems (Glenberg 1997; Slotnick 2004; Harrison and Tong 2009; Teng and Kravitz 2019): measures of perception rely on recall of the perceptual experience, and memory processes involve perception, in such a way that decrement in performances can reflect the impact on both perception and memory processing. Finally, the standard task of SPS is proposed to naïve participants. Because of the nature of body awareness, that develops through bringing attention to the body (Kinsbourne 1998), repeated exposure to the SPS task could lead to training in body awareness abilities. But these aspects are not yet well known and might motivate future studies on SPS adopting an intra-individual approach with repeated measures.

The legitimacy of the study of SPS lies within the ten years of studies that have demonstrated and replicated the involvement of many cognitive processes such as attention and vision (Michael and Naveteur 2011; Michael et al. 2012;

Naveteur et al. 2015; Tihanyi and Köteles 2017), interoception (Michael et al. 2015), or gating of motion (Beaudoin and Michael 2014). These studies infer that SPS contribute to body awareness, and thus that they could offer a window to further investigate cognition in body awareness. For example, pain and catastrophic thinking associated with fibromyalgia, a condition characterised by somatosensory amplification and/or altered interoception, have been found to greatly amplify the frequency of SPS (Borg et al. 2015, 2018). These findings correlate with the phantom limb phenomenon, where an excessive attentional focus on the representation of the missing limb would lead to phantom sensations and pain (Berlucchi and Aglioti, 1997; Kinsbourne 1998), which would be greatly reduced by visual perception of the missing limb (i.e., using a set of mirrors or a plastic limb) (Ramachandran 1998).

Finally, spatial localization abilities, rather than working memory, may explain our findings. The SPS task is mainly visuospatial since it requires participants to localize and define the shape and size of the sensations they perceive. If localizing SPS was difficult, then remembering their location would be difficult too. Spatial tactile abilities are tightly linked to small fields of receptive units on the glabrous skin, which are most abundant in the distal areas (Vallbo and Johansson 1984). Thus, localization difficulties should be associated with a steeper proximo-to-distal gradient in the perception of SPS, with greater dependence on highly sensitive areas. This is indeed what we observed in this analysis, with a steeper gradient in the SPS frequency of poor interference managers, which was interpreted in terms of abilities in managing interference (Figure 5). The differences observed might account for variability in terms of localization ability more than the ability to resist interference in visuospatial working memory. However, it could be expected that, as a low-level process, spatial localization would undermine the measures of decay and distractors' cognitive load as well, and would thus result in similar modulation of the SPS frequency. This is not what has been observed, as we found distinct patterns of clusters between the indices. The way low-level and higher-level visuospatial processes operate is difficult to catch in the present study and would need further investigation.

Individual differences in managing decay, interference, and cognitive load in visuospatial working memory produced variations in SPS perception. Visuospatial working memory abilities would play a role in body awareness, and disturbances of body awareness could be at least due to alteration of visuospatial working memory. Besides merely keeping representations active to counteract decay (Wolpert et al. 1998), visuospatial working memory processes could be involved in the updating of body representations: allowing body representations in focal awareness, and applying changes to fit the current body condition through visuospatial, proprioceptive, and tactile information (e.g., SPS) (Kinsbourne 1998; Haggard and Wolpert 2005). Hence, failures in working memory could contribute to asomatognosia symptomatology (Haggard and Wolpert 2005).

Conclusion

Spontaneous sensation perception may offer a window on body representations, allowing the study of processes involved in body awareness. As body representations decay, so may SPS; as body representations are altered, so may SPS. An interesting point is that inhibition abilities in working memory probably allows a better perception of less salient SPS. By tackling the novel theme of working memory in body awareness, this study has raised more questions than it has resolved. Future neuropsychological studies may help consolidate our claims.

Note

1. $\alpha = \text{covariance}(x,y) / \text{variance}(x)$, where x is the task complexity level (0, 1, and 2), and y is the percentage of errors.

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Entracte

Dans cet Acte II, nous avons identifié les mécanismes attentionnels responsables de la sélection dans le *background of bodily sensations* et du maintien du corps en conscience (Kinsbourne, 1998).

Le Tableau 1 a approfondi l'implication de l'attention en identifiant les mécanismes attentionnels responsables de la sélection sensorielle. L'étude qui y est présentée démontre le rôle distinct et complémentaire de l'inhibition et de la régulation des ressources cognitives. Ces résultats furent l'occasion d'appréhender toute la complexité des processus attentionnels engagés dans la conscience corporelle, et de comment nos habiletés attentionnelles influencent la manière dont nous explorons notre corps et appréhendons nos sensations. Dans le Tableau 2 nous nous sommes intéressés à ce qu'il advient des représentations une fois qu'elles sont sélectionnées. Cette étude nous a permis d'apporter des arguments quant au rôle de la mémoire de travail visuospatiale dans la conscience du corps, un rapprochement qui – à notre connaissance – a été soit rejeté soit ignoré jusqu'à présent. Nous y argumentons la nécessité de maintenir les représentations du corps en mémoire de travail pour en prendre conscience, mais également de la responsabilité de ces mécanismes dans leur intégrité et leur mise à jour en mémoire à long terme.

A travers l'étude des SPS, nous avons pu voir que l'expérience subjective corporelle dépend de processus attentionnels et en mémoire de travail non-spécifiques au corps. Ces recherches nous ont permis en plusieurs instances de discuter du rôle de ces mécanismes dans certaines distorsions perceptuelles du corps, mais aussi plus largement de comment ces habiletés cognitives sont étroitement liées à l'image que nous nous faisons de notre corps. Ce *material me* (A. D. Craig, 2009a, 2010b) n'est pas une photographie à l'identique du corps, c'est une construction subjective dépendante de ce dont nous prenons conscience et qui détermine de nombreux aspects du *Self*. Dans l'Acte III, nous clôturerons cette réflexion en explorant la relation des mécanismes neuraux à l'origine de ces construits subjectifs avec les SPS.

ACTE III. ETUDE APPROFONDIE DES CORRELATS COGNITIFS ET NEURAU

De l'origine à la raison des sensations spontanées

Tableau 1. La jonction temporo-pariétale et l'insula antérieure

Les travaux précédents ont abordé séparément la question de l'origine des SPS et celle des mécanismes qui les amènent en conscience. Nous avons pu voir que ce phénomène possède une forte dépendance à l'attention, qui se manifeste à la fois dans la fréquence des SPS qu'à travers l'activité oscillatoire corticale de SII (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015). Des aires corticales dévouées à l'intégration multimodale et à l'intéroception, TPJ et AI, seraient responsables de ces modulations en SII (Gallace & Spence, 2008, 2009, 2010; Taylor-Clarke et al., 2002).

En effet TPJ et AI sont des nœuds clés du réseau de saillance, qui engagent l'attention dans l'environnement, et du réseau cérébral par défaut, qui promeut l'attention interne (Corbetta & Shulman, 1998, 2011; Davey et al., 2016; Fox et al., 2005; Modinos et al., 2009). Ces différents états attentionnels et l'activité de TPJ et AI se caractérisent par ailleurs par des modulations de l'arousal (Chapell, 1994; Fan et al., 2012), lui-même déterminant les ressources cognitives accessibles. L'étude suivante aurait ainsi pu être présentée plus tôt dans le manuscrit, puisqu'en ciblant TPJ et AI nous étudions comment l'état d'éveil, et l'aptitude à engager l'attention dans l'environnement et hors du *Self* influencent la conscience du corps. Mais l'intérêt pour ces régions corticales n'émane pas seulement de leur appartenance à deux réseaux attentionnels distincts. La littérature autour de TPJ relève ainsi fréquemment son rôle dans l'élaboration du sentiment d'incarnation, et ses lésions dans les hallucinations autoscopiques (Arzy et al., 2007; Blanke, 2008; Blanke et al., 2004; Brosey & Woodward, 2017; Eddy, 2016; Ionta et al., 2014). Des preuves ont été avancées concernant l'implication d'AI dans ces distorsions perceptuelles (Yu et al., 2018), mais on met surtout en avant le couple de TPJ avec les aires corporelles extra-striées (EBA; (Blanke, 2008), des régions occipitales spécialisées dans le traitement visuel des parties du corps (Blanke, 2008; Lacey et al., 2017; Limanowski et al., 2014; Perruchoud et al., 2016; Urgesi et al., 2004). Cette cognition autour du *Self* étant incompatible avec l'engagement attentionnel de l'environnement, la question du rôle de TPJ et de ses échanges avec AI et EBA dans la conscience du corps reste ambiguë (voir Prologue, parties I-B-2 & 3, et partie II-A).

Acte III - ETUDE approfondie des corrélats cognitifs et neuraux

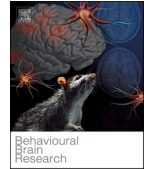
Dans l'article suivant, nous avons cherché à délier les rôles respectifs de l'attention et de l'incarnation dans la perception des SPS à l'aide de deux études. D'une part, nous nous intéressons à la connectivité fonctionnelle de TPJ-AI et TPJ-EBA, et de comment cette activité EEG de base affecte les SPS. D'autre part, à l'aide de mesures déclaratives et grâce à un enregistrement au repos de la conductance cutanée, nous apportons de nouveaux éléments concernant le rôle de l'attention et de l'arousal dans le phénomène des SPS.

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To the self and beyond: Arousal and functional connectivity of the temporo-parietal junction contributes to spontaneous sensations perception

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ABSTRACT

The temporoparietal junction (TPJ), along with the anterior insula (AI) and the extrastriate body area (EBA), play a major part in embodiment and self-awareness. However, these connections also appear to be frequently engaged in arousal and attentional processing of external events. Considering that these networks may focus attention both toward and away from the self, we set to investigate how they contribute to the perception of spontaneous sensations (SPS), a common phenomenon related to self-awareness and mediated by both interoceptive and attentional processes. In Experiment 1, resting-state EEG was recorded, as well as arousal reported via a questionnaire, followed by a SPS task. Functional TPJ-AI and TPJ-EBA connectivity were computed using eLORETA. Spatial correlational analyses showed that less frequent SPS coincided with greater TPJ-AI and TPJ-EBA functional connectivity, especially in the theta and alpha frequency bands. High self-reported arousal predicted low intensity and low confidence in the location of SPS. Resting-state skin conductance level (SCL) was recorded in Experiment 2, followed by the SPS task. Less frequent SPS coincided with greater SCL. Findings are interpreted in terms of attention and self-related processes, and a discussion of the TPJ participation in self-awareness through SPS is presented.

1. Introduction

Being aware of oneself means having access to many aspects of the self, ranging from body sensations to thoughts and emotions. Awareness requires attentional processes, allowing one to focus on the body and thus to apprehend the information it conveys, from sensory inputs to body representations [1]. Conversely, diverted attention would weaken access to body awareness.

The temporoparietal junction (TPJ) would play a key role in self-awareness. Referring to an area situated at the intersection of the inferior parietal lobule, the superior temporal sulcus, and the lateral

occipital cortex [2], and comprising the supramarginal and angular gyri [3], the TPJ is a multimodal cortical region, receiving inputs from thalamic, limbic, somatosensory, visual and auditory areas [2,4]. Interest in the TPJ persists with the lack of understanding of its precise function since it is involved in attentional processes and arousal [5–7], as well as in social cognition [8,9], or memory retrieval [9]. Besides, the TPJ is a great candidate for self-awareness, since it was associated with self-referential processes such as theory-of-mind [9], self-other discrimination [10–13], self-location [14,15], agency [16,17], and embodiment [18,19].

The focus of this paper is placed deliberately on embodiment and

Abbreviations: ADCL, Activation/Deactivation Checklist; AI, Anterior Insula; BMI, Body Mass Index; EBA, Extrastriate Body Area; EEG, Electroencephalography; eLORETA, Exact Low-Resolution Tomography; SCL, Skin Conductance Level; SPS, Spontaneous Sensations; TPJ, Temporoparietal Junction.

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self-location. As both involve the feeling of being present at a certain location, their failure results in autoscopic experiences, such as out-of-body experiences and heautoscopy, where one can see oneself from another location in space [20]. Temporoparietal junction dysfunction would lead to these bodily illusions, as would two other cortical areas. The first, the extrastriate body area (EBA), located in the lateral occipitotemporal cortex, intervenes primarily in the integration of bodily inputs [18,21–25], in body-oriented attention [26], and illusory limb ownership [27]. The second, the anterior insula (AI), located in the ventrolateral prefrontal cortex, within the Sylvian fissure, operates *inter alia* in interoception [28–31], i.e. the perception of the physiological condition of the body, but also in the looking down perspective illusion [14,15], i.e. a manipulation of the first-person perspective resulting in the feeling of looking down at the own body while being in a supine position. The TPJ shares connections with both the AI [2–4,7,32,33], and the EBA [8,15]. The TPJ connections with both the EBA and the AI appear to play a critical role in self-awareness.

Previously, we mentioned that the TPJ might participate in attentional processes and arousal, but activations of both EBA and AI were also frequently associated with high arousal [6,34,35]. Arousal refers to the level of autonomic activation sometimes due to cognitive processing frequently assumed to be attentional processing [34–40]. From a functional point of view, attentional processes seem to translate into low-frequency cortical oscillations, such as delta (0.5–3.5 Hz) [41,42], theta (4–7 Hz) [41,43–45] and alpha (7.5–12 Hz) [43,46–49]. Hence, while high arousal is associated with attentional networks mediating capture by salient environmental cues [6,36,50], areas processing interoceptive stimuli such as the AI also stand out in the generation of arousal. Along with this discrepancy, high arousal would allow attentional focus on the self and access to private information [37,51,52].

The major influence of attention and self-referential processes in body-awareness was documented in a series of studies investigating spontaneous sensations (SPS), i.e. the perception of sensations arising on the body without any external triggers. SPS are quite frequent phenomena that can be easily perceived by almost anyone. Focusing on those events may contribute to maintaining the body image in consciousness [53]. While attention taken away from the body dampens the experience of SPS [54,55], attention directed inwards enhances the perception of SPS [56,57]. These findings indicate that attention to external events and attention to thoughts and internal sensations are two competing states. As Morin [58] suggested, there is evidence that self-awareness rises through a state of focus toward the self, versus a focus toward the environment. When considering the involvement of TPJ connections with the AI and EBA in self-awareness, a discrepancy remains between self-referential processes and attention/arousal implication. There seems to be an anticorrelation between two cognitive states of focus, either toward the inner world (i.e. self-processing) or toward the outer world (i.e. salience and attentional capture). This distinction between the two states of focus can be observed in brain imaging [59] and has also been suggested within the context of SPS [56]. Many questions arise from this gathering. First, if SPS relate to self-awareness, how would SPS associate with the functional connections TPJ-EBA and TPJ-AI? Second, could arousal be negatively associated with SPS perception, even when affiliated with self-referential processes? And third, could the functional connections TPJ-EBA and TPJ-AI correlate in the same way that arousal does with SPS, or could they be dissociated?

In this paper, we present two studies investigating how these factors, as individual traits, affect SPS perception. In the first study, we focused mainly on resting-state TPJ functional connectivity with the AI and EBA, as well as the self-reported propensity to high arousal. As we have an interest in the role of cortical oscillations, we used EEG. In the second study, we investigated the question of arousal further through resting-state electrodermal activity. Specifically, we used skin conductance level (SCL), since it reflects tonic components of autonomic arousal and qualifies as a physiological trait of arousal [60]. We hypothesized that,

since arousal relates closely to attention [35,36], the propensity to high arousal would be associated with decreased perceived frequency of SPS. Given that the literature remains inconsistent regarding how functional connections in the brain, arousal, and self-referential processes interrelate, we can formulate the general hypothesis that functional connectivity of the TPJ with both the AI and EBA would be related to the perception of SPS. We might expect this relationship to translate primarily in low oscillations (i.e. delta, theta, and alpha), based on the assumption that those oscillations would reflect attentional processes involved in SPS perception.

2. Experiment 1

2.1. Participants

The study followed the Helsinki Declaration and the protocol was approved by the local ethics committee (reference number IRB 00,009,118). Participants were students at the Lumière University in Lyon, France. During the first steps of the experimental procedure, they completed a form containing questions on sociodemographic and health characteristics. Items included age, gender, height, weight, use of psychotropic medication (and if so, the reason why; antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc.), regular use of other psychoactive substances (alcohol, marijuana, etc.), and history of cardiovascular diseases or diabetes mellitus. Besides, participants could report any other information they considered to be of importance for the study. Any report of a history of neurological or psychiatric illness or psychoactive substance abuse or any disease that may affect tactile perception, such as diabetes mellitus or cardiovascular disease, led to exclusion. Thirty-eight volunteers participated in the study, ten were excluded based on the above-mentioned criteria, and one because of recording issues compromising the EEG data. Twenty-seven participants (14 female and 13 male), all right-handed, with a mean age of 22.1 ± 2.77 (age range: 19–28), and a mean body mass index of 21.2 ± 1.33 kg/m² (range: 19.26–23.89 kg/m²) were therefore included in the study. All gave their written informed consent to participate before the test.

Power analyses were conducted on the effect size of the proximo-to-distal gradient in the frequency of SPS, which is the most prominent characteristic of these phenomena. Based on published studies [53,61], the weighted average effect size expressed as Cohen's *w* is 0.52 (i.e., large) and expressed as Cramers's *V* is 0.26 (i.e., medium to large). Provided a power of 90 % to detect a similar medium effect size and an alpha at 0.05, the number of hand maps needed is 53. Given that, in the present study, two hand maps per participant are collected (one per hand), the sample size needed is 27 participants. With a sample of 27 participants (i.e., 54 hand maps) there is enough power (91 %) to diminish Type II errors.

2.2. Materials

2.2.1. Activation/Deactivation Check-List (ADCL; Thayer, 1967)

To assess a declarative measure, the propensity (trait) to arousal, participants completed a French trait version of the Activation/Deactivation Check-List (ADCL) [62,63]. It measures the activation (i.e. being actively involved in the processing of the environment) and deactivation (i.e. being prone to sleep or rest) states and was chosen because of its test-retest reliability (ranging from $\rho = .57$ to $\rho = .87$) and validity (correlation with psychophysiological measures of arousal ranging from $\rho = .43$ to $\rho = .68$). Participants must determine, for a list of 49 adjective-items, whether or not each one describes their usual functioning. Among the list of items, 27 adjectives are fillers. They had to rate each item on a 5-point Likert Scale (1=Never; 5=Very often) while taking into account the basic instruction "Usually, daily, I am:". Three main components are evaluated: General Activation (example of items: energetic, full-of-pep, active), Calm (example of items: placid, calm,

still), and General Deactivation (example of items: leisurely, sleepy, tired). High scores in those components would reflect a higher propensity to General Activation, Calm, and General Deactivation. The internal consistency for our sample, as assessed through the mean inter-item correlation was good since all values exceeded the conventional threshold of $|\rho| 0.15$ [64]: General Activation 0.61, Calm 0.62, and General Deactivation 0.27.

2.2.2. Resting-state EEG

A resting-state EEG recording was performed immediately after the completion of the questionnaire. Participants were seated comfortably in front of a computer monitor in a recording booth, fitted with the electroencephalographical equipment. An EEG ACTi Champ with active electrodes was used for this experiment. A total of 64 channel electrodes, arranged based on the revised 10/20 system [65], and 5 EOGs were used. Two EOGs were placed horizontally, on each cheekbone, and two vertically above and under the left eye to monitor blinking or eye movement. A monopolar set-up was chosen, with a reference EOG on the nose bridge. Impedances were kept below 20k Ω . Once the EEG equipment was set up, the signal quality was tested asking participants to move their eyes left to right, to blink, and to clench their jaw muscles. Then, instructions were displayed in white font on a black background. Instructions advised the participants to relax their jaw and shoulders, to try not to move, to fully relax, to close their eyes, and to resist sleepiness. To prevent any external distractions leading to an eye-opening, the light in the room was dimmed, and the screen went off when the resting session was started. The session began once the participants stated that they were ready, and the end was announced by the experimenter. The recording session lasted 3 min. At the end of the recording session, participants were asked whether they had fallen asleep. No participants reported having fallen asleep during the resting session.

2.2.3. SPS task

Participants completed the SPS task 45 min after the resting-state EEG recording. In the meantime, participants performed a distractive visuo-spatial task. This delay allowed a clear dissociation between the resting-state recording and the SPS task. Electrodes and EOGs were removed from the participants' heads. They were then seated in a quiet and normally lit room with an ambient temperature of 20–23 °C, in front of a desk. Once they were ready, SPS were introduced as normal phenomena, and to give participants some idea of what they could associate with SPS, a list of 11 sensations most likely to be felt was presented (beat/pulse, itch, tickle, numbness, skin stretch, tingling, warming, cooling, muscle stiffness, flutter, and vibration). The list used in the SPS protocol is based on the one used originally by Macefield and colleagues [66] and Ochoa and Torebjörk [67] to study microstimulation-evoked sensations, and then adapted by Naveteur and colleagues [68] to study SPS. Participants were then instructed to remove any jewelry from their hands and wrists and to roll up their sleeves if they were long enough to cover the wrist. For 15 s, they were instructed to cleanse their hands with an antiseptic gel (Aniosgel® 85 NPC, ≈ 3 mL per participant), to remove any external surface agents that could interfere with the task, and to ensure a homogenous glabrous skin surface across all participants. A 15 s latency was observed between the cleansing operation and the start of the test. Each participant was given a protocol containing the standardized reduced maps of each hand shown palm up (with a distance of 11.2 cm between the tip of the middle finger and the palm/wrist frontier), and below each map, the list of 11 SPS and two visual analog scales (i.e. two 10 cm continuous horizontal lines without markers at each end) for confidence ratings, along with a pencil and a 25 \times 25 cm piece of smooth white fabric. Once participants were familiarized with the material, the start of the test session was announced. The protocol and the pencil were placed away from the participants on the desk to prevent any interference from visual stimuli. Each hand was tested once in a balanced order across participants. They were instructed to sit with their back supported by the backrest of their

chair. The leg ipsilateral to the tested hand was turned outward by about 60 degrees from the midline. Participants placed the white fabric cotton fabric on their thigh, with the tested hand resting on it, palm up with fingers spaced slightly apart. Only a dorsal part of the hand was in contact with the fabric, apart from the fingers. The hand not being tested hung down on the outer side of the chair contralateral to the tested hand. When the "start" signal was given verbally by the experimenter, marking the start of each trial, participants gazed at their tested hand for 10 s, focusing their attention on the hand so that they could detect any sensations that might occur. They were informed beforehand that there was a possibility that they would perceive no sensation. A "stop" signal given by the experimenter marked the end of the 10 s period. Participants were immediately asked to report on the protocol whether they had detected any sensations on the tested hand or not and if they had, to (a) map the extent and location of the sensations by shading the areas where they perceived sensations on the map of the tested hands; (b) specify the perceived intensity of each sensation according to a 10 point scale (1 = just perceptible; 10 = very intense but not painful) directly on the map; (c) indicate their degree of confidence in the location and the extent of the perceived sensations according to the two visual analog scales (ranging from "not confident" to "very confident"), and (d) identify the sensations with the list of descriptors. They had the option to choose more than one descriptor and to add descriptors to the list according to what they had detected. The task lasted approximately 15 min.

2.3. Data processing

2.3.1. EEG preprocessing

The EEG data preprocessing was conducted with BrainVision Analyzer 2.1. To ensure a quality signal was processed, a passband of 0.2–120 Hz was first applied, with a 50 Hz notch, and bad electrode signals removed and replaced by the mean signal of the three nearest electrodes. On average, 2.37 ± 0.47 electrodes signals were replaced (up to 8 electrodes) and those most removed from the signal were FP1, FP2 (11 participants), FT9, TP10 (9 participants), FT10 (8 participants), and TP9 (7 participants). Those least removed were F2, POz, T8 (only one participant per electrode), and T7 (4 participants). An ocular correction with the Gratton & Coles algorithm [69], based on the left horizontal EOG and the below-eye vertical EOG, was applied, subtracting the ocular movement from the signal. For each participant, the 3-minute recording was divided into 90 epochs of 2 s, according to the processing used by Chen and colleagues [70] when studying resting-state EEG data. To ensure no evoked response was triggered by the instruction to close the eye, the first 5 epochs were removed [71]. An artifact rejection, with a maximum amplitude of 80 μ V [70] was carried out on these epochs, resulting in a rejection rate of 12.5 % epochs. A mean of 74.41 ± 12.45 epochs, ranging from 38 to 85 per participant, was obtained.

2.3.2. Functional connectivity analysis

Further analyses of the EEG data were carried out using exact Low-Resolution Electromagnetic Tomography (eLORETA; [72]). The eLORETA method is a discrete, three-dimensional distributed, linear, and weighted minimal norm inverse solution. Its validity was convincingly demonstrated by Pascual-Marqui [72]: the special weights used in eLORETA give tomography the exact localization property to test point sources, resulting in images of the current density with exact localization but with low spatial resolution; the eLORETA has no localization bias in the presence of structures noise and multiple source situations; in addition, due to the implementation of "lagged phase synchronization" that models the instantaneous and lagged components of functional connectivity, the eLORETA can robustly identify true physiological connectivity. The choice of method was further supported by the credibility provided by an array of studies investigating functional connectivity [72–75] and was influenced as well by the possibility to apply the eLORETA algorithm on filtered data to operate a frequency decomposition of the functional connectivity [72]. The cost of

electrophysiological recording compared to the quality versus the amount of information gathered considered, the eLORETA was regarded as an effective analysis method and a good fit for the study. Thus, instructions from Pascual-Marqui and colleagues were followed strictly [73,75,76].

The artifact-free epochs were analyzed to estimate the current density for five frequency bands: delta (0.5–3.5hz), theta (4–7hz), alpha (7.5–12hz), beta (13–34hz), and gamma (35–45hz). We seeded three areas forming two connections: the TPJ and EBA connectivity, and the TPJ and AI connectivity, considering only ipsilateral connectivity for both hemispheres. Regions of interest (ROI) in both left and right hemispheres were constructed with the eLORETA given MNI coordinates for the TPJ (54, -48, 7) [18], the EBA (48, -67, 3) [18] and the AI (32, 12, 20) [77]. A voxel-wise approach was applied and lagged phase synchronization, indexing the physiological lagged connectivity [72] was used to measure the functional connectivity between the TPJ and EBA first, followed by the TPJ and AI. These analyses resulted in connectivity indices for each frequency band, the value of which ranged from 0 to 1 (the greater the value, the stronger the connection; Table 1), and this was performed independently for the TPJ-EBA connection and the TPJ-AI connection in each hemisphere. Considering no hypothesis regarding the hemispheric location has been presented in this study, we used only mean indices of the right and left hemisphere functional connectivity. Due to scale differences between the connectivities of each frequency band, the indices were z-transformed for homogenization purposes. The z-transform also allowed a mean to be computed across all frequency bands for the TPJ-EBA connection and TPJ-AI connection separately.

2.4. Results and discussion

2.4.1. The topography of SPS frequency

This analysis was carried out to detect any significant effects in the spatial distribution of SPS as a function of TPJ-EBA and TPJ-AI functional connectivity. Maps filled by participants with shaded areas were projected on a 140 × 140 mm grid, with a 1mm² resolution, and converted to binary code (0=unshaded, 1=shaded cell). As a result, two binary maps per participant (i.e. right and left hand) were generated. A frequency map was obtained by superimposing these maps, in which each cell value represented the percentage of participants having shaded it (Fig. 1). SPS were reported for the whole hand but were not distributed uniformly: Fig. 1 shows the presence of a distal-to-proximal gradient in the frequency map [53,54]. Computation of the relative spatial extent of sensations, i.e. the percentage of shaded cells within a segment (distal phalanx, intermediate phalanx, proximal phalanx, and palm) in comparison to the surface of the whole hand was carried out [54]. This analysis is based on the receptor density dispersion on the glabrous surface of the hand [78]. Relative surfaces were entered into an analysis specific to proportions [79] with the anatomical segments as the unique factor. A significant segment effect was found ($Q(3) = 468.2$, $p < .000001$; Cramer's $V = .09$), with a greater SPS surface in the distal phalanx (11.68 %) than in the intermediate (11.03 %) and in the proximal (8.15 %) phalanges, as well as in the palm (7.96 %). This specific distribution is consistent with previous studies investigating SPS [53,54,56,57,61], presumably reflecting the distribution of peripheral

Table 1

Mean (SD) indices for each frequency band, for TPJ – EBA and TPJ – AI functional connectivity.

	Functional Connectivity	
	TPJ – EBA	TPJ – AI
Delta	.08 (.06)	.14 (.05)
Theta	.031 (.14)	.35 (.09)
Alpha	.40 (.16)	.56 (.11)
Beta	.06 (.02)	.09 (.02)
Gamma	.06 (.07)	.05 (.06)

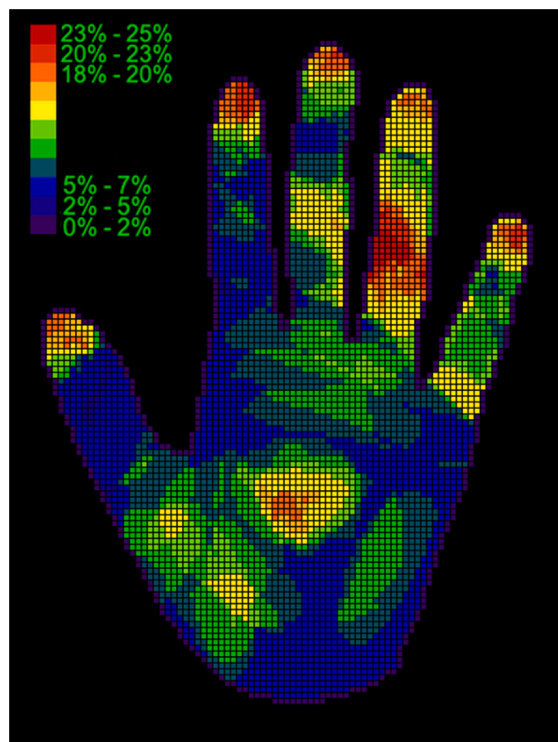


Fig. 1. Topographic map of SPS frequency (% of participants having shaded a cell) using a color scale: cool/blue colors reflect the least frequently shaded areas and hot/red colors the most frequently shaded areas.

receptive units and/or their trace within the somatosensory cortex. This gradient suggests that the task was carried out successfully.

2.4.2. Relationship between SPS frequency topography and functional connectivity

For each participant and each hand, a 140 × 140 mm grid identical to that used in the frequency processing was completed with connectivity indices. This was carried out to achieve a cell-by-cell analysis between the SPS topography and the functional connectivity. Individual connectivity indexes of the left hemisphere of each participant were used to complete the map of the right hand and individual connectivity indexes of the right hemisphere of each participant were used to complete the map of the left hand. This way, 54 individual maps reflecting the SPS frequency were correlated with 54 individual maps completed with connectivity indices, using a point biserial cell-wise correlation. This was performed separately for TPJ-EBA and then TPJ-AI connection and was performed separately for each frequency band. The correlation maps obtained were then converted into binary maps (0 = non-significant, 1 = significant), for the application of a spatial scan procedure for binary data [80] consisting of a circular window that scans, detects, and localizes significant clusters in a step-wise fashion. This also makes it possible to reduce Type 1 errors. A maximum radius of 6 cells was chosen based on previous studies [54,56]. After 999 runs of the Bernoulli (binomial) model, all detected and localized clusters were significant at least at the $p < .001$ level bicaudal. Figs. 2 and 3 display only those significant clusters for each connection.

2.4.3. SPS frequency and TPJ-EBA connectivity

Reliability analysis performed on the indices of TPJ-EBA functional connectivity suggest good to very good reliability, through a Cronbach's α at 0.83, a McDonald's ω at 0.80 and an average interitem correlation

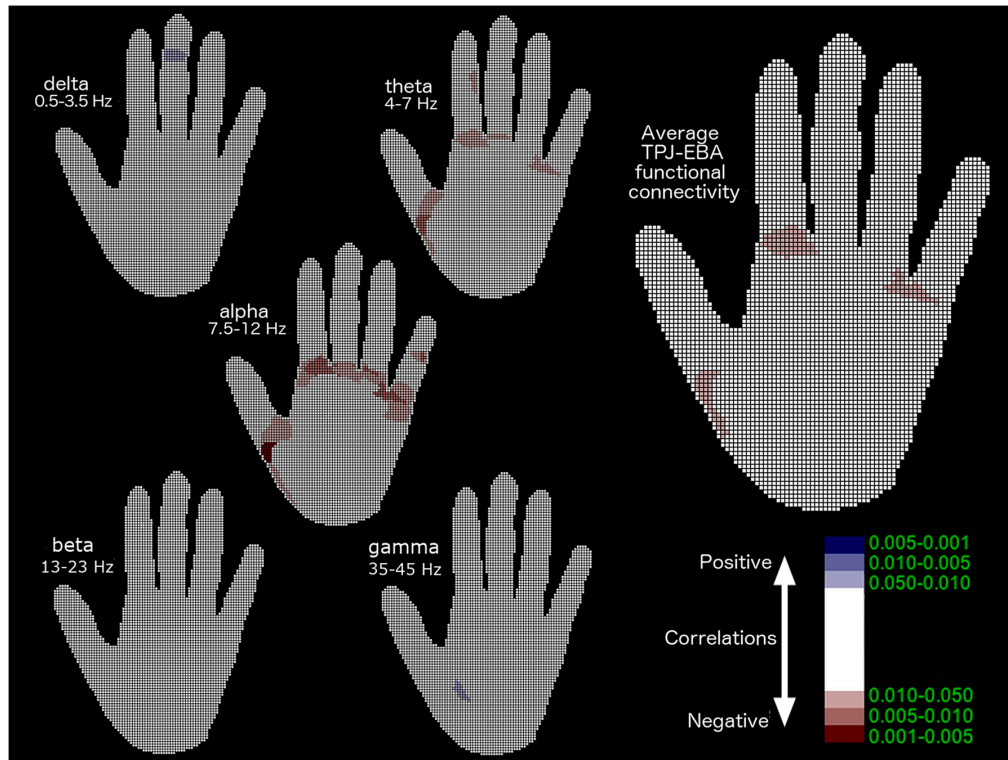


Fig. 2. Topographic probability maps of the correlations between SPS frequency and connectivity index in the delta, theta, alpha, beta, and gamma bands for TPJ-EBA connectivity. Bluish colors represent significant positive correlations and reddish colors represent significant negative correlations. The color intensity denotes the significance level.

$|\rho|$ at 0.43.

For the relationship between SPS frequency and TPJ-EBA connectivity (Fig. 2), positive significant correlations (bluish cells) were found covering a surface of 0.9 % (95 % Wilson Confidence Interval [0.66 %, 0.01 %]) in the delta band and of 0.6 % (95 % CI [0.39 %, 0.85 %]) in the gamma band, and negative significant correlations (reddish cells) were found covering a surface of 5.7 % (95 % CI [5.05 %, 0.43 %]) in the theta band and of 12.1 % (95 % CI [11.16 %, 13.10 %]) in the alpha band. To process the relationship between the SPS frequency and the functional connectivity for the average TPJ-EBA connectivity, i.e. independently of frequency band influence, SPS frequency maps were correlated with the mean z -transformed index of functional connectivity for TPJ-EBA connection in the manner described above. Only negative correlations were found in an area covering 3.5 % (95 % CI [3.00 %, 4.10 %]) of the hand.

2.4.4. SPS frequency and TPJ-AI connectivity

Reliability analysis performed on the indices of TPJ-AI functional connectivity suggest as well good to very good reliability, through a Cronbach's α at 0.77, a McDonald's ω at 0.80 and an average interitem correlation $|\rho|$ at 0.39.

For the relationship between SPS frequency and TPJ-AI connectivity (Fig. 3), negative correlations were mainly found in all frequencies, covering 10.8 % (95 % CI [9.91 %, 11.76 %]) of the hand in the delta band, 19.4 % (95 % CI [18.24 %, 20.59 %]) in the theta band, 6.5 % (95 % CI [5.81 %, 7.28 %]) in the alpha band, and 4.4 % (95 % CI [3.84 %, 5.06 %]) in the beta band. Positive correlations were observed only in the gamma band, covering a surface of 0.9 % (95 % CI [0.66 %, 1.23 %]). To process the relationship between the SPS frequency and the functional connectivity for TPJ-AI connection independently of frequency

band influence, SPS frequency maps were correlated with the mean z -transformed index of functional connectivity for TPJ-AI connection in the manner described above. Only negative correlations were found in an area covering 9.6 % (95 % CI [8.76 %, 10.52 %]) of the hand.

2.4.5. TPJ-EBA and TPJ-AI correlations

Surface percentages of significant correlations were analyzed using a Q' test (Fig. 4) [79] with the connectivity (TPJ-EBA vs TPJ-AI) and the frequency bands (delta, theta, alpha, beta, and gamma) as factors. The main effect of connectivity was highly significant ($Q'(1) = 259$, $p < .001$; Cramer's $V = .31$), with surfaces being overall larger for TPJ-AI connectivity than for TPJ-EBA connectivity. The connectivity \times frequency band interaction was also significant ($Q'(4) = 816$, $p < .001$; Cramer's $V = .28$). Multiple corrected comparisons carried out with the Q' test [79] revealed that surfaces were reliably larger in the TPJ-AI than in the TPJ-EBA connectivity in the delta ($q' = 20.15$, $p < .001$), theta ($q' = 19.51$, $p < .001$), and beta ($q' = 14.07$, $p < .001$) bands, but an opposite pattern was observed in the alpha band where surfaces were larger for TPJ-EBA connectivity than for TPJ-AI connectivity ($q' = 9.05$, $p < .001$). Finally, no differences were found in the gamma band ($q' = 1.82$, $p = .51$). The larger correlated surfaces for TPJ-AI connectivity were observed in the theta band, forming a kind of peak, whilst the larger correlated surfaces for TPJ-EBA connectivity were observed in the alpha band. It is in the latter case that TPJ-EBA connectivity surfaces were larger than for TPJ-AI connectivity.

2.4.6. Other parameters

Based on previous studies [56], other parameters of SPS, i.e. spatial extent, mean perceived intensity of SPS, confidence in location and in extent, number of areas, spatial extent per area and variety of SPS

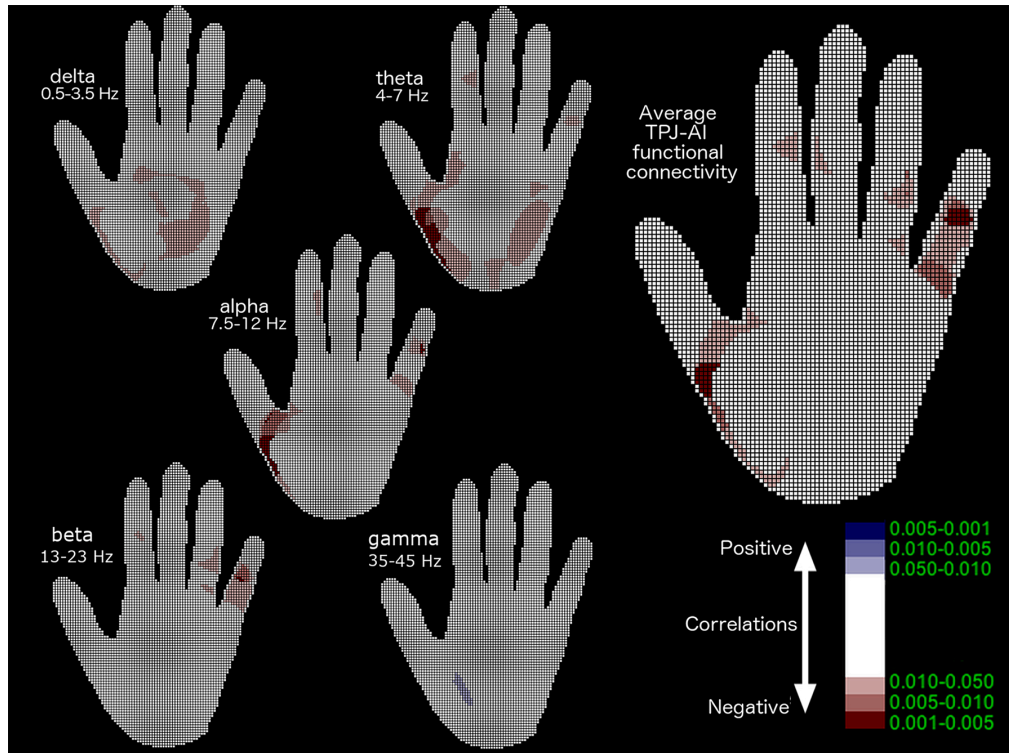


Fig. 3. Topographic probability maps of the correlations between SPS frequency and connectivity index in the delta, theta, alpha, beta, and gamma bands for TPJ-AI connectivity. Bluish colors represent significant positive correlations and reddish colors represent significant negative correlations. The color intensity denotes the significance level.

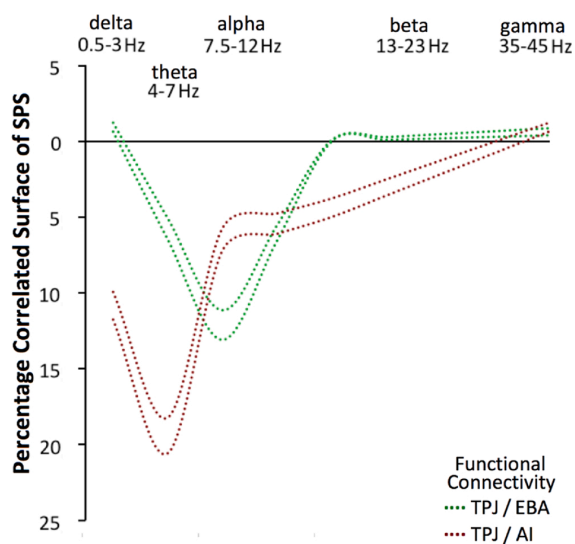


Fig. 4. Percentages of significant SPS surfaces correlated with each of the frequency bands, for TPJ-EBA and TPJ-AI connectivity, respectively. Values below 0 on the Y-axis represent percentages of negative correlations and above 0 represent percentages of positive correlations. The widths of the bands represent 95 % confidence intervals. Positive values represent positive correlations, and negative values represent negative correlations.

(Table 2), were considered for analysis. Analysis revealed good to very good reliability as suggested through the Cronbach's α at 0.78, the McDonald's ω at 0.83 and the average interitem correlation $|\rho|$ at 0.34. The predictive value of the mean z-transformed index of functional connectivity for TPJ-EBA and TPJ-AI connections and of the self-reported ADCL measures (Mean score = 20.15 ± 3.39 , Min = 13, Max = 25) on each of these parameters was examined by mean of multiple regression analyses. Furthermore, age, gender, and BMI were also included as predictors since they are known to influence perception of SPS [54,55]. The results (not Bonferroni-corrected [81,82]) are presented in Table 3. We found that the mean z-transformed index of the TPJ-AI functional connectivity negatively predicted the spatial extent of the SPS ($\beta = -1.03$, SEM = .36, $t(18) = -2.83$, $p = .01$, $R^2 = .22$) and the spatial extent per area ($\beta = -.79$, SEM = .37, $t(18) = -2.14$, $p = .05$, $R^2 = .19$). The scores in the General Activation sub-scale of the ADCL negatively predicted the intensity of SPS ($\beta = -.54$, SEM = .21, $t(18) = -2.58$, $p = .02$, $R^2 = .24$) and participants' confidence in the location of SPS ($\beta = -.51$, SEM = .22, $t(18) = -2.30$, $p = .03$, $R^2 = .13$). Finally, body mass

Table 2

Mean (SD) of the parameters collected in the SPS task in both Experiments, other than spatial distribution.

	Experiment 1	Experiment 2
Spatial extent (%)	8.94 (10.67)	11.76 (10.53)
Spatial extent per area (%)	5.84 (10.28)	2.91 (3.33)
Intensity	2.76 (1.72)	3.49 (2.28)
Variety	2.41 (1.31)	2.53 (1.47)
Number of areas	4.11 (2.98)	4.65 (3.07)
Confidence in location	6.46 (2.63)	5.26 (2.53)
Confidence in extent	5.43 (2.44)	4.73 (2.16)

Table 3

Standardized β coefficients (1 SEM) and adjusted R^2 coefficient from the multiple regression analysis carried out on each of the 7 collected dependent variables with age, gender, body mass index, mean z-transformed connectivity index for TPJ-EBA and TPJ-AI connections, and scores for the General Activation, Calm and General Deactivation items of the ADCL as independent variables. Significant predictors at least at $p < .05$ are marked with an asterisk.

	Spatial extent	Spatial extent per area	Intensity	Variety	Number of areas	Confidence in location	Confidence in extent
Age	-.09 (.21)	-.13 (.21)	-.32 (.21)	-.18 (.28)	.06 (.24)	.21 (.22)	-.08 (.24)
Gender	-.07 (.23)	-.22 (.24)	.09 (.23)	.04 (.31)	-.18 (.26)	.01 (.25)	.07 (.26)
BMI	.38 (.18)*	.47 (.19)*	.00 (.17)	.17 (.24)	-.01 (.20)	.16 (.20)	-.04 (.20)
TPJ-EBA connectivity	.56 (.35)	.35 (.36)	-.01 (.36)	-.17 (.46)	-.26 (.39)	-.24 (.37)	-.29 (.39)
TPJ-AI connectivity	-1.03 (.36)*	-.79 (.37)*	-.24 (.36)	.02 (.47)	.03 (.41)	.15 (.38)	.15 (.40)
General Activation	.02 (.21)	.02 (.21)	-.54 (.21)*	-.15 (.27)	-.48 (.23)	-.51 (.22)*	-.48 (.23)
Calm	.16 (.19)	.14 (.19)	.28 (.19)	.03 (.25)	.29 (.21)	-.06 (.20)	-.24 (.21)
General Deactivation	-.09 (.19)	-.06 (.19)	.00 (.18)	-.09 (.25)	-.18 (.21)	-.01 (.20)	-.26 (.21)
Adj. R^2	.22	.19	.24	-.33	.02	.13	.03

index (BMI) negatively predicted the spatial extent per area ($\beta = .47$, SEM = .19, $t(18) = -2.50$, $p = .02$, $R^2 = .19$).

2.4.7. Types of sensations

All SPS types were reported at least once and some participants even reported other types of sensations, such as pins and needles, weightiness, and compression. Types of reported SPS were clustered in five categories based on previous studies [83,84]: thermal (warming and cooling), deep (beat/pulse and muscle tension), paresis-like (numbness and weightiness), surface (tickle, stretch, tingling, flatter, vibration, and compression), and pain-like (pins and needles and itch). SPS types were not clustered uniformly among these five categories ($\chi^2(4) = 84.95$, $p < .001$, Cramer's $V = .42$). Surface types of SPS were most likely to be perceived and reported (51.72%), followed by deep (20.69%), thermal (14.66%), paresis-like (12.07%), and then pain-like sensations (0.86%). Each of the five categories of sensations as well as the sum of SPS reported were submitted to multiple regression analyses (not Bonferroni-corrected [81,82]) with the same predictors as before. No significant effect was observed.

Based on previous literature, the TPJ, EBA, and AI would play a role in the emergence of self-awareness, by contributing either in embodiment [19,85], or in the emergence of the "material me" [29]. However, those areas were also associated with high arousal [6] and would be strongly connected to attentional networks [7,86]. For these reasons, SPS were studied in association with at-rest functional connectivity between the TPJ and the AI, and between the TPJ and the EBA, along with a questionnaire investigating self-reported trait arousal.

The first finding of this study was that, independently of frequency bands, the functional connectivity of the TPJ was negatively associated with the propensity of perceiving SPS. Exhibiting stronger functional connectivity is associated with decreased perception of SPS.

The second finding was a distinction between TPJ-AI and TPJ-EBA connectivities. Indeed, TPJ-AI connectivity correlated with larger surfaces than TPJ-EBA connectivity and also predicted the SPS total surface and surface per area. Moreover, a dissociation appeared since the TPJ-AI dominated over the theta band whilst TPJ-EBA dominated over the alpha band. The last finding of this experiment was that non-topographic SPS parameters, such as intensity, confidence in location, were negatively predicted by self-reported General Activation. Taken altogether, the results of Experiment 1 intimate that processes reflected in the TPJ-AI and TPJ-EBA connectivities, as well as self-reported trait arousal, would play a rather inhibitory role in the perception of SPS.

Nonetheless, the arousal indices chosen in this experiment were declarative and direct, i.e. the list of adjectives was explicitly related to arousal, and this may have led to desirability bias. This may constitute a methodological flaw. The possibility of regression results stemming from desirability bias and common methodology variance needs to be ruled out. For this reason, we propose the use of a direct physiological index of arousal, i.e. skin conductance level (SCL). To our knowledge, only a single study investigated the association between SPS perception and arousal through physiological parameters and found no link

between them [87]. However, Tihanyi and Köteles [87] used a different method to investigate the perception of SPS, in which SPS topography was not explored. We further propose to use an indirect and non-explicit declarative measure of arousal, through reporting of inner speech presence. According to Alderson-Day and Fernyhough [88], inner speech or self-talk is "a subjective experience of language in the absence of overt and audible articulation" (p.931). It is a demanding sustained cognitive activity, and as such, it increases stress and autonomic arousal as demonstrated through changes in breathing patterns and electromyography [89,90]. The general hypothesis is that SCL and inner speech, as parameters of arousal, would be negatively associated with SPS perception.

3. Experiment 2

3.1. Participants

A different sample from the one used in Experiment 1 was tested here. All participants were students at the University of Franche-Comté (Eastern France) participating in psychology teaching programs. Based on the criteria listed in Experiment 1, the study included a total of 26 participants (19 female, 7 males; 23 right-handed subjects) with a mean age of 21.9 ± 2.8 (age range: 20–33), and a mean body mass index of 21.5 ± 2.7 kg/m² (range: 17.5–30.1 kg/m²). All gave their informed written consent to participate before the test. With a sample of 26 participants (i.e., 52 hand maps) there is enough power (90%) to diminish Type II errors.

3.2. Materials

3.2.1. Electrodermal recording at rest

Participants were seated in a comfortable armchair in a quiet room (room temperature ranged from 20 to 22 °C). Electrodermal activity was recorded using the BIOPAC System MP150 module and a GSR100C Amplifier with a sampling rate of 1000 Hz. Disposable Ag/AgCl electrodes (EL509) were attached to the palmar surface of the medial phalanges of the index and middle fingers of the non-dominant hand (all BIOPAC Systems, Inc., CA). Once the electrodes had been fitted, a 15-minute rest period was observed before the recordings began to allow the electrode gel to diffuse and to establish good baseline conductivity. Participants were then required to put on headphones and a sleep mask to minimize any sensory input interference. Participants then were asked to relax during the recording session and to avoid any movements and any irregular or deep breaths. The at-rest electrodermal activity recording started and lasted 5 min. An experimenter was present in the room at a distance from the participant to record any movements and deep breaths of the participant liable to produce unwanted electrodermal responses. Data were analyzed offline using AcqKnowledge 4.2 software (BIOPAC Systems, Inc., CA). A low-pass filter with a cut-off frequency of 0.05 Hz was applied. The SCL (μ S) was computed as the mean value of skin conductance measured during the 5-minute resting

phase.

3.2.2. Inner speech

At the end of the at-rest electrodermal recording session, participants received a single question on inner speech, inspired by Nikula [37]: "How present was an inner speech in your thoughts during the recordings?" (French, *A quel degré le langage interne était-il présent dans vos pensées pendant les enregistrements?*). The question was presented on a sheet of paper and participants were required to respond using a 5-point Likert scale (0 = not much; 5 = a lot). Even though some full questionnaires on inner speech exist, they are suspected to have limited validity [91]. For this reason, a single straight-forward question on the presence of inner speech was preferred here, which had already been shown to correlate with electrodermal activity [37].

3.2.3. SPS task

The task was strictly identical to that described in 2.2.3. Each participant completed an SPS task 1–3 weeks after the electrodermal recording session. This variable delay was mostly due to organizational reasons and separating the two sessions in time would avoid contamination between them. The SPS task was performed in a quiet room with an ambient temperature of 20–23 °C.

3.3. Results

3.3.1. Skin conductance level

The SCL level ranged from 2.06 to 31.1 μ S, and the mean was 15.9 \pm 7.77 μ S. No reliable difference was found between men (14.8 \pm 6.7 μ S) and women (16.3 \pm 8.3 μ S, $t(24) = .43$, $p > .67$).

3.3.2. Inner speech

The mean rating of inner speech was 2.85 (SD = 1.3), ranging from 1 to 5. Interestingly, yet in keeping with the extant literature [37], inner speech correlated positively with the mean SCL ($r(24) = .40$, $p < .05$),

suggesting that the greater the presence of inner speech, the higher the arousal.

3.3.3. SPS

3.3.3.1. The topography of SPS frequency. The same analyses described in 2.4.1 were conducted. The frequency map (Fig. 5) reveals a typical distal-to-proximal distribution of SPS [53,54] with higher frequencies over the fingertips and the center of the palm. Topographical statistics were compiled using point biserial cell-wise correlation between the presence of SPS and the mean z -transformed SCL. The significance maps were then submitted to the spatial scan procedure for binary data to isolate those clusters that reached the $p < .001$ level. Only negative correlations were found between the mean SCL level and the presence of the SPS. They covered an area of 13.4% (95% CI [11.51%, 13.48%]) of the hand (Fig. 5).

3.3.3.2. Other parameters. Regression analyses were carried out in order to understand whether the mean SCL predicted SPS parameters, i. e. overall spatial extent, spatial extent per area, intensity, variety, number of areas, confidence in location, and confidence in extent (Table 2). Once again, analysis revealed good to very good reliability as suggested through a Cronbach's α at 0.85, the McDonald's ω at 0.85 and the average interitem correlation $|\rho|$ at 0.39. Age, gender, body mass index, average and scores in the inner speech question (Mean = 2.65 \pm 1.49, Min = 0, Max = 5) were also included in the analyses as independent variables. The results (not Bonferroni-corrected [81,82]) are presented in Table 4. We found that the average SCL significantly and negatively predicted the variety of SPS ($\beta = -.43$, SEM = .19, $t(20) = -2.25$, $p = .04$, $R^2 = .30$) as well as participants' confidence in location ($\beta = -.46$, SEM = .22, $t(20) = -2.09$, $p = .05$, $R^2 = .06$). Meanwhile, inner speech significantly and positively predicted the variety of SPS ($\beta = .55$, SEM = .20, $t(20) = 2.83$, $p = .01$, $R^2 = .30$). The gender of our participants also predicted significantly but negatively the variety of SPS ($\beta =$

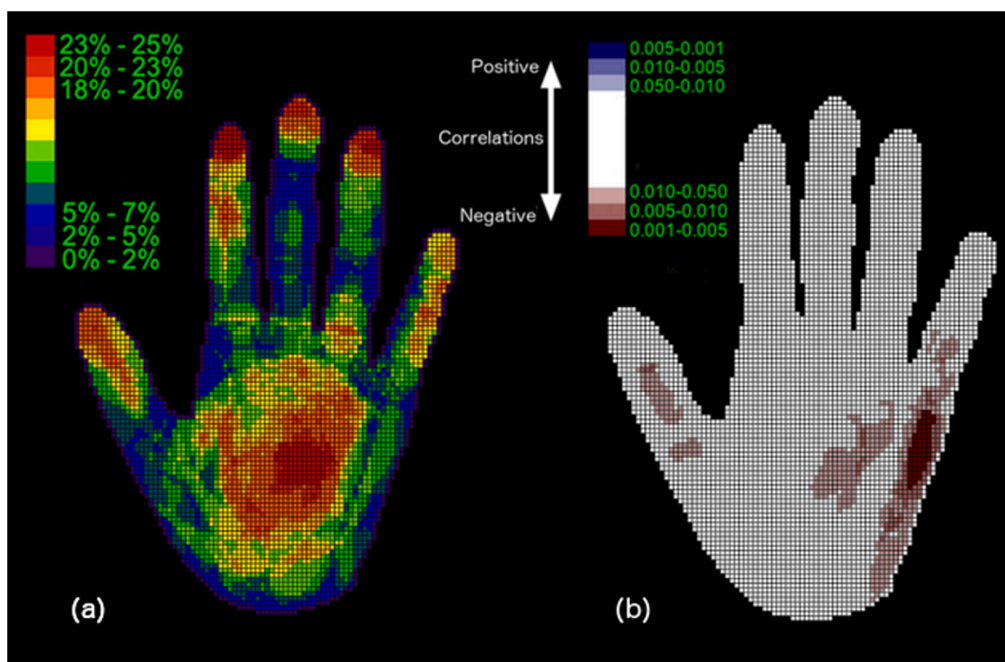


Fig. 5. Topographic maps. Left. Frequency map of SPS frequency (%) through a heat scale, cool/blue colors reflecting least frequently reported areas, and hot/red colors most frequently reported areas. Right. Probability map representing the correlations between SPS frequency and SCL. Bluish colors represent positive correlations and reddish colors represent negative correlations. The color intensity depends on the significance level.

Table 4

Standardized β coefficients (1 SEM) and adjusted R^2 coefficient from the multiple regression analysis carried out on each of the seven collected dependent variables with age, gender, body mass index, average skin conductance level, and scores for the inner speech question as independent variables. Significant predictors at least at $p < .05$ are marked with an asterisk.

	Spatial extent	Spatial extent per area	Intensity	Variety	Number of areas	Confidence in location	Confidence in extent
Age	.01 (.25)	-.06 (.21)	.53 (.20)*	-.08 (.18)	.06 (.22)	.36 (.21)	.36 (.22)
Gender	-.06 (.22)	-.27 (.20)	.03 (.19)	-.43 (.17)*	.00 (.22)	-.06 (.20)	.01 (.20)
BMI	.05 (.23)	-.13 (.21)	.20 (.20)	.07 (.18)	.23 (.22)	.23 (.21)	.18 (.22)
Average SCL	-.30 (.24)	-.13 (.23)	-.31 (.22)	-.43 (.19)*	-.41 (.23)	-.46 (.22)*	-.30 (.23)
Inner Speech	.01 (.25)	-.22 (.23)	-.11 (.22)	.55 (.20)*	.23 (.23)	.00 (.20)	-.05 (.24)
Adjusted R^2	-.15	.02	.11	.30	-.01	.06	-.05

-.43, SEM = .17, $t(20) = -2.50$, $p = .02$, $R^2 = .30$), meaning that women reported a greater variety of SPS than men. Finally, participants' age significantly and positively predicted the SPS intensity ($\beta = .53$, SEM = .20, $t(20) = 2.60$, $p = .02$, $R^2 = .11$).

3.3.3.3. Types of sensations. All 11 sensations were reported at least once, and one participant added pins and needles to the list. Since they probably reflect different underlying mechanisms, sensations were clustered in the same distinct categories as in Experiment 1. SPS types were not clustered uniformly among these five categories ($\chi^2(4) = 51.83$; $p < .001$, Cramer's $V = .31$). Surface tactile/mechanical sensations were most frequently reported by participants (38.8 %), followed by thermal (27.34 %), deep internal (16.5 %), and paresthesia-like sensations (14.39 %). Pain-like sensations were those least reported (2.9 %). Each of the five categories of sensations as well as the sum of SPS reported were submitted to multiple regression analyses (not Bonferroni-corrected [81,82]) with the same predictors as before. The mean SCL significantly predicted internal sensations, and this prediction was negative ($\beta = -.49$, SEM = .23, $t(20) = -2.17$, $p = .04$, $R^2 = .01$).

Experiment 2 was conducted to better acknowledge the association between arousal and the perception of SPS. Experiment 2 focused on a direct parameter of arousal, i.e. average SCL, as well as a self-reported and indirect parameter, i.e. inner speech, which was linked with arousal. This relationship between arousal and inner speech was confirmed here. In line with the first study, we hypothesized that these parameters would be negatively associated with SPS perception.

As a first finding, we observed that SCL correlated negatively with SPS frequency and negatively predicted SPS parameters, such as variety and participants' confidence in the location. The skin conductance level also negatively predicted deep/internal sensations. These results corroborate the hypothesis formulated earlier that arousal would exert primarily an inhibitory influence on SPS perception. Nevertheless, the self-reported inner speech seems to facilitate the perception of SPS variety, but this relationship results only when gender and inhibitory influence of SCL are taken into account simultaneously.

4. Discussion

As part of the background of bodily sensations, SPS would allow the experiencing self to come to the fore by focusing attention on body representation [1,57]. Which factors contribute to SPS perception and therefore to the emergence of body awareness? Evidence suggests that SPS depend on self-focus [57]. Also, directing attention away from the body decreases SPS [53,54,56]. In this paper, we proposed to investigate how neuronal networks reflecting attentional focus and self-referential processes, i.e. TPJ functional connectivity with EBA and with AI, were associated with SPS perception. Besides, because these two networks were associated with arousal, we investigated further how arousal was associated with SPS perception.

For the greatest interest of the reader, to present a clear and comprehensive discussion of the numerous data obtained, we will first focus on the results concerning arousal, and will then develop the results concerning brain networks.

4.1. SPS and arousal

Arousal has been investigated with the use of three indices: SCL, a self-reported arousal trait measure, and inner speech. We found that SCL correlated negatively with SPS frequency. It also negatively predicted the variety of SPS and participants' confidence in their location. Increased self-reported arousal trait predicted lower intensities of SPS and weaker confidence in their location. Finally, a greater presence of inner speech positively predicted the variety of SPS, but in interaction with gender and SCL. The variety of SPS was greater for women with a greater presence of inner speech and lower SCL. Inner speech is thought to be linked with arousal as shown both in past research [37] and in the present study. Morin and Michaud [92] suggested that inner speech would appear to be involved in the acquisition of self-information, meaning that collecting information through an inner speech about oneself raises the perception of various SPS, especially in women with low levels of arousal. All these data are in agreement with our hypothesis that increased arousal would dampen the perception of SPS. However, they also suggest that multiple other factors may determine the perception of SPS.

Contrary to Tihanyi and Köteles [87], we found relationships between SPS and arousal through SCL. This concerned the frequency of SPS perceived over the hand, as well as the intensity of SPS through the self-reported arousal trait. This discrepancy might be explained by the many differences identified in our protocol, such as (a) the use of topographical measures that have proven to be sensitive to distinct cognitive processes [54,56]; (b) the lack of restrictions considering SPS variety resulting in a greater quantity of SPS taken into account for our studies and not focusing on specific SPS; (c) the time spent focusing followed by an immediate recall of the participant's perception ensuring a low impact of visuospatial short-term memory, and enabling participants to perceive and report numerous and detailed SPS [55]. According to the extant literature, arousal indexes readiness to respond to environmental stimuli [60]. Attention to the environment results in focus away from the body and the self. In this regard, diverted attention may suppress SPS [53–55] while self-focused attention increases interoceptive processes and results in a heightened perception of SPS [56]. Also, abnormally enhanced interoception results in an abnormally enhanced perception of SPS [61].

Another line of evidence suggests that high arousal reliably predicts spontaneous brain activity, in that a subject with high arousal levels would show decreased activation of the brain network involved in self-referential processes [6], i.e. the default mode network. Indeed, previous findings showed that SPS frequency, intensity, and participants' confidence in location, were greater with increased propensity to mind wandering [57], a cognitive activity associated with the default mode network [93,94]. These findings are consistent overall with the suggestion that activity in the default mode network allows better perception of SPS, and therefore increases self-awareness [57]. Also, decreased activity of the default mode network associated with increased attention away from the body dampens perception of SPS and therefore decreases self-awareness. These observations tally well with the idea that attention directed to and maintained on the self is a necessary condition for the development of self-awareness [1,95].

4.2. SPS and brain networks involved in self-awareness

Directing attention away from the self and toward the environment involves a network that anticorrelates with the default mode network [59]. Among the key node structures of this attention network are the TPJ and the AI, which have also been associated with embodiment and self-location [15,18]. Another area, independent of this network, has also been associated with embodiment, the EBA [18]. Both the EBA and the AI are functionally connected to the TPJ [2,7,18]. However, belonging to the attention network or not suggests that these connections might serve different functions, and therefore contribute differently to self-awareness. We found that, independently of frequency bands, increased TPJ-EBA functional connectivity was associated with lower perceived frequency of SPS. In turn, high TPJ-AI functional connectivity was associated with lower SPS frequency, smaller spatial extent, and smaller surfaces per sensitive area. These results are consistent overall with our findings linking high arousal with lowered SPS perception. Indeed, TPJ and AI activation are associated with high arousal [6]. Moreover, the TPJ and AI are part of the ventral attention network, whose activity has been closely linked with arousal through the locus coeruleus noradrenergic system [36,50]. Greater connectivity among areas of this network would dampen the perception of SPS. Attention directed away from the body suppresses SPS [53–55]. Nevertheless, taken altogether, these findings indicate that high connectivity between the TPJ and structures implicated in self-awareness experiences such as the AI or the EBA will impair the perception of SPS. The TPJ is a multisensory integration hub [18], as such abnormal functioning of the TPJ would be associated with imperfect integration, resulting in disturbed self-awareness and embodiment [18,85,96]. This would present as asomatognosia and autoscopic experiences, such as out-of-body experiences, autopsychy, feeling of presence, depersonalization, failure of self-agency, etc. [20,23,97,98]. In our study, high connectivity between the TPJ and AI, and the TPJ and EBA, seems to be associated with a high propensity to altered bodily experiences as SPS.

Closer inspection of the correlation patterns between functional connectivity and SPS frequency revealed that the TPJ-AI dominated over the theta band whilst the TPJ-EBA dominated over the alpha band. Distinct cognitive processes might be reflected by these two connectivities. For instance, in an array of studies investigating neuropsychological performances and EEG frequency bands, the alpha band has been linked to broad cognitive processes such as attention and executive functions [46,48,49,99,100]. In particular, the alpha band would appear to promote sustained attention by inhibiting irrelevant cognitive and sensory processing [43,46]. This tallies well with our interpretation of the TPJ-AI connectivity influence on the perception of SPS, and overall with the assumption that SPS are suppressed when attention is directed away from the body. In turn, the theta band has been associated with memory, but also attention and executive functions [41,43,45,99], and would rather appear to reflect a global cognitive efficiency [44,101,102]. However, on another line of evidence, the alpha and theta band taken altogether have been observed respectively peaking in occipital and temporal regions with the elicitation of OBE [103]. This pattern of activity would reflect self-altered experience, such as autoscopic illusions in this specific case, and further, reinforce our interpretation of TPJ functional connectivity with the EBA and AI as deleterious for self-awareness processing.

4.3. Limitations and future directions

The findings and interpretations presented in this study are sources of limitations that should be taken into account. The main limitation of this study lies in the interpretation of attentional and self-related cognitive processes related to TPJ functional connectivity that would have an impact on the perception of SPS. Hence the lack of consensus in the literature regarding its involvement in self-awareness and the evidence of functional dissociation within the same area results in multiple

possible interpretations. Nevertheless, these two studies provide a set of quite consistent findings regarding arousal and bring new data considering the duality between attentional processes focusing on outwards and towards oneself [54–57]. Our interpretation, considering the state of the literature, appears to be the most consistent to date. The authors admit they did not directly investigate inward vs outward attention in the experiments presented here, however, they do believe these studies, along with the literature concerning SPS, contribute to a better understanding of this quite broad topic.

It is noteworthy to mention that, in Experiment 1, the resting-state task and the SPS task were separated by a 45-minute computerized visuospatial task. Separating the resting task and the SPS task by a third task reduces their contamination. However, some influence from the visuospatial task might be observed, such as tiredness.

Concerning Experiment 2, the use of an inner speech questionnaire may be debated. Inner speech is a solely subjective experience that cannot be assessed using measures other than declarative ones. The question used here required participants to decide how, according to their own experience of inner speech, it was present during the rest period, as there is no example provided to determine what is "not much" or "a lot". This can be considered as unusual since there is no external guideline to ensure an identical baseline across participants. Yet this is also the way a wide variety of subjective measures are made within other contexts (i.e., perception of pain, perception of intensity, etc). It is a very common method that does not invalidate the use of the questionnaire as inner speech. Inner speech is a matter of subjective judgment and we set to investigate the relationship between self-referential processes and their subtracts, which, by definition, depend on the perception of the self.

Finally, the association between arousal and SPS could only reflect superficial activity limited to limbs and spontaneous receptor activity. Although it is not possible to exclude this interpretation completely, the use of declarative indices shows the involvement of high-level processes through arousal in the perception of SPS. The methodology used in these two studies allows a better grasp of the processes underpinning the perception of SPS. There is still scope to investigate which neuronal connectivity is found during the perception of SPS, opening a window to a better understanding of cognitive processing found within the background of bodily sensation experience [1] and the emergence of the "material me" [28].

5. Conclusion

Our study aimed to investigate the links between self-awareness and brain networks divided into body-awareness and attention processing. We indeed found that TPJ functional connectivity with respectively the AI and the EBA, as well as arousal, was associated with decrementing SPS, a window to self-awareness. These findings indicate that the propensity to focus attention outward would affect how self-aware we tend to be.

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CRediT authorship contribution statement

Sara Salgues: Conceptualization, Investigation, Formal analysis, Writing - original draft. **Gaën Plancher:** Supervision, Writing - review & editing. **Laurence Jacquot:** Investigation. **Janick Naveteur:** Writing - review & editing. **Lison Fanuel:** Investigation. **Germán Gálvez-García:** Writing - review & editing. **George A. Michael:** Conceptualization,

Supervision, Project administration, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.bbr.2020.112880>.

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Tableau 2. Les sensations spontanées internes, de surface, et thermales

En Acte I nous avons démontré la relation entre l'activité oscillatoire spontanée de SI et SII et la topographie des SPS, dans les bandes de fréquences typiquement associées à la conscience (Seth et al., 2006) et inférant l'implication top-down de processus attentionnels destinés à moduler l'expérience perceptuelle (Kennett et al., 2001; Mima et al., 1998; Press et al., 2004; Serino et al., 2007; Taylor-Clarke et al., 2002, 2004). Et dans l'article précédent, nous avons mis en évidence une relation étroite entre les SPS et la connectivité fonctionnelle de TPJ et AI, aires qui seraient responsables de ces modulations somatosensorielles (Gallace & Spence, 2008, 2009, 2010; Taylor-Clarke et al., 2002). Par la même occasion, nous avons pu rapprocher le phénomène des SPS aux expériences subjectives de désincarnation. Nous en revenons ainsi à nos premières considérations, celles de l'origine même des SPS. Aurions-nous identifié les mécanismes neuraux responsables de ce phénomène ?

Pour clore ce travail de recherche, et dans l'objectif d'apporter des éléments de réponse supplémentaires à cette question, nous avons développé une nouvelle approche expérimentale des SPS. En effet, jusqu'à présent nous avons considéré les SPS comme un phénomène unique reposant sur des facteurs communs à la perception tactile, et avons donc axé nos recherches sur les mécanismes connus dans le domaine de la somatosensation. Pourtant, très tôt Michael et Naveteur (2011; Naveteur et al., 2005) relèvent la richesse et la variété des sensations composant ce phénomène. Une méta-analyse réalisée sur l'ensemble des études publiées sur les SPS (présentée dans Supplementary material) illustre la disparité des sensations qui sont reportées. Si les sensations de surface (comme les fourmillements) sont prédominantes, elles sont suivies de près par les sensations internes (pulsations cardiaques et flux sanguins) et par les sensations thermales (réchauffement et refroidissement). Et l'existence même de cette disparité dans les SPS les plus fréquentes infère l'implication de mécanismes déterminant la qualité des SPS.

Or l'intéroception et la thermoception n'empruntent pas les mêmes chemins périphériques et neuraux que la somesthésie. Au vu des données actuelles, nous savons que la sensibilité thermique et tactile reposent sur des unités réceptives cutanées distinctes (Paricio-Montesinos et al., 2020; Schepers & Ringkamp, 2009; Stevens et al., 1974; Vallbo, 1981; voir Prologue, partie I-A) et

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suivent un gradient différent (Filingeri et al., 2018; Li et al., 2008; Luo et al., 2020). Mais d'autre part, le cortex insulaire aurait un rôle plus prédominant dans le traitement des signaux internes et thermiques, en raison de sa somatotopie pour les signaux thermiques (A. D. Craig et al., 2000; Gallace & Spence, 2010; Hua et al., 2005) et de son activation récurrente dans les tâches intéroceptives (A. D. Craig, 2003c; Strigo & Craig, 2016; Tuthill & Azim, 2018; Vaitl, 1996). Il serait ainsi possible que les mécanismes neuraux appréhendés jusqu'à présent contribuent différemment à la perception des SPS en fonction de leur nature.

Nous nous intéressons donc de très près à ces trois types de SPS dans ce dernier article. La première étude nous permet d'introduire le protocole expérimental développé dans le but d'étudier avec fiabilité les SPS en fonction de leur type. Nous y décrivons ainsi les caractéristiques topographiques et qualitatives des SPS de surface, interne et thermique. Dans une seconde étude, nous explorons de façon détaillée l'implication de SI, SII, AI et TPJ, et de leur synchronisation avec TPJ, dans la perception de chaque type de SPS.

Article 6 : Salgues, S., Plancher, G., Michael, G. A. (in preparation). What am I feeling ? The characteristics and resting state EEG underpinnings of surface, deep and thermal spontaneous sensations

What am I feeling ? The characteristics and resting state EEG underpinnings of surface, deep and thermal spontaneous sensations

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Abstract

Perceiving spontaneous sensations (SPS) on the skin that arise in the absence of any external stimulation contributes to body awareness. Yet there is doubt whether this phenomenon has its roots in peripheral sensory processes, as it follows the distribution of cutaneous sensory units, or in central processes since it is associated to attentional modulations within the somatosensory cortices, but also in networks involving the temporoparietal junction (TPJ) and anterior insula (AI). While SPS exhibit a great variety, a preponderance of surface, deep and thermal types SPS emerges in the literature. This study aimed to investigate whether these three categories of SPS would present with specific characteristics and explored the involvement of the primary (SI) secondary (SII) somatosensory cortices, TPJ and AI in their respective perception.

Ninety-seven participants had to search, in separate sessions, only for tingling, beat/pulse and warming SPS arising on their hand. It was found that these three types of SPS had different and specific spatial distribution from the others. The electroencephalographic (EEG) activity at rest of a subgroup of 39 participants was recorded one hour prior the three-SPS task, with the assumption that inter-individual differences in spontaneous oscillatory EEG activity might relate to the phenomenology of each SPS type. It was found that each SPS was related distinctly to the current density in SI, SII, TPJ and AI, as well as to the TPJ functional connectivity with SI, SII, and AI. The spectral pattern analysis allowed to emphasize different possible mechanisms engaged in the perception of SPS in respect to their type and to highlight the contribution of SPS in different cognitive components of body awareness.

Keywords: Spontaneous Sensations; Somatosensory cortices; Temporoparietal Junction; Anterior Insula; Interoception; Somatosensation; Thermoception

1. Introduction

Kinsbourne defended that conscious awareness of the body rises from attending to the ever present background of bodily sensations (Kinsbourne, 1998), a background that would gather internal signals from the heart, viscera, joints and muscles (Tuthill & Azim, 2018; Vaitl, 1996), peripheral signals such as tactile inputs (Gallace & Spence, 2008, 2009, 2010), and perceptual traces of body-part representations. It is commonly stated that body awareness relies on the ability to detect the signals that originate from the physiological activity (Gregory et al., 2003; Pollatos, Matthias, et al., 2007; Pollatos, Schandry, et al., 2007) or that are triggered by interactions with the environment (Aspell et al., 2013; Gallace & Spence, 2010). Yet, some sensations would be perceived even though no external triggers provoke them (Beaudoin & Michael, 2014; Michael et al., 2012; Michael & Naveteur, 2011), and their study raises the question of whether some bodily signals might originate from cortical activity.

These tingling, warming or pulse sensations that are felt on the skin even though nothing seems to provoke their perception are referred to as spontaneous sensations (SPS). This phenomenon is best perceived when one is at rest, and would greatly improve when attending to one's body (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues, Plancher, Jacquot, et al., 2021). Along with attention, perceiving SPS would rely on other abilities associated to body awareness, such as interoception, i.e., perceiving the physiological bodily state (A. D. Craig, 2003c; Michael et al., 2015), embodiment, i.e., localizing one's within one's own body frontiers (Blanke, 2008; Michael, Guyot, et al., 2020; Salgues, Plancher, Jacquot, et al., 2021), or the propensity to inner speech and mind-wandering (Michael et al., 2017; Salgues, Plancher, Jacquot, et al., 2021). Besides, SPS would be sensitive to perceptual distortions in patients with atypical body awareness (Borg et al., 2015; Echalié et al., 2020). They seemingly belong to the background of bodily sensations (Kinsbourne, 1998), and are thus usually investigated as a mean to explore inter-individual differences in body awareness.

Spontaneous sensations perceived on the hands present similar topographic characteristics with tactile sensitivity: they are unequally distributed on the glabrous skin of the hand, more frequent on digits than on the palm (Michael et al., 2012; Michael & Naveteur, 2011), following a proximo-to-distal gradient similar to the cutaneous organization of mechanoreceptors (Johansson & Vallbo, 1979a; Vallbo & Johansson, 1984). This might be a clue that they originate from the spontaneous physiological peripheral activity (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi &

Köteles, 2017). There is indeed physiological evidences of spontaneous bursts in skin fascicles at rest (Vallbo et al., 1979), and of somatosensory perception resulting from single impulses of single units in high sensitivity areas of the glabrous skin (Johansson & Vallbo, 1979b; Vallbo et al., 1984). Furthermore, SPS are described as having qualitative properties that are quite like sensations triggered by actual stimuli with which the skin is in contact. While it is possible these mechanisms result in the perception of SPS (Michael et al., 2012; Michael & Naveteur, 2011), it cannot be excluded that SPS may originate from the cortical activity (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017). Indeed, attention modulates the somatosensory cortices activity in an amplification/suppression fashion (Gomez-Ramirez et al., 2016; Mima et al., 1998; Taylor-Clarke et al., 2002), a pattern that was evidenced in the perception of SPS when investigating the interactions of attention and vision (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015): attending to and looking at the hand allowed the suppression of SPS on the palm and their amplification on the fingers. Besides, fMRI studies provided evidence that attending to SPS increased the activation within somatosensory cortices (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014), and an EEG study found that the oscillatory activity at rest of the dedicated areas for digits and palm within the somatosensory cortices was associated to the perception of SPS in these respective areas (Michael et al., n.d.). This supports that SPS topographical characteristics might be linked to the cortical somatosensory homunculus, i.e., the somatotopic representation of the body within the somatosensory cortices (Huang & Sereno, 2018; Kinsbourne, 1998; Nakamura et al., 1998). There are instances of bodily hallucinations associated to the somatotopic cortical organization (Bär et al., 2002; Geoffroy et al., 2013, 2014; Jardri et al., 2008; Shergill, 2001), and evidence that phantom sensations would be perceived as having the same shape than the missing limb (Halligan, 2002).

However, SPS present another similarity with somatosensory sensations that is usually less emphasized: the type of sensations perceived varies. There is a predominance of surface-type (e.g., tingling, vibration), deep (e.g., beat/pulse, muscle stiffness), and thermal sensations (e.g. warming, cooling), and a more rare occurrence of paresis-like (e.g., numbness) or pain-like sensations (e.g., pins-and-needles) (Michael et al., n.d., 2012; Michael, Guyot, et al., 2020; Michael & Naveteur, 2011; Salgues et al., n.d.; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021). In addition, there are occurrences of modulations in the type of SPS perceived that were linked to the motion of the attended hand (Beaudoin & Michael, 2014), age and gender (Naveteur et al., 2015), arousal and attention (Michael et al., 2012; Michael & Naveteur, 2011; Salgues,

Plancher, Jacquot, et al., 2021), cognitive abilities (Michael et al., 2015, 2017; Salgues et al., n.d.; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021), and altered body awareness (Borg et al., 2015; Echalié et al., 2020). This supports the idea that some peripheral and cortical factors might also underpin the qualitative aspect of SPS. Yet studies investigating SPS always focused on the topographical distribution of sensations regardless of their type. Because of this, there is no knowledge about the respective characteristics of each type of SPS. Yet, since SPS present many similarities with somatosensory perception, it might be expected that at least the topography of SPS differs according to their type. For instance, the detection of elicited surface sensations is optimal in the fingertips and decreases in more proximal areas of the volar hand (Johansson & Vallbo, 1979a), but the perception of thermal changes is better in the palm than on fingers (Li et al., 2008; Wakolbinger et al., 2014). Even though less documented, the perception of cardiovascular events on the skin surface would most likely depend on the underlying venous network (G. E. Jones et al., 1987; Katkin, 1985; O'Brien et al., 1998; Schandry et al., 1993), which regarding the glabrous hand would mean a greater occurrence of these sensations on distal phalanges and thenar eminence (Taylor & Schwarz, 1955).

Besides there is also a great understanding that the perception of surface, deep, and thermal sensations would differently involve cerebral areas of the somatosensory pathway. The primary (SI) and secondary (SII) somatosensory cortices are frequently referred to as underlying the tactile perception, meaning the perception of sensations arising from pressure and motion of the skin (Bolognini & Miniussi, 2018; Gallace & Spence, 2008, 2009, 2010; Rapp et al., 2002). While their involvement in the detection of cardiac signals (Khalsa et al., 2018; Pollatos et al., 2005) and thermal discrimination (Peltz et al., 2011) was also documented, the perception of interoceptive and thermal signals is usually associated to the insula (Aizawa et al., 2019; Berlucchi & Aglioti, 2010; A. D. Craig, 2009a; A. D. Craig et al., 2000; Dubé et al., 2009; Hassanpour et al., 2016; Peltz et al., 2011; Wiebking et al., 2014). Disruption of the anterior insula (AI) and temporoparietal junction (TPJ) was also linked to somatosensory aberrations (Arzy et al., 2007; Bowling et al., 2019; Brosey & Woodward, 2017), and TPJ activity was found to increase the perception of surface sensations in depersonalization (Bowling et al., 2019), and autoscopic hallucinations (Persinger et al., 2010; Persinger & Saroka, 2013; Saroka & Persinger, 2013). The TPJ and AI would intervene in the multimodal integration and, while integration of visceral afferences in the AI would enable interoception (Berlucchi & Aglioti, 2010; A. D. Craig, 2003c, 2009a), back-projections from the TPJ toward SI, SII and the insula would promote feedback

mechanisms in the processing of tactile and haptic signals (Gallace & Spence, 2008, 2009, 2010). Besides, the synchronization of TPJ with AI would also underly a wide range of self-related cognitive processes, including attention (Corbetta et al., 2008; Igelström et al., 2016; Uddin et al., 2010) and embodiment (Eddy, 2016; Igelström & Graziano, 2017; Ionta et al., 2011, 2014; Mars et al., 2012). Interestingly, a previous resting state EEG study provided evidence that the functional connectivity between the TPJ and the AI would contribute to the perception of SPS (Salgues, Plancher, Jacquot, et al., 2021), and since the gradient in SPS might be related to the somatotopic cortical organization (Michael et al., n.d.), it could be hypothesized that the variety in SPS also relates to the involvement of SI, SII, TPJ and AI in their perception.

The relationship between SPS and the oscillatory activity of these ROIs might bring insight toward their cognitive underpinnings. Indeed, their perception was previously associated to alpha oscillations (7.5 – 12hz) in SI, and to beta (13 – 34hz) and gamma bands (35 – 45hz) in SII (Michael et al., n.d.), and their relationship with the TPJ – AI functional connectivity was prominent in delta (0.5 – 3.5hz) and theta bands (4 – 7hz) (Salgues, Plancher, Jacquot, et al., 2021). In somatosensory cortices, alpha and beta bands would reflect the awareness of somatosensory inputs (Haegens et al., 2011; Kilavik et al., 2013; Palva, 2005), and gamma would be associated to tactile hallucinations (Baldeweg et al., 1998). Attentional processes would be reflected by delta (Barry et al., 2010; Karamacoska et al., 2018), theta (Barry et al., 2010; Clayton et al., 2015; Finnigan & Robertson, 2011; van der Hiele et al., 2008) and alpha (Benedek et al., 2014; Çiçek & Nalçacı, 2001; Clayton et al., 2015; Keune et al., 2017; Laufs et al., 2003). But low frequency oscillations delta and theta were also proposed to underpin integration mechanisms in the insular and temporoparietal areas (Knyazev, 2012; Knyazev et al., 2009). It would be congruent that these spectral patterns are found when investigating different type of SPS.

Hence, two objectives motivated this study. The first one was to investigate the phenomenology of SPS according to their type. To this end, we used a new protocol for the collection of SPS data, the three-SPS task, in which participants had to search for a specific SPS in separate sessions: tingling (TG), beat/pulse (HB), and warming (WM). The choice for these sensations was based on a meta-analysis (see supplementary material) which exhibited the prominence of surface, deep, and thermal types in SPS, and TG, HB, and WM as the more frequently reported in each type respectively. The three-SPS task required participants to focus on these sensations one at a time, with the idea that this would allow to collect the characteristics of surface, deep and thermal SPS. Their perception was investigated on the glabrous hand, and

participants had to report their location and other characteristics such as the perceived intensity. The differences between TG, HB, and WM were investigated by conducting comparisons on their topographical and non-topographical characteristics. This is presented in Experiment 1.

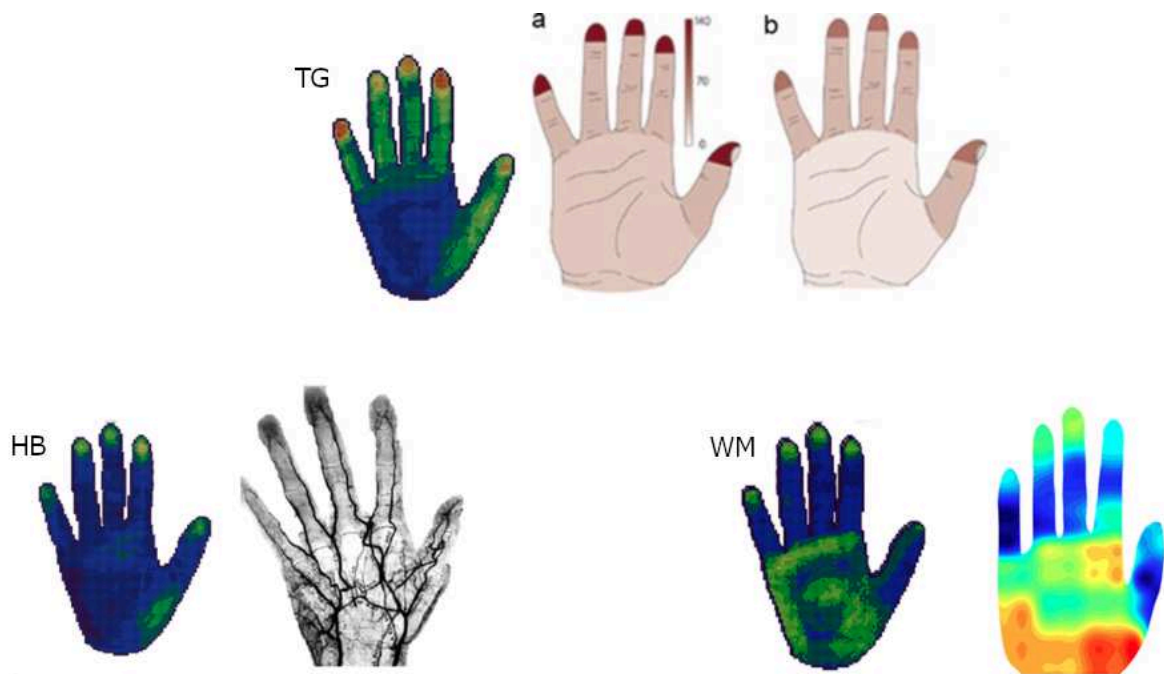


Figure 1: Theoretical distribution of SPS according to their type. On the first row, the theoretical distribution of tingling sensations (left hand map) next to the distribution of cutaneous mechanoreceptors on the glabrous hand (right hand maps; Vallbo & Johansson, 1984). On the second row, the theoretical distribution of pulse/beat sensations (left) and of warming sensations (right), next to the venous network of the hand (left; Taylor & Schwarz, 1955) and to the mapping of thermal sensitivities (right; Li et al., 2008).

A second objective was to investigate the distinct involvement of SI, SII, AI and TPJ in the perception of TG, HB, and WM. This was conducted on a portion of the sample of participants in Experiment 1. The cortical activity at rest was recorded using an electroencephalograph (EEG) one hour before the three-SPS task, with the idea that the spontaneous oscillatory activity reflects a neural trait (Berkovich-Ohana et al., 2014; Kajimura et al., 2016; Kucyi, 2018; Mennes et al., 2010; Power et al., 2011), and that the perception of SPS would relate to individual differences in the engagement of neural mechanisms (Michael et al., n.d.; Salgues, Plancher, Jacquot, et al., 2021). Using the sLORETA algorithm, current densities in all ROIs (SI, SII, AI and TPJ) and the functional connectivity of TPJ with SI, SII and AI were extracted. Spectral analyses were conducted, and as in previous studies, we expected that the relationship between the oscillatory activity and

the three-SPS would be reflected in the alpha to gamma bands for SI and SII (Michael et al., n.d.), and in the delta to alpha bands for AI and TPJ (Salgues, Plancher, Jacquot, et al., 2021). Since we investigated the topography and qualitative characteristics (i.e., non-topographic) of the three-SPS, we also hypothesized that differences among HB, TG and WM might arise (i) in the relationship with the ROIs and networks targeted, (ii) in the spectral pattern of association for a given ROI/network, and (iii) in the direction of correlations. This is presented in Experiment 2.

2. Experiment 1

2.1. Method

2.1.1. Participants

The study was realized according with Helsinki declaration guidelines and was approved by the local ethic committee (reference number IRB 00,009,118). Volunteers were from the Lumiere University (Lyon, France). They were asked to fill a form containing questions on their sociodemographic and health characteristics. Items consisted of age, gender, height, weight, use of psychotropic medication, and if so, the reason why (antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc.), regular use of other psychoactive substances (alcohol, marijuana, etc.), and medical history with a special emphasis on cardiovascular diseases and diabetes mellitus. Participants were also asked to report any other information they considered of importance for the study. They were excluded if they reported any history of neurological or psychiatric disorder, psychoactive abuse or any disease that may affect the tactile sensitivity such as cardiovascular diseases and diabetes mellitus. Ninety-seven participants (71 females and 26 males) were included, with a mean age of 21.26 ± 2.98 years (range: 17 to 33) and a mean BMI of 21.95 ± 3.62 kg/m² (range: 14.84 to 36.11). All were informed beforehand of the study objectives and consented to the use of their data for research purposes.

2.1.2. Three-SPS task

Participants realized the SPS task in a quiet and normally lit room, with an ambient temperature of 20-23°C. They were seated in a chair without armrests, in front of a table and next to the experimenter. When ready, the experimenter introduced the SPS concept, emphasizing it was a normal phenomenon that could be felt by almost anybody, and presented the three SPS investigated (i.e., heartbeat, tingling and warming) as examples so that they had an idea what to expect. It was explained that they might perceive other sensations, but that they will be asked to focus only on the three ones presented, one at a time. Participants were then asked to remove any jewelry from their hands and wrists, to roll up their sleeves if they covered the wrists and were instructed to cleanse their hands with an antiseptic gel (Aniosgel ® 85 NPC, ≈ 3ml per participants) for 15s. This last step removes any external agent on the skin that could interfere with the task and

ensure a homogenous glabrous skin surface across all participants. A 15s latency was respected before the start of the test. A document, consisting of three identical protocols (one per sensation) representing the standardized reduced maps of each hand shown palm up (with 11.2 cm between the tip of the middle finger and the palm/wrist frontier), along with a pencil and a 25 × 25 cm piece of smooth cotton fabric were given to each participant. When ready, these were placed on the desk and hidden to prevent any interference from visual stimuli. For each type of SPS, each hand was tested once, meaning there was 6 experimental conditions (i.e., HB left hand, HB right hand, TG left hand, TG right hand, WM left hand, WM right hand) that were tested in a Latin-square order across participants. Participants were asked to sit with their back supported by the backrest of their chair, the leg ipsilateral to the tested hand turned outward by about 60 degrees from the midline. The cotton fabric was placed on the thigh so that the tested hand could rest on it, palm up and fingers spaced slightly apart. In this way, only a dorsal part of the hand was in contact with the fabric. The other hand hung down on the outer side of the chair contralateral to the tested hand. A “start” signal was given verbally by the experimenter to mark the start of each trial, at which participants gazed at the tested hand for 10s and focused their attention on the hand. They were instructed beforehand of the sensation they had to focus on and were informed there was a possibility they would perceive no sensations or would perceive other non-investigated sensations. If the latter happened, they were advised not to focus on these sensations and to keep looking for the one instructed. A “stop” signal given by the experimenter marked the end of the 10s period. Participants were immediately asked if they perceived any sensation on the tested hand, and if it was the one instructed, they had to (a) map their location and extent by shading the areas on the map of the tested hand; (b) specify the perceived intensity of each sensation according to a 10-point scale (1 = just perceptible; 10= very intense but not painful) directly on the map. Each sensation was investigated with a new protocol and the other two hidden, ensuring no interference could arise from visualizing the previously reported sensations in the other conditions. The task lasted approximately 20 minutes.

2.2. Results and Discussion

To compute differences in the topographical distribution of each SPS type, maps shaded by participants were projected on a 140 × 140 mm grid, with a 1mm² resolution, and converted to binary code (0 = nil, 1 = shaded cell). For each sensation, two binary maps (i.e., left, and right

hand) per participant were created, meaning each frequency maps were built using $N \times 2 = 194$ hand maps. The superimposition of these maps, respective of the sensation they reflect, led to the generation of three frequency maps in which each cell represents the percentage of participants having shaded it (Top row of Figure 2). For each sensation, SPS were reported over the whole hand, but not uniformly on the surface of the hand.

2.2.1. Examination of the proximo-to-distal gradient

To assess the differences in the topographical distribution of each sensation, an examination of the distribution based on the relative receptor density (Johansson & Vallbo, 1979a, 1979b; Vallbo & Johansson, 1984) was first carried out: percentages of shaded cells within each segment (distal phalanx, intermediate phalanx, proximal phalanx and palm) compared to the surface of each segment were entered into an analysis of proportions (Michael, 2007). Since multiple comparisons on proportions only allows $2 \times k$ designs and that this could not allow the investigation of interactions among HB, TG and WM gradients, the SPS were compared two-by-two (see bottom graphic in Figure 2).

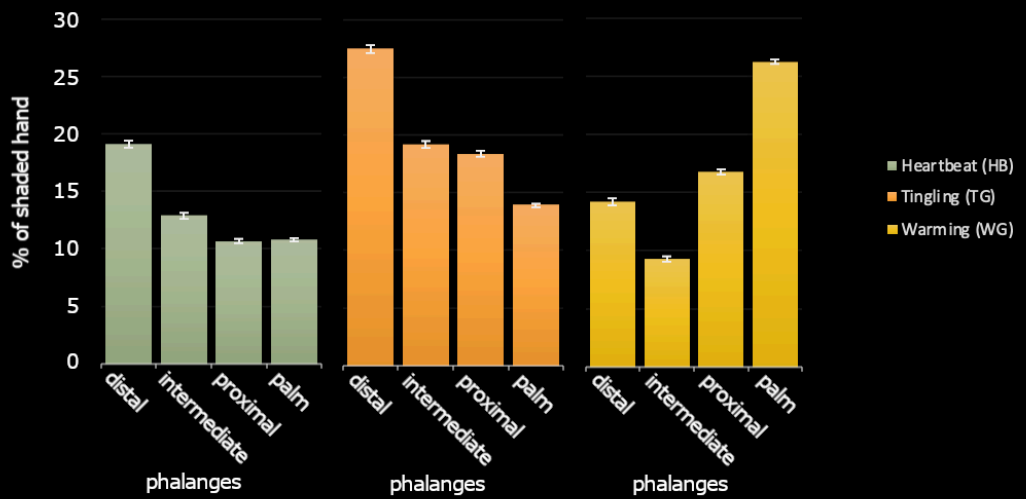
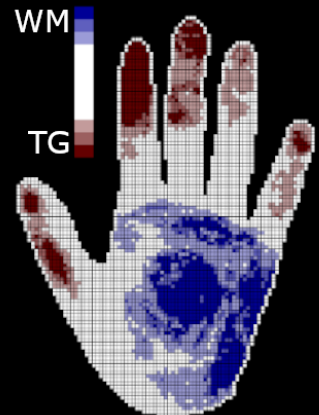
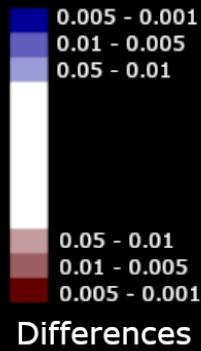
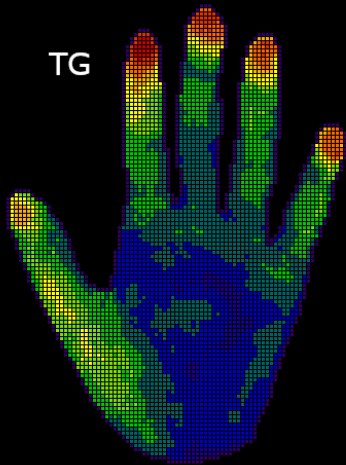
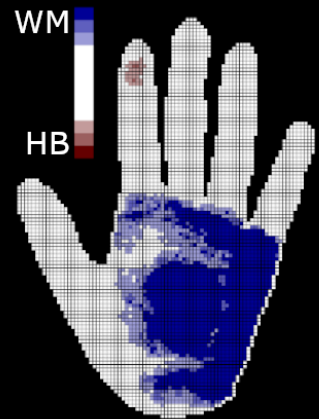
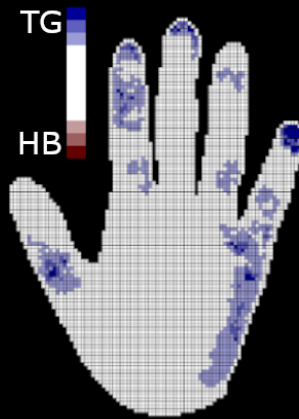
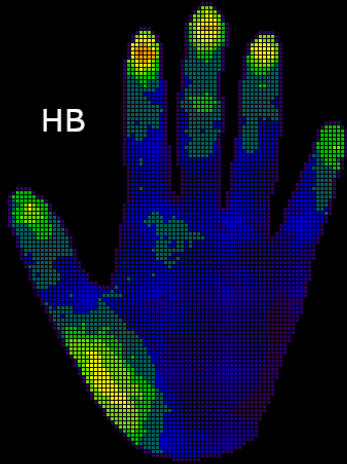
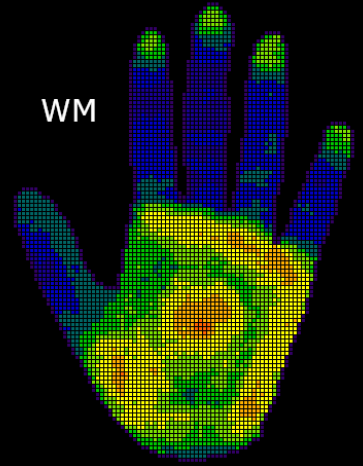
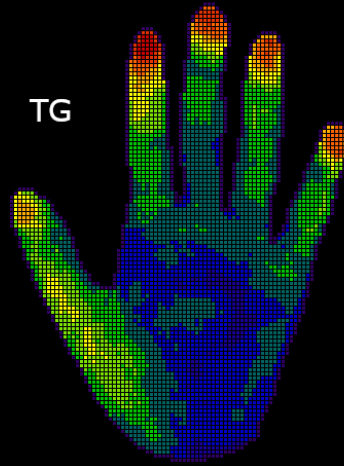
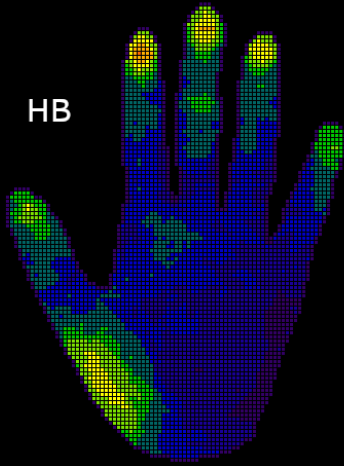
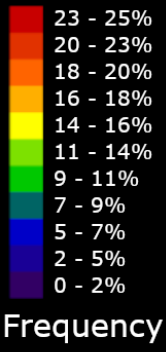


Figure 2 : Topographical maps depicting (i) in the first row, the frequency (% of participants having shaded a cell) of heartbeat (HB), tingling (TG) and warming (WM) sensations using a color scale: cool/blue colors reflect the least frequently shaded areas and warm/red colors reflect the most frequently shaded areas; (ii) right underneath, a matrix depicting the differences between each frequency maps using a color scale: bluish colors shows differences in favor of the sensation map at the top and reddish colors differences in favor of the sensation map on the left. The color intensity denotes the significance level; (iii) at the bottom, a graphic depicting the proximo-to-distal gradient (% of shaded cells within each segment) for heartbeat, tingling and warming sensations. Horizontal scale refers to segments. Error bars depict 95% Wilson confidence intervals.

The comparison performed between the relative spatial extent of HB and TG revealed a significant SPS x segment interaction ($Q^2(3) = 850.87$, $p < .001$, Cramer's $V = .05$). Significant differences were found among the segments for TG (all $ps < .002$), with a greater relative surface in the distal phalanx (27.47%) than in the intermediate (19.19%), proximal phalanges (18.38%) and the palm (13.93%). A similar pattern was observed for HB, as the relative spatial extent was greater in the distal phalanx (19.10%) than in the intermediate (12.89%), proximal phalanges (10.66%) and palm (10.80%). Almost all differences were significant (all $ps < .001$), except for the difference between the palm and of the proximal phalanx ($p = .73$). Further significant differences between HB and TG were found, as relative surfaces were greater for TG in the distal (difference = 8.37; $q^2(1) = 35.19$, $p < .001$), intermediate (difference = 6.29; $q^2(1) = 28.80$, $p < .001$), proximal phalanges (difference = 7.71; $q^2(1) = 47.47$, $p < .001$), and the palm (difference = 3.12; $q^2(1) = 30.59$, $p < .001$). Overall, relative surfaces were larger for TG than for HB (6.37%).

A significant interaction also arose between the relative spatial extent of HB and WM ($Q^2(3) = 11549.87$, $p < .001$, Cramer's $V = .17$). The surfaces of all segments were all significantly different for WM (all $ps < .001$), with a greater relative surface in the palm (26.24%) than in the proximal (16.75%), distal (14.20%) and intermediate phalanges (9.28%). Differences between HB and WM were also significant, since surface was greater for WM in the palm (difference = 15.44; $q^2(1) = 130.59$, $p < .001$) and proximal phalanx (difference = 6.09; $q^2(1) = 38.31$, $p < .001$), and greater for HB in the distal (difference = 4.90; $q^2(1) = 23.33$, $p < .001$) and intermediate phalanges (difference = 3.61; $q^2(1) = 19.29$, $p < .001$). Overall, relative surfaces were larger for WM than for HB (3.26%).

The interaction between the relative spatial extent of TG and WM was also significant ($Q^2(3) = 11549.87$, $p < .001$, Cramer's $V = .17$). Differences between their relative spatial extent were significant, it was greater for WM in the palm (difference = 12.32; $q^2(1) = 100.19$, $p < .001$), and greater for TG in the distal (difference = 13.27; $q^2(1) = 58.58$, $p < .001$), intermediate

(difference = 9.90; $q\chi(1) = 47.92$, $p < .001$) and proximal phalanges (difference = 1.62; $q\chi(1) = 9.19$, $p < .001$). Overall, relative surfaces were larger for TG than for WM (3.12%).

2.2.2. Differences in the topographical frequency

Differences in the topographical frequency of each sensation were investigated by computing topographical statistics using the previously generated frequency maps (first row of Figure 2). For each couple of sensations, cell-by-cell comparisons with the exact test for the significance of change (Liddell, 1983) were computed between their topographical frequency. The resulting probability maps were converted into binary maps (0 = non-significant cell, 1 = significant cell) and a spatial scan procedure (Kulldorff, 1997), which consists of a circular window scanning the map in a step-wise fashion, was performed to highlight significant clusters of correlated cells. A maximum radius of 6 cells and 999 iterations of the Bernoulli (binary) model were computed. Only significant clusters at $p < .002$ were kept. This procedure eliminates incidental clusters of correlations and lower the risk of type I errors. The resulting significance maps are depicted in Figure 2, organized in columns and rows in relation with the two topographical frequency maps they depict the differences.

Significant differences were found between all three sensations. When comparing TG and WM, TG were more frequent on the fingers, covering 21.70% of the hand (95% CI [20.50%, 22.95%]), and WM were more frequent on the palm, covering 37.77% of the hand (95% CI [36.33%, 39.33%]). Comparisons between WM and HB also revealed that WM was more frequent on the palm, on a surface of 44.04% (95% CI [42.57%, 45.53%]), whereas HB was more frequent on the index distal phalanx, covering only 0.76% of the hand (95% CI [0.54%, 1.07%]). This last difference might be considered as an artifact.

2.2.3. Differences in the non-topographic parameters of heartbeat, tingling and warming sensations

The other parameters investigated were the spatial extent, the spatial extent per area, the number of disjointed areas and the intensity. Their characteristics are reported in Table 1.

Table 1 : Mean (SD) values for the non-topographic parameters of heartbeat, tingling and warming sensations.

	Spatial extent (%)	Spatial extent / area (%)	Number of areas	Intensity
Heartbeat	6.22 (8.92)	3.82 (6.88)	2.82 (2.65)	2.36 (2.08)
Tingling	8.77 (15.08)	2.05 (3.39)	3.50 (2.70)	2.37 (1.82)
Warming	10.04 (14.65)	4.64 (9.70)	2.81 (3.26)	2.49 (2.10)

An analysis of variance (ANOVA) was computed on each of the SPS parameter presented in Table 1 with the SPS types (HB, TG and WM) as within-participants factors, followed by *post-hoc* Newman-Keuls tests. The main effect of spatial extent was significant ($F(2; 192)=3.07, p<.05, \eta^2_p=0.03$), with RC covering a greater overall surface than HB ($p<.05$; Cohen's $d = .32$). The main effect of spatial extent per area was significant as well ($F(2; 192)=4.81, p=.009, \eta^2_p=0.05$): TG sensations were reported on narrower areas than HB sensations ($p<.001$; Cohen's $d = .32$) and WM sensations ($p<.01$; Cohen's $d = .35$).

Previous studies showed the predominance of deep, surface, and thermal sensations in the perception of SPS (see Supplementary material). These sensations would involve distinct afferents on a peripheral level (A. D. Craig, 2003c; Granovsky et al., 2005; Tuthill & Azim, 2018; Vaitl, 1996; Vallbo, 1981; Vallbo & Johansson, 1984; Westerman & Delaney, 1991) and would elicit different processing on a neural level (Berlucchi & Aglioti, 2010; A. D. Craig, 2003c; A. D. Craig et al., 2000; Gallace & Spence, 2008, 2010; Green, 2004; Peltz et al., 2011; Shergill, 2001; Smith et al., 2017). If deep, surface, and thermal sensations in the perception of SPS do rely on different underpinnings, this would transpire through their topographical and non-topographical characteristics. Here, we aimed to assess whether the SPS standardized task could be modified so that participants would only focus on heartbeat, tingling and warming sensations, and if it allowed to collect their characteristics.

We found differences between these sensations, both in their distribution and their other parameters. All sensations were unevenly distributed, but none showed the exact same gradient or pattern. The decrement in frequency between distal and proximal areas was found for tingling and heartbeat sensations, but it was steeper in the phalanges for heartbeat sensations; in contrast, the decrement of warming sensations was almost reversed, as they were highly reported on the palm and proximal phalanx and were poorly perceived on the intermediate phalanx. Warming sensations were more perceived on the palm than heartbeat and tingling sensations, whereas tingling were more perceived than warming sensations in the fingers, and more than heartbeat sensations over

the whole hand. We also found that these sensations varied in size, as tingling sensations covered less surface than warming and heartbeat sensations.

These findings support that the task succeeded in collecting the specific topographical and non-topographical characteristics of heartbeat, tingling and warming sensations. As expected, the distribution of tingling sensations is consistent with the organization of cutaneous mechanoreceptors (Johansson & Vallbo, 1979a; Vallbo & Johansson, 1984), and reflect the gradient typically exhibited in SPS frequency irrespectively of their type (Michael et al., 2012, 2015; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues, Plancher, Jacquot, et al., 2021). In addition, warming sensations were more frequent on the palm and distal phalanges, suggesting that these SPS would be linked to thermal sensitivity (Filingeri et al., 2018; Li et al., 2008). Finally, heartbeat sensations were more frequently reported on distal phalanges and on the thenar eminence, that is to say on the areas of the glabrous hand that are the most innervated by superficial veins and arteries (Taylor & Schwarz, 1955). Overall, these findings are consistent with what was announced and reinforce the idea of multiple determinants behind SPS perception.

In the next session, we will investigate how these sensations relate to electrophysiological activity within the somatosensory cortices, that are dedicated to somatosensory perception (Gallace & Spence, 2008, 2009; Tsakiris, 2010), and the temporoparietal junction and interior insula, that – among other – underpins multimodal integration (Berlucchi & Aglioti, 2010; Casey et al., 1996; A. D. Craig, 2003c; Ionta et al., 2014; Lopez et al., 2008; Pollatos, Schandry, et al., 2007; Tsakiris, 2010; Wu et al., 2015). This was done with a subset of the participants presented here.

3. Experiment 2

3.1. Method

3.1.1. Participants

The sample was constituted of 39 participants (26 female and 13 male), with a mean age of 20.49 \pm 2.48 years (range: 17 to 28) and a mean BMI of 21.52 \pm 3 kg/m² (range: 14.8 to 33.59). All participated to the first experiment and were included based on the same criteria.

3.1.2. Resting-state EEG

A resting-state EEG was performed one hour prior to the three-SPS task. The material consisted of an EEG ACTi Champ with active electrodes, 64 channels disposed following the revised 10/20 system (Jurcak et al., 2007) and 5 EOGs: two horizontally on each cheekbone and two vertically above and under the eye that monitored blinking and eye movement, and a reference EOG on the nose bridge for a monopolar setup. Impedances were kept below 40k Ω (Ferree et al., 2001; Kappenman & Luck, 2010).

Participants were comfortably seated in front of a computer monitor in a recording booth, with dimmed lights. The task started once the electroencephalographic equipment was fitted and the signal quality was checked. Instructions were displayed in white font on a black background. Participants were informed of the importance of minimizing movements and to resist sleepiness during the recording and were asked to fully relax and close their eyes for the entire duration of the resting period. When ready, participants had to press any key – triggering the start of the resting period – and to rest with eyes closed until the participants announced the end of the session. The resting period lasted 3 min. No participants reported having fallen asleep or encountered any problem.

3.1.3. Data processing

3.1.3.1. EEG preprocessing

Data preprocessing was conducted using BrainVision Analyzer 2.1. A passband of 0.2 – 120 Hz with a 50 Hz notch was applied, and bad electrode signals were removed and replaced by the mean signal of the nearest electrodes. On average, 2.56 ± 2.35 electrodes per participant (up to 8 electrodes) were corrected. Those more replaced were P1 (11 participants), P7 (9 participants), T7 (8 participants), F8, TP10 (7 participants), P8, TP7, TP9 (6 participants), AF8, FT7, and T8 (5 participants). Those least removed were AF4, AFz, C1, C3, C4, F1, F2, F4, F6, FC1, FC4, FC5, Oz, P4, PO7, POz, Pz (one participant per electrode), C6, F5, FC6, Fz, PO3, PO8 (2 participants), AF7, F7, FT8, O1, TP8 (3 participants), FP1, C5, Fp2, FT10, FT9, and P2 (4 participants). An ocular correction was applied with the Gratton & Coles algorithm (Gratton et al., 1983). For each participant, the 3-minutes recording was divided into 90 epochs of 2 s (A. C. N. Chen et al., 2008), and the first 5 epochs were removed to ensure no interference arises from evoked response due to instructions reading or closing the eyes (Barry et al., 2007, 2011). An artifact rejection, with a decision criterion of $80\mu\text{V}$ as maximum amplitude (A. C. N. Chen et al., 2008), resulted in a rejection rate of 17.80 epochs. *In fine*, a mean of 69.87 ± 10.19 epochs per participants, ranging from 39 to 85, were considered for analysis.

3.1.3.2. Extraction of electroencephalographic indices

Two separate analyses of the signal were carried out using the sLORETA algorithm (LORETA-KEY; KEY Institute for Brain-Mind Research Switzerland): an extraction of the ROIs current sources density and of the functional connectivity index between ROIs. This was done following the same procedure described respectively in (Michael et al., n.d.) and in experiment 1 of (Salgues, Plancher, Jacquot, et al., 2021), as the present study share similar motives regarding the investigation of the electroencephalographic activity.

The sLORETA algorithm uses a realistic three-shell bead model based on the MNI 152 template provided by Brain Imaging Center of MNI (Fuchs et al., 2002) that includes the scalp, skull and brain restricted to the cortical gray matter and hippocampus (Talairach & Tournoux, 1988). Its inverse solution is based on existing neuroanatomical and physiological knowledge, and the smoothness assumption (Pascual-Marqui, 2002). sLORETA extracts the synchronously activated neuronal populations underlying EEG activity by computing their cortical localization from the scalp distribution in the electric field, with a spatial resolution of 5mm^3 (Pascual-Marqui, 2002), which is comparable with fMRI (1.5T) spatial resolution of 4mm^3 under optimal

conditions (Özcan et al., 2005; Yoo et al., 2004). sLORETA implements the “lagged phase synchronization” that models the instantaneous and lagged components of functional connectivity, which allows it to robustly identify true physiological connectivity, and can be applied on filtered data to operate a frequency decomposition of the functional connectivity (Pascual-Marqui et al., 2011). As stated in previous studies (Michael et al., n.d.; Salgues, Plancher, Jacquot, et al., 2021), the sLORETA was regarded as a good fit for the study purposes.

Four ROIs were seeded: SI, SII, TPJ, AI. To target the hand area of the somatosensory cortices, a ROI file was constructed with the MNI coordinates for 4 seed mid-points (digits and palm in SI and SII) from a total of 149 coordinates reported in the literature (35 studies) on cortical somatosensory responses to tactile stimulation of the right hand (see Supplementary material in (Michael et al., n.d.)). In the left hemisphere, the mid-point coordinates ($x = -46, y = -29, z = 55$) in SI and ($x = -51, y = -23, z = 19$) in SII were used. The Euclidian distance between the two points was 7.07mm. The coordinates ($x = -54, y = -48, z = 7$; (Arzy et al., 2006)) in TPJ and ($x = -32, y = -12, z = 20$; (A. D. Craig et al., 2000)) in AI were the same used in a previous study (Salgues, Plancher, Jacquot, et al., 2021). The primary auditory cortex ($x = -52, y = -19, z = -7$) was used as a control seed. Positive values of the x-axis were used for the right hemisphere.

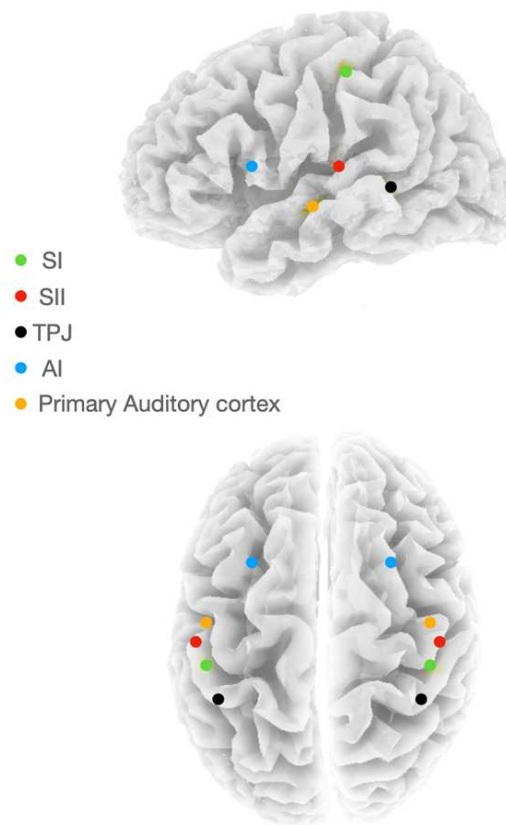


Figure 3 : Spatial MNI coordinates of the ROIs and of the control site (primary auditory cortex) used in the present study.

Analyses were performed in the frequency domain using delta (0.5–3.5hz), theta (4-7hz), alpha (7.5-12hz), beta (13-34hz), and gamma (35-45hz) bands. Artifact free epochs were entered into a cross spectral analysis to compute the current density (intensity of the current/area, measured in A/m^2). Current source density levels were extracted for each of the ROI seeds ($5mm^3$). The resulting file produced log-transformed average current source density in each frequency band, for all participants and for each seed. To make all data comparable, log values were z-transformed before any further analysis.

The lagged phase synchronization of the TPJ with SI, SII and AI were extracted from the current density, using a voxel wise approach. Only ipsilateral connectivity for each hemisphere was considered. The resulting file produced log-transformed functional connectivity index in each frequency band, for all participants and for each connection. Its value ranges from 0 to 1 (the greater the value the stronger the connection). As for the current density values, the functional connectivity indices were z-transformed.

3.2. Results

3.2.1. The topography of heartbeat, tingling and warming sensations

The same procedure described in experiment 1 to yield frequency maps was carried out. Frequency maps of HB, TG and WM sensations are displayed in Figure 4. When considered separately, SPS were not reported over the whole hand: HB sensations were lacking in 4.01% of the surface, mainly on the palm, TG in 4.35% of the surface, on the proximal phalanges of the middle and auricular digits, and WM in 2.77% of the surface on the intermediate phalanx of the middle finger.

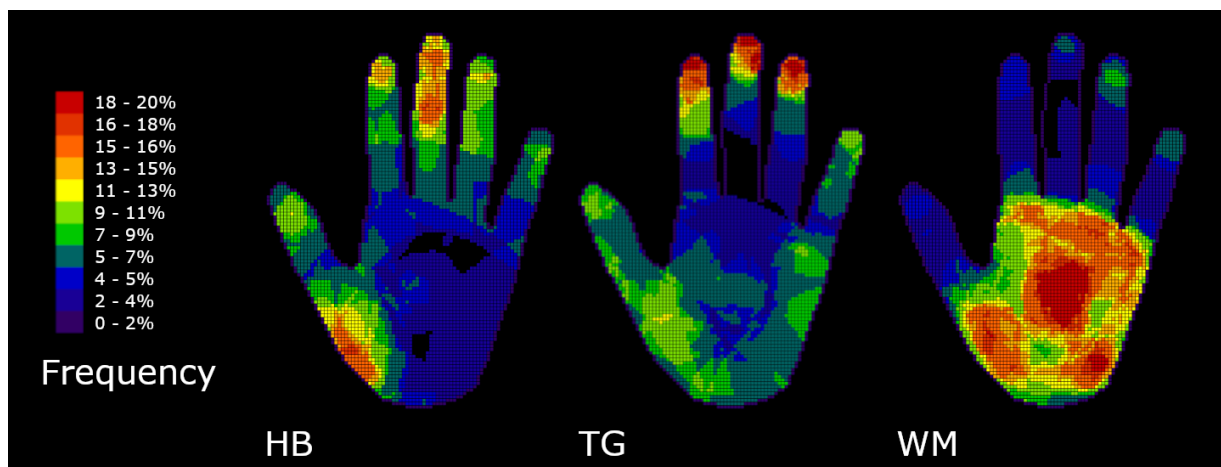


Figure 4 : Topographical maps of the frequency (% of participants having shaded a cell) of heartbeat (HB), tingling (TG) and warming (WM). The frequency is depicted using a color scale: cool/blue colors reflect the least frequently shaded areas and warm/red colors reflect the most frequently shaded areas.

An examination of the proximo-to-distal gradient as described in experiment 1 was performed, as a mean of assessing the validity of the measures.

Relative spatial extent for each sensation entered in the multiple comparison of portion analysis can be found in Figure 5. The interaction between the relative spatial extent of HB and TG sensations was significant ($Q(3) = 850.87, p < .001$, Cramer's $V = .05$). Significant differences were found among the relative spatial extent of each segment for HB (all $ps < .001$), with greater relative surfaces in the distal phalanx (10.06%) than in the intermediate (8.39%), proximal phalanges (4.98%) and palm (3.84%). They were also found for TG (all $ps < .001$), with greater relative surfaces in the distal phalanx (10.98%) than in the palm (5.53%), intermediate (4.78%) and proximal phalanges (3.88). The relative spatial extent was greater for TG in the distal phalanx

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(difference = 1.20; $q^{\chi}(1) = 5.96$, $p < .001$) and palm (difference = 1.69; $q^{\chi}(1) = 23.43$, $p < .001$), whereas it was greater for HB in the intermediate (difference = 3.61; $q^{\chi}(1) = 21.49$, $p < .001$) and proximal (difference = 1.10; $q^{\chi}(1) = 10.4$, $p < .001$) phalanges. Overall, relative surfaces were larger for HB than for TG (.45%).

The interaction between the relative spatial extent of HB and WM sensations was significant as well ($Q^{\chi}(3) = 11196.82$, $p < .001$, Cramer's $V = .28$). Significant differences were found among the relative spatial extent of each segment for WM (all $ps < .001$), as relative surfaces were greater in the palm (12.95%) than in the proximal (6.96%), distal (3.89%) and intermediate (2.12%) phalanges. The relative spatial extent of each segment differed between HB and WM, as it was greater for HB in the distal (difference = 6.17; $q^{\chi}(1) = 37.39$, $p < .001$) and intermediate (difference = 6.26; $q^{\chi}(1) = 41.76$, $p < .001$) phalanges, but was greater for WM in the palm (difference = 9.11; $q^{\chi}(1) = 97.48$, $p < .001$) and proximal phalanx (difference = 1.97; $q^{\chi}(1) = 16.23$, $p < .001$). Overall, relative surfaces were larger for HB than for WM (.34%).

The interaction between the relative spatial extent of TG and WM sensations was also significant ($Q^{\chi}(3) = 7557.37$, $p < .001$, Cramer's $V = .22$). The relative spatial extent of each segment differed between TG and WM, as it was greater for TG in the distal (difference = 7.36; $q^{\chi}(1) = 43.10$, $p < .001$) and intermediate (difference = 2.65; $q^{\chi}(1) = 21.48$, $p < .001$) phalanges, but was greater for WM in the palm (difference = 7.42; $q^{\chi}(1) = 75.61$, $p < .001$) and proximal phalanx (difference = 3.08; $q^{\chi}(1) = 26.52$, $p < .001$). Overall, relative surfaces were larger for WM than for TG (.12%).

The presence of a gradient in the distribution of sensations, and of differences between sensations relative spatial extent, suggest that the task successfully collected the topographic characteristics of HB, TG and WM sensations.

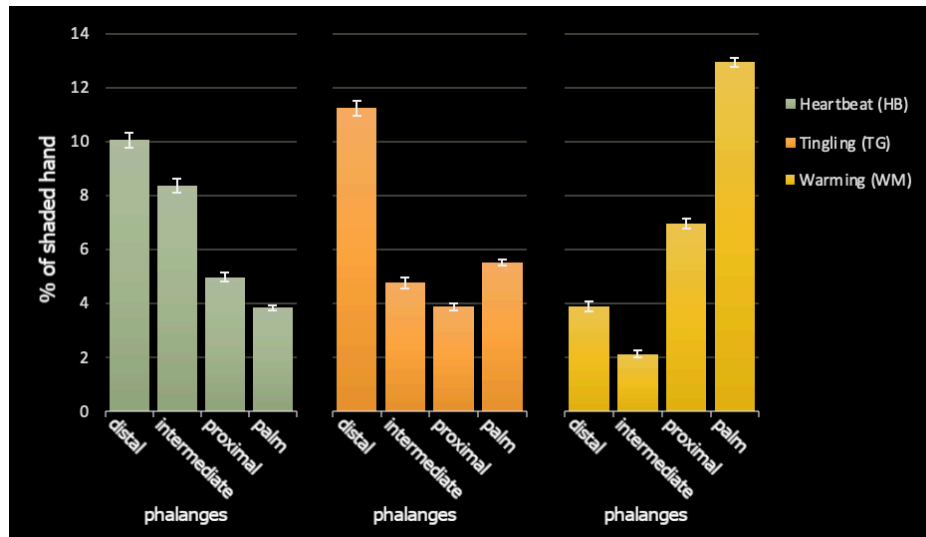


Figure 5 : Graphic depicting the proximo-to-distal gradient (% of shaded cells within each segment) for heartbeat, tingling and warming sensations. Horizontal scale refers to segments: 1 = distal phalanx, 2 = intermediate phalanx, 3 = proximal phalanx, 4 = palm. Error bars depict 95% Wilson confidence intervals.

3.2.2. The relationship between three-SPS frequencies and current densities for each frequency band

To achieve a cell-by-cell analysis, z -transformed current densities were used to fill two maps per participant, right-hand maps were filled with the values of the left hemisphere, and left-hand maps with values of the right hemisphere. This was done separately for each ROI and for each frequency band. In this way the 78 maps (left and right hand) depicting the frequency were correlated to the 78 maps filled with the contralateral z -transformed current densities. Point biserial cell-wise correlations were conducted separately between the frequency of each sensation and the z -transformed current densities. The resulting probability maps were corrected using the same spatial scan procedure described in experiment 1. The 95% Wilson confidence interval was computed for the significance of the overall proportion of area of the hand covered by deemed reliable clusters, and a threshold of 5% relative to the surface area of the hand was posited, below which the total percentage of hand surface area that correlated with a frequency band was considered an artifact (Michael et al., n.d.). This makes it possible to reduce Type I errors. Graphs of the correlated surfaces and corrected probability maps are displayed in Figure 6.

3.2.2.1. Heartbeat frequency and ROIs current densities

Correlations of the HB frequency with ROIs current densities were the most prominent compared to TG and WM. They were the only reliably associated with SI current density (see top left graph of Figure 6), and this exhibited through positive correlations in the gamma band covering 12.96% (95% CI [9.04%, 10.87%]) of the surface, and negative correlations in the theta band on 9.93% (95% CI [9.04%, 10.87%]) of the surface. Negative and positive correlations were found on distinct fingers but were restricted to intermediate and proximal phalanges and adjacent palmar areas.

Only negative correlations were found with the remaining ROIs current densities. In SII (see top right graph of Figure 6), they were found above 7hz, covering a minimal surface of 34.53% (95% CI [33.11%, 35.99%]) in the beta band and a maximal surface of 56.63% (95% CI [53.62%, 56.63%]) in the gamma band.

Regarding TPJ and AI current densities (bottom graphs of Figure 6), negative correlations were found across all frequency bands. In AI, they were the least in the delta band, covering a surface of 13.10% (95% CI [12.11%, 14.16%]), and were the most prominent in the theta band, covering 50.21% (95% CI [48.70%, 51.73%]) of the surface. In TPJ, they covered a minimal surface of 13.15% (95% CI [12.16%, 14.21%]) in the alpha band and a maximal surface of 17.73% (95% CI [16.61%, 18.92%]) in the beta band.

3.2.2.2. Warming frequency and ROIs current densities

The frequency of WM sensations was reliably associated to SII, AI and TPJ current densities only. Like HB sensations, negative correlations in SII (see top right graph of Figure 6) were found above 7hz. They were minimal in the beta band, covering 14.80% (95% CI [13.76%, 15.90%]) of the surface, and maximal in the alpha band, covering 24.53% (95% CI [23.26%, 25,85%]) of the surface. They were the only to also exhibit positive correlations in the beta band, on 9.83% (95% CI [8.97%, 10.76%]) of the surface. Negative and positive correlations were found on opposite segments of the hand, as negative were found on the hand boundaries (i.e., distal phalanges and base of the palm) whereas positive correlations were restricted to the intersection between the palm and digits.

WM frequency was negatively associated to AI current density (see bottom left graph of Figure 6) in the theta band, on a surface of 8.72% (95% CI [7.91%, 9.60%]), and positively

associated to TPJ current density (see bottom right graph of Figure 6) in the delta band, on a surface of 5.96% (95% CI [5.29%, 6.71%]).

3.2.2.3. Tingling frequency and ROIs current density

The frequency of TG sensations was the least associated to ROIs current density. Reliable negative correlations were only found with SII and AI current densities. Like TG and WM sensations, they were found above 7hz in SII (see top right graph of Figure 6). They covered a surface of 6.68% (95% CI [5.96%, 7.48%]) in the gamma band, and 11.81% (95% CI [10.86%, 12.82%]) in the beta band. Like WM sensations, they were only associated with the theta band in AI (see bottom left graph of Figure 6), on a surface of 7.21% (95% CI [33.11%, 35.99%]).

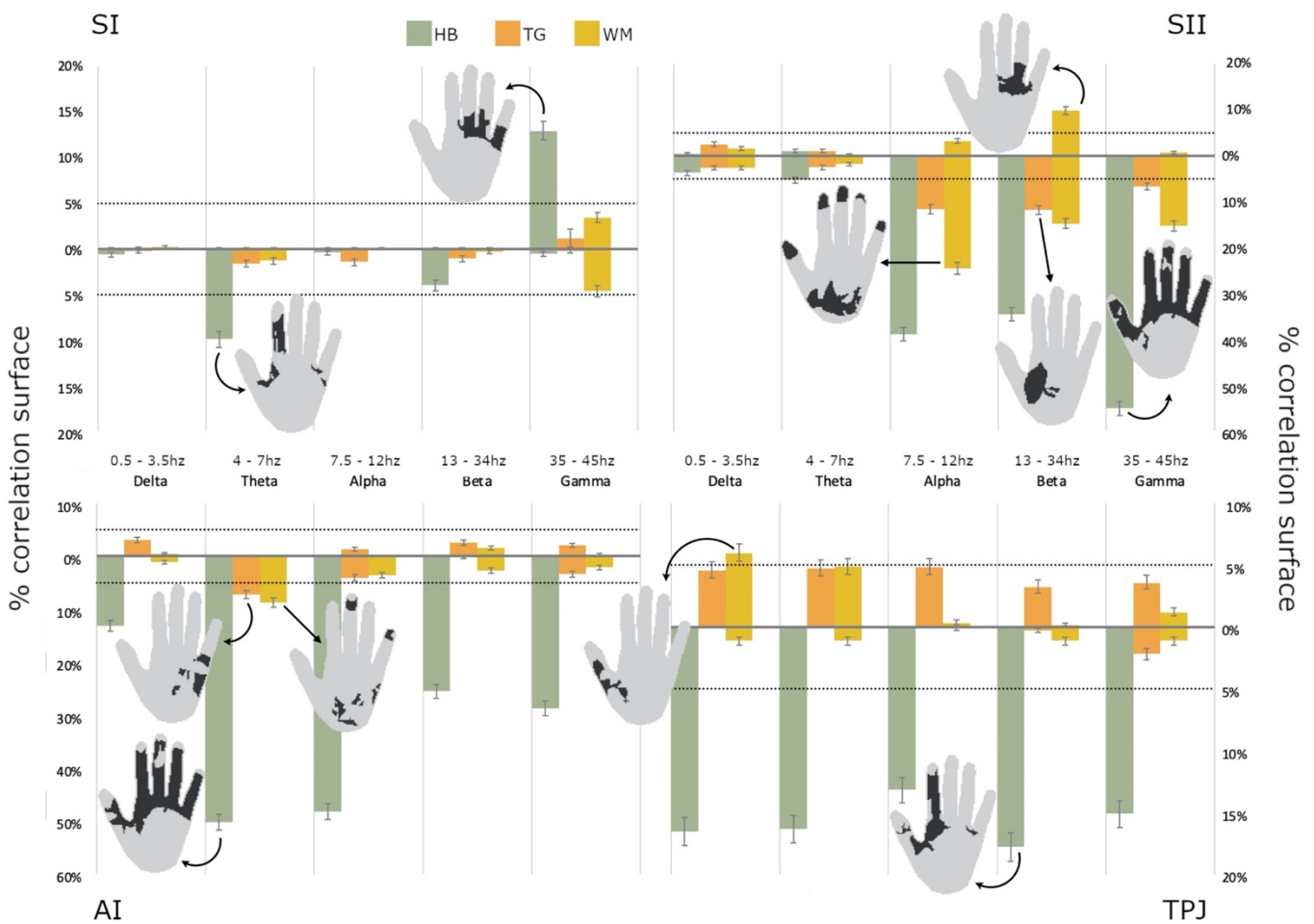


Figure 6 : Percentages of surfaces covered by significant correlations between heartbeat (HB), tingling (TG), warming (WM) frequencies, and current densities in SI (top left graph), SII (top right graph), AI (bottom left graph) and TPJ (bottom right graph). Histograms on top of the 0% value

depict the surface covered by positive correlations, those beneath the 0% value depict the surface covered by negative correlations. The dashed line marks the 5% threshold and error bars represent 95% Wilson confidence intervals. Shadowed areas of the hand depict the areas where significant correlations were observed. Only $p < .001$ clusters are shown, with the requirement that the total surface cover an area greater than or equal to 5% of the hand. When correlation surfaces were above the threshold in more than one frequency band for the same sensation and the same ROI, only the hand map with the largest correlated surface is displayed.

3.2.2.4. The three SPS frequency and the primary auditory cortex current density

The current density in the primary auditory cortex was used as a control condition. Reliable correlations were found with all 3 SPS in all frequency bands (Figure 7).

Regarding HB frequency, reliable positive correlations were found in delta on a surface of 18.59% (95% CI [17.44%, 19.80%]), in theta on a surface of 26.42% (95% CI [25.11%, 27.78%]), and in beta on a surface of 7.78% (95% CI [7.01%, 8.63%]).

For TG frequency, only negative correlations in the alpha band were deemed reliable, covering a surface of 8.65% (95% CI [7.83%, 9.54%]).

For WM frequency, reliable positive correlations covered a surface of 19.09% (95% CI [17.93%, 20.30%]) in delta, a surface of 13.74% (95% CI [12.73%, 14.81%]) in theta, and a surface of 7.21% (95% CI [6.47%, 8.03%]) in gamma. Reliable negative correlations were found as well in alpha, covering 6.31% (95% CI [5.62%, 7.09%]) of the surface, and in beta, covering 10.77% (95% CI [9.87%, 11.74%]) of the surface.

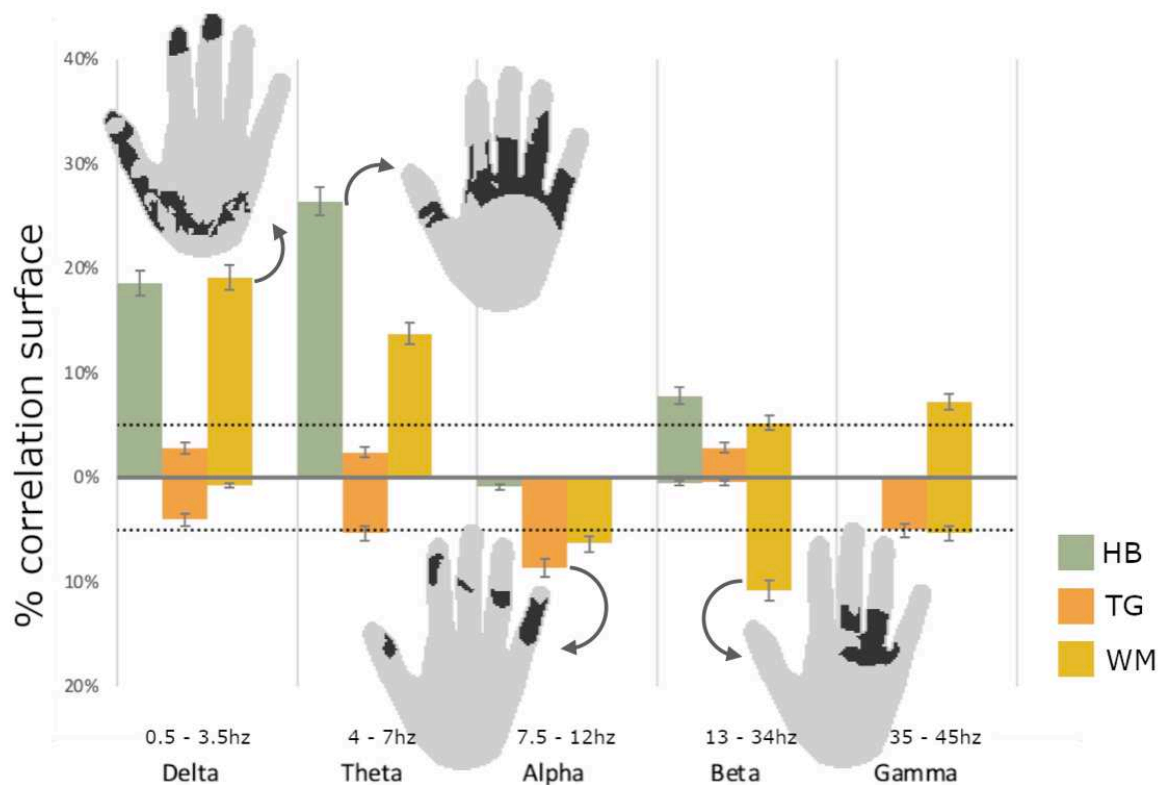


Figure 7: Percentages of surfaces covered by significant correlations between heartbeat (HB), tingling (TG), warming (WM) frequencies, and current densities in the primary auditory cortex. Histograms on top of the 0% value depict the surface covered by positive correlations, those beneath the 0% value depict the surface covered by negative correlations. The dashed line marks the 5% threshold and error bars represent 95% Wilson confidence intervals. Shaded areas of the hand depict the areas where significant correlations were observed. Only $p < .001$ clusters are shown, with the requirement that the total surface cover an area greater than or equal to 5% of the hand. When correlation surfaces were above the threshold in more than one frequency band for the same sensation, only the hand map with the largest correlated surface is displayed.

3.2.3. The relationship between the frequencies of the three-SPS and functional connectivities for each frequency bands

To achieve a cell-by-cell analysis, z -transformed functional connectivity indices were used to fill two maps per participant, right-hand maps were filled with the values of the left hemisphere, and left-hand maps with values of the right hemisphere. This was done separately for each functional connectivity and for each frequency band. In this way the 78 maps (left and right hand) depicting the frequency were correlated to the 78 maps filled with the contralateral z -transformed functional connectivity. Point biserial cell-wise correlations were conducted separately between the frequency

of each sensation and the z -transformed functional connectivity. The resulting probability maps were corrected using the same spatial scan procedure described in experiment 1 and underwent the same 95% Wilson confidence interval computation and 5% threshold applied for the correlations with current densities. They are depicted in Figure 8.

3.2.3.1. Heartbeat frequency and TPJ functional connectivity

The frequency of HB sensations exhibited more prominent reliable positive associations with each of the targeted TPJ functional connectivities, compared to the other sensations. In the TPJ-SI functional connectivity (see top left graph of Figure 8), reliable correlations were found across all frequency bands above 4Hz . They covered a surface of 7.76% (95% CI [6.98%, 8.61%]) in the gamma band, and 17.16% (95% CI [16.05%, 18.33%]) in the theta band. The prominence of the theta band was true as well in the TPJ – SII (see top right graph of Figure 8) and TPJ – AI functional connectivities (see bottom graph of Figure 8), where positive correlations covered respectively 12.41% (95% CI [11.45%, 13.44%]) and 11.24% (95% CI [10.32%, 12.23%]) of the surface. Positive correlations were also found in the gamma band for TPJ – SII, on 8.23% (95% CI [7.44%, 9.10%]) of the surface, and in the beta band for TPJ – AI, on a surface of 8.21% (95% CI [7.42%, 9.08%]).

3.2.3.2. Warming frequency and TPJ functional connectivity

WM sensations were the second most associated to each of the TPJ functional connectivities. This exhibited particularly through the gamma band, with reliable positive correlations covering a surface of 8.60% (95% CI [7.79%, 9.48%]) in TPJ – SI (see top left graph of Figure 8), 13.85% (95% CI [12.85%, 14.93%]) in TPJ – SII (see top right graph of Figure 8), and 10.16% (95% CI [9.28%, 11.10%]) in TPJ – AI (see bottom graph of Figure 8). Positive correlations were also found in the theta band for TPJ – SII, covering 6.31% (95% CI [5.62%, 7.09%]) of the surface.

3.2.3.3. Tingling frequency and TPJ functional connectivity

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The frequency of TG sensations was the least associated to the TPJ functional connectivity, as it was only found in TPJ – SII and TPJ – AI functional connectivities. They were also the only to exhibit reliable negative correlations, that were found in the delta band of TPJ – SII (see top right graph of Figure 8) covering a surface of 7.76% (95% CI [6.99%, 8.61%]). Otherwise, they were positively associated to the beta band in TPJ – AI (see bottom graph of Figure 8), on a surface of 9.92% (95% CI [9.05%, 10.86%]).

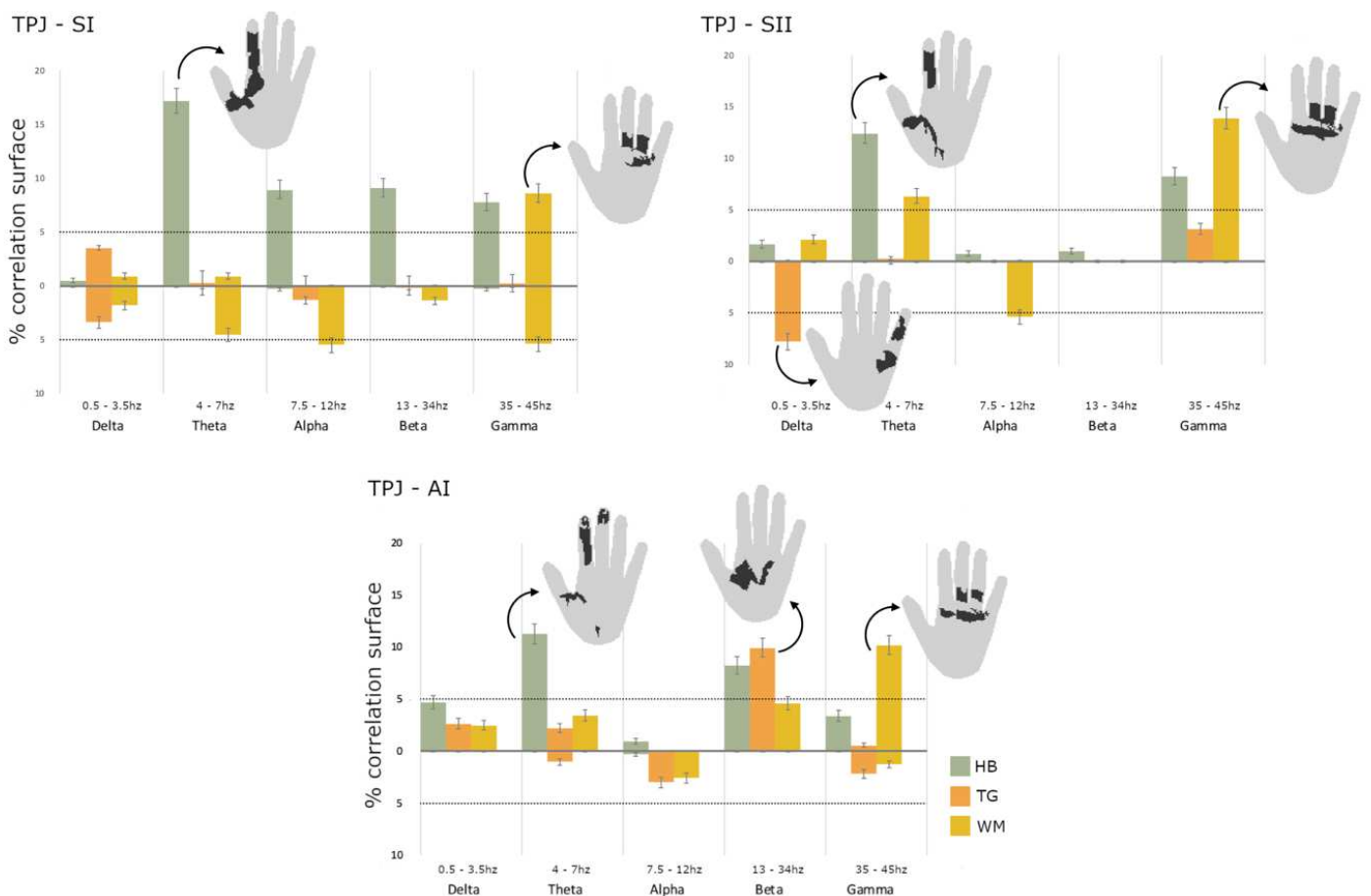


Figure 8 : Percentages of surfaces covered by significant correlations between heartbeat (HB), tingling (TG), warming (WM) frequencies, and the TPJ functional connectivity with SI (top left graph), SII (top right graph), and AI (bottom graph). Histograms on top of the 0% value depict the surface covered by positive correlations, those beneath the 0% value depict the surface covered by negative correlations. The dashed line marks the 5% threshold and error bars represent 95% Wilson confidence intervals. Shaded areas of the hand depict the areas where significant correlations were observed. Only $p < .001$ clusters are shown, with the requirement that the total surface cover an area greater than or equal to 5% of the hand. When correlation surfaces were above the threshold in more than one frequency band for the same sensation and the same connectivity, only the hand map with the largest correlated surface is displayed.

3.2.4. Other parameters and oscillatory activity

The non-topographic parameters investigated were the spatial extent, the spatial extent per number of areas, the number of disjointed areas, the perceived intensity and participants' confidence in the location and extent of sensations. Their values for each sensation are provided in Table 2.

Table 2 : Mean (SD) values for each non-topographic parameters of heartbeat (HB), tingling (TG) and warming (WM) SPS.

	HB	TG	WM
Spatial extent	5.21 (10.87)	5.78 (8.60)	8.89 (11.33)
Spatial extent / area	3.55 (9.38)	3.29 (5.08)	7.29 (9.59)
Number of areas	1.82 (2.08)	2.49 (2.49)	1.79 (1.87)
Intensity	1.95 (1.94)	1.83 (1.52)	1.96 (1.75)

To investigate whether the electroencephalographic measures for each ROIs and each targeted network had a predictive effect on the non-topographic SPS parameters, mean current density per ROI and mean functional connectivity per network was extracted by averaging values in each frequency bands and each hemisphere. Values are provided in Table 3.

Table 3 : Mean (SD), minimal and maximal values for the mean current densities in SI, SII, AI, TPJ and the primary auditory cortex.

	Mean (SD)	Min	Max
Mean current density			
SI	-1.15 (.11)	-1.43	-0.86
SII	-1.55 (.12)	-1.90	-1.28
AI	-3.06 (.26)	-3.62	-2.37
TPJ	-3.95 (.40)	-4.76	-3.08
Primary Auditory Cortex	-1.49 (.12)	-1.83	-1.25
Mean functional connectivity			
TPJ – SI	.22 (.09)	.07	.47
TPJ – SII	.14 (.06)	.06	.34
TPJ – AI	.22 (.07)	.11	.38

Multiple regression analyses were conducted with the non-topographic SPS parameters as dependent variables. The mean current density for each ROI and the primary auditory cortex, as well as the mean functional connectivity for each network was entered as predictors, along with age, gender and BMI since they are known to influence tactile (Kozłowska, 1998) and SPS

perception (Naveteur et al., 2015). All variables were *z*-transformed beforehand. The results (not Bonferroni corrected (Cabin et al., 2000; Perneger, 1998) are presented in Table 4.

Table 4 : Standardized β coefficients (t SEM) and adjusted R^2 coefficient from the multiple regression analysis carried out on each of the six collected dependent variables for heartbeat (HB), tingling (TG) and warming (WM) SPS, with age, gender, body mass index (BMI), the mean current density for SI, SII, AI and TPJ, and the mean functional connectivity of TPJ with SI, SII and AI. Significant predictors at least at $p < .05$ are marked with an asterisk.

	Spatial extent (%)			Spatial extent / area			Number of areas			Intensity		
	HB	TG	WM	HB	TG	WM	HB	TG	WM	HB	TG	WM
Age	-.01 (.16)	-.27 (.19)	-.23 (.20)	.04 (.15)	-.24 (.18)	-.32 (.19)	-.09 (.19)	-.07 (.21)	-.02 (.18)	.04 (.20)	-.07 (.21)	-.10 (.20)
Gender	-.29 (.15)	-.25 (.18)	-.23 (.18)	-.20 (.14)	-.27 (.17)	-.13 (.18)	-.18 (.17)	-.05 (.19)	-.22 (.16)	-.06 (.19)	-.05 (.20)	-.13 (.18)
BMI	-.17 (.16)	-.33 (.19)	-.23 (.19)	-.08 (.15)	-.31 (.18)	-.31 (.19)	-.16 (.18)	-.05 (.20)	.22 (.17)	.01 (.20)	-.18 (.21)	.02 (.19)
Mean current density												
SI	-.67 (.48)	.00 (.57)	-.44 (.58)	-.66 (.46)	-.08 (.54)	-.34 (.57)	.38 (.56)	.53 (.61)	-.49 (.53)	.38 (.61)	-.42 (.63)	-.70 (.58)
SII	-.61 (.24)*	-.46 (.28)	-.54 (.29)	-.56 (.23)*	-.56 (.27)	-.38 (.28)	-.13 (.28)	.16 (.31)	-.44 (.27)	.05 (.30)	-.34 (.32)	-.26 (.29)
AI	.71 (.71)	-.26 (.84)	.13 (.86)	.96 (.68)	-.13 (.80)	-.04 (.84)	-1.59 (.83)	-.97 (.91)	.62 (.79)	-1.36 (.90)	.14 (.94)	.49 (.86)
TPJ	1.56 (.66)*	.47 (.77)	.62 (.79)	1.82 (.62)*	.61 (.74)	-.23 (.77)	.24 (.76)	.73 (.83)	1.52 (.72)*	.14 (.82)	-.24 (.86)	.37 (.79)
Primary Auditory Cortex	-1.39 (.63)*	.5 (.75)	.13 (.76)	-1.93 (.60)*	.23 (.71)	1.11 (.74)	.87 (.73)	-.09 (.81)	-1.53 (.70)*	.58 (.80)	.30 (.83)	-.14 (.76)
Mean functional connectivity												
TPJ – SI	.11 (.63)	.82 (.74)	.12 (.75)	.34 (.59)	1.02 (.70)	-.02 (.73)	-1.57 (.73)*	-.84 (.80)	-.07 (.69)	-1.51 (.79)	.12 (.82)	-.93 (.75)
TPJ – SII	-.44 (.52)	-.97 (.61)	-.52 (.63)	-.44 (.49)	-1.25 (.58)*	-.30 (.61)	.11 (.60)	.95 (.66)	-.02 (.57)	.59 (.65)	-.16 (.68)	.73 (.62)
TPJ – AI	.75 (.54)	.67 (.63)	.79 (.65)	.49 (.51)	.68 (.61)	.65 (.63)	1.48 (.62)*	.23 (.68)	.28 (.59)	.61 (.68)	-.22 (.71)	.03 (.65)
Adjusted R²	.291	.017	-.028	.360	.102	.025	.046	-.147	.143	-.118	-.220	-.025

The spatial extent of HB was negatively predicted by the mean current density in SII ($\beta = -.61$, $t(38) = -2.53$, $p = .02$, adjusted $R^2 = .29$) and in the primary auditory cortex ($\beta = -1.39$, $t(38) = -2.20$, $p = .04$, adjusted $R^2 = .29$), but was positively predicted by the mean current density in TPJ ($\beta = 1.56$, $t(38) = 2.38$, $p = .03$, adjusted $R^2 = .29$). Similar effects were found in the spatial extent per area of HB for SII ($\beta = -.56$, $t(38) = -2.43$, $p = .02$, adjusted $R^2 = .36$), the primary auditory

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cortex ($\beta = -1.93$, $t(38) = -3.21$, $p < .005$, adjusted $R^2 = .36$) and TPJ mean current densities ($\beta = 1.82$, $t(38) = 2.91$, $p < .005$, adjusted $R^2 = .36$). The number of disjoined areas of HB was negatively predicted by the TPJ – SI mean functional connectivity ($\beta = -1.57$, $t(38) = -2.16$, $p = .04$, adjusted $R^2 = .31$) and positively predicted by the TPJ – AI mean functional connectivity SII ($\beta = 1.48$, $t(38) = 2.36$, $p = .03$, adjusted $R^2 = .05$).

The spatial extent per area for TG was negatively predicted by the mean functional connectivity of TPJ with SII ($\beta = -1.25$, $t(38) = -2.15$, $p = .04$, adjusted $R^2 = .10$).

The number of disjoined areas of WM was positively predicted by the TPJ mean current density ($\beta = 1.52$, $t(38) = 2.10$, $p = .05$, adjusted $R^2 = .14$) and negatively predicted by the primary auditory cortex mean current density ($\beta = -1.53$, $t(38) = -2.20$, $p = .04$, adjusted $R^2 = .14$).

4. Discussion

Many studies showed that interindividual differences impacted differently the perception of SPS according to their type (Borg et al., 2015; Echalié et al., 2020; Michael et al., 2015, 2017; Michael, Guyot, et al., 2020; Naveteur et al., 2015; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021; Tihanyi et al., 2018; Tihanyi, 2019; Tihanyi & Köteles, 2017), suggesting that distinct cognitive factors would determine the qualitative dimension of this phenomenon. Due to the current lack of knowledge toward this matter, we set to establish the phenomenology of the three most reported SPS types, i.e., deep, thermal, and surface SPS. Experiment 1 explored the perception of deep, surface, and thermal SPS, asking participants only to focus on beat/pulse, tingling and warming sensations. We found clear differences in the topographical and non-topographical characteristics between each of these types of SPS. This comforted us in our assumption that it is possible to extract the specificities of SPS according to their type.

Beside, previous studies demonstrated the involvement of the oscillatory activity of the somatosensory cortices (Michael et al., n.d.) and of the TPJ-AI functional connectivity (Salgues, Plancher, Jacquot, et al., 2021) in the perception of SPS. These areas would ensure the processing, integration and would enable awareness of bodily signals (A. D. Craig, 2003c; Ronchi et al., 2018; Tsakiris, 2010). Since their involvement in the processing of interoceptive, thermal and tactile signals was repeatedly evidenced (A. D. Craig, 2009a; A. D. Craig et al., 2000; Gallace & Spence, 2008, 2009, 2010; Green, 2004; Peltz et al., 2011), we wondered whether they would as well be involved in the perception of deep, thermal and surface SPS. Using a portion of the sample in experiment 1, experiment 2 investigated the relationship between each of these SPS and (i) the current density in SI and SII, the perceptual cortices devoted to somatosensory processing (Gallace & Spence, 2010; Tsakiris, 2010); (ii) the current density in AI and TPJ, multisensory integration areas (Arzy et al., 2006; Berlucchi & Aglioti, 2010; A. D. Craig, 2003c, 2009a; Igelström & Graziano, 2017; Ionta et al., 2011); (iii) the functional connectivity of the TPJ with SI, SII, and AI, that would support somatosensory awareness (Gallace & Spence, 2010). We found that the perception of heartbeat, tingling, and warming SPS were distinctly associated to the oscillatory activity in these areas and to their synchronization. As a control measure, we also explored the correlation between the 3 SPS frequencies and the current density in the primary auditory cortex and found reliable correlations as well. We will first discuss about the differences between deep, surface, and thermal SPS, and how they might reflect peripheral underpinnings. We will then focus

on their associations with the EEG activity and will elaborate on the neural mechanisms that may be engaged in their perception.

4.1. Differences in the characteristics of SPS according to their type

The investigation of SPS perceived on the hands repeatedly emphasized a typical distribution following a proximo-to-distal gradient (Echalier et al., 2020; Michael et al., 2012, 2015; Michael, Guyot, et al., 2020; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021). Experiment 1 provided evidence that the topography of SPS and their non-topographic characteristics were closely related to the type of sensations perceived. Deep SPS were gradually distributed only on digits and were particularly more frequent on fingertips and the thenar eminence. Besides, they were found to cover the least surface. In contrast, surface and thermal SPS exhibited a gradient over the whole hand but were differently distributed, as surface were more frequently reported on digits whereas thermal SPS were heavily reported on the palmar area. Thermal SPS were also reported on greater surface, but surface SPS were the most numerous compared to the two others. The differences exhibited in the characteristics of SPS types might relate to peripheral and physiological factors.

Although distinct, the distribution of deep and surface SPS were the most resembling and the most similar to the one repeatedly exhibited in the perception of SPS (Michael et al., 2012, 2015, 2017; Michael & Naveteur, 2011; Naveteur et al., 2015; Salgues, Plancher, & Michael, 2021; Salgues, Plancher, Jacquot, et al., 2021). It was repeatedly compared to the cutaneous sensory units organization on the glabrous skin (Ferentzi et al., 2017; Johansson & Vallbo, 1979a, 1979b; Michael & Naveteur, 2011; Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017; Vallbo & Johansson, 1976) that underpin a greater tactile acuity on the distal phalanges in comparison to the palm. This gradient is due to the optimal cutaneous mechanoreceptors' density, the narrow receptive fields (Johansson & Vallbo, 1979b; Vallbo & Johansson, 1984), and low psychophysical and neural thresholds near distal phalanges (Johansson & Vallbo, 1979b; Vallbo & Johansson, 1976), whereas when drawing near the proximal areas of the hand, the cutaneous mechanoreceptors density decreases, large receptive fields are more abundant (Johansson & Vallbo, 1979b; Vallbo & Johansson, 1984), and the neural threshold increases, meaning single impulse from the proximal areas are less likely to provoke a sensation (Johansson & Vallbo, 1979b; Vallbo, 1981; Vallbo &

Johansson, 1976). It is congruent that surface SPS would be distributed along such a gradient, as the stimulation of mechanoreceptive unit is associated to the perception of sensations like tingling, flutter or vibration (Vallbo, 1981).

Yet, the perception of deep events would rely on visceral inputs and proprioceptive units (Tuthill & Azim, 2018; Vaitl, 1996), the latter being located in the musculoskeletal apparatus (i.e., joints, muscles, tendons) (Tuthill & Azim, 2018). To our knowledge, no studies investigated the perception of cardiac events on the skin or provided evidence that mechanoreceptive units on the glabrous skin would contribute to the perception of cardiac signals. But it was proposed that visceral inputs would borrow somatosensory afferents, as some cutaneous receptive units would be sensitive to blood pressure (G. E. Jones et al., 1987; Schandry et al., 1993). Regarding the volar hand blood vessels, superficial veins create a dense network right in the thenar eminence, and arteries innervate profusely distal phalanges (Taylor & Schwarz, 1955), which are consistently the areas where deep SPS were more frequently reported. The perception of deep SPS might be linked to blood circulation causing internal pressure on the skin. This is supported by evidence of cutaneous stimulation increasing the frequency of SPS (Beaudoin & Michael, 2014; Michael & Naveteur, 2011). Besides, perceiving SPS relates to interoceptive abilities (Michael et al., 2015), but heartbeat detection would vary with the cardiovascular system dynamic (Schandry et al., 1993; Yates et al., 1985), and interoceptive accuracy would increase as a function of the systolic blood pressure level (O'Brien et al., 1998). This supports the idea that some SPS might have an origin in the spontaneous physiological activity (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017).

On their part, thermal SPS followed a different distribution that is new in the study of SPS, as they were particularly prominent on palmar areas. Yet, this pattern is similar to the one exhibited in studies mapping the thermal sensitivity to warm on the glabrous hand (Filingeri et al., 2018; Li et al., 2008). This might suggest differences in the peripheral units coding for SPS: while stimulation on the skin surface are transmitted by myelinated and unmyelinated fibers (Hallin & Torebjörk, 1976; Vallbo & Johansson, 1984), the detection of thermal events (specifically warm) would rely on unmyelinated C-fibers afferents (Darian-Smith et al., 1979; Paricio-Montesinos et al., 2020; Westerman & Delaney, 1991; Yarnitsky & Ochoa, 1991) that innervate the volar hand on solely three areas: the base of the palm, the proximal phalanx of the index and the lateral intermediate phalanx of the middle finger (Watkins et al., 2021). This imbalance between the cutaneous mechanoreceptors and thermoreceptors of the glabrous skin would result from the main purpose of prehension and tactile investigation of the hand (Watkins et al., 2021), and may explain

why thermal SPS had a greater extent than surface and deep SPS: cutaneous mechanoreceptors may be able to detect SPS arising on smaller areas, whereas thermal SPS would be detected by thermoreceptors only when covering larger areas. This would also be consistent with the finding that warming SPS relate more to muscle tension than tingling SPS (Tihanyi & Köteles, 2017).

The findings presented here advocate that deep, surface, and thermal SPS are distinct from the others, and infer that they do have many similarities with the physiological and peripheral factors underlying somatosensory perception and thermoception. Are these characteristics determined by the cutaneous sensory units (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017), or from the cortical somatotopy that follows the peripheral organization (A. D. Craig et al., 2000; Gallace & Spence, 2008, 2009, 2010) ? Even though a recent study (Article 1) demonstrated that SPS gradient was not determined by the tactile sensitivity of the glabrous hand, it hinted nonetheless that the occurrence of thermal and paresis-like sensations could be linked to peripheral factors. Overall, these findings support our claim that investigating the perception of specific SPS would bring more insight toward their underpinnings.

4.2. Neural mechanisms engaged in the perception of deep, surface, and thermal SPS

The flow of information within the neural pathway contributing to body awareness is complex and quite not well established as of today. Yet, there is a general understanding that a hierarchy exists in the processing of sensory afferents, starting from local and detailed processing in perceptual areas and ultimately ending in global processing and multi-modal integration. Somatosensory afferents would most likely activate perceptual areas that code for their specific characteristics, and SI was proposed to underpin this role due to its somatotopic organization (Blankenburg et al., 2003; Gallace & Spence, 2008, 2010; Huang & Sereno, 2018), whereas SII somatotopic organization (Ruben et al., 2001), that is less-fine grained, would depend on SI activations and would underlie a more global processing of somatosensory traces in SI (Gallace & Spence, 2010). SII was also proposed to engage awareness mechanisms (Gallace & Spence, 2008, 2010). The multisensory integration of those traces within the AI and TPJ would be next in the hierarchy, and would contribute to non-conscious self-related processes such as homeostasis (Babo-Rebelo, Wolpert, et al., 2016; Dubé et al., 2009; Sakson-Obada et al., 2018) or embodiment (Arzy et al., 2006; Igelström & Graziano, 2017; Ionta et al., 2011, 2014). Finally, back-projections from the TPJ

toward lower level neural areas would promote feedback mechanisms (Gallace & Spence, 2008, 2009, 2010) causing changes in the processing of somatosensory afferents (Barrett & Simmons, 2015; Bechara & Damasio, 2005; Gu et al., 2013; Maurer et al., 2016; Sakson-Obada et al., 2018). Yet, the AI would play a twofold role: it would constitute the perceptual cortex dedicated to thermoception, and as such it would exhibit a somatotopy only in the processing of thermal events (Baumgärtner et al., 2010; A. D. Craig et al., 2000), but would also have a prominent role in the detection of cardiac and visceral signals (Babo-Rebelo, Wolpert, et al., 2016; Berlucchi & Aglioti, 2010; A. D. Craig, 2003c; Pollatos, Schandry, et al., 2007). It might thus be difficult to infer whether the neural traces underlying SPS followed a different pathway according to their type. But the fact that they exhibited different associations with the oscillatory activity in and between these areas suggests that different neural mechanisms are at play in the processing of the 3 SPS types.

In showing that each type of sensation was associated with beta to gamma bands in SII, we replicated the findings of a previous study (Michael et al., n.d.) that suggested these oscillations would promote mechanisms contributing to the awareness of SPS. Except for isolated effects, a general trend was exhibited regardless of sensations type: the frequency decreased with the increase of the oscillatory activity in each ROI, and increased along with the TPJ synchronization with SI, SII and AI. This might suggest the involvement of suppressive mechanisms that are locally engaged, and of amplification phenomenon elicited by feedback mechanisms. Similar observations were made in previous studies, as attention contributed to the suppression of SPS arising on the palm and the enhancement of those arising on the fingers (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015). This would be congruent with the fact that many effects were found on a wide range of frequency bands if not the entire spectral distribution, a finding that suggest central attentional processes (Altenmüller et al., 2011; Barry et al., 2003; Groppe et al., 2013; Keune et al., 2017) were engaged on the processing of SPS. Besides, while there are evidence that attention modulates the cortical activity of somatosensory cortices in a suppression/amplification fashion, it was also shown that suppressive mechanisms operate earlier than amplification mechanisms (Iguchi et al., 2002; Mima et al., 1998; Taylor-Clarke et al., 2002; van Ede et al., 2014). Physiological studies demonstrated that the perceptual threshold was higher than the physiological cutaneous threshold (Johansson & Vallbo, 1979b; Vallbo & Johansson, 1976), which suggest many sensory afferents are suppressed in the early perceptual stages by attention in order to diminish the signal-to-noise ratio (Briggs et al., 2013). Regarding the TPJ, its heavy involvement in attention was repeatedly evidenced (Corbetta et al., 2008; Corbetta & Shulman, 2002; Igelström

et al., 2016; Krall et al., 2015; Vallar & Calzolari, 2018), and its modulation of the somatosensory cortices would be expressed through alpha and beta bands for anticipation mechanisms, and gamma band for somatosensory processing (Benedek et al., 2014; García-Cordero et al., 2017; van Ede et al., 2014). Consistently, we found that correlations with the TPJ functional connectivity were only above 4hz. It would be congruent that some higher-level processes underpinned by the TPJ would identify the relevance to internal goals of certain SPS and might motivate feedback mechanisms that would promote their prioritization and enhance their perception. This further emphasizes the strong involvement of attention in shaping the perceptual experience. Yet, we found these effects were not affecting equally all types of SPS.

4.2.1. The interoceptive pathway behind deep SPS

Deep SPS were those that displayed the most associations on wider oscillations ranges, notably in AI and TPJ, suggesting their processing is more likely to require central attentional processes in those areas. In addition, those were the only associated to SI oscillatory activity, through a theta/gamma dissociation that suggest that the amplification/suppression mechanisms operate early in the processing of deep SPS. Even though SI activation alone is not sufficient to enable somatosensory perception (Gallace & Spence, 2010), the fact that deep SPS were the only associated to its oscillatory activity suggest a probable engagement of specific neural mechanisms in their processing. It might be that, because deep SPS are smaller and would originate from internal events that rarely require consciousness (Barrett & Simmons, 2015; A. D. Craig, 2011), their perception would be more complex and would thus require a greater range of cognitive processes and increased attentional skills (Gregory et al., 2003; Herman et al., 2021; Matthias et al., 2009; Pollatos, Matthias, et al., 2007; Pollatos, Schandry, et al., 2007). Consistently, skilled interoceptors exhibited a greater proneness to perceive and report SPS arising on low sensitivity areas of the hand (Michael et al., 2015).

Besides, in few instances, deep SPS exhibited an association restricted to specific frequency bands. For instance, to theta and gamma in SI and in TPJ – SII connectivity. The coupling of gamma within the theta period would promote the binding of multiple sensory inputs into a neural trace in working memory (Sauseng et al., 2010), and working memory mechanisms were shown to modulate the somatosensory cortices activity (Teng & Kravitz, 2019) and would contribute to SPS perception (Salgues, Plancher, & Michael, 2021). In addition, the TPJ greatly contributes to

memory (Carter & Huettel, 2013; Igelström et al., 2015, 2016; Igelström & Graziano, 2017; Patel et al., 2019) and its back-projections toward somatosensory cortices and the insula were proposed to underpin mnemonic mechanisms in the tactile perception (Gallace & Spence, 2009, 2010). The early processing of deep SPS in SI, along with their close relationship with TPJ and AI, might be a consequence of their involvement in the updating of body-part representations (Kinsbourne, 1998; Tsakiris, 2010). This would be consistent with the nature of deep SPS, that convey information about the physiological state of the body, and with evidence that malleability of body-part representations relates to interoceptive abilities (Tsakiris et al., 2011).

Another inference could be made regarding the theta/beta pattern that arises in the TPJ – AI connectivity. It was recently evidenced as a trait of empathy toward other's pain in temporo-insular regions (Balconi & Angioletti, 2021). Indeed, along with interoception, AI contributes to emotions processing (A. D. Craig, 2011; Gu et al., 2013; Krolak-Salmon et al., 2003; Kurth et al., 2010), and the TPJ to the third-person perspective taking (Babo-Rebelo et al., 2019; Martin et al., 2020; Vogeley & Fink, 2003), whereas embodiment and empathy are closely associated (Gangopadhyay, 2014; Gieser, 2008; Jospe et al., 2018; Zahavi, 2010). This might be a clue that deep SPS are greatly anchored in self-related processes, notably maintaining homeostasis, and localizing oneself within one's body. A supplementary evidence of this claim might be the theta band that contribute to embodied perspective in the TPJ (Wang et al., 2016) and that was repeatedly evidenced in the perception of deep SPS. Overall, these findings further emphasized the resemblances between the neural processing of deep SPS and those engaged in interoception.

4.2.2. The detection of thermal SPS

Thermal SPS, although less obvious, showed some interesting association patterns with the oscillatory activity at rest. For instance, they were not associated to SI, a finding that might not be incidental and may be related to early perceptual stages of the thermoception taking place in the AI (Baumgärtner et al., 2010; A. D. Craig et al., 2000). Consistently, the frequency of thermal SPS decreased in AI and increased in TPJ, in low oscillations that would be devolved to thermoception within the temporo-insular region (Chang et al., 2005; Fardo et al., 2017; Lenoir et al., 2018). In addition, suppressive/mechanisms phenomenon were found in SII, which would receive insular efferences (Gallace & Spence, 2008, 2009, 2010) and may promote attentional mechanisms on thermal SPS through the beta band notably (Keune et al., 2017; Laufs et al., 2003; O'Gorman et

al., 2013; van Ede et al., 2014). This is rather congruent with the previous interpretations and suggest that specific neural mechanisms, similar to those deployed in thermoception, would ultimately lead to the same phenomenon of early noise-suppression and late attentional enhancement in the perception of thermal SPS.

The relationship between thermal SPS and TPJ functional connectivities was particularly prominent in the gamma band, and this might reflect the involvement of TPJ back-projections in a local and more acute processing of thermal SPS (Fardo et al., 2017). Some authors proposed that thermal changes, because they inform of unpleasant or painful events, would engage early processes dedicated to identify their nature (Chang et al., 2005; Filingeri, 2016; Lenoir et al., 2018), and only then would engage local processing as so to localize the source of relevant or harmful thermal sensations (Aizawa et al., 2019; Mancini et al., 2013; Paricio-Montesinos et al., 2020). This is rather consistent with the fact that delta, exhibited in AI, contributes to the categorization of thermal changes as it is only involved in the coding of warm changes (Chang et al., 2005), whereas theta, evidenced in TPJ and TPJ – SII connectivity, would reflect the processing of thermal changes irrespectively of the perceived temperature (Chang et al., 2005; Fardo et al., 2017; Lenoir et al., 2018). Moreover, this might also account for thermal SPS covering a greater surface. Overall, this contributes to the understanding that the perception of thermal SPS might involve the same neural mechanisms underlying thermoception.

4.2.3. Mechanisms of awareness in the perception of surface SPS

Unexpectedly surface SPS showed few associations with the oscillatory activity other than those common to all types of SPS. It might be that, because these sensations are the most frequently reported (see Supplementary material), ceiling effects compromised the correlations analysis. Nevertheless, like thermal, the perception of surface SPS decreased with theta in AI, but this is less likely to result from the involvement of similar thermosensory mechanisms, and would rather be a coincidence due to implicit somatosensory integration mechanisms also exhibiting through low oscillations (Douw et al., 2011; Knyazev, 2012; Saito et al., 2012). Another observation was that surface SPS increased with the beta band in the TPJ – AI connectivity, a finding that could reflect tactile working memory mechanisms at work in their perception (Li Hegner et al., 2007), and that is consistent with the involvement of TPJ back-projections in tactile memory (Gallace & Spence,

2009, 2010). It seems that even in the absence of attentional modulations and awareness mechanisms, integration mechanisms are engaged in the processing of surface SPS through TPJ and AI, and this might be closely related to the involvement of these areas in embodiment and tactile distortions. It would be consistent with evidences that first-person perspective and embodied feeling while engaged on a visual task rest on the neural monitoring of cardiac and viscerogastric signals, not attention (Azzalini et al., 2020; Babo-Rebelo et al., 2019; Babo-Rebelo, Richter, et al., 2016; Park et al., 2018; Tallon-Baudry et al., 2018). A further evidence of this could be in the delta band, whose increase is associated to seizure with “parasitic consciousness”, an autoscopic hallucinations that is accompanied by the perception of tingling sensations on the skin (Saroka & Persinger, 2013), and that was shown to decrease the perception of surface SPS in the TPJ – SII connectivity. Previous studies argued that SPS contribute to embodiment (Michael, Guyot, et al., 2020; Salgues, Plancher, Jacquot, et al., 2021), and the findings presented here further support this claim. Since surface SPS closely follow the proximo-distal gradient of the cutaneous units, this distribution enables them to convey information about the body boundaries, but also about its location and interactions with the environment (Gallace & Spence, 2008, 2010; Kinsbourne, 1998).

4.3. Limitations and further considerations

Some limitations should be considered when considering the findings presented in this study. Before us, Tihanyi and colleagues (Tihanyi, 2019; Tihanyi et al., 2018; Tihanyi & Köteles, 2017) tried to investigate the perception of warming and tingling SPS without instructing participants to focus specifically on them, and encountered two difficulties: One, the variety of adjectives used by participants to describes SPS is never-ending, and some type of SPS (such as surface) display a large range of sensations (see Supplementary material); Two, without instructions, SPS are unequally reported, even among the more frequently perceived (see Supplementary material). This hinders comparative studies. By asking participants to search for three specific SPS, we expected to narrow the range of SPS reported, and to trigger the perception of deep, surface, and thermal SPS only so that they would be almost equally represented.

Besides, in the second experiment, the three types of SPS were not reported over the whole hand, which is not usually encountered when studying SPS with approximately 80 hands maps (Michael et al., 2015; Michael, Guyot, et al., 2020; Michael & Naveteur, 2011; Naveteur et al.,

2015; Salgues et al., n.d.; Salgues, Plancher, & Michael, 2021). This might imply that not enough data was collected for the perception of the three-SPS types, and that Type II errors are likely to happen. Even though we provided a certain number of findings relating the perception of SPS types to distinct neural mechanisms, our assumptions regarding the lack of associations might be prone to criticisms.

We also discussed about the prominence of deep SPS in the associations with the oscillatory activity at rest, compared to surface and thermal SPS, and linked this effect to them being more complex and requiring a greater range of cognitive processes. But this may also result from the statistical analysis performed. Indeed, correlations are performed cell-by-cell but are topographically represented. Statistical bias can thus emerge due to SPS occupying a small surface – which was the case for deep SPS. There is moreover a discrepancy in the fact that the current density in AI and TPJ was deleterious for deep SPS in all frequency bands, but this did not transpire in linear regression when considering the mean current density. This raises the concern of whether only the topographical distribution was affected, or if this is a consequence of statistical biases.

Finally, to replicate a previous study methodology (Michael et al., n.d.), we explored the relationship between each SPS type frequency and the current density in the primary auditory cortex, with the expectation that no reliable correlations would be found in the process. Unfortunately, many observations were made. Surface SPS were most abundant with the reduction of alpha, while deep and thermal SPS were both positively associated to low (delta and theta) and higher frequency bands (respectively beta and gamma, which contrasts with the major negative correlations that were described with the other ROIs current density. One explanation could be that SPS share common mechanisms with another similar illusory perceptual phenomenon : tinnitus (Thut & Miniussi, 2009). Indeed, tinnitus has been linked to abnormal spontaneous oscillations within the temporal cortex, notably with a reduction of alpha and an increase in delta and gamma bands (Dohrmann et al., 2007; Kahlbrock & Weisz, 2008; Roberts et al., 2013; Weisz et al., 2005). In addition, it was shown as well that communications between the somatosensory and the auditory cortices modulated the loudness and pitches of tinnitus (Roberts et al., 2010), that out-of-body experiences can be associated to tinnitus (De Ridder et al., 2007; Donaldson et al., 2015) and that stimulation of the TPJ improves the inhibition of the perceptual auditory cortices and reduces the pathological phenomenon (Donaldson et al., 2015; Wang et al., 2016). Besides, other observations of cross-modal modulations have already been reported, such as enhanced tactile sensitivity in deaf individuals (Levänen & Hamdorf, 2001). It could be assumed

as well that deactivation of the primary auditory cortex, that would transpire through low oscillations such as delta and theta (Makeig & Jung, 1995), may help the inhibition of unrelated auditory inputs so that these attentional mechanisms would be devolved to the perception of SPS. Considering these elements, choosing the primary auditory cortex as a control site may have been misguided, and more interests should be brought toward this matter in the future.

This study aimed to explore the factors underlying the perception of SPS by adopting a new approach. Experiment 1 explored the perception of tingling, heartbeat and warming sensations and revealed that SPS types differed in their topographical distribution, in their spatial extent and in amount. We found many resemblances between the characteristics of surface, thermal and deep SPS and the organization of peripheral afferents enabling tactile acuity, thermal sensitivity, and detection of cardiac events, and suggested that the distribution of the three SPS types could reflect the cortical somatotopy of somatosensory and insular areas. Experiment 2 investigated whether differences arose as well between the types of SPS in relation to the oscillatory activity of neural areas and networks involved in body awareness. Consistently, we found that specific neural mechanisms were at stake in the perception of SPS in relation to their type, and that they were coherent with those exhibited in somatosensory perception, thermoception and interoception. Yet even though the neural mechanisms differed, similar phenomenon of early suppression and late amplification operated on all SPS and emphasized the involvement of attention in shaping the subjective experience. We discussed whether SPS would contribute to different and complementary aspect of body awareness, in relation with the nature of the information that they convey and that might be required for either body-part representations updating, homeostasis, embodiment, and detection of harmful events. The findings greatly support the role of SPS within the background of bodily sensations in unconscious and conscious body and self-related processes.

5. Conclusions

This study investigated the perception of deep, surface, and thermal SPS. We found the characteristics and neural mechanisms within the somatosensory cortices, anterior insula and temporoparietal junction, differed in respect to SPS types. We discuss of the central mechanisms responsible for the occurrence of each type of SPS, and of their distinct contribution to body awareness. Some findings emphasized the need to explore the relationship between SPS and the occurrence of other sensory hallucinations such as tinnitus.

Supplementary material

A meta-analysis was conducted on published studies using the standardized task of SPS. This restricted the number of studies included but allowed us to compile the raw data we have access to. In studies with multiple experiment, the data for all experiment was included only if it was obtained from different participants. Otherwise, only the data obtained from the main experiment was considered. In studies investigating pathologies (Borg et al., 2015; Echalié et al., 2020), only data from control participants was considered. We included 9 studies, with a total of raw data of $N = 419$. They are presented in Table 1 and Figure 1 display their distribution across all studies included.

Table 1 : Studies and raw data included in the meta-analysis.

Authors	Types				
	Thermal	Deep	Surface	Paresis-like	Pain-like
Michael & Naveteur, 2011	Warming	Beat/pulse	Tickling	Numbness	Itching
	$N = 81$	$N = 96$	$N = 39$	$N = 102$	$N = 12$
Exp. 1	Cooling	Muscular	Skin stretch		
$N = 70$	$N = 107$	tension	$N = 8$		
		$N = 60$	Tingling		
			$N = 165$		
			Trembling		
			$N = 64$		
			Vibrations		
			$N = 32$		
Exp. 2	Warming	Beat/pulse	Tickling	Numbness	Itching
$N = 23$	$N = 4$	$N = 24$	$N = 5$	$N = 9$	$N = 0$
	Cooling	Muscular	Skin stretch		
	$N = 2$	tension	$N = 4$		
		$N = 2$	Tingling		
			$N = 65$		
			Trembling		
			$N = 25$		
			Vibrations		
			$N = 6$		
Michael et al., 2012	Warming	Beat/pulse	Tickling	Numbness	Itching
	$N = 58$	$N = 76$	$N = 31$	$N = 30$	$N = 73$
$N = 80$	Cooling	Muscular	Skin stretch	Hardening*	
	$N = 48$	tension	$N = 12$	$N = 1$	
		$N = 40$	Tingling		
			$N = 73$		
			Trembling		
			$N = 46$		

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			Vibrations <i>N</i> = 47		
			Compression*		
			<i>N</i> = 7		
			Movement*		
			<i>N</i> = 4		
			Electrical flow*		
			<i>N</i> = 2		
Beudoïn & Michael, 2014	Warming <i>N</i> = 19	Beat/pulse <i>N</i> = 21	Tickling <i>N</i> = 15	Numbness <i>N</i> = 23	Itching <i>N</i> = 3
Exp. 1 <i>N</i> = 20	Cooling <i>N</i> = 19	Muscular tension <i>N</i> = 12	Skin stretch <i>N</i> = 5	Weight*	Pins-and-needles*
			Tingling <i>N</i> = 32	<i>N</i> = 2	<i>N</i> = 1
			Trembling <i>N</i> = 18		
			Vibrations <i>N</i> = 10		
Exp. 2 <i>N</i> = 28	Warming <i>N</i> = 24	Beat/pulse <i>N</i> = 44	Tickling <i>N</i> = 21	Numbness <i>N</i> = 38	Itching <i>N</i> = 7
	Cooling <i>N</i> = 5	Muscular tension <i>N</i> = 36	Skin stretch <i>N</i> = 5	Weight*	Pins-and-needles*
			Tingling <i>N</i> = 50	<i>N</i> = 4	<i>N</i> = 5
			Trembling <i>N</i> = 19		
			Vibrations <i>N</i> = 5		
Borg et al., 2015	Warming <i>N</i> = 9	Beat/pulse <i>N</i> = 12	Tickling <i>N</i> = 5	Numbness <i>N</i> = 8	Itching <i>N</i> = 8
<i>N</i> = 18	Cooling <i>N</i> = 17	Muscular tension <i>N</i> = 4	Skin stretch <i>N</i> = 3		
			Tingling <i>N</i> = 17		
			Trembling <i>N</i> = 1		
			Vibrations <i>N</i> = 2		
Michael et al., 2017	Warming <i>N</i> = 17	Beat/pulse <i>N</i> = 21	Tickling <i>N</i> = 15	Numbness <i>N</i> = 20	Itching <i>N</i> = 3
<i>N</i> = 29	Cooling <i>N</i> = 21	Muscular tension <i>N</i> = 4	Skin stretch <i>N</i> = 4		Pins-and-needles*
			Tingling <i>N</i> = 10		<i>N</i> = 1
			Trembling <i>N</i> = 14		
			Vibrations <i>N</i> = 14		

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Echalier et al., 2020 <i>N = 20</i>	Warming <i>N = 12</i>	Beat/pulse <i>N = 5</i>	Tickling <i>N = 4</i>	Numbness <i>N = 23</i>	Itching <i>N = 2</i>
	Cooling <i>N = 11</i>	Muscular tension <i>N = 13</i>	Skin stretch <i>N = 0</i>		Pins-and-needles* <i>N = 3</i>
			Tingling <i>N = 37</i>		
			Trembling <i>N = 10</i>		
			Vibrations <i>N = 0</i>		
Michael, Guyot, et al., 2020 <i>N = 55</i>	Warming <i>N = 14</i>	Beat/pulse <i>N = 34</i>	Tickling <i>N = 10</i>	Numbness <i>N = 25</i>	Itching <i>N = 1</i>
	Cooling <i>N = 19</i>	Muscular tension <i>N = 18</i>	Skin stretch <i>N = 7</i>	Weight* <i>N = 1</i>	Pins-and-needles* <i>N = 1</i>
			Tingling <i>N = 68</i>		
			Trembling <i>N = 18</i>		
			Vibrations <i>N = 28</i>		
			Compression* <i>N = 2</i>		
			Movement* <i>N = 2</i>		
			Electrical flow* <i>N = 5</i>		
Salgues et al., 2021 Exp. 1 <i>N = 27</i>	Warming <i>N = 4</i>	Beat/pulse <i>N = 20</i>	Tickling <i>N = 7</i>	Numbness <i>N = 9</i>	Itching <i>N = 0</i>
	Cooling <i>N = 13</i>	Muscular tension <i>N = 9</i>	Skin stretch <i>N = 4</i>	Weight* <i>N = 2</i>	Pins-and-needles* <i>N = 1</i>
			Tingling <i>N = 28</i>		
			Trembling <i>N = 6</i>		
			Vibrations <i>N = 8</i>		
			Compression* <i>N = 1</i>		
Salgues et al., n.d.-b <i>N = 49</i>	Warming <i>N = 26</i>	Beat/pulse <i>N = 30</i>	Tickling <i>N = 4</i>	Numbness <i>N = 13</i>	Itching <i>N = 1</i>
	Cooling <i>N = 25</i>	Muscular tension <i>N = 26</i>	Skin stretch <i>N = 12</i>	Weight* <i>N = 3</i>	
			Tingling <i>N = 55</i>		
			Trembling <i>N = 28</i>		
			Vibrations <i>N = 13</i>		

Compression*
 $N = 3$

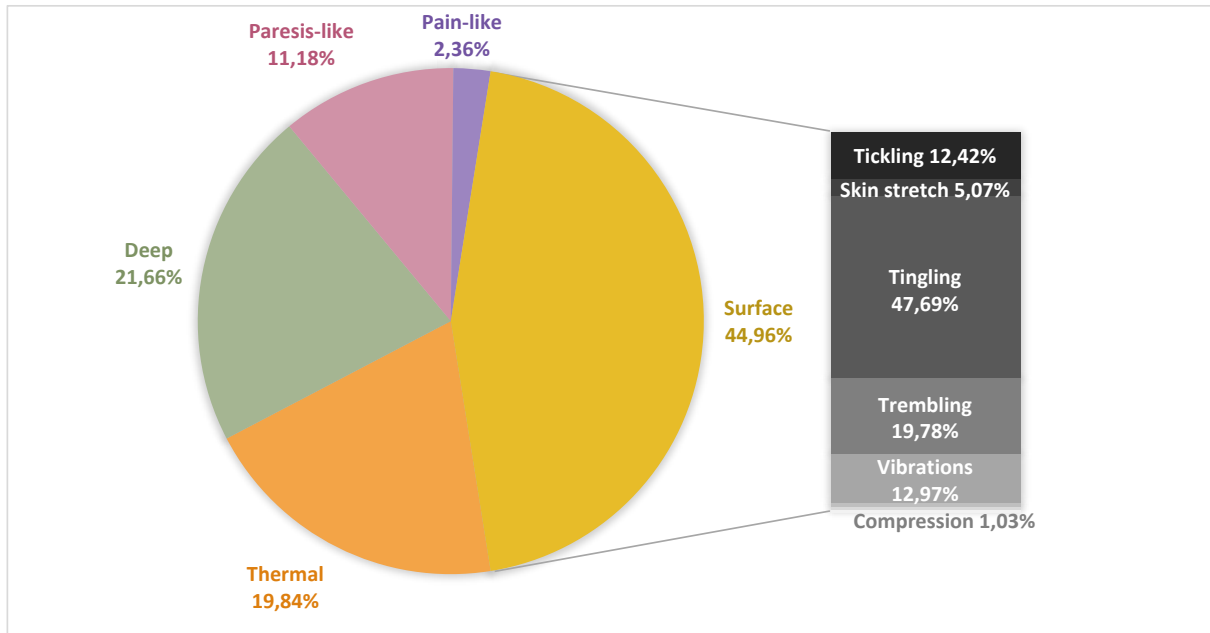


Figure 1 : Graph depicting the percentage of each type of SPS across all studies included, with a special emphasis on surface-type sensations since their variety was the greatest.

DISCUSSION GENERALE

Discussion générale

Ce travail de recherche est motivé par deux objectifs principaux : définir la nature des SPS, et identifier les opérations cognitives déterminant leur perception. Leur étude, nous permet d'enrichir les connaissances théoriques sur la conscience corporelle. A cette fin, nous avons emprunté à la physiologie, à la psychologie cognitive et aux neurosciences, et avons exploré les facteurs périphériques, cognitifs et neuraux derrière le phénomène des SPS. Dans l'Acte I, nous avons opposé deux études portant sur les mécanismes périphériques tactiles et somatosensoriels corticaux. Ces travaux ont mis en exergue une relation délétère entre la perception des SPS et la sensibilité tactile sous-jacente (article 1, p. 61), mais ont révélé un parallèle entre leur topographie et l'activité oscillatoire spontanée de SI et SII (article 2, p. 85). Dans l'Acte II, nous avons interrogé successivement la contribution des processus attentionnels et de la mémoire de travail, identifiés en amont comme des fonctions cognitives nécessaires à l'émergence de la conscience du corps et de ses sensations. Nous y décrivons le rôle distinct et complémentaire des processus supra-modaux inhibiteurs et de régulation des ressources cognitives dans la sélection des signaux corporels (article 3, p. 137), et apportons des preuves de l'implication nécessaires des mécanismes en mémoire de travail visuospatiale dans l'élaboration, le maintien et l'intégrité de l'expérience subjective du corps (article 4, p. 181). L'Acte III fut l'occasion de mêler nos deux problématiques de recherche. En portant notre intérêt sur TPJ et AI, nous avons abordé à la fois la question des processus cognitifs déterminant la perception consciente des SPS que des mécanismes corticaux pouvant être responsables de leur existence (article 5, p. 201). Dans une dernière étude, nous avons modifié l'approche expérimentale des SPS, ceci nous permettant d'introduire de nouvelles considérations quant à l'unicité de ce phénomène et des facteurs qui y sont investis (article 6, p. 219). Dès à présent, nous allons développer l'apport de ces résultats à la compréhension du phénomène des SPS, et plus globalement, à la conception fondamentale de la conscience corporelle. Par la suite, nous aborderons les limites de ce travail et proposerons de nouvelles pistes de réflexion autour de l'étude de la subjectivité du corps, avant de faire une conclusion générale sur l'ensemble de ces travaux.

I. A la source des SPS

Aux prémices de cette thèse, nous recensons seulement 11 publications scientifiques sur les SPS, tout auteurs confondus (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014; Beaudoin & Michael, 2014; Michael et al., 2012, 2015, 2017; Michael & Naveteur, 2011; Naveteur et al., 2005, 2015; Tihanyi & Köteles, 2017). Malgré ces données, nous étions confrontés à une faille majeure : nous ne savons pas d'où viennent les SPS, ni pourquoi nous les percevons. Tihanyi et Köteles (2017) proposent trois origines hypothétiques, avec en premier lieu l'activité physiologique cutanée spontanée, en second l'activité corticale spontanée, et en dernier des modifications physiologiques résultant de processus attentionnels top-down. Nous reprendrons ici les éléments confortant ou infirmant les hypothèses d'une origine corticale ou physiologique.

A. Des résultats en faveur d'une origine corticale

L'hypothèse centrale est celle qui veut associer le phénomène des SPS aux mécanismes corticaux responsables des expériences hallucinatoires. La validation de cette hypothèse repose sur deux conditions : la preuve de l'indépendance aux mécanismes périphériques, et la mise en évidence de mécanismes spécifiques aux distorsions perceptuelles du corps.

Dans l'article 2, nous avons observé un parallèle entre le gradient des SPS et la somatotopie corticale : l'activité oscillatoire spontanée de SI, dont le codage est plus fin, favorise la perception de SPS sur les doigts, tandis que l'activité enregistrée en SII, dont les traitements sont plus globaux, module leur fréquence sur la paume. Des effets qui sont cohérents avec l'implication de SI dans la perception de SPS sur le pouce (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014), et qui soulèvent la question d'un investissement cortical dépendant de la finesse des traitements topographiques et visuospatiaux. A contrario, l'article 1 a échoué à lier ce gradient au seuil de sensibilité tactile sur la surface glabre de la main. En effet, la perception de SPS est négativement affectée par la sensibilité tactile, de telle sorte qu'on ne peut attribuer aux mécanismes périphériques un rôle quelconque dans l'émergence de ces percepts. Plus encore, nous y avons décrit des effets restreints aux doigts et à la paume qui suivent la ségrégation corticale (Gálvez-García et al., 2012). Ces résultats suggèrent l'existence d'une compétition entre SPS et perception tactile : un *gating* somatosensoriel agirait sur les mécanismes périphériques afin de favoriser les mécanismes

corticaux somatosensoriels, tandis qu'une grande dépendance aux stimuli tactiles de l'environnement détournerait de ces percepts centraux. D'autres éléments confortent cette interprétation. Ainsi l'apport de SI se manifeste à travers la bande alpha, ce que nous avons interprété comme une suppression attentionnelle du fait du rôle de ces oscillations dans l'inhibition neurale (S. R. Jones et al., 2010; van Ede et al., 2011, 2014), mais qui *in fine* opère dans le but de faciliter la perception des SPS. Il serait ainsi plausible que cet effet reflète la suppression tactile en SI. Les études sur les oscillations alpha au cours de tâches impliquant la mémoire de travail discutent à de nombreuses reprises de leur rôle dans l'inhibition corticale des régions activées par les distracteurs (Cooper et al., 2003; W. Klimesch et al., 1999; Wolfgang Klimesch, 1997, 2012; Wolfgang Klimesch et al., 2007), et de leur diminution dans les aires perceptuelles dévolues au maintien de représentations suivant l'effort cognitif requis par ce maintien (de Vries et al., 2017; Fukuda & Woodman, 2017; Gevins, 1997; Myers et al., 2015). Cette inhibition corticale étant nécessaire à la priorisation des ressources cognitives sur les représentations d'intérêts. On décrit également des phénomènes comportementaux similaires dans les distorsions perceptuelles du corps, comme une altération des performances tactiles pendant l'illusion de la main en caoutchouc (Zopf et al., 2011), un émoussement progressif de la sensibilité tactile dans les hallucinations tactiles (Berrios, 1982; Liu et al., 2020), ou encore une dégénérescence rétrograde des afférents tactiles suivant la réorganisation corticale dans le syndrome du membre fantôme (Flor, 2002; Flor et al., 2006). Mais également dans un phénomène voisin, les acouphènes (*tinnitus* en anglais), caractérisées par une réduction de l'alpha dans les régions perceptuelles auditives ainsi qu'une perte progressive de l'audition (Norena et al., 2002; Roberts et al., 2010; Weisz et al., 2005). Il semblerait que le point commun de ces manifestations soit la primauté des mécanismes attentionnels sur le traitement des entrées sensorielles (Behrendt, 2006) : la suppression de ces dernières entraînant une diminution des signaux à traiter, les mécanismes attentionnels auraient le champ libre pour élaborer des percepts, donnant naissance aux SPS et aux hallucinations.

Un autre argument a été avancé dans l'article 5, où l'étude de mécanismes de plus haut niveau *via* TPJ, AI et EBA fut l'occasion de révéler un pattern oscillatoire typique des hallucinations autoscopiques (Persinger et al., 2010) dans la perception des SPS. Ce qui paraît peu relever de la coïncidence compte tenu du rôle de ces régions dans la modulation attentionnelle de la perception du corps (Gallace & Spence, 2008, 2009, 2010; Igelström & Graziano, 2017; Wu et al., 2015), de leur investissement dans les illusions tactiles (Ionta et al., 2011; Katzer et al., 2012; Limanowski et

al., 2014; Lopez et al., 2008; Romano et al., 2014), et de la sensibilité de ces dernières aux mécanismes attentionnels (Costantini & Haggard, 2007; Wawrzyniak et al., 2018).

Mais malgré tous ces résultats, l'ambiguïté de l'origine des SPS est toujours présente. Cette question reste gouvernée par le lien étroit entre l'organisation périphérique et la somatotopie corticale, la dernière étant élaborée à partir de la première (Gallace & Spence, 2008, 2009, 2010). Or, les traces corticales se développent à mesure que les interactions avec l'environnement sollicitent les récepteurs cutanés: on observe donc des représentations structurelles particulièrement développées pour les doigts de la main droite chez les bassistes et violonistes (Elbert et al., 1995; Schwenkreis et al., 2007), et une amélioration des performances tactiles avec la pratique d'un instrument de musique ou d'activités physiques telles que le tai-chi (Godde et al., 2020; Kerr et al., 2008; Kóbor et al., 2006; Ragert et al., 2004). Si nous percevons globalement les SPS en faisant abstraction des mécanismes périphériques, se pourraient-ils que certaines soient quand même le fruit de processus intérocepteurs ?

B. Pas d'origine périphérique : vous y mettriez votre main à couper ?

L'hypothèse périphérique prétend trouver l'origine des SPS dans l'activité physiologique spontanée, et défend que des processus attentionnels et visuels ainsi que des facteurs externes affectent cette activité physiologique pour en moduler la perception (Beaudoin & Michael, 2014; Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015). La récurrence d'un gradient proximo-distal identique à celui mis en évidence dans l'organisation cutanée (Johansson & Vallbo, 1979a, 1979b; Vallbo & Johansson, 1984) est l'argument principal qui motive l'idée d'un parallèle entre les SPS et la somesthésie. Si les SPS sont liées à l'activité physiologique, alors elles reposeraient sur les paramètres déterminant la sensibilité tactile. Au contraire, les résultats de l'article 1 mènent à la conclusion d'une non-dépendance des SPS aux mécanismes périphériques. Une conclusion que tirent également Echalié et collaborateurs (2020) lorsqu'ils échouent à lier l'émoussement de la sensibilité tactile dans le syndrome douloureux complexe régional à une altération des SPS. A prime abord, l'hypothèse périphérique n'a pas le vent en poupe.

Pourtant, la perception de certaines SPS pourrait être une manifestation de l'intéroception dans son sens le plus brut, c'est-à-dire la perception d'états physiologiques internes. Mais le lien n'est pas si évident. L'étude des 3 SPS (article 6) a démontré que les sous-catégories de SPS

possèdent des caractéristiques topographiques et qualitatives spécifiques et distinctes. Non seulement nous y observons que les SPS profondes et thermales ont une topographie distincte de celle des SPS de surface – identique à celle classiquement relevée jusqu'à présent – mais en plus nous relevons des similarités entre ces gradients moins habituels et les mécanismes périphériques derrière l'intéroception et la thermoception (Li et al., 2008; Taylor & Schwarz, 1955; Vaitl, 1996; Wakolbinger et al., 2014). A la lumière de ces nouveaux éléments, il est possible que notre approche *via* la sensibilité tactile dans l'article 1 ait manqué de rigueur parce que nous réduisons les SPS à une dimension appartenant à la perception tactile. Il serait ainsi plus juste de proposer une multitude de mécanismes somesthésiques, intéroceptifs et thermosensoriels à l'origine des SPS, dont certains seraient périphériques. Cela serait cohérent avec les travaux de Tihanyi & Köteles (2017) qui montrent une relation tendancielle entre la tension musculaire du bras et l'intensité subjective des SPS de réchauffement, mais pas avec celle des SPS de fourmillement. Le traitement de ces signaux périphériques ayant des buts similaires au *background of bodily sensations* (Kinsbourne, 1998), à savoir ancrer le *Self* dans les limites de son corps (Azzalini et al., 2020; Babo-Rebelo et al., 2019; Babo-Rebelo, Richter, et al., 2016; Babo-Rebelo, Wolpert, et al., 2016; Tallon-Baudry et al., 2018).

Les SPS profondes sont les premières à venir à notre esprit, puisque l'intéroception est classiquement associée à la détection des battements du cœur. Nous montrons dans l'article 6 que leur distribution est particulièrement similaire à l'irrigation veineuse de la main, faisant de la circulation sanguine un candidat parfait pour expliquer la détection de pulsations sur la peau. Nous décrivons également un investissement cortical majeur requis pour leur perception, ce que nous avons présenté comme une mobilisation très coûteuse de processus attentionnels supprimeurs. En effet, l'intéroception est fréquemment associée à des compétences attentionnelles développées (Buldeo, 2015; García-Cordero et al., 2017; Gregory et al., 2003; Matthias et al., 2009; Pollatos et al., 2005; Pollatos, Schandry, et al., 2007) dues à la difficulté de détecter un signal discret dans un bruit plus important (Buschman, 2015; Vallbo et al., 1979; Vallbo & Johansson, 1976). Pourtant, l'étude de Michael et collaborateurs (2015) a montré que les compétences intéroceptives n'influençaient pas la perception des sensations de pulsations : au contraire l'intéroception facilite la perception des SPS sur la paume, précisément l'endroit où les SPS profondes sont les moins fréquentes (article 6). Il est donc difficile de conclure que les mécanismes par lesquelles nous réussissons à détecter les battements de notre cœur sont ceux-là même qui aboutissent à la perception de pulsation sur la peau au repos.

La question se pose aussi pour les SPS thermales, qui possèdent également une phénoménologie identique à la thermoception (article 6), et dont l'occurrence est prédite par le gradient de la sensibilité tactile (article 1). Toutefois, cette relation avec la sensibilité tactile reste négative. Et s'il est vrai que leur perception varie avec l'intéroception, leur fréquence diminue avec les compétences intéroceptives (Michael et al., 2015) et augmente dans la fibromyalgie (Borg et al., 2015) et dans la schizotypie (Michael, Guyot, et al., 2020). Finalement, ce pattern semble être plus cohérent avec la première explication avancée, celle d'une prédominance corticale et d'une forte dépendance aux mécanismes attentionnels. Comme Kinsbourne (1998), qui explique le syndrome du membre fantôme par une inhibition des afférences sensorielles au profit des représentations structurales du membre absent, le dérèglement des mécanismes attentionnels dans les pathologies douloureuses et dans la schizotypie contraindrait le traitement des afférences sensorielles et contribuerait à l'élaboration d'une représentation distordue du corps, laquelle se reflète dans le percept des SPS (Borg et al., 2015; Echalié et al., 2020; Michael, Guyot, et al., 2020).

En somme, les éléments que nous avons présentés tendent à lier les SPS aux mécanismes corticaux. Il reste cependant un doute raisonnable concernant une potentielle origine périphérique, et d'autres recherches sur les soubassements périphériques des SPS en fonction de leur type permettront d'écarter définitivement cette hypothèse ou de développer celle d'un multi-déterminisme. Au-delà de ces considérations, il y a une (ou des) raison(s) à l'existence des SPS : elles seraient la trace de représentations corporelles actives, tel que Kinsbourne (1998) décrit le *background of bodily sensations*. L'étude des mécanismes cognitifs et électrophysiologiques déterminant leur perception nous permettra donc de discuter du rôle d'un tel phénomène hallucinatoire dans la conscience corporelle chez l'individu lambda.

II. Conscience du corps, mode d'emploi

Les conceptions théoriques maintiennent un flou artistique sur la question de Comment conscience du corps il y a. Mais on relève pourtant dans la littérature des convergences concernant certaines dimensions cognitives, comme l'attention, qui module la perception et élicite la conscience du corps et de ses sensations (Gomez-Ramirez et al., 2016; Kinsbourne, 1998; Schubert et al., 2006; van Ede et al., 2014), ou la mémoire, qui encode les signaux corporels, stocke les représentations du corps et les rend accessibles à la conscience sur le court ou long terme (Carruthers, 2008; Kinsbourne, 1998; O'Shaughnessy, 2003; Sirigu et al., 1991). Nous avons spécifié le rôle des mécanismes attentionnels centraux et en mémoire de travail visuospatiaux non-spécifiques au corps (article 3, 4 & 5). Or si certaines preuves ont déjà été avancées quant à la dépendance de la conscience corporelle aux compétences attentionnelles supramodales (Gregory et al., 2003; Matthias et al., 2009; Pollatos, Matthias, et al., 2007), nous sommes les premiers à apporter des éléments confortant l'investissement de mécanismes en mémoire de travail visuospatiale dans l'expérience subjective du corps. Nous avons également décrit à de nombreuses reprises des mécanismes d'amplification et de suppression typique de l'attention et des patterns oscillatoires associés aux mécanismes mnésiques dans l'activité EEG de SI, SII, TPJ et AI (article 2, 5 & 6), et avons décrit leur interaction avec les processus tactiles (article 1). Nous reprenons ces différents éléments en les incorporant petit à petit dans une modélisation théorique.

A. Des stratégies attentionnelles qui détermineraient l'accès en conscience

La perception des SPS implique une focalisation attentionnelle, grâce à des mécanismes d'inhibition et de régulation des ressources identiques à ceux requis dans l'extéroception (article 3), et diriger ces ressources vers l'environnement aurait des répercussions négatives sur la conscience corporelle, au contraire de les diriger sur les pensées (article 5). Ces différences entre conscience de l'environnement et conscience du corps se manifestent à travers des changements physiologiques, de telle sorte qu'un arousal bas favorise la perception de SPS. La loi Easterbrook (1959) nous explique qu'un arousal bas marque une baisse des performances aux tâches comportementales, dû à l'impossibilité de maintenir une attention sélective sur les signaux de l'environnement sensoriel. Ce qui semble aller à l'encontre de Kinsbourne (1998) et son argument d'une sélection élicitant la

conscience du corps. Mais cette relation linéaire négative des SPS avec l'arousal physiologique marque la distinction déjà connue entre le traitement de l'environnement et celui du *Self*: en diminuant l'arousal, l'activation du système parasympathique contraindrait la réactivité aux signaux environnementaux et favoriserait l'attention sur le *Self*, le corps et ses sensations (Chapell, 1994).

Admettons que nous voulons porter attention à notre main pour x ou y raisons (comme par exemple, y percevoir des sensations). Selon le modèle MAM (Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014), la représentation de l'environnement générée par la carte MAM est ajustée afin de refléter les représentations pertinentes (ici celles de la main). Les éléments saillants, eux, ne sont pas affectés par ces objectifs internes ; comme l'environnement de sensations corporelles qui fait office de musique d'ascenseur lorsque nous sommes engagés dans des opérations cognitives externes (Kinsbourne, 1998), la conscience du corps émergerait dans un environnement de sensations à la fois corporelles et extéroceptives. De meilleures capacités d'inhibition favoriserait la perception de SPS pertinentes (article 3 & 6) en supprimant ces afférences distractives et en priorisant les représentations de la main. Au niveau neural, la suppression du réseau de saillance permettrait la mise en place de mécanismes attentionnels contrôlés (Corbetta et al., 2008; Corbetta & Shulman, 1998, 2002) *via* l'engagement du réseau cérébral par défaut et la mobilisation de l'attention interne (Buckner et al., 2008; Raichle & Snyder, 2007). La désynchronisation de TPJ et AI et l'arousal faible seraient donc bénéfiques à la perception de SPS en ce qu'ils marquent une dépendance faible à l'environnement lorsque l'attention est portée sur soi (article 5). Perception de SPS, propension au vagabondage de pensée et détection intéroceptive seraient ainsi liées par ces corrélats neuraux communs, mais également par leur dépendance aux habiletés attentionnelles (Borg et al., 2015; Gregory et al., 2003; Matthias et al., 2009; Michael et al., 2015, 2017; Pollatos, Matthias, et al., 2007; Smeekens & Kane, 2016; Welhaf et al., 2018).

Au contraire, lorsque nous sommes activement engagés dans le traitement de signaux externes, les représentations composant l'environnement de sensations corporelles sont peu pertinentes pour les opérations cognitives en cours, et sont donc inhibées. Mais avec la diminution de l'arousal vient une diminution de l'efficacité des mécanismes inhibiteurs et une allocation des ressources à une plus grande variété de signaux sensoriels – notamment ceux qu'on nomme distracteurs (Egeth & Kahneman, 1975; Hanoch & Vitouch, 2004; Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014). Ainsi, et ce malgré un focus visuel toujours porté sur l'environnement, le déplacement de l'attention vers le corps court-circuite les mécanismes supprimeurs et amplifie la fréquence des SPS perçues (Michael et al., 2012; Michael & Naveteur,

2011; Naveteur et al., 2015). Cette non-sélectivité de l'attention permettrait donc à certaines sensations corporelles d'entrer en conscience lorsque nous sommes engagés dans d'autres opérations cognitives, ce qui serait délétère à tout point de vue.

La conscience corporelle d'une part en serait affectée. Dans l'article 6, nous montrons que la perception de SPS profondes dépend fortement de mécanismes suppresseurs élicités par TPJ et AI, destinés à influencer le ratio signal/bruit pour faciliter la détection de signaux discrets. Ces SPS demandant plus d'efforts et de ressources cognitives, leur perception serait particulièrement difficile lorsque TPJ et AI sont déjà engagés dans le traitement de l'environnement. Au contraire, nous relevons en plusieurs instances que d'autres types de SPS moins fréquents sont plus reportés lorsque les ressources cognitives sont divisées et réduites (articles 3, 4 & 5). Ce déséquilibre dans le type de signaux corporels perçus accroît le bruit en défaveur du signal et affecterait l'homéostasie. Preuve en est de la fibromyalgie, où l'hypervigilance permanente sur le corps permet une perception élevée de signaux corporels discrets et peu pertinents, menant à une anxiété exacerbée et un comportement inadapté vis-à-vis du corps et de ses besoins (Borg et al., 2015; A. D. Craig, 2011, 2013; Tsakiris & De Preester, 2019). De plus, l'étude du syndrome douloureux régional complexe a également démontré que le détournement attentionnel du membre douloureux modifie la conscience et le comportement vis-à-vis du corps (Echalier et al., 2020; Lewis et al., 2007; Marinus et al., 2011; Schwoebel et al., 2001).

La conscience de l'environnement souffrirait également des interférences provenant du corps. Ainsi, du fait de la relation étroite entre perception de SPS et propension au vagabondage de pensée (Michael et al., 2017), on peut assumer que ces signaux corporels entrant inopinément en conscience provoqueraient distractibilité endogène (Mason et al., 2007; Rajan et al., 2019; Scheibner et al., 2017) et baisse des performances (Couffe & Michael, 2017). L'incapacité à supprimer les interférences corporelles est d'ailleurs une manifestation typiquement observées dans les syndromes douloureux (Borg et al., 2015; Echalier et al., 2020), où la douleur pathologique et son emprise sur l'attention affectent l'efficacité cognitive (Boehme et al., 2020; Borg et al., 2018; Hart et al., 2003; Kim et al., 2017; McCracken & Iverson, 2001; Moriarty et al., 2011, 2017).

B. La mémoire du corps, de la perception au *Material me*

1. Maintenir en conscience

L'accès des représentations corporelles à la mémoire de travail est médié par la focalisation attentionnelle (Cowan, 1999; Woodman et al., 2013). Mais cette mémoire de travail étant sujette à un déclin temporel naturel, ces représentations sont vouées à retrouver un état d'inactivation dès lors qu'elles sortent du focus, causant l'oubli. Les résultats que nous décrivons en article 4 confortent cette hypothèse, puisque la fréquence des SPS diminue avec la rapidité du déclin en mémoire de travail visuospatiale. De manière similaire, Wolpert (Haggard & Wolpert, 2005; Wolpert et al., 1998) décrit un patient avec lésion du lobule pariétal supérieur qui perd la conscience du membre affecté en quelques secondes s'il ne le garde pas en focus visuel. Une asomatognosie unique à ce jour, qui montre bien qu'éliciter la conscience n'est pas suffisant : l'expérience subjective du corps doit être continuellement alimentée pour perdurer.

Un mécanisme de rafraîchissement attentionnel contrecarrerait l'oubli en mémoire de travail en redirigeant le focus sur les représentations en déclin (Barrouillet et al., 2004, 2012; Barrouillet & Camos, 2012; Plancher & Barrouillet, 2020; Vergauwe et al., 2014). Or, dans le même esprit que Kinsbourne (1998), qui attribue à l'attention le rôle de sélectionner et de maintenir les représentations du corps en conscience, les effets présentés dans l'article 4 suggèrent que ces mécanismes attentionnels seraient identiques à ceux discutés précédemment. En effet, l'augmentation de la charge cognitive diminue les ressources mobilisables et affecte négativement la fréquence des SPS – d'une manière assez similaire à ce que nous observons dans l'article 3 ou 5. Et le maintien de représentations malgré une tâche interférente, dont le succès dépend de compétences d'inhibition, favorise la perception de SPS sur la paume aux dépens des doigts. Une dissociation entre paume et doigt que l'on relève dans toutes les études sur les SPS impliquant plus ou moins directement l'attention (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2015). D'autres études démontrent par ailleurs que le maintien de représentations visuelles en mémoire de travail repose sur la sélectivité attentionnelle (Williams et al., 2013; Woodman et al., 2013). En somme les mécanismes attentionnels qui amènent les représentations en conscience contribueraient à les y maintenir.

2. L'intégration multimodale, entre maintien et manipulation

Pourtant, nous montrons dans les articles 5 et 6 que la perception de SPS requiert également d'autres mécanismes neuraux, qui se manifestent dans la synchronisation entre TPJ et les aires somatosensorielles et insulaires. Ces échanges sous-tendraient l'intégration multi-sensorielle des afférences perceptuelles et la génération de représentations complexes en TPJ, lesquelles nous permettraient de percevoir notre corps comme un tout, d'y localiser notre *Self*, et de nous situer dans l'espace environnant. Et ces mécanismes, identifiés dans la perception de SPS internes et de surface, appartiendraient à la mémoire de travail (article 6).

Or maintien et manipulation de représentations en mémoire de travail sont compétitifs, ils reposent sur une réserve commune de ressources non-divisibles et ne peuvent pas opérer simultanément (Barrouillet et al., 2004, 2012; Barrouillet & Camos, 2012; Plancher & Barrouillet, 2020; Vergauwe et al., 2014). Du fait de ces exigences cognitives, la manipulation de représentations en focus générerait de nouvelles représentations complexes, forçant le déclin des premières afin que de nouvelles représentations plus pertinentes accèdent et soient intégrées en mémoire de travail. La flexibilité cognitive entre maintien et manipulation serait donc primordiale en ce qu'elle permettrait d'enrichir l'expérience perceptuelle. Ainsi, à l'instar des bons intérocepteurs (Michael et al., 2015), les individus capables d'alterner efficacement maintien et manipulation en mémoire de travail perçoivent plus aisément des SPS apparaissant sur des aires moins saillantes de la main (article 4). Bien que cette interprétation soit à prendre avec des pincettes, puisque dans l'article 4 nous avons regardé les performances à la tâche de maintien uniquement et pas à celle de manipulation; nous ne pouvons donc pas affirmer avec certitude que ces performances sont liées à de meilleures capacités d'inhibition (comme nous l'avons présenté jusqu'à présent), ou à une plus grande flexibilité cognitive. Cependant, une étude publiée récemment a démontré qu'une plus grande aisance à se désincarner volontairement, *via* une transformation mentale de son corps, est délétère pour la perception de SPS (Michael, Guyot, et al., 2020). La manipulation des représentations du corps empêchant le maintien d'opérer, l'expérience de désincarnation serait sauve tant que la perception de nouveaux signaux corporels est court-circuitée. Nous savons également que maintenir le corps en vision perturbe plus la détection tactile que regarder un objet neutre, et ce alors que l'apport visuel n'est pas informatif dans les deux cas (Press et al., 2004) : parce que la représentation discordante est activement maintenue en focus, son

intégration biaise les performances tactiles et empêche le renouvellement des représentations en mémoire de travail. On trouverait également une potentielle explication au cas décrit par Wolpert (Haggard & Wolpert, 2005; Wolpert et al., 1998). En effet, au-delà du déclin rapide sans focus visuel, la lésion de TPJ et des aires somatosensorielles provoque un « oubli » du membre affecté dans l'espace, le patient le laissant trainer dans le couloir d'un bus jusqu'à ce qu'un passant trébuche dessus. L'incapacité à maintenir et manipuler les représentations affecterait ainsi l'intégration multi-sensorielle et la génération de représentations dans l'espace, empêchant l'individu de concevoir où se situe son membre affecté dès lors qu'il ne l'a pas en focus.

C. Une proposition de modélisation théorique

Ce travail de recherche approfondi sur les mécanismes de la conscience corporelle à travers la perception de SPS nous a permis de comprendre le rôle distinct et complémentaire de l'attention et de la mémoire de travail. Les interprétations que nous avançons étant cohérentes entre elles et avec de nombreuses conceptions théoriques, nous avons décidé de modéliser les processus par lesquels nous percevons le corps et ses signaux, qu'ils soient d'origine périphérique ou centrale. Ce modèle est adapté à partir du modèle MAM (Michael et al., 2006, 2013; Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014) et reprend certains éléments des modèles de mémoire de travail (Barrouillet et al., 2004, 2012; Barrouillet & Camos, 2012; Cowan, 1999; Plancher & Barrouillet, 2020; Vergauwe et al., 2010, 2014).

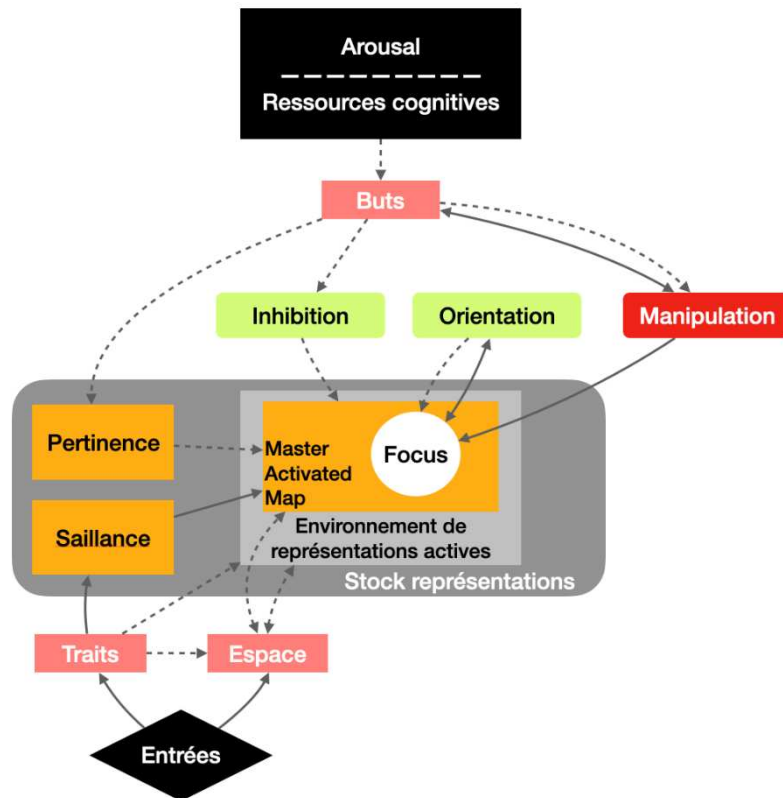


Figure 1 : Proposition de modélisation théorique de la conscience.

Basée sur le modèle MAM (Michael et al., 2007; Michael, Dorey, et al., 2020; Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014).

1. Les représentations

Comme Cowan (1999), nous avons placé au centre le stock de représentations en mémoire, lequel concentre les représentations à long terme de l'environnement, du corps et du *Self*, et avons distingué différents niveaux d'activation. Les afférences sensorielles continueraient certaines représentations en stock, ces percepts composant l'environnement de représentations actives (L. M. Chen et al., 2003; Flor, 2002; Gallace & Spence, 2010; Wawrzyniak et al., 2018). De nombreuses études ont démontré que les activations de SI et SII ne reflètent pas les stimulations tactiles mais le percept tactile illusoire (Blankenburg et al., 2006; L. M. Chen et al., 2003; Wawrzyniak et al., 2018; Zopf et al., 2011), ce qui est cohérent avec les résultats que nous décrivons dans l'article 2. Puisque nous n'agissons pas sur l'afférence sensorielle mais la trace neurale qu'elle élicite, l'environnement de représentations actives rassemble sans distinction percept élicite par une stimulation externe et percept élaborée par l'activité corticale. Cela correspondrait au *background of bodily sensations* qui est introduit par Kinsbourne (1998), à la différence que cet environnement

n'est pas spécifique à une dimension. Grâce aux objectifs internes et entrées sensorielles, une carte d'activation principale (MAM) serait élaborée à partir des percepts pertinents et saillants de l'environnement de représentations actives. Y resteraient les représentations non-pertinentes et discrètes, dont l'activation seule permettrait d'ancrer l'expérience subjective dans un contexte spatio-temporel sans mobiliser de ressources attentionnelles (Azzalini et al., 2020; Babo-Rebelo et al., 2019; Babo-Rebelo, Richter, et al., 2016; Park et al., 2018; Tallon-Baudry et al., 2018). Lorsqu'elles appartiennent à cet environnement, les SPS contribueraient à la conscience corporelle même si elles ne sont pas perceptibles. Nous décrivons en effet en article 6 que les SPS de surface reposent sur des mécanismes d'intégration entre TPJ et AI, mais pas sur des modulations attentionnelles corticales. Au même titre que les afférences tactiles en continue, les SPS de surface et leur distribution topographique suivant les frontières du corps trouveraient une utilité en marquant la distance du *Self* avec l'environnement, et en l'ancrant dans le corps (Gallace & Spence, 2008, 2009, 2010).

Lorsqu'elles sont compilées dans la MAM, les représentations seraient accessibles aux mécanismes attentionnels (Michael et al., 2007; Michael, Dorey, et al., 2020; Michael, Mizzi, et al., 2014; Michael, Pannetier, et al., 2014) : les mécanismes d'inhibition supprimerait les représentations interférentes, priorisant les représentations pertinentes sur lesquelles l'orientation dirige le focus attentionnel. Mais nous ajouterions ici que l'inhibition de représentations supprimerait leur activation, les rendant plus difficiles à récupérer car hors de la MAM. Cette supposition est faite compte tenu du phénomène mis en évidence avec l'amorçage négatif : le traitement d'un percept ayant été inhibé en amont est particulièrement coûteux, et nécessite une levée de l'inhibition (Tipper, 1985, 2001). Dans le syndrome du membre fantôme par exemple, on reporte que les représentations structurales du membre absent sont maintenues en focus au détriment des signaux sensoriels (Kikkert et al., 2018). Les percepts périphériques seraient inhibés afin que les percepts corticaux soient priorisés, ces derniers étant tout aussi pertinents et plus saillants du fait de la réorganisation corticale, qui entraîne une activité spontanée atypique et génère des sensations douloureuses (Andoh et al., 2017; Flor, 2002, 2003; Flor et al., 2006; Moseley & Flor, 2012). Une preuve en serait du parallèle entre suppression tactile (article 1) et facilitation corticale (article 2) qui sous-tendent la perception des SPS. Comme Kinsbourne (1998) le suggère, l'attention est donc focalisée sur des percepts corticaux qui, normalement, appartiennent à l'environnement de sensations actives. Avec la levée de l'inhibition, la réduction de la sélectivité

attentionnelle permettrait de passer d'une dimension à l'autre, que ce soient des percepts sensoriels aux percepts corticaux, ou du corps à l'environnement.

2. L'expérience subjective du corps

L'expérience subjective du corps, émergerait en mémoire de travail, au cœur du focus grâce à la sélectivité attentionnelle. L'interdépendance entre focalisation attentionnelle et manipulation de représentations permettrait d'élaborer de nouvelles représentations plus complexes. TPJ et AI seraient des candidats parfaits pour ces mécanismes. Les projections de TPJ vers les aires somatosensorielles et insulaires sous-tendant modulation attentionnelle et mémoire tactile (Gallace & Spence, 2008, 2009, 2010; Igelström et al., 2015; Wu et al., 2015), et AI promouvant attention interne, intéroception et homéostasie (A. D. Craig, 2003c, 2008, 2009a, 2010b, 2011; Strigo & Craig, 2016).

La compétition entre maintien et manipulation proviendrait potentiellement de l'incompatibilité des mécanismes corticaux attentionnels et d'intégration en TPJ. Nous relevons en effet que les modulations attentionnelles top-down influencent directement l'activité oscillatoire de SI, SII et AI (articles 2 et 6), tandis que les mécanismes d'intégration se mettent en place dans leur synchronisation avec TPJ (articles 5 et 6). Mais également que les mécanismes d'intégration multimodaux et d'incarnation entre TPJ et AI sous-tendent la perception des SPS (notamment celles de surface dans l'article 6), et ce même lorsque l'attention n'est pas dirigée sur les représentations du corps. Le pattern typique des expériences de désincarnation relevé dans l'article 5 en serait une manifestation : l'engagement du réseau de saillance marquerait une dépendance à l'environnement et une plus grande sensibilité à la capture attentionnelle par les percepts saillants (Corbetta & Shulman, 1998, 2002; Shulman, 2002). Des interférences naîtraient entre les représentations externes qui capturent l'attention et celles internes manipulées, perturbant l'intégration en TPJ et AI, et causant fatalement expériences de sortie du corps, héautoscopie et sentiment de présence (Arzy et al., 2007; Blanke et al., 2004; Blanke & Arzy, 2005; Cazzato et al., 2015; Easton et al., 2009; Ionta et al., 2011; Maurer et al., 2016; Sperduti et al., 2011; Yu et al., 2018). Un mécanisme identique a d'ailleurs été proposé pour expliquer les hallucinations auditives dans la schizophrénie, où les pensées internes seraient confondues et intégrées comme des afférences sensorielles auditives (Behrendt, 2006; Garbarini et al., 2016; Garrison et al., 2017; Perrone-Bertolotti et al., 2014; Pynn & DeSouza, 2013).

3. L'oubli

Un dernier point de ce modèle concerne l'après conscience. Les représentations actives suivraient un déclin naturel jusqu'à retrouver leur place dans le stock de représentations. Mais les modifications réalisées en mémoire de travail seraient conservées dans la trace neurale. En effet, les mécanismes en mémoire de travail modulent directement l'activité des aires corticales perceptuelles pour affecter la perception (Harrison & Tong, 2009; Pisella, 2017; Slotnick, 2004; Teng & Kravitz, 2019), et les représentations structurales du corps sont mises à jour avec les changements de position (Tamè et al., 2017). Ces considérations ont été apportées en article 4, où nous discutons des distorsions des représentations corporelles par les mécanismes mnésiques. L'accès en conscience déterminerait donc le contenu stocké par la suite en mémoire à long terme, mais également le comportement vis-à-vis du corps. Dans le syndrome du membre fantôme, l'incapacité à mener en conscience les percepts sensoriels au lieu des percepts centraux contraindrait la mise à jour des représentations structurales. Et dans les cas d'hémi-asomatognosies, où les lésions temporo-pariétales et insulaires provoquent une négligence de l'hémicorps, le patient est convaincu d'avoir un membre absent, est incapable de situer le membre affecté dans l'environnement, et manifeste des somatoparaphrénies où il l'attribue à un individu tiers (Dieguez et al., 2007; Dieguez & Annoni, 2011; Haggard & Wolpert, 2005).

III. Limites et autres considérations

Les travaux présentés dans ce manuscrit ont permis d'enrichir les connaissances actuelles sur la conscience corporelle. Nous y avons présenté des preuves de l'existence de phénomènes hallucinatoires normales chez l'individu lambda, et avons présenté un modèle théorique permettant d'expliquer à la fois comment nous en prenons conscience, mais également leur rôle dans la cognition humaine. Certains points sont sujets à critiques, et d'autres mériteraient d'être appréhendés dans de futures études.

A. L'expérimentation cognitive et la subjectivité

Un premier point concerne la question de la subjectivité même, une critique qui revient à chaque fois que les travaux sur les SPS sont soumis à publication ou présentés à un public. Il est vrai que l'étude des SPS est biaisée par cet aspect subjectif, qui influence fortement leur phénoménologie d'un protocole expérimental à un autre. Par exemple, l'étude pilote de Bauer et collègues (C. C. C. Bauer, Barrios, et al., 2014; C. C. C. Bauer, Díaz, et al., 2014) montre que les SPS sont perçues assez tardivement, et qu'une minute de focus est nécessaire à leur récolte avec leur protocole expérimental. Au contraire celles menées par Michael et Naveteur (Michael et al., 2012; Michael & Naveteur, 2011; Naveteur et al., 2005, 2015) montrent que 10 secondes sont suffisantes à leur perception : dans les travaux de 2005, les SPS apparaissent aux alentours de 3.83 secondes et sont perçues durant en moyenne 5 secondes. Avec ce protocole, dépasser ces 10 secondes provoquerait un effet plafond avec un effacement des différences interindividuelles.

Nous démontrons également le poids de cette subjectivité dans l'article 6, où pour permettre l'analyse comparative des 3 SPS nous adaptons les consignes et demandons explicitement aux participants de rechercher une sensation prédéfinie à la fois. En conséquence, les sensations de réchauffement ont été reportées beaucoup plus fréquemment, et leur distribution étant concentrée sur la paume, le gradient proximo-distal des SPS indépendamment du type est différent de celui observé classiquement. Cet effet pourrait être attribué à un biais de réponse. En effet, les premiers travaux de Naveteur et collaborateurs (Naveteur et al., 2005) ont montré que les SPS différaient des sensations induites par la consigne de détecter des électrochocs subliminaux. Leur variété est en effet plus riche et leur distribution n'est pas restreinte aux doigts portant de fausses électrodes.

Avons-nous inféré un biais de réponse en restreignant les consignes à trois SPS ? Au contraire, avons-nous amélioré leur perception en informant les participants de leur pertinence ? En effet nous avons déjà apporté de nombreux arguments quant au rôle de la sélectivité attentionnelle dans le phénomène des SPS, il serait logique que ces capacités d'inhibition (article 3) profitent également à la priorisation de sensations spécifiques en supprimant celles qui ne correspondent pas à la cible énoncée par l'expérimentateur.

Une dernière remarque concerne l'absence de délimitation entre l'expérience subjective normale et la distorsion perceptuelle. Cette question ne se pose pas lorsque les expériences incluent directement des populations pathologiques, dont les performances sont comparées à un groupe contrôle (Borg et al., 2015; Echalié et al., 2020). Elle commence à se poser dans les études proposant plusieurs conditions expérimentales : par exemple, comment peut-on conclure que leur perception est optimale au repos, quand on voit que le contact tactile augmente leur fréquence (Beaudoin & Michael, 2014) ? Si nous avons déjà confronté ces remarques dès l'introduction, les nouveaux travaux présentés ici soulèvent de similaires interrogations. Nous avons en effet décrit à plusieurs reprises des variations dans le type de sensations reportées liées à des traits attentionnels, cognitifs ou électroencéphalographiques, et avons interprété ces effets comme des distorsions de l'expérience subjective (voir discussion article 4). Par exemple, en article 4, les individus avec de mauvaises performances en mémoire de travail visuospatiale dues à la charge cognitive de la tâche interférente ressentent plus de sensations parétiques, des SPS rarement reportées et dont la perception élevée serait supposément délétère à la conscience corporelle. Pourtant ces mêmes sensations sont mieux perçues par les bons intérocepteurs (Michael et al., 2015). Il reste ainsi encore des points d'ombre à élucider sur la phénoménologie des SPS.

Toutefois, la subjectivité est-elle vraiment un biais ? Quel autre moyen aurions-nous pour étudier les SPS ? Et confronté à la problématique de la conscience corporelle (Borg et al., 2018; Echalié et al., 2020; Michael et al., 2015), ce protocole expérimental n'est-il pas tout à fait adapté pour en saisir les aspects personnels, privés, et non-objectivables ? Si l'on relève de nombreux outils déjà adaptés dans la littérature pour étudier et évaluer le ressenti de la douleur chez le patient, très peu d'outils nous permettent d'approcher la question de la forme du corps en conscience. Ces outils manquent cruellement à l'étude des asomatognosies, et notamment à celle du membre fantôme où le support « physique » est absent et contraint la manipulation expérimentale.

B. Le gradient cortical

Un résultat assez intéressant que nous avons décrit est le parallèle entre la topographie des SPS et la précision somatotopique en SI et SII (article 2). Car à ce jour, les études en imagerie cérébrale ne réussissent à distinguer en SI que les représentations des doigts et celles de la paume (pour références, voir Acte I, Tableau 2 – Supplementary Material). Or, le gradient proximo-distal des SPS est particulièrement précis, notamment sur les phalanges, et cela n'est pas expliqué par l'organisation physiologique cutanée (article 1). Et cette précision est d'autant plus appréciable lorsque nous nous focalisons sur les fourmillements (article 6), ces SPS similaires aux sensations tactiles véhiculées par les mécanorécepteurs, eux-mêmes distribués selon ce même gradient. Nous n'avons pas comme objectif d'étudier la somatotopie corticale, mais il est important de le relever : si les SPS sont déterminées par des mécanismes centraux – comme beaucoup d'éléments l'indiquent – alors leur distribution topographique serait une preuve de la finesse des traitements somatotopiques en SI. De futures études pourraient confirmer ces allégations, notamment en étudiant la perception de SPS sur le membre fantôme chez l'individu amputé.

C. ... Et l'insula antérieure alors ?

A notre grand regret, beaucoup des éléments discutés nous ont permis de justifier le rôle des SPS dans la génération du sentiment d'incarnation, et très peu d'appréhender leur appartenance à l'intéroception. En effet c'est seulement en article 6 que nous avons apporté l'idée de déterminants multiples aux SPS, et où nous avons supposé un rôle des mécanismes périphériques cutanés dans la détection d'événements cardio-vasculaires. Nous ne pouvons pas pour autant l'affirmer, car l'implication de ces mécanismes a été rejetée dans l'article 1. Nous avons cependant montré l'existence de mécanismes d'intégration entre TPJ et AI dans la perception de SPS internes, sous-tendant vraisemblablement l'élaboration du sentiment empathique à la douleur d'autrui. Selon les modèles de l'émotion incarnée, nous comprenons les émotions des autres parce que nous les répliquons dans notre propre corps (Keysers et al., 2010; Niedenthal, 2007). On sait en effet que l'intégration des afférences viscérales et cardiovasculaires en AI génèrent des représentations des états émotionnels, et que ces représentations guident la prise de décision (Bechara & Damasio, 2005; A. D. Craig, 2008; Strigo & Craig, 2016). A visée homéostatique, des mécanismes feedback insulaires influenceraient l'activité physiologique afin d'anticiper un événement dès qu'une

représentation complexe déjà existante est activée par une nouvelle afférence sensorielle (Apps & Tsakiris, 2014; Barrett & Simmons, 2015; Gu et al., 2013; Walter et al., 2020). Par ces mêmes mécanismes, la reconnaissance d'une émotion chez autrui entrainerait des modifications physiologiques perceptibles suivant une organisation topographique précise (Nummenmaa et al., 2014). Il serait donc possible que ces mécanismes prédictifs insulaires soient à l'origine de certaines SPS, notamment internes et thermiques (article 6). Intéroception et conscience émotionnelle étant étroitement liées, la détection de signaux intéroceptifs activerait ces représentations complexes, engageant des mécanismes prédictifs et provoquant des modifications physiologiques à l'origine des SPS. En ce sens, bons intérocepteurs percevraient plus de SPS sur la paume (Michael et al., 2015) non pas parce que l'acuité tactile y est plus basse, mais parce que les représentations insulaires sont engagées. La somatotopie du cortex thermo-sensoriel serait vraisemblablement moins fine que celle en SI, d'une part car les extrémités glabres du corps sont très peu innervées en thermocepteurs (Watkins et al., 2021), et d'autre part car les traitements insulaires visent à coordonner en parallèle identification et localisation topographique (Baumgärtner et al., 2010; A. D. Craig et al., 2000; Hua et al., 2005). En conséquence, la thermoception est facilitée sur la paume (Li et al., 2008; D. Schmidt et al., 2020; Wakolbinger et al., 2014), et les sensations de réchauffement y sont plus fréquentes (article 6). D'ailleurs, l'intéroception n'affecte pas la perception de battements, mais influence celle du refroidissement (Michael et al., 2015).

Nous avons pris le parti d'appréhender l'insula à l'aide de l'EEG. Et bien que d'autres chercheurs aient défendu l'intérêt de l'algorithme *LORETA* pour cibler cette région (Berkovich-Ohana et al., 2012, 2014; Hata et al., 2016; Knyazev et al., 2009), nous sommes bien conscients des limites qu'imposent l'étude d'une structure enfouie à l'aide d'un outil d'imagerie cérébrale de surface. Il paraît donc nécessaire que les futures études, qui seront sensiblement dirigées sur les SPS et la conscience émotionnelle à travers l'insula, le cortex cingulaire et le cortex préfrontal, exploitent d'autres techniques d'investigation cérébrale.

Conclusion

Ce travail de thèse a enrichi les connaissances théoriques et fondamentales de la conscience corporelle. En explorant le phénomène des SPS chez l'individu lambda, nous avons appréhendé la question des représentations corporelles et des mécanismes déterminant leur accès en conscience. Notre approche méthodologique stable et rigoureuse et la variété des outils expérimentaux utilisés nous ont permis d'obtenir des mesures comportementales et électrophysiologiques à même de répondre à nos interrogations.

Nous avons ainsi montré que les SPS dépendaient fortement de mécanismes centraux et suscitaient au contraire la suppression de mécanismes périphériques, et avons proposé que ces phénomènes reflétaient l'accès en conscience de représentations corporelles structurales. Nous avons exploré les processus attentionnels à travers les mécanismes d'inhibition et de régulation des ressources, l'arousal, et la synchronisation des régions TPJ et AI, et avons intégré ces effets dans un tout cohérent. Nous avons également démontré l'investissement de mécanismes visuospatiaux en mémoire de travail dans la conscience corporelle, ce qui n'a jamais été prouvé à ce jour, et avons proposé un rôle de ces mécanismes dans l'intégrité de l'expérience subjective, l'élaboration de représentations complexes, et la mise à jour des représentations en mémoire à long terme. Enfin, nous avons mis en évidence les mécanismes neuraux sous-tendant les SPS à travers TPJ et sa modulation des aires somatosensorielles et insulaires. Nous discutons ainsi du rôle des SPS principalement dans la génération du sentiment d'incarnation et dans l'homéostasie, et posons la question de leurs liens avec la conscience émotionnelle.

Ainsi, ces résultats nous ont permis de combler des points d'ombres théoriques fondamentaux. Nous avons proposé une modélisation théorique sur la base de nos travaux et de la littérature scientifique, afin d'expliquer comment représentations, attention et mémoire de travail s'intriquent pour provoquer la conscience du corps dans l'environnement. Nous y argumentons que représentations du corps et de l'environnement sont intrinsèquement liées, en ce qu'elles permettent d'ancrer l'expérience subjective dans un contexte spatial et une perspective donnée. Et nous prouvons que ces mécanismes même amènent à la perception de SPS.

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