

Interdependent relationships between the mental representation and psychophysiological correlates of action

Thiago Ferreira Dias Kanthack

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INTERDEPENDENT RELATIONSHIPS BETWEEN THE MENTAL REPRESENTATION AND PSYCHOPHYSIOLOGICAL CORRELATES OF ACTION

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I dedicate this work to my family.

To my parents, for having started me in the way I should go since I was a child. And for always remembering me the right paths that should be followed.

To my sister for her unconditional support and encouragement in the hardest experience of my life. Finally, to my wife. For her present love, despite the distance. You are the reason God gave to always try to be a better person. This work is partially yours.

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Finally, I express my gratitude to my wife, Raíssa Kanthack, the greatest gift God ever gave me. Thank for never let me give up, for understanding the hard moments and for showing me that things will be all right, as long as we have each other. I love you, and I will continue so for the rest of my life.

L'objectif de ce travail était d'apporter des données encore inconnu sur la relation entre les corrélats neurophysiologiques de l'action et la représentation mentale. Un ensemble de six expérimentations ont été menées. Celles-ci nous ont permis de mieux comprendre les modalités d'utilisation de l'imagerie motrice qu'elle soit concomitante ou réaliser après la pratique réelle. Les effets de la pratique physique sur la capacité d'utilisation de l'imagerie motrice ont aussi été explorés. Nos résultats montrent que l'imagerie motrice est très efficace, qu'elle soit pratiquée de manière concomitante à la pratique réelle ou après celle-ci lorsque la fatigue physique est importante. Nous démontrons que des capacités d'imagerie élevées ne sont pas systématiquement reliées à une amélioration de la performance. De manière inédite nous démontrons que la pratique réelle peutêtre bénéfique pour la capacité d'imagerie motrice d'une habilité fortement automatisée. De plus, des sessions de pratique physique prolongées et intermittentes semblent plus perturber la capacité d'imagerie motrice qu'une pratique continue. L'ensemble de ces résultats est une contribution importante aux connaissances relatives à l'utilisation de l'imagerie motrice dans la réhabilitation ou encore dans la pratique physique.

MOTS CLÉS : Fatigue, entrainement intégrée, imagerie motrice.

The main purpose of the present work was to add substantial data regarding the psychophysiological correlates of action with respective mental representation. A total of six experimental protocols were developed to understand the mechanisms of using motor imagery concomitant and after actual practice, and the effects of exercise on motor imagery ability. According to our findings, motor imagery can very be usefull when performed concomitant with actual practice and even after an exercise session, when fatigue is most present. We demonstrate that higher levels of motor imagery ability are not always linked with greater performance enhancement. Unprecedentedly, we reported that an exercise session might even be beneficial for motor imagery ability of high-automated task. In addition, prolonged intermittent exercise session are more likely to impair motor imagery ability in comparison with continuous exercise. These findings are of special interest of sports coaches and rehabilitation professionals, which usually incorporate motor imagery into their physical training sessions.

KEYWORDS : Fatigue, Integrated training, motor imagery.

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ABBREVIATIONS LIST

ADP : Adenosine Diphosphate	M ₁ : Primary Motor Cortex	
ANS : Autonomic Nervous System	MEP : Motor-Evoked Potential	
AT : Anaerobic Threshold	MG-A : Motivational General Arousal Imagery	
ATP : Adenosine Triphosphate	MG-M : Motivational General Mastery Imagery	
CEMP : Cervico-Medular Evoked Potential	MI : Motor Imagery	
CG : Cognitive General Imagery	MIIMS: Motor Imagery Integrative Model in Sport	
CNS : Central Nervous System	MRCP : Motor-Related Cortical Potential	
CS : Cognitive Specific Imagery	MS : Motivational Specific Imagery	
EDA : Electrodermal Activity	MVC : Maximal Voluntary Contraction	
EEG : Electroencephalography	PP : Physical Practice	
EMG : Electromyography	RPE : Rate of Perceived Exertion	
EVI : External Visual Imagery	SMA : Supplementary Motor Area	
GSR : Galvanic Skin Resistance	TMS : Transcranial Magnetic Stimulation	
HR : Heart Rate	VMIQ-2 : Vividness of Movement Imagery Questionnaire 2	
IVI : Internal Visual Imagery	VT : Ventilatory Threshold	
KI : Kinesthetic Imagery		

FIGURE LIST

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The capacity to (trans)form images is one of the most amazing abilities of human cognition. Humans can mentally rehearse past events but also simulate inexistent ones at their convenience, both in presence or absence of the corresponding motor/perceptual outputs. For decades, this ability to mentally create images has fascinated scientists and philosophers:

"I am enough of an artist to draw freely upon my imagination. Imagination is more important than knowledge. Knowledge is limited. Imagination encircles the world." Albert Einstein, Physics Nobel Prize laureate (1921), in "What life means to Eistein: An Interview by George Sylvester Viereck" in The Saturday Evening Post p. 17 (October 26th, 1929).

Conceptually, this emphasizes that inexistent experiences or even impossible ones can be easily created in our mind, hence further highlighting the small frontier between imagery of real situations and imaginary events.

"Acho que damos pouca atenção àquilo que efetivamente decide tudo na nossa vida, ao órgão que levamos dentro da cabeça: o cérebro. Tudo quanto estamos por aqui a dizer é um produto dos poderes ou das capacidades do cérebro (...). Fora da nossa cabeça não há nada.

I think we give few attention to what effectively decides everything in our lives, the organ we carry inside our heads: the brain. Everything we are about here saying is a product from the powers or the capacity of the brain (...) Outside our head relies nothing." (José Saramago, Literature Nobel Prize 1998, in Tabu, april 19th, 2008)"

The present work focuses on one of these remarkable capacities of human cognition, namely the capacity to mentally simulate actions. We can simulate every kind of motor tasks, that is motor skills we perform every day since years, but also movements we are not even capable of doing, like a novice athlete imagining himself performing movements that only professionals would be skilled enough to do. In the scientific literature, Motor Imagery (MI) refers to the voluntary process of mentally rehearsing a motor task without engaging actual body movements (Jeannerod, 1994, Moran et al., 2012). Crucially, MI is more than thinking about a movement:

"(...) imagery and execution are on a continuum, with imagined movements inadvertently generating muscle activity when facilitation of corticospinal excitability crosses a threshold for activating the alpha motor neuron pool" (Stinear, 2010 in Guillot and Collet, The Neurophysiological Foundations of Mental Motor Imagery, p. 58).

Early postulates from the first half of the 20th century claimed that MI practice might be relevant to improve motor learning (Sackett, 1934, 1935). MI practice, at the time referred to as "symbolic rehearsal", was compared to drawing practice to improve the speed by which a maze would be completed. Participants performed the maze task with one week of interval, and were asked to either drawn the maze, hence physically perform the task, "think" about completing the maze or remain passive during a control condition. Both drawing and thinking resulted in decreased times to complete the maze when compared to the control condition. However, the MI group remained slower compared to the physical training group after completion of the intervention (Sackett, 1934). In the same vein, Sackett (1935) sought to delineate whether there was a relationship between the amount of MI training (i.e., the number of MI trials completed during the intervention) and performance gains. They found no correlation between the

amount of MI practice and the performance after one week, but all MI groups (i.e., 1, 3 and 5 trials per day during a week) outperformed the control group.

Since the early insights from Sackett et al., there has been a continuous and increasing interest in the use of MI to enhance motor performance and learning. Scanning the Pubmed/MEDLINE[®] database combining "motor imagery" with "motor performance" keywords yielded 28 results between the years 1990-95. Amazingly, the same search from 2012 to 2017 leaded to 748 results (Figure

1).



Figure 1. Overview of Pubmed/Medline[®] indexed articles combining "motor imagery" and "motor performance" since 1990. Until 2011, the number of indexed articles were always bellow one hundred (Red columns). From 2012 until 2017, the exponential grown surpassed one hundred articles per year (Blue columns). The year of 2018 (Black column) was still in February at the moment, however it already had more indexed articles than all the years until 2003.

Combining MI with actual physical training has been shown to yield greater benefits on motor performance than PP training alone, and outperform the control practice conditions (e.g. Driskell et al., 1994, Yágüez et al., 1998, Jackson et al., 2004, Allami et al., 2008, Guillot et al., 2010, Seif-Barghi et al., 2012, Kanthack et al., 2014). However, motor performance gains achieved through PP training usually remain superior to those resulting from MI practice alone (Yue and Cole, 1992, Jackson et al., 2004, Ranganathan et al., 2004, Gentili et al., 2006, Fontani et al., 2007, Allami et al., 2008). The well-known study by Pascual-Leone et al. (1995) revealed that participants subjected to MI practice during 5 days achieved a level of performance comparable to that attained by participants assigned in the PP group after 3rd day. Interestingly, only 2h of additional PP allowed participants from the MI group to achieve the same final level of performance.

There are several factors behind the growing interest for MI interventions in research. MI practice is easy to implement and cost-effective. Crucially, to the best of our knowledge, no negative side effects associated with MI practice have yet been reported. MI practice can thus be considered a relevant form of additional training to improve motor performance.

A large body of research addressed the optimal guidelines for efficient MI practice. In a recent systematic review, Schuster et al. (2011) examined the key components to achieve success when performing MI, in five different disciplines: Education, Medicine, Music, Psychology and Sports. They included in their metaanalysis a total of 133 articles published between 1975 and 2010. The authors concluded that MI was an effective intervention to boost motor performance, specifically when sessions where individual, supervised and applied after PP. Evidence-based models like the PETTLEP approach (Holmes and Collins, 2001, see also Wakefield et al., 2013, Collins and Carson, 2017) and the MIIMS sport-specific approach (Guillot and Collet, 2008) further aimed at assisting sport

psychologists to deliver fruitful MI interventions. The use of these models as intervention frameworks is now well-documented (e.g. Callow et al., 2006, Smith et al., 2007, Wright and Smith, 2007, Wright and Smith, 2009). The PETTLEP model cites seven elements to be considered when adopting a MI intervention, namely:

Physical – The physical nature of imagery, the task to be imagined is of high (e.g. a maximum force exercise) or low (e.g. crossbow shooting competition) arousal. In this case, arousal would be described as the level of excitement necessary to achieve maximum performance.

Environment – To create an environment that ease the mental rehearsal, like performing motor imagery in an ecological and usual environment, using videotape for demonstration and personalizing instructions according to each participant's needs.

Task – Integrates performers' previous knowledge of the task, the nature of the task and the imagery perspective to be adopted.

Timing – How MI and PP have similar temporal features.

Learning – Since task knowledge evolves with training, so should MI sessions be reviewed to match functional equivalence of performers current state.

Emotional – To include individual emotional aspects on MI scripts. Perspective – How internal and external MI should be applied according to the motor skill.

The MIIMS emphasizes that MI guidelines should be adapted according to the purpose of the intervention. The MIIMS reviews several factors that should

be considered to have a successful outcome consecutive to the MI intervention (Figure 2). This model starts with the postulate that the content of MI should always be positive. The types of MI practice are then divided into five subcategories. Those categories (imagery components) are: Cognitive Specific imagery (CS), involving the rehearsal of specific motor skills. Cognitive General imagery (CG), focusing on task strategies and tactical points, Motivational Specific imagery (MS) used to mentally create an outcome and the ways to achieve it, increasing intrinsic motivation. Motivational General Arousal imagery (MG-A), used to regulate anxiety into the optimum level for physical performance. Finally, Motivational General Mastery imagery (MG-M) is used to enhance self-confidence and beliefs on performer's capacity.



Figure 2. Adapted illustration of the Motor Imagery Integrative Model in Sport proposed by Guillot and Collet (2008), considering four specific imagery outcomes and functions. The key components should be controlled according to the model in order to have a successful MI intervention.

Interestingly, the different frameworks used to achieve optimal MI practice

systematically encourage combining MI with PP during training interventions.

Embedded forms of MI practice are therefore highlighted, e.g. MI sessions during the rest periods of physical training, concomitantly to the physical training, or right after. In accordance with this viewpoint, Schuster et al. (2011) reported, in their systematic review, that running MI sessions during the time allocated to physical training or immediately after might be a key component to increase performance gains. Despite such conceptual guidelines, this remains a limited scientific investigations of the efficacy in support of such combined and embedded forms of MI interventions in the experimental scientific literature. For instance, very few studies focused on the effects of physical fatigue elicited by PP. If MI should be embedded into PP training, it is logical to assume that physical fatigue might be effective as well. Generally speaking, there is therefore a gap in the scientific literature regarding the implications of embedded forms of MI practice on performance, in which we were specifically interested in the present doctoral work.

First, a theoretical framework is built to detangle the similarities between MI and PP at the psychological, behavioral and neurophysiological levels. These similarities are crucial to understand the scientific rationale behind the potential to enhance motor performance through MI. Second, we focus on fatigue, i.e. an intrinsic component and aspect of PP training. We specifically discuss fatigue models. The relationships between MI and fatigue in the context of PP training then give rise to a series of experimental contributions. First, we investigated the effect of MI practice under a fatigued state. We were specifically interested in how MI might impact performance under a fatigued body state. Second, we investigated how fatigue might impact MI, specifically in terms of accuracy, and how this might affect the outcome of such embedded MI interventions. A total of

six experiments were designed and developed to achieve our goals. At the end we draw a general discussion to approach the most significant findings and discuss future research perspectives.

I) MOTOR IMAGERY

A) DEFINITION

Motor Imagery (MI) is the mental representation of an action without concomitant body movements (Jeannerod, 1994). Similarities between MI and PP are reported from behavioral (e.g., temporal congruence Decety et al., 1989, Guillot et al., 2005a, Gueugneau et al., 2008, Papaxanthis et al., 2012, Di Rienzo et al., 2014b, Fusco et al., 2014) to neurophysiological (Hanakawa et al., 2008, Munzert et al., 2009, Guillot et al., 2014, Case et al., 2015) parameters. Classically, while MI is by default a multimodal process, different MI modalities are considered according to the type of sensory information processed during the mental representation of the action. The most frequent MI modalities encountered in scientific protocols are *i*) internal and external visual MI, and *ii*) kinesthetic MI. Internal visual imagery is a form of MI where the person visualizes herself performing the action from a first-person perspective (Figure 3 left), while during external visual imagery, the persons sees herself performing an action from a third-person perspective (Figure 3 right). Kinesthetic is a form of MI emphasizing the feel of the movement, force, effort, and spatial sensations, where the action is mentally represented from proprioceptive information. Overall, MI consists in the voluntary recall of procedural motor memories.



Figure 3. Motor imagery visual perspectives. Left image represent a first-person perspective of a free-throw in basketball, the imager mentally rehearses the visual information encountered by his/her eyes during the task. The right image represent a third-person perspective of the same task, imager creating images a camera would capture from a given distance.

Looking for the specificity of MI modalities, White and Hardy (1995) reported that internal MI would be more effective than external MI in goal-oriented motor tasks relying on perception (e.g., a downhill slalom). Conversely, external imagery would be better for form-based tasks, since it extracts higher order aspects of a skill (Whiting and Den Brinker, 1982, Morrison, 1991). Accordingly, Hardy and Callow (1999) examined different types of MI training designed to learn distinct motor skills, i.e., a karate kata, a gymnastic routine, and a rock climbing task. They confirmed their initial proposal (White and Hardy, 1995), that external MI might be predominantly effective when rehearsing form-based tasks (see also, Guillot et al., 2012b).

B) NEUROFUNCTIONAL BASES

Defining MI as a purely mental processes would imply that it is intrinsically distinct from the physical performance. However, MI represents an emulation of an internal state of action preparation (Jeannerod, 1994). There is now compelling evidence that during MI, motor command signals are processed and

inhibited at some stage of the motor system (for a review, see Guillot et al., 2012a). According to Jeannerod (2001), MI shares common neural substrates with both action preparation and execution, as attested by the recruitment of cortical structures during each task (Hanakawa et al., 2008). In general, kinesthetic imagery superior benefit to motor performance is due to a greater activation of neural regions related to motor activation compared to visual imagery (Guillot et al., 2014). Further, this form of MI has been reported to elicit greater corticospinal facilitation (Stinear et al., 2006a).

Here, we discuss to which extent MI and PP share overlapping neural substrates. Firstly, we will focus on the shared cortical and spinal activations between the two tasks.

(1) CORTICAL OVERLAPPING ACTIVITY

(i) **PRIMARY MOTOR CORTEX**

Since the major contribution by Jeannerod (2001), where the author reviewed experimental evidence that MI mirrors the preparation phase of actual motor performance at the cortical level, there has been a considerable increase of findings supporting the neurofunctional equivalence between MI and PP (for more recent reviews, see Lotze and Halsband, 2006, Munzert et al., 2009, Guillot et al., 2012a, Guillot et al., 2014, Ruffino et al., 2017). Methodologies such as functional magnetic resonance imagery (fMRI) and electroencephalography (EEG) have been largely adopted by researchers to better understand MI neurofunctional correlates. It is now well-accepted that MI and PP share overlapping substrates at the cerebral level, even though activation patterns are not strictly identical (See Figure 4).



Figure 4. fMRI recordings of brain activity during motor imagery and physical practice of an upperlimb task. Main areas activated by motor imagery are: frontoparietal areas (mainly supplementary motor areas, ventral and dorsal premotor areas), frontal and temporal opercular areas, inferior parietal regions and cerebellum. Only a few areas of the premotor cortex and cerebellum were more active during more imagery than during physical practice. This figure was adapted from Hanakawa et al. (2008).

For instance, the primary motor cortex (M₁) has been wildly reported as being active during MI. This region plays a critical role by sending the signals that control movements. Its activation during MI has been debated for a long time, since the first neuroimaging studies dealing with the mental simulation of actions (for a review, see Hétu et al., 2013). A pioneering study from Roland et al. (1980) using fMRI did not report activation of the contralateral M₁ during MI. This finding was further supported by other studies which did not report M₁ activation during MI (Binkofski et al., 2000, Gerardin et al., 2000, Hanakawa et al., 2003, Kuhtz-Buschbeck et al., 2003, Dechent et al., 2004, Hanakawa et al., 2008). At the meantime, a large amount of experiment using comparable methods to investigate the central nervous system activity reported peaks of activation in this region during MI (Leonardo et al., 1995, Sabbah et al., 1995, Porro et al., 1996, Roth et al., 1996, Lotze et al., 1999, Porro et al., 2000, Miyai et al., 2001, Ehrsson et al., 2003, Nair et al., 2003, Solodkin et al., 2004, Lacourse et al., 2005, Michelon et al., 2006, Guillot et al., 2008, 2009, Burianová et al., 2013). Anatomically speaking, M₁ can be divided into an anterior part, mainly of executive nature, and a posterior part, subserving primary cognitive functions (Sanes and Donoghue, 2000). Sharma et al. (2008) reported a smaller cluster distribution of the anterior part during MI compared to PP, while the posterior part had a similar activation between imagined and real task. Even with substantial literature attesting the activation of M₁ during MI, an explanation to controversial data is required before adopting a conclusion. One important scientific consideration that may explain this inconsistent pattern of results is the temporal resolution of the technique used to map brain activations (Lotze and Halsband, 2006). Also, the MI modality is likely to elicit changes in the spatial distribution of cerebral activations. Kinesthetic MI is, for instance, known to induce greater M1 activation compared to visual imagery (Solodkin et al., 2004, Lorey et al., 2011, see Figure 4, adapted from Guillot et al., 2014 for visual representation of cortical activation during visual and kinesthetic imagery). Interestingly, Guillot et al. (2008) compared cortical activations of good imagers and poor imagers. To separate the groups, authors used an well-accepted questionnaire to evaluate MI ability (Hall and Martin, 1997), participants' capacity to preserve temporal characteristics of the task during MI (Guillot et al., 2005a, Malouin et al., 2008) and electrodermal responses (Guillot and Collet, 2008) (All those parameters will

be explained in details in following sessions). Authors reported brain activation differences between good and poor imagers, including selectively different M₁ activity (see also Guillot et al., 2009, Lotze and Zentgraf, 2010). Kuhtz-Buschbeck et al. (2003), combining fMRI and TMS measurements in complex vs simple imagined finger movements, reported an increased involvement of M₁ during complex movements. This supports the postulate by Jackson et al. (2001), who argued that differently from PP, MI requires previous knowledge from task components by the participants before engaging in mental training (see also, Sharma et al., 2008, and Lotze and Zentgraf, 2010). To summarize, MI modality, MI ability and task-knowledge might substantially influence M₁ activation during mental representation. Despite such early controversial studies, the debate is somewhat resolved and there is now a growing consensus that M₁ is active during MI.

(ii) SECONDARY MOTOR AREAS

There is converging evidence that secondary motor areas, strongly involved in movement planning, programming and predicting, exhibit a comparable activity during PP and MI. Activation intensities observed during MI remain either lower (e.g., in the cerebellum, supplementary motor area and parietal operculum, Macuga and Frey, 2012) or higher (e.g., left superior frontal sulcus, bilateral superior precentral sulcus, superior frontal gyrus and right occipital cortex, Hanakawa et al., 2008), compared to PP. The overlap between PP and MI involves the following regions:

Ventral and dorsal premotor cortices: these regions have been extensively found to be active during imagined movements (see Lotze and

Halsband, 2006, Guillot et al., 2008, Munzert et al., 2009). While the ventral part is responsible for cognitive aspects of action, the dorsal part is more related to movement preparation and execution (Rizzolatti et al., 1998). The ventral part was usually found to be more active during MI than during PP (Gerardin et al., 2000).

Supplementary Motor Area: This region is anatomically divided in three functional parts: *i*) the pre-SMA, involved in movement control, *ii*) the rostral part, involved in motor imagination, and *iii*) the caudal part, highly connected with motor execution (Vorobiev et al., 1998, Gerardin et al., 2000). Gerardin et al. (2000) reported two functional subdivisions for this area during MI, the post-SMA, where a rostro-caudal gradient was found between MI and PP, and the pre-SMA, more involved in imagination of the movement. While the SMA has punctually been emphasized for its role in the inhibition of M1 activity during MI (Kasess et al., 2008), its activation during imagined movements is well-admitted and systematically reported in the literature (Lotze et al., 1999, Hanakawa et al., 2003, Solodkin et al., 2004, Guillot et al., 2008, Olsson et al., 2008a, Guillot et al., 2009, Munzert et al., 2009).

Basal Ganglia: While this region is strongly involved in the storage of learned sequence movements and motor preparation (Alexander and Crutcher, 1990, Parent and Hazrati, 1995), there is now converging evidence of its activation during MI (see Gerardin et al., 2000, Nair et al., 2003, Lotze and Halsband, 2006, Guillot et al., 2008, Munzert et al., 2009), although little is known about its specific function (Guillot et al., 2014). Recently, Hanakawa et al. (2017) analyzed basal ganglia-cortical circuits during both PP and MI. When both tasks were completed in a faster pace, basal ganglia was more activated during PP

and MI, compared with regular speed. Furthermore, due to the reduced activity observed in this regions in the Parkinson Disease group, authors concluded that basal ganglia may play a critical role in movement control during MI as well, through dopaminergic neurons.

Parietal Regions: Parietal regions include the somatosensory cortex and the parietal lobules (inferior and superior, as well as the precuneus). These areas were frequently found to be active during MI (see Lotze et al., 1999, Binkofski et al., 2000, Gerardin et al., 2000, Hanakawa et al., 2003, Nair et al., 2003, Guillot et al., 2009, Munzert et al., 2009). Lesions in the superior part of the parietal cortex is known to perturb the temporal congruence between MI and PP (Sirigu et al., 1996, Malouin et al., 2004, Sabaté et al., 2007), hence suggesting that this area would most likely be involved in planning processes during MI. In a seminal case-study, Schwoebel et al. (2002), asked a patient with bilateral parietal lesions to perform MI of hand movements. Surprisingly, the patient executed the movement during pure MI, without any awareness, thus demonstrating his incapacity to inhibit the motor command as usual. More recently, Kraeutner et al. (2016) induced a virtual "lesion" of the left inferior parietal lobule using continuous theta burst stimulation, and reported that intrinsic learning was impaired, therefore highlighting a disruption in MI-based skill acquisition.

To summarize, motor systems, including motor and premotor regions, basal ganglia and the cerebellum, as well as parietal regions, are activated during MI (Figure 5).



Figure 5. Graphic representation of brain networks activation and corresponding functions during MI. A) Blue: Areas mainly activated during kinesthetic imagery, including M₁, the premotor cortex, the supplementary motor area, the cerebellum and the inferior parietal cortex Basal ganglia are also selectively activated during kinesthetic imagery, but does not appear in the figure .Red: Areas strongly recruited during visual imagery, including occipital regions (visual areas) and the superior parietal lobule (including the precuneus). B) Summary of cortical areas involved in motor task functions during MI.

(2) CORTICOSPINAL EXCITABILITY FACILITATION

Although there is no any overt action during MI, there is converging evidence for a facilitation in corticospinal excitability. Some researchers consider that the most reliable condition to evaluate brain activity during MI is to verify, via electromyography, the absence of muscle activity related to the task (see Stinear, 2010 for a discussion on the topic). This lack of muscular activity has been extensively reported in the literature (e.g., Shick, 1970, Decety et al., 1993, Yahagi et al., 1996, Herbert et al., 1998, Mulder et al., 2004, Mulder et al., 2005, Gentili et al., 2006, Personnier et al., 2008). However, the existence of a subliminal muscular activity during MI was earlier postulated by the psychoneuromuscular theory (Jacobson, 1930, Wehner et al., 1984). In a famous review, Feltz and Landers (1983) emphasized previous research comparing internal visual imagery and kinesthetic MI with external MI, and found that internal MI coupled with kinesthetic induced greater muscle activation (see also, Jacobson, 1932, Lang, 1979). Internal visual imagery alone further produced greater muscle activity compared to external MI (Hale, 1982).

Cortical activity during MI is inhibited by, still, obscure mechanisms in the brain (for review, see Guillot et al., 2012a). However, this inhibition is not complete as it may produce muscle activity with reduced magnitude (Gandevia et al., 1997), reaching the spinal tract and eliciting a corticospinal excitation. Data supporting that MI is capable to induce cortical gains over spinal system primarily stems TMS experiments. TMS typically consists in measuring the Motor Evoked Potential (MEP) elicited by a magnetic stimulation applied to MI. TMS pulses usually focus on trans-synaptic activation of cortical neurons (Rothwell, 1991, Curra et al., 2002, Terao and Ugawa, 2002), the somatotopic parts of M1 supporting the representation of the targeted somatic effectors and a MEP being observed by placing an electrode on the contralateral muscle (Barker et al., 1985). TMS is considered a non-invasive and reliable tool to probe the level of corticospinal excitability, including during MI (for a recent review, see Ruffino et al., 2017). MEP can be measured as peak-to-peak amplitude (Rossini et al., 1999) as well as the time to be elicited. Also, protocol with multiple stimulations with different intervals and intensities are used to investigate the isolated processes of facilitation and inhibition (Curra et al., 2002, Reis et al., 2008).

A large number of studies recorded MEPs with and without concomitant MI. It is well-evidenced that the amplitude of MEPs is higher during MI compared to control conditions (Abbruzzese et al., 1996, Stephan and Frackowiak, 1996, Bonnet et al., 1997, Kasai et al., 1997, Fadiga et al., 1998, Facchini et al., 2002,

, for reviews check Munzert et al., 2009, Grosprêtre et al., 2015a, Grosprêtre et al., 2015b, Ruffino et al., 2017. See Figure 6).



Figure 6. MEPs for the flexor carpis radialis during MI of maximal wrist flexion adapted from Grosprêtre et al. (2015a). Gray bars in the left are depicted results for each participant in the study. The MEPs had greater amplitude when applied concomitantly to MI. The increase in the amplitude during MI of the MEP elicited by TMS demonstrate that the corticospinal track was facilitated (Kasai et al., 1997, Yahagi and Kasai, 1998).

(i) <u>SPECIFICITY OF CORTICOSPINAL RECRUITMENT DURING</u> <u>MI</u>

According to Stinear (2010), "Imagery and execution are on a continuum, with imagined movements inadvertently generating muscle activity when facilitation of corticospinal excitability crosses a threshold for activating the alpha motor neuron pool". This claim is supported by a large amount of TMS data attesting the high degree of specificity of M₁ facilitation during MI, which closely parallels that observed during the physical performance of the task. MI does not only induce synaptic modifications in M₁, altering representation patterns, i.e., modulating the size of a movement representation and stimulation intensity necessary to induce a MEP (Rossi and Rossini, 2004). The facilitation of the corticospinal tract mirrors several features of the motor command elicited during the physical performance of the action. Corticospinal facilitation during MI is *i*) muscle specific, meaning that facilitation only occurs in muscles which are the agonists of the imagined action (Fadiga et al., 1998, Yahagi and Kasai, 1998, Rossini et al., 1999, Stinear and Byblow, 2003, Stinear et al., 2006a, Stinear et al., 2006b, Marconi et al., 2007); *ii*) content specific, since they reflect several features of the motor preparation, such as imagined force level (Mizuguchi et al., 2013, , see also Mizuguchi et al., 2014 on cortical activation depending on imagined force level), MI content (Yahagi and Kasai, 1998, Li et al., 2004) and task phase, with moment "on", i.e., stimuli given at the same time as task is mentally imagined, increasing MEP and decreasing intracortical inhibition (Stinear and Byblow, 2004).

(ii) <u>CORTICOSPINAL ACTIVATION THROUGH A PARALLEL</u> <u>PATH</u>

For years, researchers looked for spinal facilitation induced by MI. A reliable approach is the recording of the H-reflex, a reflectory reaction from muscle after electrical stimulation of la afferent neurons causing muscles to contract (Palmieri et al., 2004). A large number of studies did not report any influence of MI (Facchini et al., 2002, Patuzzo et al., 2003, Stinear and Byblow, 2003, Stinear et al., 2006a, Stinear et al., 2006b, Mouthon et al., 2016), but the lack of H-reflex modulation by MI is not a consensus. Contradictory data is equally found in the literature (Taniguchi et al., 2008, Ichikawa et al., 2009, Hara et al., 2010, Fujisawa et al., 2011, Nakagawa et al., 2018). Recently, Grosprêtre et al. (2015a) applied two types of stimulation to further investigate whether MI

facilitated the spinal level of the motor system. They specifically recorded the cervico-medular evoked potential (CMEP) and the Hoffman reflex (H-reflex). While CMEP gives a measurement of pyramid-motoneuronal junction (Taylor, 2006), H-reflex rather measures the transmission between Ia afferences and alpha-motoneurons. During rest, CMEP increased, without changes in H-reflex, demonstrating facilitation in descending spinal tracks but no activation on alpha-motoneurons. The authors used two techniques known to activate spinal inhibitory presynaptic circuit (i.e., presynaptic interneurons), which reduce H-reflex (Mizuno et al., 1971, Pinniger et al., 2001). The first technique was muscle lengthening via an isokinetic dynamometer, and the second H-reflex conditioning with stimulation of the antagonistic nerve (Daniele and MacDermott, 2009, Duclay et al., 2011). When applied, MI managed to modulate H-reflex avoiding decreases. These data attest that MI runs a parallel path through low-threshold interneurons to la afferents modulating their activity (See Figure 7).



Figure 7. Illustrated representation of motor imagery parallel path into corticospinal excitability. Corticalspinal activity provoked by MI is strong enough to activate low-threshold interneurons (dashed lines, Grosprêtre et al., 2015a). Those structures would be responsible to intermediate la afferent signals from agonist and antagonist muscles, and regulate α motoneuron signal transmission.

(3) MOTOR INHIBITION DURING MOTOR IMAGERY

The absence of movement during MI is somewhat intriguing considering the activation of M₁ during mental rehearsal. Basically, the neurophysiological processes mediating motor inhibition during MI remain poorly understood. It has been early postulated that the cerebellum would be responsible, at least partially, for inhibiting the signal before reaching the pyramidal tract (Lotze et al., 1999, Guillot et al., 2014). Literature reports that by using Transcranial Magnetic Stimulation (TMS) on cerebellum, prior to TMS of M₁, the motor evoked potential is inhibited (Ugawa et al., 1995, Daskalakis et al., 2004, Cengiz and Boran, 2016). Recently, Tanaka et al. (2017), using cerebellar TMS to induce M₁ inhibition, reported that during MI of muscle contraction the cerebellum contributed to the facilitatory control of M₁ excitability, with no alterations of muscle relaxation during MI, with or without cerebellar TMS. Based on these findings, one can postulate that the cerebellum is likely to inhibit M₁ excitability during imagined muscle contraction, but not during imagined muscle relaxation. Even with such evidence in support of a cerebellar contribution to the suppression of motor command signals, other cerebral areas were also emphasized for their potential involvement in inhibitory processes during MI. This is the case for the parietal (Lebon et al., 2012b) and the ipsilateral premotor cortices (Kasess et al., 2008, Bäumer et al., 2009). A very interesting report is the case-study conducted by Schwoebel et al. (2002) in a patient with bilateral parietal lesions. When imagining
hand movements, the patient simultaneously executed the imagined motor act without being aware of the movements. Surprisingly, these movements were also significantly more accurate than volitional movements. Such finding confirms that MI may normally involve the inhibition of movements and underlines the possible suppressive influence that parietal regions may exert over M₁ during MI. Several authors have further shown that reduced M₁ activation during MI is related to the suppressive Influence of other motor-related brain regions, including the SMA, thus suggesting that motor inhibition during MI may also intervene at the early stages of motor planning (e.g., Solodkin et al., 2004, Kasess et al., 2008).

More recently, Bruno et al. (2018) investigated whether MI has a facilitatory/inhibitory influence on M₁. In this TMS study, they manipulated the instructions given to the participants as both the experimental and the control group were asked to imagine a finger-to-thumb opposition task, but only the experimental group received explicit information to avoid unwanted finger movements during MI. Data revealed a facilitatory effect (increased MEPs amplitude) in the control group and inhibitory effects (decreased MEPs amplitude) in the experimental group. Bruno et al. (2018) argued that the facilitatory effects during MI may be explained by the subliminal EMG activity collected during imagined movements, due an uncomplete motor inhibition (Jeannerod, 1994, Bonnet et al., 1997, Guillot et al., 2012a). When "pure" MI is performed, however, MI may have an inhibitory effect, lowering MEPs amplitude.

C) MOTOR IMAGERY ABILITY MEASUREMENT

An important factor when applying MI into any motor training program is to control the users' MI ease and ability, as well as their compliance with instructions and (Guillot and Collet, 2008). In theory, better imagers would have greater benefits from MI training than poor imagers (Martin et al., 1999). A thorough procedure requires to combine neurophysiological, psychological and behavioral measures (Guillot et al., 2005a, Lotze and Halsband, 2006).

(1) BEHAVIORAL MEASURES

(i) TEMPORAL CONGRUENCE

Mental chronometry refers as to the duration needed to process an information (Posner, 1978), and the temporal congruence principle is somewhat supported by the fact that PP and MI of the same action obey to Fitts law (average duration of responses is directly proportional to the minimum average amount of information per response, Fitts, 1954, see Decety and Michel, 1989, Bakker et al., 2007, Personnier et al., 2010) (average duration of responses is directly proportional to the minimum average amount of information per response, Fitts, 1954). The temporal congruence between PP and MI is a reliable index of MI (Roure et al., 1999, Malouin et al., 2008, Guillot et al., 2012c). The idea is that changes in PP would equally change MI temporal parameters, and vice-versa. Modulations in MI time constrains can therefore directly affect PP. For instance, Louis et al. (2008) asked participants to intentionally modulate MI speed during 3

weeks of MI practice. At the end, fast MI practice resulted in faster PP speed, and slow MI practice resulted in slower PP speed (see also, Boschker et al., 2000). Thus, MI practice should carefully be guided by time measurements of mental representation. From a conceptual viewpoint, The main important recent MI models highlight that MI should be performed with a high degree of isochrony compared to PP (Holmes and Collins, 2001, Guillot and Collet, 2008), even though some literature defends the idea of using faster/slower MI practice might selectively and punctually contribute to successfully improve motor performance (O and Munroe-Chandler, 2008, Jenny and Hall, 2009).

In a review, Guillot et al. (2012c) underlined the main factors likely to influence the ability to achieve temporal congruence between MI and PP (Figure 8). They argued that if the imager is first of all able to perform MI with high level of temporal congruence, then MI time could be voluntarily and temporarily modulated with the intention of changing PP speed. However, inaccuracy in temporal constraints might represent a low level of imagery ability, and should be developed before applying MI with distinct timings from PP.



Figure 8. Factors underlined in experimental research for their potential to influence the temporal congruence between MI and PP. Figure extracted from Guillot et al. (2012c) with authorization from Taylor & Francis Group.

In conclusion, recording MI time and comparing with real task is an applicable and accessible method.

(ii) **PSYCHOMETRIC MEASURES**

Self-evaluation methods such as questionnaires and oral debriefs are frequently used during MI practice (Di Rienzo et al., 2014a). For such, standardized questionnaires, frequently validated in health participants such as the Vividness of Visual Imagery Questionnaire (VVIQ - Marks, 1973), the Vividness Movement Imagery Questionnaire (VMIQ - Isaac et al., 1986) and its revised version (VMIQ-2 - Roberts et al., 2008) are among the most common. For the interest of the present manuscript, we will further discuss and explain the VMIQ-2. Additionally to questionnaires, self-reports which are not standardized can be applied, especially when questionnaires do not attend a specific population or task.

(a) <u>VIVIDNESS OF MOVEMENT IMAGERY QUESTIONNAIRE</u> 2 (VMIQ-2)

MI vividness is a self-report from attesting the intensity of the sensory experience associated with MI. MI vividness can be collected for each type of MI modality/type. Subjective reports range from "no visual/proprioceptive sensory" experience" to "comparable visual/proprioceptive experience to that encountered during the physical performance of the task". To standardize and quantify MI vividness reports, Isaac et al. (1986) early developed the VMIQ, a standardized questionnaire designed to measure visual and kinesthetic imagery in many different motor tasks (e.g. running downhill and jumping from a high wall). MI vividness demonstrated a valuable method to access MI ability. For instance, high level athletes related higher level of vividness in their sport when compared do low level athletes (Isaac and Marks, 1994, Eton et al., 1998). Isaac (1992) reported higher performance improvement after MI training in participants with higher vividness compared with low vividness participants. Finally, high and low imagers exhibited significant differences in neural activation, measured by electroencephalography (Marks and Isaac, 1995). More recently, Roberts et al. (2008) developed a revised version of the VMIQ, due to i) confused conceptualization of visual and kinesthetic imagery presented in the literature when the questionnaire was first created, *ii*) detailed conceptualization of external

imagery i.e., watch *someone else* or *oneself* performing the movement, and *iii*) lack of rigorous psychometric validation. Consisting of 12 different movements to be imagined (e.g. Run, Throw a rock in the water, ride a bike), the VMIQ-2 (Appendix 1) clearly separates imagery in three well-defined categories: Internal Visual Imagery (IVI), External Visual Imagery (EVI) and Kinesthetic Imagery (KIN). Participants must first imagine all the tasks using EVI, followed by all items in IVI and finally KI. For each type of imagery, participants report a vivacity score ranging from 1 "mental representation perfectly clear and real" to 5 "no mental representation, I just thought about the movement" (Reliability = .95 for IVI; .95 for EVI and .93 for KIN).

(b) SELF-REPORT SUBJECTIVE MEASURES

One of the most applicable ways to measure MI abilities consists in collecting participant's self-evaluations. The idea is to measure MI ease and vividness using a Likert scale (Lotze et al., 2001, Moseley, 2007, Gustin et al., 2010). Participants are argued with questions like "How vivid was the mental representation?" and have to rate from 1 – "*not vivid at all*" to 7 – "*Highly vivid, it was almost like doing*". The question and answer may slightly variate according to the type of MI (e.g., visual or kinesthetic). The ability to mental represent an action may further vary according to imagers specific knowledge of the task. For instance, a soccer player may be a good imager when mentally simulating soccer tasks and daily motor activities (leading to a high score in MI questionnaire abilities), but may struggle in mentally recreating basketball shooting, tennis

serve, climbing (see Reed, 2002). The greatest advantage of using self-reports instead or in addition to MI questionnaires is the possibility to be applied in any MI task (See Di Rienzo et al., 2014a for futher devolopment on the topic).

(iii) PHYSIOLOGICAL MEASURES

MI is associated with motor preparation and planning (Jeannerod, 2001). Similarly as during the actual motor preparation, mental representation therefore engages anticipatory physiological adaptations of the body, which are in part under the control of the autonomic nervous system (ANS - Collet et al., 2013).

(a) AUTONOMIC NERVOUS SYSTEM

The ANS is mainly responsible for the maintenance of homeostasis in the body. By regulating the activity of organs, it adapts the physiological demands to adapt to internal (e.g., postural changes or physical effort) or external (e.g., temperature and altitude) constraints (Appenzeller and Oribe, 1997). ANS is functionally divided into sympathetic and parasympathetic pathways, which work in the system by the liberation of acetylcholine (sympathetic and parasympathetic) and catecholamines (adrenaline and noradrenaline, for both systems; McCorry, 2007). In general, a functional unity from the ANS consists in two neurons, one pre-ganglionic (with neurons' body located in the Central Nervous System) and a post-ganglionic (body located in an autonomic ganglion). Sympathetic nervous system has pre-ganglionic neurons in the thoracic-low back division, while for Parasympathetic system the same neurons are found in brain

stem and in the sacral region. While the sympathetic branch of the autonomic nervous system is primarily linked to body activation (awareness, fight or flight), the parasympathetic branch is primarily involved in the downregulation of physiological activity (Cannon, 1929). There is a general consensus that the sympathetic and parasympathetic branch of the autonomic nervous system share antagonistic characteristics (Figure 9).



Figure 9. Antagonist functions of the sympathetic and parasympathetic branches of the autonomic nervous system networks (adapted from Bear et al. (2007).

Those adaptations are meant to adjust the metabolic activity to the expected demands of the forthcoming action. For instance, heart and respiration rate changes during MI reflect the energetic cost of the imagined actions (Decety et al., 1993, Bolliet et al., 2005, Fusi et al., 2005, Demougeot et al., 2009, Collet et al., 2013). However, some organs represent exceptions to the principle of dual innervation by the sympathetic and parasympathetic branchs. This is the case of

eccrine sweat glandes, which are completely under the sympathetic command (Shields et al., 1987). Eccrine sweat glands range from 1.6 to 5 millions in the human body, and are located in the skin whit a high density in the fingers' skin (Wilke et al., 2004. Figure 10).



Concentration of eccrine glands per cm²

Figure 10. Concentration of eccrine glands per square centimeter in the human body (adapted from Wilke et al. (2004)

Many receptors (e.g. mechanical, chemical and baroreceptors) are responsible for scanning the body and detect both external and internal changes. Afferent pathways mediate reflex adaptation responses of the visceral system (oligosynaptic), and some more complex circuits projects the information to nuclei in the brain and the brain stem (Mitchell and Victor, 1996). For the last 30 years, the development of microneurographic techniques leaded to important discoveries regarding the reflex regulation of sympathetic nerve in skeletal muscle (Mitchell and Victor, 1996). They highlighted that muscle nerve sympathetic activity was sensitive to the variation of blood pressure whereas hand eccrine sweat glands remained silent (see Wallin and Fagius, 1986 for a review on the subject). Indeed, eccrine sweat glands are only innervated by the sympathetic system, thus do not suffer inhibition from the parasympathetic system as muscle endings.

<u>ELECTRODERMAL ACTIVITY</u>

The use of ANS variables is considered a good objective approach to measure MI quality. However, those techniques are yet scarcely considered in the MI literature (Collet and Guillot, 2010, Collet et al., 2011, Collet et al., 2013). Based from early reports dating from the XIXth century, researchers postulated that EDA might convey relevant information regarding mental states (Féré, 1888, Tarchanoff, 1890). EDA can be measured as skin resistance or conductance, one being the opposite of the other. Since eccrine glands are under the mere control of sympathetic branch of the autonomic nervous system (Shields et al., 1987), EDA measurement follow the principle of conductivity, where the skin becomes a better conductor when eccrine glands are active and sweet is present, due to sympathetic activity over sweet glands, fillings the sweet channels. Sweat release increases skin conductance and, therefore, reduces skin resistance. Skin

principle of dual innervation, and makes electrodermal activity (EDA) a reliable dependent variable attesting physiological arousal. Vernet-Maury et al. (1995) developed a system to measure skin electric conductivity and described the "ohmic perturbation durarion", a robust temporal index of sympathetic system activation (Figure 11). An electric current (15 μ A, with 0.2 μ A.mm⁻² of density) originating from an electrode placed in the index finger passes the skin, is captured by a second electrode placed on medium finger. Compared to basal level, a decrease in skin resistance tonic values should be expected as motivation/engagement towards the task increases, attesting greater activity of the sympathetic nervous system (Collet et al., 2011). The phasic activity, i.e., electrodermal responses, is characterized by a sudden drop in EDA slope, with a slow and steady return to baseline (Vernet-Maury et al., 1995). So far, EDA is known to reflect significant stimulation (internal or external to subject). Indeed, EDA increase is correlated with motor preparation and movement execution (Critchley, 2002), and similar EDA response during PP and MI is a reliable index of MI ability (Collet et al., 2011, Collet et al., 2013).



Figure 11. Electrodes positioning for electrodermal activity recordings (MLT116F GSR Finger Electrodes, ADInstruments, Dunedin, New Zeland). Electrodes are always positioned in the index and medium fingers, at the second phalanx (Vernet-Maury et al., 1995).

Others autonomic responses related to task preparation and MI are reported in the literature, such as heart rate (Oishi et al., 2000, Bolliet et al., 2005), blood pressure (Wang and Morgan, 1992) and respiration rate (Wang and Morgan, 1992, Oishi and Maeshima, 2004). For instance, EDA modulations (i.e., increase in skin conductivity) has been associated with increases in heart rate and respiration rate (Oishi et al., 2000, Oishi and Maeshima, 2004).

II) MENTAL REPRESENTATION AND PERFORMANCE

MI is frequently practiced to enhance motor performance and since the early 19's, as emphasized in several seminal meta-analyses (e.g., Feltz and

Landers, 1983, Driskell et al., 1994). Research in the field of MI has extensively grown in the last 15 to 20 years (see Figure 1 in Di Rienzo et al., 2016). The similarities between MI practice and PP, specifically with regards to the involvement of the brain motor system, support the usefulness of MI to increase motor performance and promote motor mearning (Ruffino et al., 2017). Coupling MI with PP is usually recommended to achieve peak performance (Holmes and Collins, 2001, Guillot and Collet, 2008, Schuster et al., 2011). Thus, MI practice has been extensively tested in motor performance improvement, including motor skill (Pascual-Leone et al., 1995, Gentili et al., 2006, Gentili et al., 2010) and strength gains (Ranganathan et al., 2004, Grosprêtre et al., 2017). A more recent question remains to determine in greater details when/how integrating MI practice into PP to enhance performance gains. Should it be decoupled, combined with, or directly included/embedded into PP? All those terms will be further explained and developed according to existent literature.

A) MENTAL REPRESENTATION DECOUPLED FROM ACTION

(1) SKILL PERFORMANCE AND LEARNING

Developing motor skills, such as soccer, basketball, playing an instrument or even writing, is a time-consuming process with several interdependent components. Human capacity to plan, learn and retain new motor skills is essential in daily life. This ability is requested, for instance, when a good eyebody coordinated task is demanded, such as grabbing a knife without hurting oneself or hitting a golf ball in a multiple-joint task. A great deal of research was

conducted to better understand the neural and behavioral aspects involved into motor learning. Motor learning may come from the acquisition of a new motor skill, through an incremental learning process, or the ability to compensate for environmental changes (for reviews, see Doyon and Benali, 2005, Shadmehr et al., 2010). For the acquisition of a new motor skill, it may come from a skill which participants had previous explicitly knowledge (Kami et al., 1995, Doyon et al., 1996, Karni et al., 1998, Doyon et al., 2002, Penhune and Doyon, 2002, Kincses et al., 2008). New motor skill acquisition may also result from implicit learning through repetitive training (Doyon et al., 1996, Grafton et al., 1998, Seidler et al., 2002, Robertson et al., 2004b, Albouy et al., 2006) and from self-experience, i.e., try and error (Jenkins et al., 1994, Jueptner et al., 1997a, Jueptner et al., 1997b, Sakai et al., 1998, Toni et al., 1998). With training and experience, our system not only mechanically adapts for the trained task (e.g., muscle hypertrophy, blood hemoglobin concentration and heart pumping capacity), but also learns how to adequately activate the motor system. This is called skill acquisition (i.e., motor learning), and according to Doyon and Benali (2005), this process can be divided in five phases: i) Fast phase – performance enhancement is visible right after the first PP training session; ii) Consolidation phase - performance enhancement occurs after a few (6+) hours passed the PP training; iii) Slow phase - Several PP training sessions are requested to begin to automatize the task; iv) Automatic phase - Task is performed without low cognitive demand due to high capacity of future state prediction, sparing energy from both CNS and muscles; v) Retention phase - Task can be performed after a considerable time in the absence of training.

Skill acquisition and learning are possible due the dynamic process in the nervous system named neural plasticity (Dayan and Cohen, 2011), which is the capacity to produce adaptive modulations in the structure and function of the nervous system (Zilles, 1992). For instance, Wu et al. (2004) measured motor cortex activity before and after automatization (i.e., when task is performed with low cognitive demand without decreasing performance). Authors reported less activity of the motor cortex in automated task execution, with less activity in bilateral cerebellum, pre-supplementary motor area, cingulate cortex, left caudate nucleus, premotor cortex, parietal cortex and prefrontal cortex when task is automated compared with first stages of learning. Thus, less workload to the central nervous system is required, due a more precise and accurate muscle activation (see also, Elbert et al., 1995, Kami et al., 1995, Pearce et al., 2000, Svensson et al., 2003). Additionally, neuron connectivity is susceptible to be modulated, reinforcing their communication trough synaptogenesis in the cerebellar (Black et al., 1990, Anderson et al., 1994, Kleim et al., 1996) and motor cortex (Kleim et al., 1996, Kleim et al., 2002). For instance, Yang et al. (2009) reported that after 2 days of PP in rats, the number of dendrites in the motor cortex increased, and that retention of the learned task were associated with the number of new dendrites. However, it is important to highlight that this synaptogenesis induced by PP remains activity-dependent, i.e., appears only in the regions of the motor cortex related with the trained task (Kleim et al., 2002, see also, Ganguly and Poo, 2013 for a review).

In order to elicit neural plasticity and all its components, a stimulus is required. The most common and obvious path to increase motor performance is trough PP (Robertson et al., 2004a). Similarly, due to the shared overlapping

substrates between PP and MI, MI is known to induce neuroplasticity (Pascual-Leone et al., 1995, Jackson et al., 2003, Lacourse et al., 2004, Nyberg et al., 2006, Olsson et al., 2008a, Avanzino et al., 2015) and has being extensively proved to enhance skill performance in healthy subjects (Boschker et al., 2000, Gentili et al., 2006, Robin et al., 2007, Gentili et al., 2010, Guillot et al., 2010, Guillot et al., 2013a, Battaglia et al., 2014, Kanthack et al., 2014, Afrouzeh et al., 2015, see also Di Rienzo et al., 2016, for a review).

(i) MOTOR IMAGERY EFFECT ON SKILL PERFORMANCE

Controlling the movement to achieve a perfect speed-accuracy trade-off is of critical importance. To our knowledge, Boschker et al. (2000) were the first to report that MI practice is likely to alter PP durations, specifically by accelerating/reducing the speed of the actual execution. Participants were requested to physically and mentally perform rhythmic based tasks (sequence of steps inside a square drawn in the floor) in different speeds, i.e., slower and faster than baseline conditions. The groups which performed fast MI/PP yielded reduced actual times during the retention test. As well, the slow groups (MI practice and PP) took more time to perform the task during the retention test. This results were later confirmed and extended by Louis et al. (2008), who reported similar results in expert athletes with high automated skill. Some challenging data were found by O and Munroe-Chandler (2008). In this study, participants were requested to dribble across a series of cones with a soccer ball, and the time needed to complete the task and unsuccessful performance (e.g., missed cone, ball touching the cone) were recorded. All imagery conditions, i.e., real-time, slow

and fast MI were found to improve performance by decreasing task duration and unsuccessful performance. However, this was a single day intervention, and not a MI practice (several days of mental representation). Thus, MI may have enhanced performance by retrieving forward models from motor memory instead of inducing neuroplasticity (see also, Avanzino et al., 2009, and Debarnot et al., 2011).

In the sport domain, MI has been widely used and studied, and there is converging evidence that MI contributes to enhance performance (Morris et al., 2005, Cumming and Williams, 2013) and improve movement kinematics. For instance, Guillot et al. (2013a), with a sample of young elite tennis athletes, applied MI with an "external focus" along with regular training to improve serve accuracy and velocity. Using an ecological approach, i.e., in game measures, the authors reported an increased accuracy, velocity, number of successful first servers and won points during a match, in the MI practice group compared to regular training alone after four months. Similarly, MI (using the PETTLEP model) training coupled with video observation was found to enhance movement performance in the Hopping and Drop Jump test in rhythm gymnastics (Battaglia et al., 2014). Positive results in movements performance were also be found in the bar clearance skill of active high jumpers (Olsson et al., 2008b), and hip and pelvis kinematics in dancers (Girón et al., 2012).

Overall, motor skill enhancement strongly benefits from MI practice. These gains might rely on a unitary process of neuroplasticity resulting from the consistent recruitment of the brain motor networks during the imagined task (e.g., movement accuracy, speed and efficacy. See Di Rienzo et al., 2016). For instance, Pascual-Leone et al. (1995) targeted, using TMS, the cortical motor

area representing the long finger flexor and extensor muscles. Researchers then taught a piano sequence during five consecutive days using PP and MI practice separately. The PP group outperformed the MI group after the intervention, and the performance of both PP and MI practice groups was better than that recorded in the control group. Surprisingly, motor system reorganization elicited by training was similar between the PP and MI practice group (Pascual-Leone et al., 1995). Basically, the cortical maps representing the flexor and extensor muscles of the long finger increased and the MEP threshold decreased. The MI practice group was able to achieve the same performance as the PP group with the adjunction of only one single session of 2 hours with PP. Stronger brain mapping techniques later distinguished differences in cortical activation between MI and PP (i.e., fMRI and positron emission tomography). For instance, Lacourse et al. (2004), during one week of a sequential task learning, reported that while PP training increased striatal and decreased cerebellar activation, MI practice lead to increased cerebellar, premotor and striatal activation (see also Lafleur et al., 2002, and Jackson et al., 2003). According to Ruffino et al. (2017) "...these differences in activation and performance may arise from the absence of sensory feedback while imagining". Interestingly, these authors proposed a neural adaptation conceptual model with MI for the different phases of skill knowledge (See Figure 11 below, and see Jackson et al., 2001 for a pionnering study on this topic discussion).



Figure 12. Neural adaptation model of mental practice with motor imagery (Ruffino et al., 2017). 1) During the first phases of learning, corticospinal excitability would increase and gradually decrease as learning approaches the automated phases. 2) At cortical and spinal levels, the low motor command generated would strengthen the synapses in the corticospinal tracks. 3) Finally, at the spinal level, MI may influence the pre-synaptic inhibition by activating low threshold interneurons, facilitating signal conductivity. Figure copied with authorization from Elsevier©.

(ii) MOTOR IMAGERY AND STRENGTH PERFORMANCE

While the benefits of MI practice for skill learning are well-accepted, findings supporting the efficacy of MI practice for force development remain sparse. The pioneering study in the field was conducted by Cornwall et al. (1991). In a test-retest design, the authors measured maximal isometric quadriceps torque before and after four days of MI practice (20 minutes per day). They reported an increase in MI practice group by 12.6% compared to the control group (Figure 13). Later, Yue and Cole (1992) trained two groups during four weeks in a fifth digit abduction task using the non-dominant hand. Interestingly, both MI and PP practice groups increased their maximal isometric strength, the increase being more pronounced in the PP compared to the MI practice group (29.7% vs.

22%, respectively). In addition, the ulnar nerve was stimulated during rest, and no changes was observed between the pre and the posttest, thus attesting that the increase in strength was from a neural origin and did not account for changes in muscle hypertrophy (see also Ranganathan et al., 2004). Finally, when force was measured in the untrained hand, improvements were present but without difference between the MI practice and PP groups. Authors argued that changes in the motor program were partially transferred to the contralateral hand (Enoka, 1988, Sale, 2008). In the same vein, Ranganathan et al. (2004) measured strength performance in a little finger abduction and elbow flexion task, before and after several weeks of MI practice. They also recorded movement cortical potential during the real and imagined practice of the tasks. The authors reported that strength increased for both tasks, and further found a significant increase in electroencephalogram-derived cortical potentials, concluding that MI practice enhanced cortical output, hence confirming that performance enhancement was linked to cortical neuroplasticity, which likely leaded to better recruitment of motor units (see also Yao et al., 2013). Finally, Lebon et al. (2010) introduced MI during the intervals between each exercise series for 12 training sessions. The maximal voluntary contraction (MVC) in the bench press in the MI group was significantly greater than the control group. This protocol, so far, is the only one who measured the effect of embedded MI into strength training in a longitudinal design. This form of embedded intervention (see also Reiser et al., 2011, Grosprêtre et al., 2017) fits the most classical literature recommendations regarding MI practice (Feltz and Landers, 1983, Holmes and Collins, 2001, Guillot and Collet, 2008, Schuster et al., 2011).



Figure 13. Effect of 4 days of MI intervention, 20 minutes per day, on isometric quadriceps muscle torque. MI group (Pre – 137.1 \pm 27.6 Nm, Post – 154.4 \pm 20.5 Nm) significantly increased performance while no change was observed in Control (Pre – 127.1 \pm 16.6 Nm, Post – 125.9 \pm 18 Nm). Reproduced with permission from Cornwall et al. (1991, DOI: 10.2519/jospt.1991.13.5.231). Copyright © Journal of Orthopaedic & Sports Physical Therapy[®].

So far, data supporting the practical relevance of MI practice to enhance strength development emphasized the impact of training on cerebral plasticity. Yet, until recently, no studies have investigated the sub-cortical adaptations of MI practice specifically from strength gains. Recently, Grosprêtre et al. (2017) investigated the effect of one week of MI practice focusing on strength gain for the plantar flexors in a maximal isometric task. Authors reported that after one week of MI practice, the MI group increased MVC and rate of torque development for the gastrocnemius. Followed by increased H-reflex response during rest, increased V-wave (an index of the amount of supraspinal neural drive addressed to the motoneuronal pool during voluntary contraction) and increased EMG activity on MVC plato. No changes were observed in the control group, for any variable. Such data provided, for the first time, evidence that one week of MI practice not only increased the supraspinal command, but also enhanced spinal excitability at rest.

(a) <u>SPECIFICITIES OF MOTOR IMAGERY ON STRENGTH</u> PERFORMANCE

Even with strong evidence of MI usefulness to enhance strength performance, differences in methodologies prevent from drawing final conclusions. Recently, Paulo Manochio et al. (2015) designed a systematic review, with an eligibility process, accounting for the population investigated (health young adults), intervention (with an isolated MI group), comparators (control or placebo group), outcome (analyze of muscle strength performance) and study design (randomized and/or longitudinal studies). After literature databases screening, authors included with only 4 articles, hence concluding that there is not enough evidence that MI alone can be effective to induce strength gains. Among them, Wright and Smith (2009), in a six week MI practice intervention study, measured strength gain on arm curl in five different groups: "traditional MI" (i.e. mental recreation of PP while seated in a quite room"), PETTLEP based MI, PP, PP + PETTLEP, and control. Results showed no significant difference in post compared to pre-test in "traditional MI" (+13.75%) and control (+5.12%) groups. However, both PETTLEP (+23.29%) and PP (+26.56%) exhibited strength gains, while the combination of PETTLEP MI practice and PP yielded marginally greater performance improvement (+28.03%). the authors suggested that MI might partially replace PP (see also Reiser et al., 2011).

Even with positive results of MI practice in strength performance, supported by neuro-adaptive mechanisms (Yue and Cole, 1992, Ranganathan et al., 2004, Yao et al., 2013, Grosprêtre et al., 2017), many gaps must thus be filled in the field. For instance, behavioral measures of MI ability might indirectly reflect the degree of motor networks stimulation (Meulen et al., 2014), and fatigue elicited by exercise may alter behavioral measures of MI ability, and should thus be considered in greater details (see session || -Β. MENTAL **REPRESENTATION COMBINED WITH ACTION).**

B) MENTAL REPRESENTATION COMBINED WITH ACTION

MI is capable to enhance motor performance based on its neurofunctional equivalence with PP (Di Rienzo et al., 2016). Furthermore, this neurofunctional equivalence is correlated ones' MI ability (Meulen et al., 2014). So far, most MI recommendations postulate that MI should be included (i.e., combined) within physical training (Holmes and Collins, 2001, Guillot and Collet, 2008). However, many factors remain to be considered when interpreting and applying such recommendation. For instance, when exactly should MI be included in the training session? Schuster et al. (2011) argued that the majority of protocols with positive results included MI after PP. However, the selective effects of physical fatigue on MI might modulate athletes' disposition towards mental rehearsal. So far, prolonged or intense sessions of exercise are known to impair motor performance, and recent literature suggest that MI ability might be impaired as well. For instance, Demougeot and Papaxanthis (2011) measured the duration of real and imagined arm point movements. After a maximal isometric exercise for

shoulder muscles, MI duration decreased while PP duration increased. Interestingly, PP durations recovered faster along with additional practice, compared to MI durations. These authors argued that the forward model was recalibrated through afferent feedback from current body states, which remain absent during MI. In addition, both real and imagined duration changed for the exercised arm, but not for the rested contralateral arm. Authors concluded that modulations in imagined durations originated from a local perception of fatigue. Di Rienzo et al. (2012), with a sample of twelve swimmers, investigated the effects of an intense session of physical fatigue on both internal and external visual imagery. After 45 minutes of a physically-fatiguing protocol where participants swam from 70% to 100% of their maximal aerobic speed, no subjective changes were reported in self-reports about difficulty to imagine. However, internal visual imagery durations exhibited a significant decrease compared to both pretest and real execution. This decrease was associated with shorter electrodermal responses durations. No such changes were present for external visual imagery. Authors argued a real-time updating of motor representations derived from sensory feedback are likely to affect internal MI accuracy. Thus, degradation of actual motor performance is likely to induce changes in MI accuracy. Such detrimental effects of physical fatigue was not systematically reported in the literature. Guillot et al. (2005b) measured the duration and autonomic response of imagined countermovement jumps before and after an exercise protocol for lower limbs. No alterations in the behavioral and neurophysiological correlates of MI ability were found after the fatiguing exercise. Authors argued that their protocol elicited only peripheral, but not central fatigue, hence suggesting that MI might be coupled with PP during

training. Based on these contrasting results, there is clearly a gap in the literature regarding MI x PP relationship, especially regarding the effects of PP on MI. Understand this relationship in greater details is one of the main purposes of this manuscript.

(1) MENTAL REPRESENTATION ASSOCIATED WITH ACTION

So far, only one study aimed to use MI to control the deleterious effects of PP on performance. Guillot et al. (2015) used MI practice of forehand and backhand strokes in young tennis athletes. The MI practice intervention was delivered during the rest periods of a high intensity interval training. Participants were evaluated for stroke accuracy and velocity in backhand and forehand (see Pialoux et al., 2015). Even with a high arousal level elicited by exercise (i.e., evaluated through heart rate), MI use avoided the deleterious effect of intense exercise over performance. In this experiment, the MI ability was thoroughly controlled. This prevents from concluding that only MI practice with a high degree of MI ability is effective to prevent the deleterious effects of fatigue elicited by PP. Authors argued that MI increased focus on movement preparation and facilitated forthcoming execution (Ramsey et al., 2010) despite the deleterious effect of intense exercise on cognitive and physiological process (Tomporowski and Ellis, 1986). Along with the gap regarding the effects of physical training on MI ability, researches should focus on the possibility to use MI as mean to avoid motor performance degradation across exhaustive sessions of exercise.

(2) MENTAL REPRESENTATION INCLUDING ACTION

While it remains unanswered whether MI efficacy to improve performance can be affected by the fatigue elicited by PP during training, specifically through decreased MI accuracy, embodied forms of MI practice have been shown to increase both MI ability and MI practice efficacy over performance. This is the case of dynamic motor imagery (dMI). dMI was recently described by Di Rienzo et al. (2016) as:

"A type of MI where athletes adopt a congruent body position and embody spatial and/or temporal invariants of the movement without entirely performing it".

Gould and Damarjian (1996) early postulated that dMI might increase the sensations associated with PP by adding proprioceptive information into the modeling, and thus be preferential for MI ability and motor performance enhancement. One of the first implementations of dMI was conducted by Callow et al. (2006). These authors measured MI vividness, self-confidence and performance in a sample of ski athletes during a down-hill ski-slalom. While static MI was performed seated in a quiet room, dMI was performed with ski equipment on and positioned in the start line of the down-hill and participants were instructed to move their bodies from side to side as they imagined the curves. Both mental trained groups were compared to a control group, which performed stretching exercises for an identical duration. Performance was tested right after the intervention. While dMI seemed to be the most relevant condition, static MI group did not differ from control group. These findings supports that dMI might be more beneficial to increase performance than MI. Surprisingly, MI did not facilitate the performance (see Vergeer and Roberts, 2006, for similar results when

investigating imagery *during stretching* vs imagery *before stretching*). This is, however, not the first report of the absence of effects consecutive to a MI practice intervention (Hall and Erffmeyer, 1983, Lamirand and Rainey, 1994). It was argued that MI practice would possibly need more time to be effective, even though one single session of MI is reported as being beneficial for motor performance (e.g., Kanthack et al., 2014, Guillot et al., 2015). Following a similar approach, Guillot et al. (2013b) measured vividness and duration by using dMI or static MI in a single training session, and subsequent motor performance in high jump athletes. During dMI, participants related higher vivacity compared to static MI. Additionally, the duration of dMI was compared to PP, while static MI overestimated the duration. In addition, the dMI group had better performance than static MI group (45% of success in bar clearance against 35%, respectively), and better kinematics evaluation by experts. Figure 14 was retrieved from Guillot et al. (2013b) as a good example of how dMI surpass static MI in enhancing performance and MI ability.



Figure 14. Mean and SD for duration (left) and performance (right) in dMI and static MI (here called motionless Imagery) groups. Each variable evaluated by the experts is considered crucial during a perfect bar clearance in high jumps. © Guillot et al; licensee BioMed Central Ltd. 2013.

Finally, Fusco et al. (2014) confirmed, through a more fundamental approach, that MI is not only a task-dependent process, but that dMI is also better

to achieve greater temporal congruence. Participants performed four walking tasks (normal walking, light running, lateral walking and backward walking), both physically and mentally (dMI or static MI). During dMI, duration was similar to PP duration, while the number of steps was underestimated for backward walking and lateral walking, hence demonstrating a good temporal but not spatial similarity. Meanwhile, static MI resulted in underestimated durations for light run and lateral walking, compared to PP.

Spurred by the findings mentioned above, there is enough to believe that dMI in better than static MI in enhancing performance due to increased MI ability, hence increasing functional equivalence with PP (Lebon et al., 2012a, Williams et al., 2012).

(3) MENTAL REPRESENTATION CONCOMITANT WITH ACTION

As frequently mentioned, MI is recommended to be coupled with PP (Holmes and Collins, 2001, Guillot and Collet, 2008, Schuster et al., 2011). So far, only one study investigated the use of MI concomitantly with MI only (Vergeer and Roberts, 2006). This gap in the literature is comprehensible, since the tasks where MI can be used *at the same time* without disengaging the imager from the task and thus, impairing performance, is somewhat limited, and certainly unusual. Similarly, in this case, MI might be confounded with a kind of "*focus on oneself on the task one are doing and the sensations it creates*". In their study, Vergeer and Roberts (2006) used MI during stretching training, where participants either imagined anatomical/physiological stretching process or the stretching movement while performing the real task. Authors reported no performance

enhancement, but an increased perceived comfort compared to control group after four weeks of training. The authors argued that MI may have a psychological, rather than physiological, influence on stretching performance, when used concomitantly with PP.

I) EFFECT OF MOTOR IMAGERY COMBINED WITH PRACTICE ON PERFORMANCE

EXPERIMENTAL CONTRIBUTION #1 : Thiago KANTHACK FERREIRA DIAS, Aymeric GUILLOT, Charalambos PAPAXANTHIS, Théophile GUIZARD, Christian COLLET, Franck DI RIENZO. *"Neurophysiological insights on flexibility improvements through motor imagery"*. Brain Behavioral Research, 331, 159-168, 2017.

In the majority of literature, MI practice is usually performed decoupled from the actual task (e.g., Weinberg et al., 1981, Lamirand and Rainey, 1994, White and Hardy, 1995, Yágüez et al., 1998, Dijkerman et al., 2004, Guillot et al., 2013a, Battaglia et al., 2014, Kanthack et al., 2014, Grosprêtre et al., 2017). For the first time, Vergeer and Roberts (2006) applied MI practice during an stretching exercise paradigm. After 4 weeks of training, MI group showed similar improvement compared to control group. However, MI practice group felt more comfortable performing stretching training than control group. Their result was contested by Guillot et al. (2010), that reported that MI practice, yet decoupled from actual training, enhanced stretching performance, overcoming the control group. The main question raised by those two studies is whether MI can influence physiological parameter related to stretching performance enhancement. Recently Grosprêtre et al. (2015a) demonstrated when MI is performed during muscle stretching, low threshold neurons are activated, inhibiting signals from

afferent muscles. Considering that integrated use of MI is recommended by the main MI frameworks (Holmes and Collins, 2001, Guillot et al., 2005a, Guillot and Collet, 2008, Schuster et al., 2011), the main objective of this first experimental contribution was to examine the effect of MI practice during stretching on maximal flexibility and agonist / antagonist muscle activation.

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Neurophysiological insights on flexibility improvements through motor imagery



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ABSTRACT

The efficacy of motor imagery (MI) practice to facilitate muscle stretching remains controversial and the underlying neurophysiological mechanisms unexplored. We evaluated the effects of MI practice during a sit-and-reach task. Healthy participants were randomly assigned to a MI practice (n = 15) or Control (n = 15) group and completed 2 blocks of 5 sit-and-reach trials. During the first block (B1), participants performed 5 maximal stretching trials of 10s. During the second block (B2), trials were divided into two consecutive parts: *i*) reproducing the maximum performance of B1 (10s, B2 part 1), and *ii*) attempting to outperform the maximum performance of B1 (10s, B2 part 2). Participants performed kinesthetic MI of hamstring and *rectus femoris* of the dominant leg. We also processed skin conductance as an index of sympathetic activity. We measured greater performance improvements from B1 to B2 part 2 in the MI practice group compared to Control (p < 0.001) and B2 part 2 (p < 0.001) compared to Control. Skin conductance revealed higher sympathetic activation during B2 part 2 compared to both B1 and B2 part 1 in the two groups. Thus, performing MI *during* actual movement is likely to improve stretching performance through reduced muscle activation. Such improvement may be grounded in a cortical gain over spinal reflexes.

1. Introduction

Motor imagery (MI) is the mental representation of an action without concomitant body movement [1,2]. Experimental data suggest that MI practice engages cerebral motor networks controlling actual motor preparation and execution [3–6]. Parallel patterns of brain activation are systematically reported during the physical performance and MI of the same action [7]. Both tasks recruit the premotor, primary sensorimotor and parietal cortex, as well as the basal ganglia and cerebellar networks [8–10]. Although not systematically [11,12], some experiments reported a subliminal muscle activity during MI [13,14]. These neuromuscular correlates of MI matched the intensity [15,16] and nature (i.e., eccentric, concentric and isometric) of the corresponding contractions [17,18]. Applied research on MI practice addressed its efficacy to improve various aspects of motor performance [for reviews see 6,19,20]. Since Cornwall, Bruscato and Barry [21], several experiments focused on muscle activation enhancement, particularly isometric force [22–27]. In keeping with the statements of the psychoneuromuscular theory [28,29], these experiments early postulated that MI practice might prompt cortical reorganizations leading to a more efficient neural drive to motor units [2].

Whether central nervous system activation during MI extends to the spinal and peripheral levels remains a debated issue [for review,see 30]. Transcranial magnetic stimulation, by varying the number, intensity and timing of pulses applied to the motor cortex [31–33], have provided compelling evidence for both increased intra-cortical facilitation and reduced intra-cortical inhibition during MI [e.g.,34,35]. As underlined by Stinear [36], most studies failed to detect a facilitation of spinal motor neurons during MI, as attested by unchanged Hoffman's reflexes amplitudes [37–39]. Yet, Cowley, Clark and Ploutz-Snyder [40] reported increased Hoffman's reflex amplitudes albeit the changes were not specific to the muscles targeted by MI. Nonetheless, few experi-

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Received 30 January 2017; Received in revised form 28 April 2017; Accepted 2 May 2017 Available online 06 May 2017 0166-4328/ © 2017 Elsevier B.V. All rights reserved. ments recently reported the facilitation of spinal motor neurons by recording F-waves, which are not influenced by pre-synaptic inhibitory or Ia afferent input [41–43]. Grosprêtre, Lebon, Papaxanthis and Martin [44] further investigated the amplitude of Hoffman (H) reflexes and cervico-medullar-evoked potentials during MI. They found reduced H-reflexes by about 20% after a conditioning stimulation of the antagonist nerve, thus activating presynaptic inhibitory interneurons. However, no such changes occurred in H-reflexes amplitudes during MI following the conditioning stimulation. The authors concluded that MI might activate low-threshold spinal structures without changing alpha motor neurons excitability. There is thus a pool of inconsistent findings regarding the issue of spinal motor neurons facilitation during MI. As underlined by Stinear [36], discrepancies between findings remain congruent with an assumption of an action-states continuum separating MI from the physical execution:

"(...) Imagery and execution are on a continuum, with imagined movements inadvertently generating muscle activity when the facilitation of corticospinal excitability crosses a threshold for activating the alpha motor neuron pool". Stinear [36].

According to this framework, changes in intra-cortical facilitation/ inhibition would determine whether facilitation of the motor system occurs at the spinal level. The origin of such subtle modulations remains uncertain [45]. For instance, differences in the nature of MI tasks, the accuracy of the MI instructions, or the individual MI ability were not systematically reported, controlled or discussed across experiments.

Few studies investigated the efficacy of MI practice to improve stretching performance, and the relationship between flexibility gains and muscle activation in target muscles remains unexplored. Williams, Odley and Callaghan [46] first reported improvements of hip joint range of motion when MI practice was associated with a 15-sessionsstretching program of proprioceptive neuromuscular facilitation scheduled within a span of 3 weeks. Improvements in the MI practice group outperformed those in the control groups who performed proprioceptive neuromuscular facilitation training. Progress lasted up to 3 days after the cessation of training. Later, Vergeer and Roberts [47] tested the effects of 11 training sessions of "stretching imagery" over 4 weeks (mental representation of the physiological and anatomical stretching processes) and "movement imagery" (imagining overall movements of the stretched limb during stretching). The authors reported similar hip joint range of motion in both groups, during both passive and active stretching. Nonetheless, "stretching imagery" and "movement imagery" groups reported higher perceived comfort, thus suggesting that MI may facilitate stretching due to psychological, rather than physiological, effects. Guillot, Tolleron and Collet [48] evaluated stretching performance in elite synchronized swimmers, before and after 15 training sessions delivered within a span of 5 weeks. They reported higher stretching gains in participants of the MI practice group compared to the control group, for hamstring, front split and ankle stretching performance. Unfortunately, none of these studies included correlative neurophysiological recordings during MI, hence limiting the conclusions that could be drawn to explain the processes leading to flexibility gains.

The respective contribution of psychological and physiological factors to flexibility gains after MI practice remains uncertain. In the study by Guillot, Tolleron and Collet [48], the MI practice intervention was delivered *after* the stretching exercises. Since MI practice did not occur *during* the stretching exercises, there was no possibility for immediate effects on comfort and pain perception due to psychological factors. Accordingly, range of motion increases after the experimental intervention possibly originated from physiological factors [48]. In most experiments, MI practice was decoupled from the physical practice. Yet, integrated/embodied uses of MI are recommended in MI frameworks [49,50–52] and currently receive increased attention [53–56]. Accordingly, as pioneered by Vergeer and Roberts [57], detangling the effects of MI practice *during* stretching might be of specific relevance in both fundamental and applied perspectives.

Spurred by the above mentioned results, the present study intended to examine the effect MI practice *during* stretching on flexibility and muscle activation along with the corresponding neurophysiological correlates. We hypothesized that MI practice might facilitate flexibility by affecting the muscle activation [44,58].

2. Material and methods

2.1. Participants

Thirty male students $(22.6 \pm 3.2 \text{ years}; 178.3 \pm 5.3 \text{ cm}; 72.8 \pm 9.8 \text{ kg})$ participated in the experiment. All were recreational practitioners in terrestrial sports (e.g., soccer, basketball, running, boxing). To avoid expertise bias, participants who dedicated more than 1 h/week to stretching development were not deemed eligible. This ruled out recreational practitioners of artistic sports requiring high levels of flexibility (e.g., gymnasts, ice skaters, dancers). Additionally, none of the participants was involved in any sports training/rehabilitation programs targeting the development of flexibility at the time of the experiment. No information regarding the aims and scopes of the study was provided until completion of the design. All participants finally provided a written informed consent according the statements of the Declaration of Helsinki (1982).

2.2. Experimental design

Participants were randomly assigned to the MI practice (n = 15) or Control group (n = 15). All completed a stretching paradigm (Fig. 1) adapted from the sit-and-reach task [59] under the form of individual sessions scheduled at the same daytime (1 pm before lunch).

The experimental session took place in a quiet experimental room. After a 10 min warm-up (i.e., 3×10 squats, 4×5 counter-movement squat jumps and 20 s of static tapping with 30s of passive rest between each exercise), participants completed 2 blocks of 5 trials on the sitand-reach task (120s of passive rest between blocks). During the first block (B1), participants performed 5 maximal stretching trials of 10s (10s of rest between each trial). During the second block (B2), the 5 stretching trials lasted 20s, and were divided in two consecutive parts (10s each). During the first part, participants stretched until they reached the maximum stretching point achieved throughout B1 trials (B2 part 1). To prevent participants from achieving better performance a blocking apparatus was placed at the maximal stretching point achieved during B1. After B2 part 1, participants were instructed to achieve their maximum stretching performance irrespective of B1 trials (B2 part 2, 10s). A software command triggered each step of the paradigm. We assumed that the effect of the experimental intervention would be quantifiable both in terms of stretching performance (as assessed during B2 part 2 where the maximum/unrestricted performance was required) and stretching efficiency, namely a reduced energy expenditure to achieve the same performance. This was assessed by EMG recordings during B2 part 1, where a performance restricted to the best trial of B1 was required. This appeared relevant to assess improvements occurring at a submaximal level of stretch demands while concomitantly controlling for habituation from B1 to B2.

2.3. Experimental conditions

Participants received MI practice or Control instructions during the 120s rest period separating B1 from B2. The MI practice group completed the 5 trials of B2 (part 1 and 2) while continuously performing kinesthetic MI of hamstring relaxation according to the following instructions:

"As you start stretching, imagine the feeling of your posterior leg muscles relaxing and accepting the stretch as you go further and further ahead"

The Control group completed the 5 trials of B2 (part 1 and 2) while

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Fig. 1. Flowchart of the experimental design. EMG: Electromyography, EDA: Electrodermal activity, MI: Motor Imagery.

concomitantly performing a mental calculation task (iterated multiplications by 2). This was expected to control for attention distraction effects from the pain/discomfort elicited during stretching.

and-reach trials (i.e., MI and mental calculation) was similar in both groups. In addition, participants from the MI practice group reported "How vivid was your imagery of the movement?" from 1 ("Absence of visual/proprioceptive perception of the movement") to 10 ("Same visual/proprioceptive perception of the movement as during physical practice").

2.4. Dependent variables

2.4.1. Psychometric variables

2.4.1.1 Perceived exertion

We collected the perceived exertion scores immediately after both warm-up and completion of the stretching paradigm, using a 10-point Borg Scale for perceived exertion [60]. The Borg Scale is a well-known psychometric tool. For both short and long duration exercises, the perceived intensity exhibited strong correlations with physiological variables such as heart rate (correlation coefficient range: 0.80-0.90), lactate blood concentrations (correlation coefficient range: 0.90-0.95) [60–62]. Here, the Borg scale enabled to control that the level of perceived exertion was similar in both groups as participants were included in the design, and that the fatigue elicited by the stretching paradigm was comparable in spite of the different nature of the cognitive task performed during the sit-and-reach trials (i.e., comparable cognitive demands in terms of mental resources allocated to parallel processing).

2.4.1.1. Motor imagery ability. All participants completed the VMIQ-2 [63] before performing the sit-and-reach paradigm. The VMIQ-2 assesses MI vividness according to different modalities, namely visual (both through first and third-person perspectives) and kinesthetic. The VMIQ-2 includes 12 different items rated from 1 ("Perfectly clear and vivid mental representation") to 5 ("No mental representation, I just thought about the movement") for each modality. The factorial structure of the VMIQ-2 questionnaire was validated by mean of confirmatory factor analyses, while the construct validity study of the VMIQ-2 provided Cronbach's alpha coefficients superior to 0.90 for all subscales [63]. The VMIQ-2 was addressed to the participants from both the MI practice and Control groups to ensure the homogeneity of experimental procedures and time spent in the presence of the experimenters.

After completion of the sit-and-reach paradigm, participants from the MI practice and Control groups also rated "*How difficult was it to remain focused on imagining/counting during stretching?*" on a Likert-type scale ranging from 1 ("*No difficulty at all*") to 10 ("*Impossible to imagine/ count*"). The subjective report was expected to control that the level of mental strain elicited by the cognitive task performed during the sit-

2.4.2. Behavioral variables

We measured stretching performance during B1 and B2 part 2 with reference to the maximal point reached by both hands on the anteroposterior axis. There was no dependent measure of the stretching performance during B2 part 1 since participants' performance was limited to the maximal performance achieved during B1. Performance, i.e., the point reached from the initial sit-and-reach position, ranged from 0 to 60 cm (30 cm corresponding to the feet sole level, see Fig. 2). To control baseline effects across groups, stretch performance during B1 and B2 part 2 was expressed in percentage of the maximal stretch performance achieved during B1 according to the following formula:

Stretchingperformance (B1trials, B2part2trials)-Stretchingperformance

```
(maximumB1trial)
Stretchingperformance(maximumB1trial)
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Participants were instructed to maintain a 180° knee extension throughout the sit-and-reach trials (including the 10 s rest). During the 120 s between B1 and B2, participants folded their legs in a comfortable position.

2.4.3. Physiological variables

We continuously recorded electromyography (EMG) and electrodermal activity (EDA) data (Fig. 2). Data were processed online and synchronized by the LabChart ProV8© software (ADInstruments Pty Ltd, 2014).

2.4.3.1. Electromyography. We recorded EMG from the hamstrings (HT) and rectus femoris (RF) muscles. The HT was the main stretched muscle, but we also measured RF activity as an index of the agonist demand required to keep the legs straight. Indeed, pilot recordings revealed co-activation patterns between these two muscles during maximal sit-and-reach trials, due to the tension from the stretched HT on the knee joint at high amplitudes.

After shaving and cleaning the skin with alcohol, EMG wireless surface silver electrodes (Patented parallel-bar technology, sampling rate 2000 Hz) were positioned according to Surface Electromyography for the Non-Invasive Assessment of Muscles (SENIAM) recommenda-



Fig. 2. A. Experimental settings. Upper right panel shows electrodes positioning on the second phalanx of the second and the third digits of the non-dominant hand for the recording of electrodermal activity. Lower right panel shows electrodes positioning on the *Rectus Femoris* and Hamstrings for EMG recording. B. Experimental design. Demonstrative flowchart from B1 to B2 (part 1 and 2).

tions [64]. To avoid impedance bias, we elevated the sit-and-reach experimental settings to prevent any physical contact between the floor and the back of the tight where the EMG electrodes of the HT were positioned (Fig. 2). We used the TrignoTM Wireless EMG System© (2014, Delsys Incorporated) for data acquisition. We filtered the EMG signal offline, then rectified and smoothed with a bandpass of 20–450 Hz (Butterworth filter, 4th order) with respect to the 10s period corresponding to sit-and-reach trials. The smoothed EMG (sEMG) was finally expressed in percentage of the maximal sEMG value achieved during B1 trials according to the following formula:

<u>sEMG</u>(B1trials,B2part1trials,B2part2trials)-<u>sEMG</u>(maximumB1trial) <u>sEMG</u>(maximumB1trial)

2.4.3.2. Electrodermal activity. We continuously measured electrodermal activity through skin conductance (µS, i.e., 1 m^{-2} .kg⁻¹.s³.A².10⁻⁶) using two unpolarizable 50 mm² bipolar electrodes attached to the second phalanx of the second and third digits of the non-dominant hand (MLT116f GSR Finger Electrodes, ADInstruments, Dunedin, New Zealand). Skin conductance varies according to the activity of eccrine sweat glands, which are under the unique control of the sympathetic branch of the autonomic nervous system [65]. Changes in skin conductance tonic level are correlated with arousal changes while phasic activity (skin conductance responses) attest stimuli perception and cognitive processing during both physical practice and MI [for a review, see 66]. Skin conductance increase originates from increased sympathetic output. Conversely, skin conductance decrease match reduced sympathetic output. After checking that the tonic activity exhibited a similar pattern in both groups throughout the stretch paradigm, we collected electrodermal response amplitude (EDR) during sit-and-reach trials. EDR are typically characterized by a sudden increase in skin conductance, followed by a more prolonged and regular return to the pre-stimulus values [67]. Due to the great inter-individual difference of skin conductance basal values among all participants, EDR were expressed in percentage of the

maximal EDR value achieved during B1 trials according to the following formula:

EDR (B1trials,B2part1trials,B2part2trials)-EDR (maximumB1trial) EDR (maximumB1trial)

2.5. Statistical analysis

We used R [68] to construct a linear model of VMIQ-2 scores as a function of Group (MI practice and Control). Likewise, we investigated the Group effect on participant's perceived exertion after the warm-up and the sit-and-reach task.

We used R and lme4 [69] to run a linear mixed effect analysis on stretching performance. We built a series of random-coefficient regression models with random intercepts by subjects [70]. As fixed effects, we entered GROUP (MI practice and Control) and BLOCK (B1 and B2 part 2), with interaction term. We also entered TRIALS (Trials 1-5) since we expected a systematic habituation effect of the muscles to stretching across trials of B1 and B2 part 2. The TRIAL factor was included in the linear mixed model as a numeric regressor. This enabled to quantify performance changes across the successive trials for each block of the sit-and-reach task. The statistical significance threshold was set for a type 1 error rate of 5%. We used contrast tests (least square means difference) for post-hoc investigations and applied Holm's sequential corrections to control the false discovery rate [71]. We followed the same procedure for processing the physiological dependent variables, i.e., sEMG and EDR (n.b., BLOCK included one additional class since we considered physiological data collected during B2 part 1 trials).

3. Results

3.1. Participants

As we assumed that data distribution was non-Gaussian (visual

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Table 1 Comparison of participant's characteristics in MI practice and Control groups.

	Control	MI practice	W	p-value
Age (y)	22.27 ± 3.26	23.07 ± 3.35	96.00	0.50
Weight (kg)	75.40 ± 10.44	70.20 ± 8.91	142.00	0.22
Height (m 10 ⁻²)	179.60 ± 6.23	177.06 ± 4.16	138.50	0.29

inspection of Q–Q plots), we used Wilcoxon's tests to assess the homogeneity of participant's characteristics between groups (age, weight, height). The results are summarized in Table 1.

3.2. Psychometric data

The perceived exertion was similar in both groups after both the warm-up (MI practice: 3.26 ± 1.33 ; Control: 3.80 ± 1.15 , F(1,28) = 1.73, p = 0.25), and B2 (MI practice: 5.33 ± 2.09 ; Control: 5.8 ± 1.66 , F(1,28) = 0.46, p = 0.50).

Linear models revealed no GROUP effect on VMIQ-2 scores for firstperson visual imagery (MI practice: 22.8 ± 5.70 ; Control: 25.27 ± 6.18 ; F(1,28) = 1.29, p = 0.26, NS), third-person visual imagery (MI practice: 23.80 ± 8.92 ; Control: 26.67 ± 7.54 ; F(1,28) = 0.90, p = 0.35, NS), and kinesthetic imagery (MI practice: 35.67 ± 6.26 ; Control: 32.33 ± 6.22 ; F(1,28) = 2.13, p = 0.15, NS). Likewise, the perceived difficulty at achieving the MI/mental calculation task during B2 was similar in the two groups (MI practice: 6.33 ± 1.63 , Control: 6.40 ± 1.99 , W = 126, p = 0.58). Finally, the MI practice group reported a level of MI vividness during B2 stretch trials of 5.80 ± 2.39 on the 10-point Likert scale.

3.3. Behavioral data

Raw averages (\pm standard deviation) stretching performance across groups are provided in Appendix A. The stretching performance was 29.95 cm \pm 8.13 in the MI practice group and 33.14 cm \pm 10.77 in the Control group during B1.

The linear mixed effect analysis on stretching performance yielded a significant GROUP by BLOCK interaction ($\chi^2(1) = 11.90$, p < 0.001), as well as a main TRIAL effect corresponding to a 1.20% \pm 0.19 of performance increase across the successive trials ($\chi^2(1) = 37.98$, p < 0.001). The performance increase from B1 to B2 part 2 in the MI practice group (12.33% \pm 0.08, p < 0.001) was greater than that in the Control group (8.62% \pm 0.06, p < 0.001) (Figure 3).

3.4. Physiological data

3.4.1. Electromyography

Raw averages (\pm standard deviation) sEMG across groups are provided in Appendix A. The raw sEMG of the HT during B1 was 102.21 mV \pm 20.84 in the MI practice and 104.68 mV \pm 34.36 in the Control group. The raw sEMG of the RF during B1 was 102.49 mV \pm 33.45 in the MI practice and 106.42 mV \pm 39.19 in the Control group (for an illustration of sEMG data across blocks, see Fig. 4).

The linear mixed effect analysis carried on the normalized HT sEMG yielded a significant GROUP by BLOCK interaction ($\chi^2(2) = 31.01$ p < 0.001) although there was no effect of TRIAL ($\chi^2(1) = 0.16$, p = 0.68). The respective sEMG decreases from B1 to B2 part 1 (42.96% ± 2.42, p < 0.001) and B2 part 2 (42.24% ± 2.45, p < 0.001) (Fig. 5) in the MI practice group were greater compared to those in the Control group during both B2 part 1 (27.98% ± 2.11, p < 0.001) and B2 part 2 (28.23% ± 2.01, p < 0.001) (Fig. 5).

The sEMG from the RF muscle exhibited a comparable pattern to that observed in the HT with a significant GROUP by BLOCK interaction ($\chi^2(2) = 24.13$, p < 0.001) and a main TRIAL effect (3.28% ± 0.67, $\chi^2(1) = 23.53$, p < 0.001). The decrease in sEMG from B1 to B2 part 1

STRETCH PERFORMANCE



Fig. 3. Stretching performance during B1 and B2 part 2 for MI practice and Control groups. *** = p < 0.001, NS=No statistically significant difference.

in the MI practice group (35.21% \pm 2.63, p<0.001) was greater compared to that observed in the control group (12.93% \pm 2.87, p<0.001) (Fig. 5). Likewise, the sEMG decrease from B1 to B2 part 2 in the MI practice group (24.69% \pm 3.37, p<0.001) was greater compared to that in the Control group (8.51% \pm 3.38, p<0.01) (Fig. 5).

3.4.2. Electrodermal activity

Raw averages (\pm standard deviation) electrodermal activity data across groups are provided in Appendix A.Tonic skin conductance exhibited a comparable profile during B1 and B2 in both MI practice and Control groups (Fig. 6).

EDR amplitude was 6.98 μS \pm 9.51 in the MI practice and 4.33 μS \pm 4.75 in the Control group during B1.

The linear mixed effect analysis revealed no GROUP by BLOCK interaction ($\chi^2(2) = 2.89$, p = 0.24), but we observed a main BLOCK effect ($\chi^2(2) = 68.55$, p < 0.001). EDR amplitude in B2 part 2 was larger compared to that recorded during both B1 (366.89% ± 50.92, p < 0.001) and B2 part 1 (394.44% ± 55.42, p < 0.001) (Fig. 6). Lastly, there was no difference between B1 and B2 part 1 (p = 0.37).

4. Discussion

The present study aimed at investigating the effects of MI practice during stretching on flexibility and their neurophysiological correlates. We implemented a transversal design with two independent groups to prevent carryover effects from one experimental session to another. Warm-up and perceived exertion after completion of the paradigm were similar in MI practice and Control groups. Both groups also reported comparable levels of mental strain after completing the experimental conditions at B2. This indicates that neither MI practice nor mental calculation yielded additional mental load likely to confound the results, e.g., distracting participants' attention from the discomfort/ pain sensations elicited by stretching. The parallel processing framework underlines the relative importance of afferent signals depending on social/physical contexts [for further development,see 72,73]. During the sit-and-reach trials of B1, MI practice and Control groups exhibited the same level of performance. HT and RF activation, as well as EDR amplitudes were also comparable in both groups. This attests that the baseline was comparable in the MI practice and Control groups. During B2 part 1, participants were asked to replicate the maximal performance achieved during B1, while concomitantly engaging in either


Fig. 4. A. Electromyography (Butterworth filter 20–450 Hz, 4th order) of the rectus femoris during B1 (left panel) and B2 part 1 and 2 (right panel). B. Electromyography (Butterworth filter 20–450 Hz, 4th order) of the hamstring during B1 and B2 part 1 and 2. Data were extracted from a representative participant of the Control group.

kinesthetic MI or mental calculation. EDR amplitudes remained unchanged in both groups compared to B1. This result was expected considering that the two tasks involved the same demand in terms of physiological arousal.

A first original finding is the decreased muscle activation from B1 to B2 part 1 and from B1 to B2 part 2 in the HT and RF. Interestingly, only few studies investigated lower limb muscle activity during stretching *in vivo* [e.g.,74,75,76]. The authors reported unchanged EMG in spite of

flexibility gains, which contradicts the present findings. The authors argued that the progressive viscoelastic relaxation of non-contractile connective tissues underpinned flexibility enhancements. Nonetheless, these past experiments investigated muscle activation during passive stretching exercises, the legs being stabilized by splint systems. During passive stretching, agonist/antagonist efficiency is not crucial to achieve high joint amplitudes, due to external forces. Contrary to past experiments [e.g.,74,75,76–79], the present sit-and-reach task cannot



HAMSTRINGS

RECTUS FEMORIS

Fig. 5. Standardized smoothed EMG in hamstring (left panel) and rectus femoris (right panel) muscles during the sit-and-reach paradigm in MI practice and Control groups. ** = p < 0.01, *** = p < 0.001, NS—No statistically significant difference.



Fig. 6. A. Average skin conductance (plain line) with standard deviation (grey area) during B1, B2 part 1 and B2 part 2. Values are reported to basal level for each participant. B. Electrodermal responses amplitude in the MI practice and Control groups during B1, B2 part 1 and B2 part 2. *** = p < 0.001, NS=No statistically significant difference.

be considered a passive stretching paradigm per se. During active stretching, the force demand on the agonist muscle is related to the amplitude of the stretch reflex. Accordingly, neural factors (i.e., stretch reflex and agonist/antagonist coordination) directly affect the flexibility performance [for further development,see 80,81-83]. For instance, a high resistance of the HT would not only limit hip flexion, but also make more difficulty to stabilize the lower limbs posture (i.e., 180° of knee extension), hence resulting in an increased RF activation. The MI practice group exhibited additional decrease of HT and RF activation compared to the Control group during B2 part 1. This indicates reduced stretch reflex amplitude during trials reproducing maximal B1 performance. This represents a second original result, extending pioneering findings on the effects of MI practice on stretching performance [46,48]. This result supports the working hypothesis that MI might affect muscle activity during stretching through a cortical gain over spinal reflexes, in keeping with the postulates by Alter [84 p. 135]:

"(...) Motor imagery might facilitate the development of flexibility by decreasing motor neuron activation, resulting in greater relaxation and altered programming of the motor system"

There is now a large body of research on the effects of MI on corticospinal excitability [85–88], which leaded to divergent conclusions with regards to the recruitment of spinal networks [36]. Recently, Grosprêtre, Lebon, Papaxanthis, and Martin [44] reported that MI of maximal muscle contractions facilitated both corticospinal and cervico-medullary excitability, but not Ia-alpha synapses. MI also cancelled the downregulation of Hoffman's reflex elicited by various conditioning stimuli at rest, including muscle stretching. The authors inferred a modulatory role of MI on spinal networks, specifically low-threshold interneurons mediating Hoffman's reflexes. Considering the modulatory effect of MI over spinal networks, the cortical gain elicited by MI over spinal interneurons mediating the stretch reflex possibly contributed to decrease its amplitude during sit-and-reach trials. This could account for the additional flexibility gains during B2 part 1 compared to B1 in the MI practice group compared to Control.

During B2 part 2, participants were instructed to achieve maximal performance on the sit-and-reach task. B2 part 2 thus involved an additional demand compared to B2 part 1. This was attested by increased EDR amplitudes in both groups. As expected, both groups improved their stretching performance compared to B1. Furthermore, the MI practice group exhibited additional gains compared to the Control group. Interestingly, while the MI practice group exhibited reduced muscle activation compared to Control during B2 part 2, the difference in RF and HT sEMG was similar to that already recorded during B2 part 1. This finding suggests that performance improvements from B1 to B2 part 2 might not directly account from neural factors. We suggest that the reduced activation of HT in the MI practice group, observed during B2 part 1 and B2 part 2, potentially yielded a more effective stretch of the connective tissues. Indeed, lower resistance from the HT emphasizes the stretching demand on the viscoelastic tissues of the muscle, while concomitantly reducing the demand on the RF to keep the 180° knee extension and assist the hip flexion. Present results confirmed the hypothesis of a beneficial influence of MI practice on flexibility [89,90]. Yet, literature findings are sparse and crossover with previous experiments remains difficult since they combined active and passive exercises [57,89]. MI practice research focusing on muscle function primarily addressed the development of isometric force [91–93]. Interestingly, the beneficial effects of MI practice on force and flexibility might rely on a unitary neurophysiological processes, namely a cortical gain over motor units prompting/facilitating the forthcoming/ongoing physical performance. This is in agreement with the hypothesis of a functional equivalence between MI and physical practice [for pioneering insights, see 94], but also with the statements of the psycho-neuromuscular theory, which early postulated the facilitation through MI practice of the neural pathways mediating the forthcoming physical performance [95,96]. In the case of isometric force development, MI practice contributed to increase the cortical output to the muscles, thus mediating force gains [11]. In the case of flexibility development, MI would facilitate pre-synaptic inhibitory circuits [44], hence resulting in reduced muscle activation during stretching.

MI practice during stretching facilitated both the maximal (B2 part 2) and submaximal (B2 part 1) performances. By lowering the muscle stretch response, MI practice participated to enhance the stretch demand on the viscoelastic tissues, which is a major component of flexibility development [for a review,see 97]. One major practical implication of the present study is that MI practice during stretching may be relevant in terms of prophylaxis and performance, for instance in sporting activities where high joint amplitudes achieved through active stretching are seminal (e.g., artistic sports, fight sports). Also, MI practice guidelines insist on reproducing the features of the correspond-

ing task in terms of content, vividness, temporal organization, modalities and arousal [50–52,98–100]. Accordingly, both in sports training and rehabilitation, kinesthetic instructions focusing on antagonist muscle relaxation in addition to agonist muscle activation during MI practice may be relevant. This might prompt, at a spinal level, neural drives mediating efficient agonist/antagonist coordination during future executions.

4.1. Conclusions

Overall, the present data bring new insights on the neurophysiological processes underlying enhanced flexibility through MI practice. Future studies should contribute to further address the hypothesis of a cortical gain over spinal reflexes as a possible origin to the reduced muscle response to stretching. A first limitation is that we involved EMG recordings of the two main agonist/antagonist muscles of the stretching task. Future studies should consider EMG measures from other muscles to assess whether the effects of MI practice are effectorspecific [13,16,17,28,88,101], or may be generalized to other motor units. In the present study, we investigated behavioral and peripheral neurophysiological recordings. Electroencephalographic recordings during MI practice concomitant to stretching might be specifically relevant to further investigate cortical changes associated to the reduced muscle activation in response to stretching. Likewise, transcranial magnetic stimulation designs should also be relevant to address the issue of intra-cortical facilitation/inhibition changes associated with MI practice during stretching. Another complement to the present work would be to select a sample of athletes' with a high experience of stretching. While the choice of a sample of athletes with a limited experience of stretching was initially expected to control for expertise bias, this also prevents from generalization of the findings to expert performance. For instance, MI practice efficacy could be hampered due to ceiling effects associated with a high flexibility performance at baseline. Finally, future experiments should address whether MI practice interventions over more prolonged time periods, during and/ or decoupled from actual stretching, can result in comparable improvements.

Appendix A. Raw (mean \pm standard deviation) electromyography (mV), electrodermal activity (μ S) and performance (cm) data in MI practice and Control groups for Block 1 and Block 2 (part 1 and 2).

	Control											Motor imagery											
	Performar (cm)		EMG (mV)					EDR (µS)			Performance (cm)		EMG (mV)					EDR (µS)					
			Rectus Femoris			Hamstrings								Rectus Femoris			Hamstrings						
Time	B1	B2 (2)	B1	B2 (1)	B2 (2)	B1	B2 (1)	B2 (2)	B1	B2 (1)	B2 (2)	B1	B2 (2)	B1	B2 (1)	B2 (2)	B1	B2 (1)	B2 (2)	B1	B2 (1)	B2 (2)	
Mean SD	34.24 11.71	37.12 11.44	102.85 17.17	84.68 21.51	96.07 31.15	105.48 19.60	71.57 27.46	82.81 58.63	-2.18 1.77	-2.84 1.54	-0.38 1.20	31.70 9.22	33.49 8.29	102.3 14.49	82 39.77	87.14 38.84	102.32 8.65	60.35 25.16	63.26 26.44	-3.81 1.34	-3.11 1.35	1.25 1.17	

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EXPERIMENTAL CONTRIBUTION #2 : Thiago KANTHACK FERREIRA DIAS,

Aymeric GUILLOT, Damien SABOUL, Franck DI RIENZO. "Breathing with your mind: Using inverse motor imagery to increase breath-holding time". To be submitted.

In experimental contribution #2 the use of motor imagery during actual task is still in evaluation. MI is known to reproduce the internal state of motor preparation (Decety et al., 1993, Jeannerod, 1994, Fusi et al., 2005), and is generally accepted that MI should be congruent with actual task in order to enhance sport performance. So far, incongruent forms of MI were not studied, especially during an actual task. Incongruent forms of MI could modulate autonomic nervous system responses linked with performance (Collet and Guillot, 2010) Thus, the aim of experimental contribution #2 was to evaluate the effect of incongruent MI practice, compared with congruent MI and a control condition, on physiological and behavioral variables of a maximal breath-holding performance. Since this study was the first to use incongruent MI practice, a short communication format was chosen. Hoping to provide future references in the use of incongruent forms of MI.

SHORT COMMUNICATION

BREATHING WITH YOUR MIND: USING INVERSE MOTOR IMAGERY TO INCREASE BREATH-HOLDING TIME

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Abstract

Motor Imagery (MI) is the mental representation of a movement without executing it, and is known to share overlapping neural substrates with the actual motor preparation and execution. MI reproduces physiological arousal state recorded during the physical practice, hence attesting the incomplete inhibition of motor command signals addressed to neurovegetative effectors. According to the classical guidelines, MI practice should be practiced in a comparable physiological arousal state to that encountered during physical practice, and reproduce the main features of the physical practice (e.g.,). Hence, classical guidelines advocate for a congruent MI practice with regards to the requirements of performance. Here, we aimed at studying whether an incongruent form of MI practice could enhance performance. Participants engaged in maximal breathholding trials while concomitantly practicing i) MI of breathing, ii) MI of breathholding. Performance was predicted by the cardiac activity and blood oxygen saturation. Performance was improved during MI of breathing compared to both MI of breath-holding and a control condition. We discuss the possibility of delayed central breath reflex due the internal stimulation of a breathing body state during MI.

INTRODUCTION

Motor imagery (MI) is the voluntary process of mentally representing an action without executing it (Decety, 1996). MI and physical practice of the same action engage overlapping cortical and subcortical substrates (Munzert et al., 2009, Hetu et al., 2013, Guillot et al., 2014). MI can thus be considered a "motor cognition" process, due to the involvement of the brain motor system in the absence of physical practice (Jeannerod, 2001). At the peripheral level, MI reproduces autonomic nervous system response patterns recorded during physical practice along with effort increment, e.g., increases in cardiac and respiratory activity (Decety et al., 1991, for a review, see Collet et al., 1994). It was early postulated that MI engaged the autonomic nervous system to anticipate forthcoming physiological demands associated with the mentally stimulated action, hence reproduced an internal state of actual motor preparation (Decety et al., 1993, Fusi et al., 2005).

MI has been extensively used to enhance motor performance in sports and rehabilitation settings (see Di Rienzo et al., 2016 for a review). Research on MI practice guidelines emphasized that MI should be practiced in conjunction with physical training (Holmes and Collins, 2001, Guillot and Collet, 2008). MI should be practiced in environmental and physiological arousal contexts comparable to that encountered during physical training. There is a general consensus advocating for *congruent* forms of MI practice with respect to the endogenous (e.g., physiological arousal) and exogenous (e.g., environmental context) features of physical training (Holmes and Collins, 2001, Guillot and Collet, 2008). Could *incongruent* forms of MI practice enhance performance in specific sporting situations? To the best of our knowledge, this issue was not addressed in the

existing literature. Here, incongruent refers to a MI practice with opposite endogenous and/or exogenous demands to those encountered during the physical practice. To address this issue, we used a breath-holding paradigm. Indeed, MI is known to adequately reproduce the internal states encountered during breath-holding (Di Rienzo et al., 2014). The breakpoint of voluntary breathholding involve both psychological and physiological factors (see Parkes, 2006). Specifically, autonomic nervous system response patterns yielding changes in cardiac activity (e.g., increases in variability of inter-beat internal) have been linked to the maximal breath-hold performance (Trzebski and Śmietanowski, 1996, Javorka et al., 2001, Javorka et al., 2002). We thus specifically aimed at evaluating the effect of congruent and incongruent MI practice behavioral and physiological variables quantifying the maximal breath-hold performance.

METHODS

I) Participants

Healthy adult participants without any history of chronic disease or neurologic disorder were recruited from the Sports Sciences department of the University Claude Bernard Lyon 1 (n= 18, 9 men, age range: 20 – 35 years). They had no previous experience of breath-holding training but a regular practice of terrestrial sports (e.g., soccer, climbing, jogging, rugby). All volunteered to participate in the experiment and provided a written consent from in agreement with the statements of the declaration of Helsinki (1982).

II) Experimental design

The repeated-measures design involved three experimental sessions of 30 min. Experimental sessions were scheduled within a span of 1 week and took place in a quiet room of the Sport Sciences department. Experimental sessions were scheduled at the same daytime to avoid the influence of circadian rhythms (i.e., 12 am before lunch). Participants were specifically instructed not to eat or consume coffee during the 3 hours preceding each experimental session.

Experimental sessions consisted in repeated measures of the maximal breath-holding performance. Maximum breath-holding performance trials were performed seated with the hands and forearms on the thighs. Participants remained motionless with the knees at 90°. Participants faced a white wall without windows around to avoid possible distraction effect on breath-holding performance (see Parkes, 2006). Across the three experimental sessions, the maximal breath-holding performance was recorded under three distinct experimental conditions. During each experimental condition, subjects performed three maximal breath-holding trials. Five minutes of passive recovery were allocated between each maximal breath-holding trial (according to the recommendations by Ratmanova et al., 2016). The following experimental conditions were administered during maximal breath-holding performance trials: i) MI practice focused on the proprioceptive information related to breathing movements (i.e., MIINCONGRUENT), ii) MI practice focused on the proprioceptive information of holding breath (i.e., MICONGRUENT) and finally, iii) focus on a cross fixed in front of then at eye sight (CONTROL). Importantly, all experimental conditions were performed *during* the maximal breath-holding performance trials. Experimental conditions were administered in a fully counterbalanced order at

the group level, i.e., three participants allocated to each of the six possible order conditions (i.e., block randomization; Snow, 2013).

III) Dependent variables

A) Performance recordings

Fifteen seconds before each trial, participants were warned of prepare themselves and to perform a maximal inspiration before starting. Participants were instructed to hold their breath after completion of the ventilation routine for the as long as possible. breath-holding performance was quantified as the time separating the onset of breath-holding up to the first uncontrollable inspiration. Before each breath-holding trial, participants were equipped with a nose clip (Ergonomic shaped Pro Nose Clip Arena[®]). This enabled a rigorous control of the absence of inspiration/expiration movements during the breath-holding trials (Shykoff et al., 1991, Heusser et al., 2009).

- B) Physiological recordings
 - (1) Cardiac activity

Before each experimental condition, participants remained motionless for 10 minutes lying on their back in an adjustable reclining seatback. This standardized position enabled a baseline measure of heart rate (HR) and HR variability, using a thoracic heart rate monitor (SUUNTO®, Finland). The first and last 2.5 minutes of signal were not considered in the baseline measure. HR and HR variability were calculated during the median 5 min time range of signal acquisition. During breath-holding trials, HR and HR variability were calculated from a time window corresponding to a plateau of cardiac signal (i.e., time window duration \geq 30 s) (Figure 1). Indeed, HR variability measures specifically require a stationary signal (Vanderlei et al., 2009). The root mean square of successive differences (RMSSD) and the standard deviation of R-R intervals (SDNN) were then collected. These heart rate variables are known to respectively reflect the parasympathetic nervous system activity and the global activity of autonomic nervous system (Vanderlei et al., 2009). Heart rate variability measures were processed using the Kubios HRV Standard 3.0.1 software (MATLAB[®], © 2017 The Mathworks, Inc), and normalized relative to the 10 min baseline recording.



Figure 1. Visual representation of HR (beats per minute) and RR (seconds) for one participant in one condition. HRV plato is highlighted by the blue area (from ~15s to ~62s). A – Bradycardia as response of breath-holding (Foster and Sheel, 2005). B – Time of breath out. C – Signal noise. Here it is present outside plato, when inside it would be removed by filters. D – Maximum breath-hold performance. In 100% of the cases where plato was found, it ended a few seconds before expiration.

(2) Blood oxygen saturation

Blood oxygen saturation (SO₂) was measured at the end of the 10 min rest, before and at end of each trial using a finger oximeter placed at the first

finger of the dominant hand (AccU-Rate® Pro Series CMS 500DL). Before each trial, SO₂ was checked for return of basal values.

C) Psychometric recordings

After completion of the MI_{CONGRUENT} and MI_{INCONGRUENT} experimental conditions, participants were requested to determine which experimental condition they perceived as their best breath-holding performance (i.e., MI_{CONGRUENT}, MI_{INCONGRUENT} and CONTROL).

After completion of MI_{CONGRUENT}, MI_{INCONGRUENT} and CONTROL experimental conditions, participants reported their perceived commitment to engage in a *maximal* breath-holding performance on a Likert-type scale ranging from 1 (i.e., *"I did not engage in a maximal breath-holding trial, I just hold my breath up to the first feelings of discomfort"*) to 10 (i.e., *"I did engage in a maximal breath-holding trial, I could not hold breath any longer by any means*".

After completion of the MI_{CONGRUENT} and MI_{INCONGRUENT} experimental conditions, participants rated the perceived vividness of MI on a Likert-type scale ranging from 1 (i.e., "*No feeling at all, I only though about the movement*" to 10 (i.e., "*Similar breathing/holding my breath feeling to that during physical practice*").

IV) Statistical Analyses

We used R (R Core Team, 2015) and *nlme* (Pinheiro et al., 2011) to run a linear mixed effects analysis of i) the breath-holding performance and ii) the psychometric variables, with a by-subject random intercept. For the breath-holding performance analysis, we used EXPERIMENTAL CONDITION (i.e.,

MI_{CONGRUENT}, MI_{INCONGRUENT} CONTROL), TRIAL (i.e., TRIALS 1-3), with interaction term. We also included SO₂, HR, RMSSD and SDNN (without interaction term). TRIAL was included as numeric regressor in the model since we expected an habituation to breath-holding from trials 1-3. For the analysis of psychometric variables, we used the EXPERIMENTAL CONDITION (i.e., MI_{CONGRUENT}, MI_{INCONGRUENT}, CONTROL) as fixed effect. A backward stepwise procedure was used to fit the randomcoefficient regression model formulae (Hocking, 1976, Draper and Smith, 2014). Effect sizes were calculated in terms of proportion of variance explained by the linear mixed effects model, according to the Ω_0^2 method recommended in Xu (2003). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. The statistical significance threshold was set for a type 1 error rate of 5%. For post-hoc investigations, we used contrast tests (i.e., least square means difference) and applied Holm's sequential corrections to control the false discovery rate (Holm, 1979).

RESULTS

IV)Analysis of the breath-holding performance

Statistical interactions were removed during the backward stepwise procedure (i.e., all p > 0.05). The backward stepwise procedure eventually revealed that breath-holding performance was affected by the main effects of the EXPERIMENTAL CONDITION, TRIAL, HR_{NORM}, SDNN_{NORM} and SO₂ ($\Omega_0^2 = 0.29$). Breath-holding performance was affected by the main effect of EXPERIMENTAL CONDITION ($\chi^2(2) = 7.25$, p = 0.02). Post-hoc analyses revealed that the breath-holding performance during MI_{INCONGRUENT} outperformed that during both MI_{CONGRUENT}

(+5.58 ± 2.42, p = 0.05) and CONTROL (+5.78 ± 2.53, p = 0.05) (Figure 2). There was no difference between $MI_{CONGRUENT}$ and CONTROL (p > 0.05).



Figure 2. Effects influencing breath-holding performance. * Significant difference from all other experimental conditions (p < 0.05).

The linear mixed effects analysis also revealed that TRIAL had a positive predictive relationship on breath-holding performance (fitted estimate: +4.46 s ± 1.26; $\chi^2(1) = 12.54$, p < 0.001), HR_{NORM} (fitted estimate: +0.31 s ± 0.11; $\chi^2(1) = 7.56$, p < 0.01), SDNN_{NORM} (fitted estimate: -0.16 s ± 0.05; $\chi^2(1) = 8.58$, p < 0.01) and SO₂ (fitted estimate: -1.26 s ± 0.55; $\chi^2(1) = 5.28$, p < 0.01). breath-holding performance was not predicted by RMSSD_{NORM} (p > 0.05) (Figure 2).

V) Analysis of the psychometric data

Conformity Chi-squared test on the proportions of experimental condition perceived as the best breath-holding performance at the group level (i.e., against proportions corresponding to the chance level) revealed that CONTROL was the most frequently perceived as eliciting the best breath-holding performance (55 %), followed by MI_{INCONGRUENT} (38 %) and MI_{CONGRUENT} (5 %) ($\chi^2(2) = 7.18$, p < 0.02).

The backward stepwise linear mixed effects analysis revealed no effect of EXPERIMENTAL CONDITION on participants' commitment to engage in a maximal breath-holding performance (p > 0.05). The overall self-reports of perceived commitment was 8.40 ± 0.20 on the 10-points Likert scale.





The statistical interaction between EXPERIMENTAL CONDITION and TRIAL was removed during the backward stepwise procedure (p < 0.05). The linear mixed effects analysis revealed that EXPERIMENTAL CONDITION and TRIAL both affected the MI vividness ($\Omega_0^2 = 0.13$). MI vividness was affected by the EXPERIMENTAL CONDITION ($\chi^2(1) = 3.97$, p = 0.04). Self-reports of

perceived MI vividness were higher during $MI_{CONGRUENT}$ that during $MI_{INCONGRUENT}$ (+0.48 ± 0.24, p = 0.04). TRIAL positively predicted the self-reports of perceived MI vividness (+0.48 ± 0.15, p < 0.001) (Figure 3).

DISCUSSION

The purpose of the present study was to investigate the efficacy of congruent and incongruent MI practice on breath-holding performance. We implemented a maximal breath-holding paradigm where the sparing energy expenditure through reduced physiological arousal was crucial to perform (Klocke and Rahn, 1959, Ferrigno et al., 1986, Overgaard et al., 2006). Notably, motivation also represents one of the most crucial psychological factor involved in maximal breath-holding performance (Parkes, 2006). Throughout conditions, participants reported identical levels of comittment to achieve a maximal breath-holding performance. Yet, we found that Mlincongruent, i.e., where participants mentally recreated the sensations of breathing, but not Ml_{CONGRUENT}, where participants mentally rehearsed the sensations of holding breath and remaining motionless, improved the duration of breath-holding.

According to the early conceptual framework by Paivio (1985), MI can positively affect performance through its effects on cognitive motor processes (i.e., "*Cognitive*" function of MI). According to this framework, MI can also influence motivational processes involved in the generation of performance (i.e., *"Motivational*" function of MI). Paivio (1985)'s conceptual framework was updated at the scope of recent applications of MI practice in sport sciences and rehabilitation where the complementarities between "*Cognitive*" and *"Motivational*" functions of MI are necessary to implement effective training interventions (Guillot and Collet, 2008). Fear and anxiety negatively affect breathholding performance (Eke and McNally, 1996, Roth et al., 1998, Eifert et al., 1999, Brandt et al., 2012). Barwood et al. (2006) reported that 2 weeks of psychological intervention including MI practice, goal-settings, and coping strategies (i.e., selftalk and relaxation) significantly increased breath-holding durations in cold water immersion, without altering breath-holding performance in normal, nonthreatening air environment. Albeit performed decoupled from breath-holding, these findings demonstrate that MI participated to decrease threat perception linked with breath-holding in a hostile condition (i.e., cold water), hence contributing to delay the breakpoint of breath-holding. Accordingly, a first interpretation to the benefits of MI_{INCONGRUENT} is the generation through the *Motivational* function of MI of a more sustainable mental state during the breathholding performance, e.g., greater appraisal of threat perception associated with breath-holding.

A second interpretation relates to the well-established capacity of affecting through MI practice the activity of the peripheral autonomic nervous system effectors. MI involves central processing of motor command signals targeting the autonomic effectors, which are incompletely inhibited up to reproduce autonomic nervous system response patterns comparable to those recorded during the physical practice (Collet and Guillot, 2009, Collet et al., 2011, Collet et al., 2013). Further, it was hypothesized that the incomplete inhibition of autonomic motor command signals may feedback information to the central nervous system, hence affecting physiological arousal (for a more exhaustive discussion, see Collet and Guillot, 2009). Past studies underlined the possibility of eliciting, during MI, ventilatory responses corollary of the actual intensity of the mentally rehearsed exercise (Decety et al., 1993, Fusi et al., 2005). This involves, at a

neurophysiological level, the activation of limbic structures controlling ventilation during MI. Upregulation of the activation of the cerebral respiratory centers determine the breakpoint of breath-holding (Parkes, 2006), i.e., the neurons in the brainstem respiratory center control the breath reflex by influence of an feedforward loop over phrenic motorneurones, responsible for diaphragm contraction (Feldman, 1986). When motor command is no longer inhibited, muscular contraction will occurs. To maintain itself on voluntary breath-holding after this point requires a voluntary control over the chest respiratory muscles (Parkes, 2006) MIINCONGRUENT, but not MICONGRUENT, might participate to the perception of a central respiratory rhythm in spite of the current breath-holding state. Indeed, hypoxia, hypercapnia, decreasing lung volume and increased metabolic rate increases central respiratory rhythm (see Parkes, 2006). Hypoxia and hypercapnia during breath-holding would thus have reduced leverage over the psychological and emotional responses influencing the "will to survive" (see Kreider, 1967, Tipton, 1992), i.e., increase the neural excitability within pathways targeting the cerebral respiratory centers mediating the breath reflex. However, this remain only a hypothesis, since the factors affecting central respiratory rhythm remain poorly understood. Furthermore, it is impossible to perform directly analyses of the phrenic nerve to better understand central respiratory rhythm in humans. Most theories rely to date on animal experimentations (e.g. Noble et al., 1971, Bartoli et al., 1973, Feldman, 1986, Balkowiec and Katz, 1998).

Participant's maximal breath-holding performance was predicted by the SDNN, HR and SO₂. SDNN reflects all the cyclic components responsible for variability in the period of recording, thus represents an index of the global activity of the autonomic nervous system, a workload placed upon the autonomic nervous

system to balance homeostasis, and its decrease can be interpreted as a diminishment in body arousal (Malik et al., 1996). A decrease in HR variability has been linked with reduced physiological arousal during maximal breathholding in the literature (Trzebski and Śmietanowski, 1996, Javorka et al., 2001, Javorka et al., 2002). The decrease in HR variability was particularly prevalent in non-breath-holding athletes (Bain et al., 2018). A state of hypoxia is elicited during breath-holding. This hypoxia state can be prolonged in spite of O_2 deprival, through the involvement of anaerobic pathways. While an increase in HR is recorded during the early stages of breath-holding, a subsequent decrease occurs as the autonomic nervous system regulates physiological arousal to spare energy expenditure (Javorka et al., 2001). This might appear contradictory with the positive relationship measured between the HR and maximal breath-hold performance. Interestingly, bradycardia effects in response to breath-holding are more pronounced during face immersion compared with dry breath-holding without face immersion (Moore et al., 1972). Due to the absence of face immersion in the present paradigm, HR may thus primarily represent an index of efficient supply of available energy substrates within the body rather than an index of energy sparing through reduced physiological arousal response to breath-holding. This postulate is congruent with the fact that HR was calculated by averaging HR recordings at the level of the whole breath-holding trial. A more pronounced HR increase during the early stages of breath-holding possibly yielded an increase in O₂ supply to the tissues, hence facilitating the forthcoming breath-hold performance.

Participants reported higher levels of vividness during MI_{CONGRUENT}. This is in keeping with the predictions of existing MI frameworks, which underlined that

the MI content should reproduce the features of actual task (Holmes and Collins, 2001, Guillot et al., 2005, Guillot and Collet, 2008). Martin et al. (1999) emphasized that higher levels of MI ability contributed to greater performane improvement. Here, we demonstrated for the first time that an incongruent form of MI practice with regards to the actual task demands, yielding to lower levels of perceived vividness, was nonetheless the most relevant approach to increase the behavioral performance. Participants percieved that their breath-holding performance during MI_{INCONGRUENT} outperformed that during MI_{CONGRUENT}. It is thus suggested that the beneficial effects of MI_{INCONGRUENT}, operating either through a *"Motivational"* function of MI and/or by the effects of MI on autonomic nervous system response patterns, triggered participant's awareness of increased the cognitive workload and elicited discomfort compared to CONTROL, since the participants perceived an increased breath-holding performance during the latter experimental condition.

CONCLUSION

To the best of our knowledge, the present study is the first to demonstrate a beneficial effect of an incongruent form of MI practice with regards to the actual task demands in terms of voluntary motor control. Yet, the mechanisms underlying the efficacy of incongruent MI on breath-holding performance remain uncertain and require further experimental investigations. Future studies should consider comparing breath-holding athletes, which have a better control of the breathing reflex, with non-athletes. Also, measures of sympathetic nervous

system, such as electrodermal activity could provide interesting data about the arousal modulation.

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I) PSYCHOPHYSIOLOGICAL CORRELATES OF ACTION

Movements cannot be repeated unlimitedly as repeated physical practice yields to the decline of performance. Performance decreases as a function of time and an increased perception of effort representing the well-accepted definition of physical fatigue. Physical fatigue represents a unitary process affecting all types of motor behaviors (Pageaux, 2014, Bigliassi, 2015). Several theoretical models encompassing a wide range of psychophysiological factors have been advanced to account for its impact on performance.

A) PHYSICAL FATIGUE

Homeostatic imbalance elicited by fatigue represents a unitary process triggering adaptive psychophysiological responses. This corresponds to the central process involved in performance gains. Hence, physical fatigue is expectedly the focus of most training interventions. The concept of fatigue has been strongly debated in the literature for the last 15 years, and debates regarding the nature of fatigue and its underlying mechanisms are still ongoing. Before exposing the most recent models to explain fatigue, a travel through the history of this discussion is necessary.

An early definition of fatigue lied on a representative inability to sustain an expected or required force (Edwards, 1981). This definition was however considered incomplete since it did not acknowledge for the transitional state of

fatigue. Researchers therefore pointed that fatigue is a process instead of a unique moment, with the body continually performing adjustments to sustain the task (See figure 15). Bigland-Ritchie et al. (1983) investigated the concept of fatigue by measuring force and electromyography during maximal voluntary contraction (MVC) of the adductor pollicis sustained during 60 seconds. They postulated that the resulting fatigue, attested by a progressive decrease in force output and contraction speed, originated from the reduction of neural output to targeted muscles. Such definition, however, did not account for the proprioceptive alterations resulting from such sustained contraction (McComas et al., 1995). In a seminal review, Enoka and Stuart (1992) later argued that fatigue might be considered as an acute performance impairment. They proposed that effort perception would directly impair physical performance and the capacity to produce the required force. Their conclusions emphasized that psychological factors might also play a key role in the processes of fatigue.

Importantly, fatigue should be distinguished from exertion (Bigland-Ritchie and Woods, 1984). Exertion is the momentary inability to achieve a demanded force level, but does not necessarily involves an impairment. For instance, in order to lift a certain object with a given weight, the neuromuscular system will contract an appropriate pool of motor units. The heavier the weight, the more motor units will be contracted to match the gravity of the object. To keep holding the object, more motor units as a more frequent recruitment will be required, once it takes time for muscular energy to recover. In this case, the increase in motor unit's recruitment as a function of time represents the onset of Fatigue, while the total incapacity of lifting the object at some point of the performance corresponds to the Exertion (Figure 15).

For years, scientists sought to delineate the processes of fatigue and exertion (for a short and descriptive review, see Barry and Enoka, 2007). The discussion initially revolved around two main hypotheses: *i) the peripheral origin hypothesis, i.e.,* we stop due to a fall in the cardiovascular system to supply O₂ to the targeted muscles, leading to an incapacity of the neuromuscular junction to sustain the required levels of force; *ii) the central origin hypothesis,* i.e., fatigue originates from a reduction of central output to the muscles, hence hampering force production (Taylor et al., 2000, Gibson and Noakes, 2004). Yet, due to the strong connections between central and peripheral mechanisms accounting for both fatigue and exertion, these should not be considered separately but rather as distinct components of a unitary process (Nybo and Secher, 2004).



Time / Repetitions / Trials

Figure 15. Fatigue and Exertion visual illustration. Performance decreases along time (Fatigue) and until it can no longer be sustained to keep the task (Exertion). Fatigue process is the space between the dotted and dashed lines. The fall in performance (black line) after the exertion point represents a continuous attempt to re-achieve the minimum demanded performance.

B) FATIGUE MODELS

(1) CATASTROPHIC MODEL

Early studies dealing with fatigue focused on the muscular system. Understanding of the process underlying fatigue was thus somewhat limited to a peripherally, metabolite-induced failure of the muscle to elicit contractions. Hence, fatigue was primarily studied through physiological variables attesting energy expenditure during muscle contractions, e.g., metabolic output, cardiovascular activity, heat production (Hill, 1924, Hill et al., 1924). These variables were considered crucial in the muscle fatigue process. The main idea was that anaerobiosis resulting from the limited capacity of the circulatory system to provide oxygen to muscles caused exertion. One of the main scientific rationales in support of this theory was that the fatigue process leading to exertion was corollary of an increase in lactate concentration (Barr and Himwich, 1923, Barr et al., 1923, Hartree and Hill, 1923, Long, 1924). Specifically, Hill et al. (1924) emphasized that the increase in lactate concentration was responsible for inhibiting muscle contractions. According to the catastrophic model of fatigue, i.e., the catastrophic theory (Edwards, 1983), muscles face, at some point of exercise, a biochemistry collapse determining the exhaustion point. Analyses of cardiovascular system provided a new view for the model. Noakes (2000) stated that the first muscle to suffer a biochemistry collapse during exercise would be the heart itself, since it would face an increased workload to sustain both blood supply to the skeletal muscles and cardiac muscle tissues. Comparable limitations to the catastrophic model of fatigue were initially postulated by Hill et al. (1924).

However, according to Noakes (2000), these were largely ignored (for a short critic on the catastrophic model, see Noakes and Gibson, 2004).

(2) CENTRAL GOVERNOR MODEL

When the muscle demands in energy output increases, there is a corollary demand in terms of oxygen and substrates mediating ATP resynthesizes and necessity to remove metabolic products. A heart rate increase is required to face the resulting increase in blood supply. In a seminal work, Green et al. (1989) measured lactate concentration after a progressive cycle exercise to exhaustion in various simulated altitudes, including an altitude of 8848 meters (i.e., equivalent to the Mont Everest summit). One might assume that a greater demand placed on the anaerobic system due to the shortage of oxygen would elicit a greater lactate production. Considering the hampering effects of altitude on heart rate (Sutton et al., 1988), it was hypothesized that the anaerobic contribution to energy output should be particularly important. However, at the highest simulated altitudes (282 Torr or 8848 meters), lactate concentrations consecutive to exercise were lower compared to lower simulated altitudes conditions, including sea level. This finding demonstrated that the anaerobic system is not fully functional in spite of a comparable muscle glycogen depletion elicited by the maximal exercise. Noakes (2000) highlighted in discussion about the physiological models of fatigue and exertion:

"(...) This unexpected finding can be explained only if there is a 'governor', probably in the central nervous system, whose function is likely to prevent the development of myocardial ischemia". (Noakes, 2000 p. 128).

Later, Kayser et al. (1994) reported, during exhaustive dynamic exercise for the forearm and lower limbs, decreased integrated EMG along with increased altitude. Yet, EMG suddenly increased when oxygen supply was administrated. This data corroborated the assumption that the central nervous system was somehow able to recognize intrinsic and extrinsic information and might limit the deleterious impact of exercise on homeostasis by downregulating energy output. These findings support the hypothesis of a central governor model of physical fatigue. Figure 16 is a visual representation of the model with the possibility of a central governor.



Figure 16. A limited oxygen supply to the central governor would inhibit commands toward exercising skeletal muscle. Figure extracted from Noakes (2000) with authorization from Elsevier© (lincense number 4261450458442)

Factors focusing the different physiological systems participating to the overall energy output during exercise were proposed within the framework of the Central Governor. Noakes (2000) emphasized the following factos:

 Energy supply: intra-muscular capacity to adapt along with exercise and training, enhancing ATP storage and optimizing its use.

- II) Energy depletion: Carboydrate, main source of intramuscular. Energy, would benefit from enhanced capacity of using body fat as source of energy, delaying onset of carbohydrate depletion.
- III) Muscle recruitment and muscle power : decreased muscle contractile capacity and/or neural efficiency would directly cause fatigue
- IV) Biomechanical: an increased movement efficiency would produce less heat production. Moreover, body composition and elasticity would directly influence the fatigue curve

Altogether, these factors would be constantly controlled by the central governor and could be responsible for increasing fatigue until exhaustion point. Overall, the "central governor" seems to play an important role in the fatigue processes. Central governor models nonetheless fail to fully account for fatigue processes in that they consider a very limited number of physiological systems (i.e., the cardiovascular and muscular systems, see Noakes, 2000, Noakes, 2004, Rauch et al., 2005). To summarize, the cardiovascular system is not the only one mediating fatigue processes. Many physiological systems should be accounted for, and multiple cross-talk would be necessary to evaluate to which extent a given physiological system adjusts according to the current state of others. Nonetheless, it is well-admitted that the central nervous system (CNS) constantly controls and integrates information from each physiological system, even during the process of fatigue. There is also evidence that the CNS directly influences fatigue process and exertion (Noakes, 2006, Pageaux, 2014, Bigliassi, 2015, Bigliassi et al., 2017). In the next topics, we will discuss the main pathways by which CNS can act over somatic effectors to infer or delay fatigue.
(i) CENTRAL NERVOUS SYSTEM AND FATIGUE

The theoretical physiological models of fatigue are congruent with an evolutionary viewpoint. The capacity of the body to use energy substrates until energy systems collapse would provide a great advantage in hunting and running away from threats. Nonetheless, the body is primarily confronted with the constant challenge of maintaining homeostasis. Engaging physiological systems until failure to match increases in energy demands thus makes little sense from an evolutionary viewpoint. Maintaining a control upon physiological systems to regulate energy expenditure below a certain threshold is therefore essential. The hypothesis of a central control of fatigue would imply a hierarchy between physiological systems. Theoretically, one physiological system could cause the collapse of less important systems to keep life-essential system working (e.g., skeletal muscle involved on the task).

In the late 90's, a distinct fatigue framework was proposed, namely the Central Fatigue Model (Bigland-Ritchie et al., 1986, Gandevia, 1992, Gandevia et al., 1996, Gandevia, 1998, Taylor et al., 2000, Gandevia, 2001). According to this framework, the CNS would constantly integrate the current state of the physiological systems. Before one of them achieves a critical life-treating point, the CNS would downregulate the system to stop/reduce its activity. During exercise, for instance, the energy demand faced by the cardiovascular system would at some point cause the CNS to stop driving outputs to the muscles to sustain the exercise (Gandevia et al., 1996, Taylor et al., 2006). It has been postulated that the CNS would no longer provide the amount of efferent signals required to keep the required activity. The CNS activity would thus be the main

limiting factor affecting performance during exercise (Gandevia, 2001, Meeusen et al., 2006). Such control from CNS might be modulated by peripheral and central levels (Gandevia, 1992, Windhorst and Boorman, 1995, Taylor et al., 2000, Gandevia, 2001, Ross et al., 2007). For instance, during an isometric contraction, the electric stimulation over the alpha-motoneuron pool yields an increase in force output, hence attesting that muscles cannot be voluntarily contracted to their maximal (McKenzie and Gandevia, 1991, Allen et al., 1995, Herbert and Gandevia, 1996). Furthermore, when he force level required during voluntary exercise can no longer be sustained, an electrical stimulation is able to restore the demanded force output (Löscher et al., 1996). Such progressive failure in motor command drive to the muscles still capable of producing the contraction levels required by the exercise was interpreted as a sign of central fatigue, and imputed to a preventive inhibitory mechanism (for reviews, see Gandevia et al., 1995, Gandevia, 1998). In summary, the central fatigue model support that the brain works to preserve energy, always making adjustments through central motor drive to save energy and avoid physiological systems to collapse (see Figure 17).



Figure 17. Visual illustration of the supraspinal reflex inhibition during exercise. Repeated muscle contractions alter the homeostasis and the resulting afferent signals to the brain participate to regulate efferent motor commands (red line). (This figure was adapted from the work of Amann and Dempsey, 2009).

(a) NEURONAL FEEDBACK AND FATIGUE PERCEPTION

To drive the somatic effectors during exercise or hamper their activity, the CNS constantly integrates information regarding the internal milieu and external environment (e.g., temperature, metabolite accumulation, etc). The interaction between the CNS and the muscles is a forward and backward relationship. The CNS controls the muscles and the muscles generate proprioceptive feedbacks through afferent pathways.

We know that commands coming from spinal or supraspinal structures are responsible for muscle contraction. Corollary to muscle contraction, a series of modulations occurs in the body. In order to address feedback to the CNS regarding those modulations, the periphery is full with afferent innervations (e.g., spindles, baroreceptors, mechanoreceptors and chemoreceptors), capable of transmitting a wide range of body state information to the CNS, such as temperature (Gandevia, 1998, Amann and Dempsey, 2008), muscle tension (Garland and Kaufman, 1995, Gandevia, 2001), pain (Adreani et al., 1997) and metabolites resulting from catabolic reactions accumulation (Adreani et al., 1997).

Several experiments investigated the influence of internal and external factors in CNS motor commands. For example, if the CNS aims to protect the heart or other vital organ sensitive to O₂ concentration, exercise under hypoxic

conditions should lead to a reduced cardiovascular activity. Literature findings support this assumption. Kayser et al. (1994) reported that integrated EMG increased with time during a sustained contraction at sea level condition. However, in a high altitude environment (i.e., 5050 m), integrated EMG remained the same until exhaustion (for reviews, see Noakes et al., 2001, Noakes, 2006). Similarly to O₂ concentration, environment temperature modulates central command to exercised muscles, as reported by Tucker et al. (2004) where high temperature (35 °C) impaired muscle recruitment during 20 km of cycling timetrial. Impaired muscle activity was attested by an early reduction in integrated EMG during high temperature compared with the same task in low temperature (15 °C). Authors argued that this was a anticipatory response to adjust thermal homeostasis, since it occurred before any abnormal increase in rectal temperature, heart rate of perceived effort (see also Crewe et al., 2008). Briefly, there is a strong scientific rationale supporting that fatigue involves changes in efferent commands addressed to the muscles by the CNS. This is referred in the scientific literature as central fatigue. Thus, fatigue cannot be considered as a strictly peripheral entity, but the product of regulatory mechanisms (Gibson et al., 2001).

The Central Governor Model of fatigue postulates that exercise is regulated from its onset, exertion being the point of self-awareness of a critical state. Therefore, fatigue must be apprehended as the result of complex interactions between the physiological systems, and not as an isolated failure of a given system to match the demands during the process of energy expenditure.

Later, researchers argued that the Central Governor model was somehow incomplete due to its focus on physiological systems, without considering

psychological components (Gibson et al., 2001). Baden et al. (2005) analyzed VO2, HR, RPE and affection (i.e., how pleasurable it is to perform the task) during a treadmill task. Participants were asked to run at a certain speed in different conditions. In a first condition, they knew they would run during 20 minutes, while in a second they were told they would run for 10 minutes, but at the end they were asked to run for 10 additional minutes. Higher values of RPE and lower levels of affection were reported in minute 11, when participants were asked to run 10 additional minutes compared with when they knew they would run for 20 minutes. Authors concluded that RPE is not purely a measure of physical exertion, as treadmill speed was constant. The changes in affection scores at similar time that RPE supported the hypothesis that RPE have psychological components, such as affection and motivation to complete the task (see also Meeusen et al., 2006, Brink-Elfegoun et al., 2007, Marcora et al., 2008, Marcora, 2009).

Along with these findings, additional factors were included in the central governor model of fatigue. Supported by the findings of Baden et al. (2005) and Albertus et al. (2005), Task Knowledge and Pacing were considered important factors in the fatigue process. Participants' knowledge of the time/distance remaining up to completion of the task influenced pacing and RPE development. Not informing participants would trigger the CNS to limit motor commands in order to prevent higher energy expenditure (Okada et al., 2015). Accordingly, the Functional Systems limit, i.e., the mechanical or physiological limit of body system, was added to the model. To exemplify, the amount of stocked muscular glycogen before starting an endurance task would directly interfere in muscle energy availability during the task. In attempt to maintain the muscular system

working, the CNS would regulate motor commands to sustain the task (Ulmer, 1996, Hampson et al., 2001, Albertus et al., 2005). Finally, the evolution of RPE was added to the model. By altering work rate, RPE would be altered, following a positive correlation. Tucker (2009) proposed a synthesis of the Central Governor model in a very detailed review (Figure 18), showing RPE as a main factor.



Figure 18. The Central Governor Model for fatigue and exercise (Tucker, 2009). Black shading indicates afferent inputs to the brain and gray reflects efferent signals. CNS would constantly process information from external and internal environments, as well as motivation, aiming to finish the task with the minimal perception of exertion and energy expenditure. Figure copied with authorization.

(3) PSYCHOBIOLOGICAL MODEL OF FATIGUE

Does our body always look for efficient performance while concomitantly preserving of the homeostatic balance and keeping low levels of effort

perception? Surprisingly, recent findings emphasized that afferent signals from fatigued muscles may not affect endurance performance (Marcora et al., 2008). Specifically, blocking afferent feedback from III-IV receptors sensitive to metabolites produced during fatigue did not improve performance in a 5-km cycling time trial (Amann et al., 2008, for contradictory results, see Amann et al., 2009). Rotstein et al. (2005) examined the relationship between energetically optimal transition speed, i.e., speed where running is energetically more advantageous than walking, and preferred transitional speed, i.e., speed at which participants (including runners and non-runners) prefer to run instead of walking. Interestingly, they reported that walking in preferred transitional speed yielded greater rates of perceived exertion (RPE) than running. This result challenges the postulates of Amann and Dempsey (2009) and Tucker (2009). Indeed, since the energy required for running is higher than walking a higher RPE should be expected. Overall, this result contradicts important predictions made by the Central Governor models of fatigue, which predicts that RPE should increase along with energy expenditure.

As number of researches investigating the influence of afferent information over CNS and RPE increased, psychobiological models of fatigue emerged (Marcora et al., 2008). According to Pageaux (2014) the psychobiological model can be defined as:

" (...) An effort-based decision-making model (Marcora, 2010) based on motivational intensity theory (Brehm and Self, 1989), and postulates that conscious regulation of pace is determined primarily by five different cognitive/motivational factors;

- *i)* Perception of effort
- *ii)* Potential motivation
- *iii)* Knowledge of the distance/time to cover
- *iv)* Knowledge of the distance/time remaining
- v) Previous experience/memory of perception of effort during exercise of varying intensity and duration."

Psychobiological models of fatigue postulate that afferent feedback from fatigued effectors also affect psychological factors, and conceptualize exercise as a primarily goal-directed behavior. For instance, in Psychobiological Models, the constructs III, IV and V, i.e., knowledge of the distance/time to cover, knowledge of the distance/time remaining and previous experience with RPE during exercise, would not be affected by somatosensory feedback (Marcora, 2010, Pageaux, 2014). However, these factors are presented as explanation for the "end-spurt phenomena", i.e. where participants are no longer able to sustain a required muscle performance but, when strongly encouraged by researchers, can restore an equivalent or higher performance level by a short period of time (Marcora, 2014). Additionally, psychobiological model factor II, i.e., potential motivation, refers to:

" (...) Maximum effort an individual is willing to exert to satisfy a motive, and could be easily influenced by external factors (e.g. higher motivation during an event with competitors than during laboratory testing" (Pageaux, 2014, p. 1).

A central aspect of the psychobiological model is the perception of effort, i.e., the conscious sensation of how hard, heavy and strenuous a physical task is (Marcora, 2010). Effort perception is typically measured by RPE and represents the perceived difficulty while performing a task. Effort perception is known to influence the pace. For instance, athletes modulate their pace in endurance events as anticipatory behavior to increase their chances to finish the race (Joseph et al., 2008). In other words, athletes adjust their pace to manage their resources during exercise (De Koning et al., 2011). Both external (e.g., temperature, adversity, dioxygen concentration) and internal (e.g., motivation, affection, task-knowledge) factors would directly influence RPE. This might account for the recorded alteration in competitor's pace (Pageaux, 2014). An important question is whether peripheral somatosensory feedback are likely to influence the RPE. Studies focusing on the cardiovascular and neuromuscular systems addressed this central postulate of psychobiological models of fatigue. Braith et al. (1992) compared the final RPE after moderate and high intensity exercise in 11 heart transplanted participants, compared to a matched control group. Heart transplanted participants represent a unique model, since they do not have afferent heart innervations. The heart in these patients cannot convey afferent signals to the CNS. At the end of exercise, no difference was found for RPE between heart transplanted and control group, hence attesting that heart afferent signals may not play a critical role in RPE. Similarly, Fernandes et al. (1990), using epidural anesthesia at L-3 and L-4, showed that during a cycling exercise, blood pressure was altered, compared with the control group. However, no difference was found for ventilatory, heart rate or RPE for groups with and without anesthesia (Innes et al., 1992, Friedman et al., 1993, Kjær et al., 1999).

Overall, environmental, psychological and, of course, physical factors related to exercise are likely to influence RPE. However, peripheral changes are only partially related with RPE modulation (Pollak et al., 2014). Research failed to disclose one factor systematically causing RPE changes corollary of exercise. Since the CNS can integrate the effort even in the absence of afferent signals, it has been suggested that the brain might be informed of exercise parameters through parallel signals, i.e., corollary discharges (Morree et al., 2012). Corollary discharges represent duplicates of efferent motor commands built by the CNS. Every time the brain processes a motor command in motor networks, motor command parameters would be sent to regions linked with fatigue and decision making, e.g., the thalamus, insular cortex and anterior cingulate cortex (see Marcora, 2009). Dde Morree et al. (2014) analyzed the effect of caffeine consumption on the motor-related cortical potentials (MRCP). They were specifically interested in the relationship between MRCP and RPE. Caffeine decreased MRCP. After an exhaustive session of isometric knee extensions, caffeine reduced effort perception through reduced in MRCP in premotor and motor areas. This finding supports that central processing in premotor networks is directly linked with RPE, and is congruent with the hypothesis of corollary discharges.

Additional support for the theory of corollary discharges comes from studies under hypnotic states (Williamson et al., 2002). Hypnosis was used to focus the mind on environmental conditions and scenarios which did not correspond to the reality. For instance, during cycle ergometer exercises, hypnosis can be used to induce the perception of downhill or uphill, which require different levels of effort (Williamson et al., 2001). During hypnosis, only the participant's perception was found to be affected. The required force to sustain the exercise remains similar. Williamson et al. (2001) implemented an hypnosis

intervention during a cycling exercise, i.e., hypnosis was used to suggest a downhill and uphill condition for the last 5 min on a 15 min constant load exercise. Downhill suggestion through hypnosis yielded decreased RPE and blood flow in the left insular cortex and anterior cingulate cortex, as attested by coregistered single-positron-emission computed tomography and magnetic resonance measures. No changes in blood pressure or heart rate were recorded during the downhill hypnotic suggestion. During uphill suggestion, an increase in RPE, heart rate and blood pressure, right insular activation and right thalamus activations were recorded. Thus, concluding that increase of the RPE can activate both insular and thalamic regions, and elevate cardiovascular responses even when power output is not altered.

Another important evidence of corollary discharges control over RPE is the use of distractive techniques to modulate both performance and fatigue perception (see Bigliassi, 2015 for a short review). According to the theory of parallel processing (Rejeski, 1985), a way to modulate RPE is to add distractors external to exercise such as auditory or visual stimuli (Loizou and Karageorghis, 2015) to compete with brain corollary discharges. Parallel attention would then be responsible for increasing motivation and reduce fatigue-related symptoms, such as RPE (Bigliassi et al., 2014, Jones et al., 2014). Recently, Bigliassi et al. (2017) used an ambulatory EEG device to record brain activity during low-to-moderate exercise in a cycle ergometer. Participants were administrated a distractive intervention under the form of either music or listening to an audiobook during exercise. Authors reported that music reduced RPE by dissociating attentional focus from exercise. The audiobook did result in decreased RPE compared to a control condition without attention distraction. This probably

originated from a lack of components in audiobook which are central in music, i.e., melody and harmony. Notably, music also participated to reduce EEG alpha waves amplitude. This was followed by an increase of vastus lateralis activation, as attested by EMG. Overall, it was hypothesized that music facilitated muscle activation during exercise through relocation of the attentional focus.

A visual representation of the psychobiological model is presented in Figure 19:

"Regardless of the source of internal processes (corollary discharges or afferent feedback), environmental influences compete for attention throughout the exercise cycle. Therefore, selective attention between external and internal sensory cues is in charge of initiating cascade reactions to psychophysical responses." (Bigliassi, 2015, p. 02)



Figure 19. Psychobiological model of endurance performance (Bigliassi, 2015). Plus signs represent an incremental effect on the resulting response. Conversely, minus signs represent the opposite, a diminishing effect on following response.

The psychobiological model is currently the most acceptable account of the fatigue process (Pageaux, 2014, Bigliassi, 2015, McMorris et al., 2018). The model integrates both physiological and cognitive accounts as triggering factors to the process of physical fatigue. For instance, the increased metabolites production would not alone trigger the process, but it is know that a drop in muscle pH caused by the presence of free H+ impairs muscle functionality (Fuchs et al., 1970). In conjunction to others limiting factors underlined in the scientific literature (e.g., environmental constraints, motivation, etc.), the CNS might adjust the neural drive to the somatic effectors while concomitantly feeding itself with parallel information, hence building the RPE (Bigliassi, 2015, McMorris et al., 2018).

C) <u>PSYCHOPHYSIOLOGICAL MEASURES OF PHYSICAL FATIGUE</u>

(1) CARDIORESPIRATORY MEASURES

Human cells maintain vital functions through energy consumption. In order to achieve the requested energy, unique enzymes convert adenosine triphosphate (ATP) in adenosine di-phosphate (ADP). During ATP-ADP conversion, both energy in the form of heat and a mono-phosphate are released. Muscular cells have three principal metabolic pathways to dispose from ATP, namely *i*) Anaerobic Alactic – immediate demand (~0 to 10 sec) and low energy *ii*) Anaerobic Lactic – fast demand (~10 to 2 min) low to medium energy production and *iii*) Aerobic – Long term demand (+2 min) and high energy production. All three ways are constantly functional, the only difference is the percentage of contribution of each one during different exercises (McArdle et al., 2010). The aerobic system, responsible for high and long-term demands, uses oxygen at mitochondrial level to generate a large amount of ATP, followed by CO₂ production.

(i) VENTILATORY AND ANAEROBIC THRESHOLD

The relationship between oxygen consumption and CO₂ release via cardiopulmonary system can be used to determine the ventilatory threshold. The ventilatory threshold is marked by a first sudden increase in the O₂ consumption without achieving anaerobic states (Figure 20 A). Below the ventilatory threshold, there is a prevalence of the aerobic system to energy expenditure with low or without lactate accumulation in the muscles. The anaerobic threshold is marked

by the sudden increase in CO₂ production and may be more difficult to determine visually (Figure 20 B). Exercise above the anaerobic threshold is marked by a high demand from anaerobic system, and the production of lactate and H⁺ overcomes the removal capacity (Mader and Heck, 1986). Measuring the ventilatory and anaerobic threshold is considered, as well as heart rate evaluation, as the most trustable method for endurance performance evaluation (Boulay et al., 1997). Theoretically, one should be able to sustain exercise intensities below the anaerobic threshold for an unlimited duration if others factors such as the depletion of energy substrates and hydration were ignored. The maximal capacity to uptake and use O₂ for ATP production is called VO₂max.



Figure 20. Visual representation of O_2 (Blue line) and CO_2 (Red line) during an ergocycle incremental test (Green line). A. Ventilatory equivalent (V'E) for O_2 and CO_2 . Ventilatory threshold (VT) is represented by a sudden deflection on O_2 consumption curve, due a greater percentage of the breathed O_2 being used for energy production. B. Volume of used O2 and CO2 expired. Increase on anaerobic metabolism and blood pH is countered by stimulation of ventilation to increase CO2 excretion. Thus, Anaerobic Threshold (AT) is represented by a sudden deflection on CO2 volume curve.

(ii) VO2max measure

In order to measure VO2max and establish exercise intensities corresponding to both ventilator and anaerobic thresholds, incremental exercises

completed until exhaustion are usually administered (e.g. Ahmaidi et al., 1993, Okushima et al., 2016, Machado et al., 2017). Starting from low intensities, O₂ consumption and CO₂ production are continuously recorded. Exercise intensities increase under the form of successive stages (duration of 2 to 3 min per stage), hence leaving enough time for the body to adjust its energy output to the exercise demands without dehydration or complete depletion of energy substrates.

The incremental test finishes with the exhaustion of the participant, attested at a behavioral level by the incapacity to continue the exercise for a given intensity. Self-motivation and/or rewards are important factors to guarantee participants' commitment to the maximal effort (as explained by the psychobiological model of fatigue). Both VO2 and heart rate are strongly correlated physiological variables. In particular, the slope from HR-VO2 curve represents an individual parameter of aerobic fitness. The capacity to achieve higher levels of VO2 (until VO2max) with lower HR represents a better cardiovascular effeciency (McArdle et al., 2010). Therefore, measuring heart rate during VO2max analyses is advisable (Achten and Jeukendrup, 2003).

However, classical incremental tests to determine the VO_{2max} tests have been criticized (Noakes, 2008). As incremental tests control both work load and pace, key components of anticipatory central control become externally cued (see Noakes, 2008). In the VO2max assessment methods used in the experiment of this doctoral dissertation, participants were instructed to sustain the exercise as long as possible. We used, for instance, a braked cycle ergometer which allowed participants to use their preferential pace. For each level of incremental

task (2 min per stage), a pre-determined power (90W + 30W per stage) was requested according the formula:

$$P = F.v$$

 $P = Power (Watts)$
 $F = Force (Newtons)$
 $v = Speed (m/s)$

Since the power is predetermined for each stage of the incremental test, i.e., adjusted by the brakes of the cycle ergometer, participants can chose their own pace to match the demand in terms of power output, partially solving the problem from classical incremental testes (Noakes, 2008). A high pace, i.e., high velocity in terms of pedal rotations per minute, participants face a reduce force level. Conversely, a low pace require a higher force level.

(iii) <u>HEART RATE</u>

210 years ago, i.e., before Rene Laennec invented the stethoscope, placing one's hear against someone's chest was the most common approach to evaluation the heart rate. But it was only in the beginning of the 20th century that the Dutch physiologist Willen Eithoven developed the first electrocardiograph. Heart activity involves three main phases: *i*) the P wave corresponds to the depolarization of the atria, *ii*) the QRS wave complex corresponds to the depolarization of the ventricles, and *iii*) the T wave repolarization of the ventricles (See figure 21). In the 1980s, the first wireless HRM was created, and over the

last 30 years, heart rate monitors (HTMs) developed fast up until becoming one of the most widely used measures in the domains of sport and exercise.



Figure 21. Visual representation from P, QRS and T waves from a full regular heartbeat.

Training programs practically consist in three main components: Frequency, duration and intensity. All those components are considered training impulse triggering adaptive response yielding performance improvements (Banister, 1991). Incorrect balance between training impulse and recovery periods lead to overtraining (Jeukendrup et al., 1992, Lehmann et al., 1992). Duration and frequency are relatively easy to control. However, controlling and monitoring training intensity, i.e., the energy expenditure per minute required during exercise, represents a methodological challenge. A limited number of methods can be used without requiring rigorous laboratory procedures (Jeukendrup and Diemen, 1998).

Heart rate and volume of oxygen consumption share a linear relationship (Åstrand, 2003). HR can thus be used to infer VO2, hence providing indirect information about energy consumption. HR can be easily measured during exercise by means of ambulatory heart rate monitors. The American College of Sports Medicine recommends its use for training cardiorespiratory, muscular fitness and stretching in healthy adults (Stand, 1990). There are nonetheless some limitations regarding the use of such heart rate monitors to quantify energy expenditure. While Conconi et al. (1982) recorded heart rate to estimate anaerobic threshold in 210 athletes, measures could not be replicated (see the review from Bodner and Rhodes, 2000). Specifically, an overestimation of the lactate threshold was reported (Kuipers et al., 1988, Leger and Tokmakidis, 1988, Tokmakidis and Léger, 1992). Nonetheless, the usefulness of heart rate as dependent variable quantifying exercise intensities makes it relevant for research purposes, particularly when combined with measures of lactate concentrations and VO₂ consumption.

(2) <u>SUBJECTIVE MEASURES</u>

(i) RATE OF PERCEIVED EXERTION (RPE)

The rate of perceived exertion (i.e., RPE) is a psychometric measure of effort perception. RPE is classically evaluated using self-reports, i.e., Likert-type ratings. The Borg scale is the most frequently used tool to assess RPE (Borg, 1982). RPE measures involve answering to the question "How exhaustive is/was the exercise?". Initially, the Borg scale involved 15 levels ranging from 6 "*No exertion*" to 20 "*maximal exertion*". Later, the Borg scale was adapted to a scale from 0 (i.e., "*rest*") to 10 (i.e., "*very, very intense*", Appendix 2). Borg Scale was also used as a psychometric tool to quantify fatigue processes (Marcora and Staiano, 2010, Kanthack et al., 2014, Bigliassi et al., 2015, Kanthack et al., 2016).

The Borg scale reports are indeed correlated to HR (Foster et al., 2001, Wallace et al., 2009), lactate production (Demello et al., 1987, Boutcher et al., 1989, Hetzler et al., 1991), muscle recruitment attested by EMG (Hasson et al., 1989, Guo et al., 2017) and VO₂ modulation (Jakicic et al., 1995, Ueda and Kurokawa, 1995). Thus, represents a good measure that combines both central and peripheral modulations during exercise.

I) EFFECT OF FATIGUE ON MOTOR IMAGERY

EXPERIMENTAL CONTRIBUTION #3 : Thiago FERREIRA DIAS KANTHACK,

Franck DI RIENZO, Yoann BLACHE, Aymeric GUILLOT. "Effector-specificity modulation of motor imagery ability elicited by local muscle fatigue". To be submitted.

The capacity to enhance performance through MI practice is directly linked with the imager capacity to create and sustain a good mental representation (Martin et al., 1999, Lebon et al., 2012a, Williams et al., 2012). A good measure of MI ability is the equivalence in duration between mental and actual task (Malouin et al., 2008). According to Louis et al. (2008), when MI is systematically performed in different duration, the subsequent task time will be equally modulated. Meaning that MI in a faster pace would decrease time in actual practice, while slower MI increase actual practice duration. Thus, it is important to control for internal / external factors that may affect MI duration if duration of actual task is important. Demougeot and Papaxanthis (2011) reported that fatigue elicited by an isometric muscle contraction until exhaustion affected MI temporal congruence only for the fatigued arm. Di Rienzo et al. (2012) later reported a exhaustive sport training session was likely to affect MI time. Thus, there is still a lack of experiments to better understand the possible selective effects of fatigue on MI ability. In experimental contribution #3 we evaluated if MI ability is selectively affect by fatigue for a daily walking task.

EFFECTOR SPECIFICITY MODULATION OF MOTOR IMAGERY ABILITY ELICITED BY LOCAL MUSCLE FATIGUE

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Abstract

Motor imagery (MI) is the mental representation of an action without overt body movement, and it is known to engage similar cortical activations. Quite recently, fatigue has been showed to impair MI time accuracy, whit a lack of evidences regarding fatigue-specificity. Thus, we aimed to evaluate MI ability of a walking task before and after a resistance training protocol eliciting a local muscle fatigue from leg (CONGRUENT FATIGUE) and arm (INCONGRUENT FATIGUE) muscles. Participants (n = 14) were requested to walk a pre-defined 22 meters at their own regular pace. Before (PRETEST) and after (POSTTEST) the fatiguing resistance training protocol, participants completed four trials of MI. After the POSTTEST, four additional trials of physical practice of the walking task, each followed by MI, were completed to evaluate the effect of administering physical practice on the recovery of MI abilities. Electromyography of the quadriceps was recorded during the physical practice trials of the walking task. Mental chronometry measures of the isochrony between MI and physical practice durations, as well as MI vividness scores were collected as behavioral and psychometric indexes of the MI ability, respectively. Both CONGRUENT FATIGUE and INCONGRUENT FATIGUE positively affected isochrony. Results are discussed in terms of task nature and MI neurophysiological correlates. We support the use of MI embedded in physical training to motor performance improvement.

INTRODUCTION

Motor Imagery (MI) is the mental representation of an action without overt body movement (Jeannerod, 2001). This remarkable capacity of the human mind represents a multisensory process of action stimulation, with visual imagery (i.e., imagining the movement trough an internal or external visual perspective) and kinesthetic imagery (i.e., imagining the sensations elicited by the movement) being the two most frequently investigated modalities in the scientific literature. There is now ample scientific evidence in support of a neurofunctional equivalence between MI and physical practice of the same movement. The neural networks mediating these two tasks are extensively overlapping (e.g., Decety et al., 1994, Lotze et al., 1999, Jeannerod, 2001, Munzert et al., 2009, Hetu et al., 2013). Both tasks involve activation of the primary motor cortex (Ehrsson et al., 2003, Munzert et al., 2009). Further, MI and physical practice engage comparable patterns of connectivity between brain motor system regions (Gao et al., 2011). Theoretical frameworks postulate that MI represents an emulation to the internal model of the action, hence reproduces forward modeling processes inherent to the planning and programming stages of voluntary movements (Wolpert et al., 1995, Kawato, 1999). MI thus requires central processing of motor command signals, which do reach the peripheral somatic effectors (for a review dealing with motor inhibition during MI, see Guillot et al., 2012a).

Activity-dependent neural reorganizations are now considered the primary neurophysiological process underlying the benefits of MI training programs on performance (Di Rienzo et al., 2016). There is a large scientific background providing evidence of such positive effects of MI practice in sports training and

rehabilitation (for reviews, see Feltz and Landers, 1983, Driskell et al., 1994, Guillot and Collet, 2008, Schuster et al., 2011, Malouin et al., 2013). Among the wide range of variables likely to impact the efficacy of MI training programs on performance, the state of physical practice is currently receiving increased attention. Yet, while researchers recently started questioning the influence of MI practice on physical fatigue (Rozand et al., 2014a, Rozand et al., 2014b, Rozand et al., 2016), whether the physical fatigue state might influence the effects of MI on performance has still received little attention.

Physical fatigue is classically defined as a decrease in performance along with exercise (Enoka and Stuart, 1992). At a behavioral level, physical fatigue has been shown to impair motor coordinations and reduce maximal force production (Gandevia, 2001, Schmid et al., 2006, Feeney et al., 2015). Despite challenging data (e.g., Guillot et al., 2005), physical fatigue has been found to selectively affect MI, and more particularly its temporal congruence with physical (as attested by mental chronometry). Demougeot and Papaxanthis (2011) provided evidence that muscular fatigue elicited by isometric contraction to exhaustion affected both actual and imagined movement durations. Interestingly, the temporal congruence between MI and physical practice was restored after additional physical practice, which might account for the role sensory feedbacks to the update of internal model relating to current body states. These authors did not observe any deleterious effect of physical fatigue on MI for the non-fatigued arm, hence suggesting that local muscular fatigue affected the ability to reproduce the temporal organization of the movement during MI. However, Di Rienzo et al. (2012) later demonstrated that the general physical fatigue elicited by an incremental aerobic exercise was likely to affect MI accuracy, and most specificallyperforming internal visual MI. Considering that most training frameworks recommend the use of MI embedded with real practice during actual training sessions to maximize its benefits on performance (Holmes and Collins, 2001, Guillot and Collet, 2008), questioning the specific effect of physical fatigue appears critical to design efficient MI training interventions.

Experimental studies looking at the relationship between PF and MI practice remain sparse and failed to provide a comprehensive and congruent results pattern with regards to the relationship between physical fatigue elicited by various forms of training and the capacity to perform MI accurately. The present work was designed to evaluate whether MI was selectively affected by muscle fatigue. We were specifically interested in disentangling whether physical fatigue affected MI selectively with regards to the somatic effectors involved in the mental representation (i.e., fatigued or non-fatigued by the preceding exercise).

METHODS

I) Participants

Fourteen healthy young adults without history of neurologic disease volunteered to participate in the present experiment (for a summary of participant's characteristics, see Table 1). None had experienced any recent injury, nor was engaged in a regular resistance training program at the time of the experiment. Participants were blind to the aim of the study until the end of the experiment. All provided a written and informed consent in agreement with the

principles and statements of the Declaration of Helsinki (1982). Prior ethical approval was granted by the Research Ethics Committee of the Center of Research and Innovation in Sports.

	Age (years)	Height (cm)	Weight (kg)	IMC (kg/m2)	Leg Extension Load (kg)	Arm Curl Load (kg)
Men (n = 9)	25.0 ± 4.4	180.1 ± 5.2	74.6 ± 7.4	23.0 ± 2.4	33.9 ± 3.4	28.7 ± 2.8
Women (n = 5)	26.8 ± 2.8	164.8 ± 4.6	57.2 ± 6.2	21.0 ± 2.1	22.0 ± 2.3	15.2 ± 1.6

Table 1. Participant's characteristics (M ± SD)

II) Experimental Design

A) Experimental conditions

Two experimental sessions were scheduled within a span of two weeks (Figure 1). All participants performed MI of a walking task under the following experimental conditions: *i*) a fatigue condition where MI was performed before and after an exerting resistance training exercise engaging somatic effectors poorly involved in walking (i.e., biceps arm curl with a barbell; INCONGRUENT FATIGUE), and *ii*) a fatigue condition where MI was performed before and after and exerting resistance training exercise engaging somatic effectors strongly involved in walking (i.e., biceps arm curl with a barbell; INCONGRUENT FATIGUE), and *ii*) a fatigue condition where MI was performed before and after and exerting resistance training exercise engaging somatic effectors strongly involved in walking (i.e., machine leg extension; CONGRUENT FATIGUE).



Figure 1. Flowchart of the experimental design. Sequence: WT followed by four MI trials (Pre) \rightarrow Experimental condition \rightarrow Four MI trials (Post) \rightarrow Four WT, each followed by one MI trial (R1 to R4). EMG = Electromyography, m = meters, rep = repetitions, min = minutes, RPE = Rate of Perceived Exertion, WT = Walking task, MI = Motor Imagery, R1, R2, R3, R4 = Each individual recovery trial.

C) MI ability evaluations

Three markers were aligned on the floor, with 1 m of distance separating markers *a-b*, and 5 m separating markers *b-c*. Participants were first requested to walk at a comfortable pace, and complete the sequence *a-c-b-c-a*. They were then instructed to mentally reproduce the same motor sequence, using first person visual and kinesthetic MI. A set of four successive MI trials was performed after the initial walking practice, before engaging in the fatiguing exercise protocol (i.e., PRETEST). Immediately after completion of the fatiguing exercise protocol (see below), participants completed four additional MI trials (i.e., POSTTEST). Finally, participants completed physically four additional walking sequences, each of which immediately followed by a MI trial. This enabled to investigate to which extent physical practice might influence the recovery of MI ability on a trial-to-trial basis after eliciting a fatigued state (i.e., RECOVERY TRIALS1-4).

(1) Isochrony between MI and physical practice durations

Physical practice duration for the walking task was collected by the experimenter using a manual chronometer. MI durations for the walking task were collected by the participants, who triggered the onset and offset of MI by holding the chronometer. Walking tasks has systematically being used in the literature to evaluate MI ability, and demonstrate a good reliability in both behavioral (Decety et al., 1989, Fusco et al., 2014) and physiological level (Decety et al., 1991). During both the PRETEST and POSTTEST, we averaged the MI durations corresponding to the four trials. Isochrony between physical practice and MI durations for the walking task was calculated according to the following formula (Beauchet et al., 2010):

$$Isochrony = \frac{(Physical practice duration-MI duration)}{(\frac{Physical practice duration-MI duration}{2})} * 100$$

For RECOVERY TRIALS1-4, we calculated isochrony using the physical practice trial of the walking task as the reference for the subsequent MI trial. The closer isochrony data approached 0, the closer were physical practice and MI durations.

(2) Self-report ratings

MI vividness was finally measured from self-report ratings on a Likert-type scale ranging from 1 (i.e., "*Not vivid at all, I only thought about the movement*")

to 10 (i.e., "Perfectly vivid image, as if I was physically performing the movement").

D) Resistance training protocols

The maximal individual strength performance for the leg extension and arm curl (i.e., load corresponding to the one maximal repetition) was first estimated from anthropometric measures according to Heyward and Gibson (2014). We carried on pilot recordings to determine the poundage and repetition range eliciting fatigue of the muscles targeted by the resistance training exercises implemented during the INCONGRUENT FATIGUE and CONGRUENT FATIGUE. More specifically, we evaluated the resistance training poundage suitable to elicit a fatigue state if the participants reported a perceived exertion ranging from 7-9 on the 10 point Borgs' scale (Borg, 1982) after 60% of performance decrease in the capacity to achieve sets of 90 s of externally cued repetitions. The correspondence between strength conditioning level and body weight for men and women are presented in the description of each protocol condition (see below).

The fatiguing exercise administered during the INCONGRUENT FATIGUE experimental condition targeted muscles which were not primary agonists of the walking tasks supporting MI ability evaluations (i.e., elbow flexor muscles). We chose biceps arm curl movements with a barbell performed from a standing up position (Figure 2B). Participants stood with their back against a wall and were instructed to not perform any trunk movement. Resistance training poundage was set up at 38.5% of the body weight for men, and 26.5% for women from pilot recordings. A warm-up was administered before the fatiguing exercise protocol,

including 10 repetitions at 50% of the resistance training load. This was followed by a 1 min rest-period, immediately followed by 5 additional repetitions at 100% of the resistance load. Small poundage adjustments were considered if the participant reported some difficulties to complete the warm-up. The fatiguing resistance training protocol was scheduled 3 min after the warm-up. Participants were asked to perform sets of 90 s of externally cued repetitions, followed by 90 s allocated to passive recovery. Durations of the concentric and eccentric phases was externally cued by auditory stimuli (i.e., 1 s duration for both phases). The sets were iterated until the experimenter measured a drop in performance corresponding to a decrease of 60% in the number of repetitions completed. Participants were naïve to this information, and were only instructed to perform repetitions according the externally cued repetition timing. Verbal encouragement were provided throughout the fatiguing resistance training protocol. The fatiguing exercise administered during the CONGRUENT FATIGUE experimental condition targeted muscles which were primary agonists of the walking task supporting MI ability evaluations (i.e., leg extensor muscles). We chose the machine leg extension, which was performed from a comfortable seated position (Figure 2C). The load was set up at 45.5% of body weight for men, and 38.5% for women. Both warm-up and exercise protocol procedures followed the methods described for the INCONGRUENT FATIGUE condition. For both CONGRUENT FATIGUE and INCONGRUENT FATIGUE, we collected the number of sets completed until the fatigued state.



Figure 2. Walking task and congruent/incongruent fatigue exercises. A) Walking task to be performed at experiment start (Before Trial 1) and before MI in Trials 3, 4, 5 and 6. Sequence = *a-c-b-c-a*. B) Arm curl exercise performed during the incongruent fatigue condition. C) Leg extension exercise performed during the congruent fatigue condition.

- (1) Monitoring of physical fatigue elicited by the resistance training protocols
 - (i) Rate of perceived exertion

After the warm-up and the fatiguing protocol, the rate of perceived exertion (RPE) was measured by answering the question "How exhaustive was the warm-up/protocol?" on a Borg scale ranging from 0 (i.e., "*Rest*") to 10 (i.e., "*Maximal exhaustion*") (Borg, 1982).

(ii) Electromyography

We continuously recorded the electromyograms (EMG) from the three superficial leg muscles: *Rectus Femoris* (RF), *Vastus Medialis* (VM) and *Vastus Lateralis* (VL). After shaving and cleaning the skin with alcohol, EMG wireless surface silver electrodes (Patented parallel-bar technology, sampling rate 1000 Hz) were positioned according to Surface Electromyography for the Non-Invasive Assessment of Muscles (SENIAM) recommendations (Hermens et al., 2000). We used the TrignoTM Wireless EMG System© for data acquisition (2014, Delsys Incorporated). We filtered the EMG signal and rectified offline using a bandpass of 20-450 Hz using a 0.5 s time window (Butterworth filter, 4th order). A Fourier fast transform was applied to calculate root mean square for each trial on the walking task (EMG_{RMS}). EMG_{RMS} data was finally normalized with reference to the first trial of the fatigue task (i.e., %EMG_{RMS}).

E) Statistical Analyses

We used *R* (Team, 2012) and *nlme* (Pinheiro et al., 2011) to run a linear mixed effect analysis of the dependent variables quantifying i) the physical fatigue elicited by the resistance training protocols (i.e., number of sets completed before the fatigued state, RPE scores, %EMG_{RMS}), and ii) MI ability (i.e., isochrony, vividness scores). For the analysis of the physical fatigue elicited by the resistance training protocols, we built random-coefficient regression models with a by-subject random intercept. For the number of sets completed before the fatigued state, we entered the fixed effect of EXPERIMENTAL CONDITION (i.e., INCONGRUENT FATIGUE, CONGRUENT FATIGUE). For RPE scores, we entered in addition to the EXPERIMENTAL CONDITION (i.e., INCONGRUENT FATIGUE, TATIGUE, CONGRUENT FATIGUE).

CONGRUENT FATIGUE) the fixed effect of the MEASURE (i.e., POST WARM-UP, POST EXERCISE). For the %EMG_{RMS}, we entered the fixed effects of the EXPERIMENTAL CONDITION (i.e., INCONGRUENT FATIGUE, CONGRUENT FATIGUE), TEST (i.e., PRETEST, POSTTEST, RECOVERY TRIALS1-4) and MUSCLE (i.e., RF, VL, and VM), with interaction terms. TEST was included as a numeric regressor to account for the effect of the successive repetition of the physical practice walking trials on %EMG_{RMS}. For isochrony and vividness variables, we entered the fixed effect of the EXPERIMENTAL CONDITION (i.e., INCONGRUENT FATIGUE, CONGRUENT FATIGUE) and TEST (i.e., PRETEST, POSTTEST, RECOVERY TRIALS1-4), with interaction term. TEST was included as a numeric regressor to account for the effect of the successive repetition of the physical practice walking trials on on isochrony.

We implemented a backward stepwise procedure to fit the randomcoefficient regression model formulae (Hocking, 1976; Draper and Smith, 2014). Inspection of the residual plots did not reveal any obvious deviation from the hypotheses of homoscedasticity or normality. The statistical significance threshold was set up for a type 1 error rate of $\alpha = 5$ %. As effect sizes, we calculated the amount of explained variance, i.e., partial coefficients of determination (Rp²). We used the ad hoc procedure implemented for linear mixed effects models in the *r2glmm* package (Edwards et al., 2008; Jaeger et al., 2017). Statistically significant main effects and interactions were investigated using general linear hypotheses testing of planned contrasts (Bretz et al., 2016). We used the *multcomp* package (Hothorn et al., 2008), and applied Holm's corrections to control the false discovery rate.

RESULTS

I) Physical fatigue elicited by the resistance training protocols

A) Number of sets completed before fatigued state

The number of repetitions completed during the resistance training exercise was affected by the EXPERIMENTAL CONDITION ($Rp^2 = 0.38$, $\chi^2(1) = 13.95$, p < 0.001). Participants performed a higher number of series during the CONGRUENT FATIGUE (6.93 ± 1.83) compared to INCONGRUENT FATIGUE (4.64 ± 1.78) (fitted difference: 2.28 ± 0.61 s.e., p < 0.001).

B) RPE scores

The two-way EXPERIMENTAL CONDITION × MEASURE interaction was removed during the backward stepwise model selection ($\chi^2(1) = 0.04$, p > 0.05). The linear mixed effects analysis revealed the main effect of the EXPERIMENTAL CONDITION (Rp² = 0.17, $\chi^2(1) = 4.47$, p = 0.03) and MEASURE (Rp² = 0.62, $\chi^2(1) = 140.26$, p < 0.001). Indeed, participants reported greater RPE scores after the CONGRUENT FATIGUE (6.32 ± 2.52) compared to INCONGRUENT FATIGUE (5.60 ± 2.42) (fitted difference: 0.71 ± 0.34 s.e., p < 0.001). Also, participants reported greater RPE scores POST WARM UP (3.96 ± 1.69 s.d.) compared to POST EXERCISE (7.96 ± 1.17) (fitted difference: 4.00 ± 0.34 s.e., p < 0.001).
C) Electromyography

The three-way EXPERIMENTAL CONDITION × TEST × MUSCLE interaction ($\chi^2(2) = 1.42$, p = 0.49), the two-way MUSCLE × TEST ($\chi^2(2) = 0.29$, p = 0.86), MUSCLE × EXPERIMENTAL CONDITION ($\chi^2(2) = 2.03$, p = 0.36) and EXPERIMENTAL CONDITION × TEST ($\chi^2(1) = 2.59$, p = 0.10) interactions, and the main EXPERIMENTAL CONDITION effect ($\chi^2(1) = 0.63$, p = 0.43) were removed during the backward stepwise model selection. The linear mixed effects analysis eventually revealed a main effect of MUSCLE (Rp² = 0.07, $\chi^2(2) = 53.52$, p < 0.001) and TEST (Rp² = 0.04, $\chi^2(1) = 53.52$, p < 0.001) on %EMG_{RMS}. The %EMG_{RMS} measured on the VM (109.30 % ± 10.48) was higher compared to both VL (79.31 % ± 8.83) (fitted difference: 32.47 % ± 8.99 s.E., p < 0.01) and RF (fitted difference: 64.13 % ± 8.77 s.E., p < 0.001). The %EMG_{RMS} measured on the VL was also higher compared to that measured in the RF (74.31 % ± 8.40) (fitted difference: 32.58 % ± 8.95 s.E., p < 0.001) (Figure 3).



Figure 3. Normalized RMS values for each WT across time. * Significant difference in VL between conditions (P <0.05). Notes: RMS – Root Mean Square; REL – Leg exertion condition; INC – Arm exertion condition; RF – Rectus

Femoris; VM – Vastus Medialis; VL – Vastus Lateralis. R1, R2, R3, R4 = Each individual recovery trial.

II) Effect of physical fatigue elicited by the resistance training protocol on mi ability

A) Analysis of isochrony

The two-way EXPERIMENTAL CONDITION × TRIAL interaction ($\chi^2(1) = 2.21$, p =0.14), as well as the main effect of EXPERIMENTAL CONDITION ($\chi^2(1) = 0.27$, p = 0.61) was removed during the backward stepwise model selection. The linear mixed effects analysis finally revealed a main effect of TEST (Rp² = 0.11, $\chi^2(2) = 12.64$, p < 0.001). There was indeed a negative relationships between the repeated measures from the PRETEST to RECOVERY TRIAL4 and isochrony (PRETEST: 9.14 % ± 21.94, POSTTEST: -1.25 % ± 28.45, RECOVERY TRIAL1: 2.49 % ± 24.76, RECOVERY TRIAL2: -0.07 % ± 20.65, RECOVERY TRIAL3: -2.78 % ± 18.81, RECOVERY TRIAL4: -6.08 % ± 24.01; fitted estimate: -2.40 ± 0.67 s.E., p < 0.01). Noteworthy, from the PRETEST up to RECOVERY TRIAL2, TRIAL affected isochrony towards closer value from the 0 reference value, i.e., corresponding to identical physical practice and MI durations.



Figure 4. Mental Isochrony and MI vividness across time for CONG (black circles) and INC (white triangles). ISO – Moments Pre and Post were calculated based on the walking task performed at the beginning of experiment. For R1, R2, R3 and R4 a walking task was performed before each motor imagery trial to be used as reference. * Significant difference with Pre (p < 0.05); ** Significant difference with Pre (p < 0.05); # Statistical trend with Pre (p = 0.08).

B) Analysis of MI vividness

The two-way EXPERIMENTAL CONDITION × TRIAL interaction ($\chi^2(1) = 2.39$, p = 0.12) was removed during the backward stepwise model selection. The linear mixed effects analysis revealed the main effects of the EXPERIMENTAL CONDITION (Rp² = 0.05, $\chi^2(2) = 5.72$, p < 0.05) and TRIAL (Rp² = 0.13, $\chi^2(1) = 15.59$, p < 0.001) on MI vividness scores. Participants reported higher MI vividness scores during CONGRUENT FATIGUE (7.04 ± 1.19) compared to INCONGRUENT FATIGUE (6.74 ± 1.03) (fitted estimate: 0.29 ± 0.12, p < 0.05). Also, there was a positive relationship between the successive trials of TEST (PRETEST: 6.75 ± 1.29, POSTTEST: 6.32 ± 1.28, RECOVERY TRIAL1: 6.89 ± 0.91, RECOVERY TRIAL2: 7.00 ± 0.92, RECOVERY TRIAL3: 7.07 ± 1.02, RECOVERY TRIAL4: 7.28 ± 1.05) and MI vividness scores (fitted estimate: 0.14 ± 0.04, p < 0.001) (Figure 4).

DISCUSSION

The aim of the present study was to evaluate whether MI ability of walking might be selectively affected by different types of local muscular fatigue. Our findings confirmed that the effort was subjectively perceived as being comparable in both conditions, despite volume and intensity differences. Also, we investigated whether administering physical practice under a fatigued state might contribute to restore the MI ability (Demougeot and Papaxanthis, 2011, Rozand et al., 2016). Unexpectedly, both types of fatigue, i.e. congruent and incongruent, were found to positively influence the MI ability, as attested by the increased capacity of participants to reproduce the temporal organization of the movement during mental rehearsal. Furthermore, we measured no deleterious effect on the

vividness of the mental representation. At first glance, these findings tend to confirm previous studies supporting that physical fatigue may not systematically hamper the MI ability (Guillot et al., 2005). More specifically, it is suggested that the general perception of fatigue, rather than local fatigue, would be more likely to negatively influence isochrony (Di Rienzo et al., 2012).

Relating the present findings to previous research on the effects of physical fatigue on MI ability remains at this point difficult due to the important variability in the nature of the motor tasks supporting MI ability evaluations (e.g., jumping, swimming, pointing, and walking) and the features of the fatiguing protocols administered. Improved temporal congruence between actual and imagined duration of has already been reported in the literature for walking tasks, e.g., when participants were asked to perform MI in conjunction to body movements of small amplitudes reproducing the temporal invariants of the physical execution (Fusco et al., 2014). This form of MI was conceptualized as "Dynamic MI" (for original research articles on dynamic imagery, see Callow et al., 2006, Guillot et al., 2013, Kanthack et al., 2016). Locomotion represents a developmental coordination which is learned, consolidated and automated during childhood (Bril and Brenière, 1993). Noteworthy, locomotion represents a low attentional demand, since the coordination is not under the unique control of supraspinal structures of the brain motor system (MacKay-Lyons, 2002, Zehr and Duysens, 2004). Walking is a complex task that requires several brain areas working in conjunction (Fukuyama et al., 1997, Hanakawa et al., 1999, Miyai et al., 2001, Mihara et al., 2007, Harada et al., 2009). However, the spinal network involved in walking has historically demonstrated the capacity to activate itself and maintain the rhythmicity in the absence of any supraspinal activation (Shik and Orlovsky, 1976, Lundberg, 1979, Grillner, 1985, Jordan, 1998, Rossignol, 2000, Jordan et al., 2008). Even though the motor control of walking is well stablished in animal, the specificities of how it works in human are still under investigation (Koren et al., 2018). By contrast, MI is well accepted to engage brain motor system regions involved in the planning, programming and control of voluntary movements (Decety et al., 1994, Roth et al., 1996, Jeannerod, 2001, Munzert et al., 2009). Furthermore, MI facilitates corticospinal excitability and alpha motor neurons by downregulating the inhibitory influence of low-threshold interneurons (Stinear, 2010, Grosprêtre et al., 2015, Ruffino et al., 2017). Accordingly, MI involve a high demand in terms of attentional focus in order to engage the executive parts of the brain motor system associated with the generation of accurate and vivid motor images from proprioceptive and visual informations (Lorey et al., 2009, Lorey et al., 2011, van der Meulen et al., 2012). Accordingly, it is suggested that the local physical fatigue elicited by the resistance training protocols, attested by the increased perceived exertion and muscle activation during the POSTTEST, increased the demand in terms attentional control of walking. While one might objectivate that the INCONGRUENT FATIGUE did not elicit local fatigue within the prime agonist muscles of the walking task, upper limb movements nonetheless play a central role in anticipatory postural regulations maintaining body balance during sways associated with selfpaced locomotion (Winter, 2009). Increased attentional focus may explain, at least partially, why participants achieved increased temporal congruence between MI and actual practice of walking under a state of local fatigue. This postulate is also congruent with theoretical frameworks of fatigue development (Pageaux, 2014, McMorris et al., 2018). The increase in perceived effort caused

by prolonged exercise increases the cognitive demand of a task (Rejeski, 1985) by driven greater attention to the task instead of internal/external afferent signals. The influence of physical fatigue on the spontaneous motor tempo (Temperley, 1963, Mishima, 1968, Fraisse, 1982) and its relationships to the internal clock processes (Hoagland, 1933, Treisman, 1963, Church, 1984), might bring further perspectives to the positive effect of CONGRUENT FATIGUE and INCONGRUENT FATIGUE on MI ability. The spontaneous tempo is the individual preferred tempo to perform self-paced movements, whereas internal clock refers since Hoagland (1933) to the central representation of temporal features built from "physiological pacemakers" (e.g., the lick rate in rats; Treisman, 1963). The physiological pacemaker produces pulses at a given rate stored within short-term memory and compared with a long-term memory model (for an overview, see Church, 1984, Meck and Church, 1984). Internal clock processes are generally involved in time estimation ability. Dosseville et al. (2002) observed an increased spontaneous motor tempo for a finger tapping task in trained cyclists after 15 minutes of pedaling at a spontaneous moderate intensity. This increase was accompanied by a corollary increase in heart rate. Interestingly, the heart is assumed to play the role of the pacemaker (e.g., Jamin et al., 2004). HR increases is a wellestablished neurophysiological response to a weighted resistance training exercise (Fleck, 2003, Rezk et al., 2006, Figueiredo et al., 2013, Figueiredo et al., 2015). Alterations in MI duration according to the physiological arousal state, indexed through measures of the HR; were previously reported in the literature (Louis et al., 2011, Di Rienzo et al., 2012). Specifically, athletes exhibited isochrony between MI and physical practice durations when MI was performed in a physiological arousal state corresponding to the actual demand of physical

practice (Louis et al., 2011). Conversely, isochrony was altered when MI was performed after a period of relaxation. Recently, Di Rienzo et al. (2014) reported that breath-holding athletes required more time to perform MI of a diving task performed under apnea compared to MI performed while breathing. In the same experiment, even while imagining a non-apnea task, the HR increase corollary of breathing yielded shorter MI durations. Overall, the influence of the HR increase associated with resistance training possibly affected the internal clock processes, hence affecting MI durations towards greater isochrony due to a more congruent physiological arousal sate with the corresponding physical performance under both CONGRUENT FATIGUE and INCONGRUENT FATIGUE states. Albeit speculative, this postulate is congruent with theoretical frameworks of the motor tempo and its relationships time estimation abilities, hence should be more specifically considered in future studies.

CONCLUSION

Present data support that the temporal features of MI ability were positively influenced by a local physical fatigue elicited by resistance training exercises. Both congruent and incongruent fatigue contributed to improve the MI ability, as attested from validated behavioral methods (Guillot et al., 2012b). These findings outline new perspectives to the relationships between fatigue states elicited by exercise and MI, and corroborate the claims in support of embedded MI practice within actual training sessions (Holmes and Collins, 2001, Guillot et al., 2005). As with all research, however, the present study has some limitations that need to be considered before drawing firm conclusions. First, the experimental design did

not include a pure control condition without physical fatigue. Previous data provided strong evidence that MI times did not change under such control conditions (e.g., Demougeot and Papaxanthis, 2011, Rozand et al., 2015). Nonetheless, including a no-fatigue condition might provide relevant guarantees for designing fruitful MI interventions. Future studies should also consider comparing the effect of physical fatigue on MI of more complex and attentiondemanding coordinations.

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EXPERIMENTAL CONTRIBUTION #4 : Thiago FERREIRA DIAS KANTHACK,

Aymeric GUILLOT, Michel CLÉMÉNÇON, Franck DI RIENZO. *"Effect of physical fatigue elicited by continuous and intermittent exercise on motor imagery ability"*. To be submitted.

MI literature report that exercise might modulate MI time disrupting the congruence with actual practice (Demougeot and Papaxanthis, 2011, Di Rienzo et al., 2012). Controversially, Guillot et al. (2005b) reported that an exhaustive exercise for the lower limbs did not change MI time of a jumping task. So far, the little literature regarding the effect of fatigue induced by exercise on MI ability is little and strongly differentiate on physical approach to induce fatigue. Also, protocols were always considered extremely exhaustive, while sports training and rehabilitation sessions may use both continuous and intermittent training, and normally result on fatigue level below the exhaustion threshold. In experimental contribution #4 aimed to compare the effect fatigue elicited by intermittent and continuous exercise on MI ability. We also implemented a walking task, in comparison with experimental contribution #3 and a pointing task to investigate the specificity of fatigue on MI ability.

EFFECT OF PHYSICAL FATIGUE ELICITED BY CONTINUOUS AND INTERMITTENT EXERCISE ON MOTOR IMAGERY ABILITY

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Abstract

The ability to perform motor imagery (MI), i.e., the mental representation of an action without concomitant body movement, might be impaired by the physical fatigue elicited during actual training sessions. This issue has received limited scientific investigation and yielded conflicting results. Here, we evaluated MI ability before and after two distinct exercise protocols: i.e., i) a continuous exercise of 20 min performed on a cycle ergometer at 80 % of the secondary ventilatory threshold (CONTINUOUS EXERCISE) and ii) an intermittent exercise of 20 min involving sprints at maximal intensity performed regular intervals (INTERMITTENT EXERCISE). The exercise protocols were expected to reproduce fatigue states encountered during actual training. MI ability evaluations were carried on using validated behavioral (i.e., mental chronometry) and psychometric (i.e., self-report Likert ratings) methods. MI ability evaluations included i) mental rehearsal of a motor sequence which involved the main somatic effectors of the exercise protocols (i.e., walking), and ii) mental rehearsal of a motor task which did not involve the main somatic effectors of the exercise protocols (i.e., pointing movements with the upper limbs). Rate of perceived exertion revealed that the exercise load was comparable between CONTINUOUS EXERCISE and INTERMITTENT EXERCISE. Mental chronometry revealed that MI ability was degraded after INTERMITTENT EXERCISE only. Self-report measures of MI vividness revealed that MI ability was primarily impaired during MI of the walking task compared to the pointing task. Present results suggest that INTERMITTENT EXERCISE engaging anaerobic processes of energy expenditure, but not CONTINUOUS EXERCISE engaging aerobic processes of energy expenditure, might impair MI ability. The physical fatigue state elicited by exercise primarily affected the mental representation of the task involving the main somatic effectors of the fatiguing exercise. Findings are discussed with reference to the effect of intermittent exercise on cognitive functions, and possible changes in current body states affecting forward predictive models during MI.

INTRODUCTION

Motor imagery (MI) is the mental representation of an action without engaging its physical execution (Jeannerod, 1994). MI is a relevant approach to improve motor performance and has now many applications in sports sciences and rehabilitation (Feltz and Landers, 1983, Driskell et al., 1994, Di Rienzo et al., 2016). Motor performance gains originate from a similar pattern of cortical and subcortical recruitment to that recorded during the physical performance of the corresponding movement (Jackson et al., 2001, Munzert et al., 2009, Hetu et al., 2013). MI thus increases the cognitive demand placed upon the brain motor networks, and yields activity-dependent neural reorganizations (see Ruffino et al., 2017, for a recent review). The similarities between MI and physical practice can also be measured at a behavioral level. Mental chronometry is a wellestablished investigation method of the time course of information processing by the central nervous system (Posner, 1978). The temporal congruence between MI and physical practice has been widely used as an index of MI ability. Comparable durations, i.e., isochrony, specifically attests that the temporal organization and invariants of the movement are adequately reproduced during mental rehearsal (for an exhaustive review, see Guillot et al., 2012). Practical guidelines for efficient MI interventions suggest practicing MI in conjunction with physical practice, which has been shown to elicit additional performance gains compared to physical training alone (Driskell et al., 1994, Yágüez et al., 1998, Jackson et al., 2004, Guillot et al., 2010). Schuster et al. (2011) underlined in a seminal review pointed that positive effects of MI were more frequently observed when MI interventions were administered consecutively to physical practice.

More specifically, theoretical MI frameworks insist that embedded practice with actual physical training might be the most effective to improve performance (e.g. Holmes and Collins, 2001, Guillot and Collet, 2008). Indded, including MI during training intervals have being recently proved to attenuate the effects of fatigue (Di Rienzo et al., 2015, Guillot et al., 2015).

Motor performance decreases as a result of repeated exercise is a now well-accepted definition to the concept of fatigue (Enoka and Stuart, 1992). Recent, psychobiological frameworks conceptualized fatigue as the product of an increased in effort perception originating from the physiological and psychological effects of repeated exercise (Bigliassi, 2015, McMorris et al., 2018). Fatigue is thus an intrinsic component of training. Surprising little literature have searched for possible effects of fatigue on MI ability. This issue is of specific relevance since previous studies underlined that MI ability had a direct influence on i) the recruitment of brain motor networks (Guillot et al., 2008, Lorey et al., 2011, Meulen et al., 2014), and ii) the efficacy of training MI interventions (Martin et al., 1999, Roure et al., 1999). For instance, Louis et al. (2008) reported that practicing MI at a faster pace also accelerate real task, while when practiced in a slower pace the real task duration increased, even for high trained movements. In a pioneer study, Guillot et al. (2005) reported no effect of the fatigue elicited by halfsquat repetitions at 70% of the maximum workload isochrony. Skin resistance measures, attesting the involvement of the sympathetic branch of the autonomic nervous system during MI, also remained unchanged. This suggests MI engaged the motor system into anticipatory regulations of energy expenditure that characterize the actual motor preparation in spite of the fatigued state (see Collet et al., 1994). Demougeot and Papaxanthis (2011) later reported that a fatiguing

paradigm involving an isometric contraction of elbow flexor muscles sustained until exhaustion decreased MI durations of pointing actions. The MI ability impairment was only recorded during MI of pointing actions performed with the fatigued arm. These two experiments provided conflicting results with regards to the short-term effects of resistance training-induced fatigue on MI ability. More recently, Di Rienzo et al. (2012) evaluated in swimmers MI ability of a somersault turn, before and after 45 minutes of swimming at incremental speed up to the maximal aerobic threshold. In the fatigued state, participants reported no changes in their perceived difficulty to complete MI of the somersault turn from either an internal or external perspective. Yet, isochrony of MI from the first person perspective exhibited a significant decrease compared to the pre-fatigued state. This decrease was associated with a reduced autonomic nervous system correlates of anticipatory regulations of energy expenditure during MI. Overall, the effect of fatigue elicited by exercise on MI ability remains poorly understood. This issue needs to be addressed in a more integrative approach, specifically with regards to i) the type of fatiguing exercise and ii) whether MI ability evaluations involve mental rehearsal involves the primary effectors of the fatiguing exercise.

Past research focused on fatiguing protocol completed until to exhaustion. Yet, from practical standpoint, physical training in both sports sciences and rehabilitation primarily involves continuous and/or intermittent forms of exercise resulting in fatigue states that remain below the exhaustion threshold. The present study aimed at comparing the effect of two types fatiguing protocols on MI ability. Specifically, we measured the effect continuous and intermittent exercise on the psychometric and behavioral correlates of MI ability. A walking

task (i.e. an automated supraspinal controled task, see MacKay-Lyons, 2002, Zehr and Duysens, 2004) and an arm pointing task were used to investigate the specificity of fatigue effects over MI. We hypothesized i) that MI ability of walking task would not be impaired by fatigue, ii) MI of pointing task would most likely be impaired by fatigue as reported by Demougeot and Papaxanthis (2011) and iii) intermittent exercise will induce greater impairment on MI ability compared with continuous exercise.

METHODS

I) Participants

Participants (n = 13) were recruited from the Sports Sciences department of the University Claude Bernard Lyon 1 (F-6100, Villeurbanne). They were healthy adults without history of injury or neurologic disorder. Instructions regarding the experimental design were provided individually. No information regarding the purpose of the study was provided until after completion of the repeated measures design. The local review board approved the present experiment. Participants finally provided a written signed consent from to participate in the experiment, in agreement with the ethical statements of the declaration of Helsinki (1982). Participants' characteristics are summarized in Table 1.

II) Experimental design

A) Incremental test

During a first experimental session, participants performed an incremental test on a cycle ergometer (CycleOps Phantom 3, PowerTap®). The incremental test started at 30 Watts (i.e., 1.kg.m².s⁻³) and increased by 30 Watts every 2 minutes until exhaustion. Participants were requested to keep pedaling until they could no longer perform the exercise. The cycle ergometer adjusted the resistance to participant's cadence to match the requested power throughout the incremental, according to the formula:

Power
$$(1.kg.m^2.s^{-3}) = F(N).v(m.s^{-1})$$

Heart rate (HR) and the volume of oxygen uptake (VO₂) were continually monitored. The maximal VO₂ and the second ventilatory threshold (VT2) were calculated offline. At the cessation of the incremental test, the rate of perceived exertion (RPE) was measured using a 10-points Borg scale (Borg, 1982). Measures of the saddle high distance from handlebar and handlebars high were recorded for each participant. This enabled to control the cycling body posture throughout experimental conditions.

B) Experimental conditions

Participants performed a 10 min warm-up in the cycle ergometer at 40% of the individual VT2. After the warm-up, participants were equipped with a gas analysis device (Metamax 3B Cortex, Leipzig, Deutschland) and completed a fatiguing protocol according to the following experimental conditions: *i*) A continuous fatiguing exercise where participants were requested to complete 20

minutes at 80% of the individual VT2 on a cycle ergometer (i.e., CONTINUOUS EXERCISE), and ii) an intermittent fatiguing exercise where participants were requested to complete a series of 20 sprints of 6 s without lifting from the saddle, loaded at 0.06% of their body weight on a Wingate-type cycle ergometer (Monark 874E) (i.e., INTERMITTENT EXERCISE). Sprints onset and offset were externally cued every minute by a computer (Presentation, Neurobehavioral systems®, 240 Hz, 50 Db).

Experimental conditions where scheduled within a span of 4 days, i.e., 3 entire no-recording day between each experimental session. To prevent carryover effects due to residual fatigue from one experimental session to another, we implemented a fully counterbalanced design, with > 6 participants allocated to each of the two possible order conditions. All visits occurred at the same day time for each participant (\pm 1h) to avoid confounding effects of circadian rhythms. The experimental conditions are summarized in Figure 1A.

- C) Dependent variables
 - (1) Evaluation of experimental conditions' workload
 - (i) Spiroergometer measures

Physiological measures during both experimental conditions were carried on a breath-by-breath basis using and ambulatory spiroergometer specifically designed for cardiorespiratory exercise testing (METAMAX®3B, ©CORTEX, Biophysik, Germany). Gas exchange calculations were carried on using the MetaSoft® Studio (©CORTEX, Biophysik, Germany). According to the manufacturer's recommendations, the ambulatory spirometer was calibrated for pressure, gas concentration (i.e., 15% O₂, 5% CO₂ balanced with N₂) and volume prior to each recording. No data recordings were performed during warm-up to avoid excessive time with the VO₂ mask, which might cause discomfort. We first measured participant's VO₂. The spiroergometer also afforded recordings of heart rate (HR) and ventilatory rate. The latter was used to calculate VT2. For both CONTINUOUS EXERCISE and INTERMITTENT EXERCISE, data were averaged using a 30 s sliding time windows over the last 3 minutes of each experimental condition to avoid at maximum the VO₂ kinematics differences due the accumulated O₂ deficit (Medbo et al., 1988).

(ii) Blood lactate measures

A micro sample of blood was collected from the third finger 3 min after completion of each experimental condition. Blood lactate concentration was measured using the portable Lactate Pro (LT-1710, Arkray, Japan).

(iii) Perceived Exertion

After warm-up and at the end of exercise session, participants rate their perceived exertion level by answering the 10 points Borg scale (Borg, 1982). Participants had to answer the question "how exhaustive was the exercise session they just did" ranging from 1 *(i.e., "it was exhaustive as resting"*) to 10 *(i.e., "the most exhaustive possible"*).

(2) Evaluation of the MI ability

Immediately after warm-up and immediately after completion of the fatiguing exercise, we evaluated the MI ability using a mental chronometry approach (Malouin et al., 2008, Collet et al., 2011a).

(i) Mental chronometry

We first investigated the isochrony between MI and physical practice. MI ability evaluations were carried on two distinct tasks: i) a walking task and ii) a pointing task. The tasks were administered in a fully counterbalanced order at the group level. For the walking task, participants were requested to perform a sequence of self-paced walking displacements between 3 cones separated from each other by 1 m and 5 m, respectively. They first walked from the first to the last cone (i.e., 6 m), and then walked back to the second cone (i.e., 5 m). The pointing tasks was adapted from the paradigm by Demougeot and Papaxanthis (2011). Three targets were set according to each participants high. The line between the head of the humerus and the point A, located at participants feet, was considered as 0°, target B (40°) and C (110°) were placed in a wall 1 m in front of the participant. At their own pace, participants were instructed to point to the three targets according to a predetermined sequence A-B-A-C-A-B-A. Each physical trial was video recorded using a GoPro®HERO4. Capture points were attached to the head of the humerus and top of the hand. Data were processed using the Kinovea software (v. 0.8.25). Physical practice trials exhibiting a pointing error $> 5^{\circ}$ for each target would were excluded from the forthcoming analyses (7% of trials excluded overall). An illustration of the walking and pointing

tasks is provided in Figure 1C. Participants first performed the tasks physically, followed by MI. Participants completed MI from an identical standardized body position to that during the physical practice. Indeed, previous experiments underlined that an incongruent body posture could bias the ease to perform MI (Sirigu and Duhamel, 2001; Vargas et al., 2004). Participants were instructed perform MI according to the first person visual and kinesthetic modalities, concomitantly. Participants completed 4 trials of physical practice followed by the corresponding MI for both tasks. MI durations were collected using a manual chronometer (Digital Sport Stopwatch, PC894, LEAP) held by the participants. They were instructed to manually trigger the chronometer at the beginning and at cessation of MI (Lebon et al., 2012; Guillot et al., 2013; Kanthack et al., 2013; Fusco et al., 2014). For each trial, isochrony was calculated and averaged across trials of the pretest and posttest based on the following formula (Beauchet et al., 2010):

$$Isochrony = \frac{(Physical \ practice \ duration - MI \ duration)}{(\frac{Physical \ practice \ duration - MI \ duration)}{2}} * 100$$

(ii) Self-reports

After completion of the MI ability evaluations, participants provided a selfreport of the MI vividness on a 10-points Likert scale ranging from 1 (i.e., *"Absence of visual/proprioceptive sensations during MI, in just thought about the movement*" to 10 (i.e., *"Comparable visual/proprioceptive sensations to those experienced during the physical performance of the task*". Participants also selfreported of the perceived ease/difficulty to perform the MI tasks on a Likert scale ranging from 1 (i.e., "No difficulty at all") to 10 (i.e., "Impossible to mentally represent the movement").



Figure 1. Experimental design and procedures. A) Sequence of experimental design for each day, and variables acquired. B) Walking Task design for both physical and mental practice, sequence = A-B-C. C) Pointing Task design for both physical and mental practice, sequence = A-B-A-C-A-B-A, adapted from Demougeot and Papaxanthis (2011).

D) Statistical analyses

We used R (R Core Team, 2015) and *nlme* (Pinheiro et al., 2011) to run a linear mixed effects analysis of i) exercise workload (i.e., % of VO2max, HR, Blood lactate concentration, RPE), and ii) MI ability dependent variables (i.e., isochrony and self-report ratings of MI vividness and difficulty), with a by-subject random intercept.

For the exercise workload analysis, we entered EXPERIMENTAL CONDITION (i.e., CONTINUOUS EXERCISE, INTERMITTENT EXERCISE) as fixed effect. For the MI ability analysis, we entered as fixed effect the EXPERIMENTAL CONDITION (i.e., CONTINUOUS EXERCISE, INTERMITTENT EXERCISE), TEST (i.e., PRETEST, POSTTEST) and TASK (i.e., WALKING, POINTING), with interaction terms. We implemented a backward stepwise procedure to fit the random-coefficient regression model formulae (Hocking, 1976; Draper and Smith, 2014). Inspection of the residual plots did not reveal any obvious deviation from the hypotheses of homoscedasticity or normality. The statistical significance threshold was set up for a type 1 error rate of α = 5 %. As effect sizes, we calculated the amount of explained variance, i.e., partial coefficients of determination (Rp²) using the ad hoc procedure for linear mixed effects models implemented in the r2glmm package (Edwards et al., 2008; Jaeger et al., 2017). Main effects and interactions were post-hoc investigated using general linear hypotheses testing of planned contrasts form the *multcomp* package, as recommended for mixed effects models (Hothorn et al., 2008; Bretz et al., 2016). We applied Holm's corrections to control the false discovery rate.

RESULTS

I) Participant's characteristics

Table 1 summarizes participant's characteristics (M ± SD) after the first experimental session (i.e., incremental test).

Table 1. Participants' characteristics, i.e., anthropometry and incremental test results on the cycle ergometer. W: Watts, VO2max: Maximal oxygen uptake, VT2: Second ventilatory threshold.

_	Body mass Index (kg/m²)	Age (years)	Cycle ergometer load at exhaustion (W)	VO2max (ml/kl/min ⁻¹)	VT2 (W)
Women (n = 3)	21.00 ± 0.30	25.00 ± 3.00	200.00 ± 10.00	41.00 ± 2.00	150.00 ± 17.00
Men (n = 10)	23.00 ± 0.70	26.00 ± 1.00	276.00 ± 8.00	53.00 ± 2.00	204.00 ± 20.00

II) Exercise workload analysis

Physiological data (i.e., VO₂, HR, Blood lactate) recorded at the group level for CONTINUOUS EXERCISE and INTERMITTENT EXERCISE are provided in Table 2. Participants' RPE after CONTINUOUS EXERCISE and INTERMITTENT EXERCISE is also provided in Table 2.

Table 2. Group level workload data after completion of the experimental design $(M \pm SD)$. VO2: Oxygen uptake, HR: Heart rate, RPE: Rate of perceived exertion.

	Continuous exercise	INTERMITTENT EXERCISE	R ²	χ^2	Ρ
VO2 (% of VO2max)	70.42 ± 9.99	48.50 ± 6.64	0.65	35.09	< 0.001
HR (bpm)	154.90 ± 17.34	132.91 ± 19.05	0.30	9.97	< 0.01
Blood lactate (mmol/L)	5.55 ± 3.13	9.18 ± 4.29	0.22	6.25	< 0.05
RPE (a.u.)	5.08 ± 1.51	5.60 ± 1.17	0.04	0.91	> 0.05

The linear mixed effects analysis revealed a main EXPERIMENTAL CONDITION effect for all physiological variables and RPE (Table 2). For both VO₂ and HR measures, recordings during CONTINUOUS EXERCISE outperformed

that during INTERMITTENT EXERCISE (fitted difference: 21.92 % \pm 3.70, p < 0.001; 21.59 bpm \pm 6.83, p < 0.01, respectively). There was also a main EXPERIMENTAL CONDITION effect for blood lactate concentration, which was higher during INTERMITTENT EXERCISE compared to CONTINUOUS EXERCISE (fitted difference: 3.66 mmol/l \pm 1.46, p < 0.05). Finally, there was no effect of the EXPERIMENTAL CONDITION on RPE measures, i.e., rated between 5-6 in the 10-points Borg scale for both CONTINUOUS EXERCISE and INTERMITTENT EXERCISE (i.e., corresponding to a "*Strong*"-"*Very strong*" perceived exertion).

III) MI ability analysis

A) Isochrony

The three-way interaction between EXPERIMENTAL CONDITION, TEST and TASK, as well as the two-way interaction between EXPERIMENTAL CONDITION and TASK were removed during the backward stepwise model selection (i.e., both p > 0.05). The linear mixed effects analysis revealed i) a twoway interaction between EXPERIMENTAL CONDITION and TEST, and ii) a twoway interaction between TASK and TEST ($\Omega_0^2 = 0.07$). Isochrony was affected by the EXPERIMENTAL CONDITION by TEST interaction ($\chi^2(1) = 3.40$, p = 0.05). The PRETEST (7.58 % ± 19.55) versus POSTTEST (11.09 % ± 23.50) difference for INTERMITTENT EXERCISE was higher than the PRETEST (12.55 % ± 22.83) versus POSTTEST (10.84 % ± 22.70) difference recorded for the CONTINUOUS EXERCISE (fitted difference: 5.21 % ± 2.82, p = 0.05). The linear mixed effects analysis also revealed that isochrony was affected by the TASK by TEST interaction ($\chi^2(1) =$ 4.30, p = 0.03). As shown in Figure 2, the PRETEST (11.72 % ± 23.37) versus POSTTEST (15.43 % ± 25.75) difference for the WALKING TASK was higher than the PRETEST (8.61 % ± 19.24) versus POSTTEST (6.48 % ± 19.04) difference recorded for the POINTING TASK (fitted difference: 5.85 % ± 2.82, p = 0.03).



Figure 2. Linear mixed effects analysis of isochrony data (i.e., fitted estimates). A. EXPERIMENTAL CONDITION by TEST interaction effect from isochrony measures. B. TASK by TEST interactions from isochrony measures. *p < 0.05; *** p<0.01.

B) MI vividness and difficulty ratings

The three-way interaction between EXPERIMENTAL CONDITION, TEST and TASK, as well as the two-way interactions between EXPERIMENTAL CONDITION and TASK and between TEST and TASK were removed during the backward stepwise model selection carried on vividness ratings (i.e., all p > 0.05). The linear mixed effects analysis revealed i) an EXPERIMENTAL CONDITION by TEST interaction, and ii) a main TASK effect ($\Omega_0^2 = 0.17$). Vividness ratings were first affected by the EXPERIMENTAL CONDITION by TEST interaction $(\chi^2(1) = 4.18, p = 0.04)$. As shown in Figure 3A, the PRETEST (6.59 a.u. ± 1.59) versus POSTTEST (5.77 a.u. ± 1.93) difference for INTERMITTENT EXERCISE was higher than the PRETEST (6.50 a.u. ± 1.64) versus POSTTEST (6.46 a.u.± 1.67) difference for CONTINUOUS EXERCISE (fitted difference: 0.78 a.u. ± 0.38, p = 0.04). Also, a main TASK effect was present ($\chi^2(1) = 18.00, p < 0.001$), attesting higher vividness ratings during the POINTING TASK (6.74 a.u. ± 1.76) compared to the WALKING TASK (5.93 a.u. ± 1.58) (fitted difference: 0.80 a.u. ± 0.19, p < 0.001).



Figure 3. Linear mixed effects analysis of MI vividness data (i.e., fitted estimates). A: Effect of the EXPERIMENTAL CONDITION by TEST interaction on vividness ratings. B: Main effect of TASK on vividness ratings.
The three-way interaction between EXPERIMENTAL CONDITION, TEST and TASK and the corresponding two-way interactions were removed during the backward stepwise model selection carried on MI difficulty ratings (i.e., all p > 0.05). The main effect of EXPERIMENTAL CONDITION was also removed (p > 0.05). The linear mixed effect analysis eventually yielded a main effect of TASK and that the main effect of TEST approached the statistical threshold ($\Omega_0^2 = 0.04$; Figure 3). MI difficulty ratings were marginally affected by the TASK ($\chi^2(1) = 2.58$, p = 0.06). MI difficulty ratings during the WALKING TASK (4.17 a.u. ± 1.87) were higher than those recorded for the POINTING TASK (3.80 a.u. ± 2.15) (fitted difference: 0.37 a.u. ± 0.23). MI difficulty ratings were marginally affected by the TEST ($\chi^2(1) = 2.06$, p = 0.08). MI difficulty ratings during the PRETEST (3.80 a.u. ± 1.96) were indeed marginally lower compared to the POSTTEST (4.17 a.u. ± 2.06) (fitted difference: 0.37 ± 0.25, p = 0.08).

DISCUSSION

The present study investigated MI ability before and after intermittent and continuous exercise of moderate intensity. MI ability was evaluated using a combination of validated behavioral (i.e., isochrony between MI and physical practice) and psychometric (i.e., MI vividness and difficulty self-reports) methods (Guillot and Collet, 2005; Collet et al., 2011a; Guillot et al., 2012). Albeit different, the exercise protocols elicited similar RPE for both experimental conditions (i.e., CONTINUOUS EXERCISE and INTERMITTENT EXERCISE). The fatigue elicited by the continuous and intermittent exercise protocols thus yielded and identical fatigue perception. However, the energy expenditure for CONTINUOUS EXERCISE engaged

to a greater extent aerobic metabolic pathways, whereas INTERMITTENT EXERCISE required a greater contribution from anaerobic metabolic pathways. This was attested by the difference in VO₂ and blood lactate concentrations between the two experimental conditions. Workload data overall corroborate pilot recordings from our team which were carried on in order to build up a reproducible experimental design where the two distinct exercise protocols would emphasize either aerobic or anaerobic metabolic pathways to meet the energy demand without altering effort perception.

At a behavioral level, mental chronometry revealed that MI ability was impaired by the intermittent, but not by the continuous exercise. This finding is congruent with past reports on the effects of exercise on cognitive functions. Brisswalter et al. (2002) distinguished in a seminal review the effects of aerobic and anaerobic exercise on cognitive performances. The authors underlined that 20 minutes of aerobic exercise might actually enhance cognitive functions, most likely due a facilitation on brain oxygen delivery. On the contrary, the authors concluded that exercise primarily engaging anaerobic metabolic pathways impaired cognitive functions. Here, the exercise protocols corresponding to the two experimental conditions were primarily intended to reproduce training contexts, hence focused on the continuous or intermittent nature of the effort rather than controlling the respective contribution of aerobic or anaerobic metabolic processes to the overall energy expenditure. Nonetheless, physiological measures of the workload elicited by the two exercises revealed that the present experimental conditions prioritized either aerobic (i.e., CONTINUOUS EXERCISE) and anaerobic (i.e., INTERMITTENT EXERCISE) metabolic pathways. Overall, behavioral evaluations of MI ability support that the

conclusions by Brisswalter et al. (2002) also apply to motor cognition processes. Intermittent exercise possibly impaired MI ability by affecting cognitive functions. To perform a physical exercise induce a series of afferent signals, which modulate brain activity (Sutoo and Akiyama, 1996; Sutoo and Akiyama, 2003; Van Praag, 2009). Exercises with higher demand of force production are linked with greater muscle micro lesions (Chen and Hsieh, 2001; Chen and Nosaka, 2006; Brentano and Martins Kruel, 2011), and by consequence, greater presence of muscle metabolites in the vascular system. During our intermittent approach, participants were requested to perform a maximal, albeit short, sprint. This could be linked with a greater release of calcium in the blood, increasing dopamine concentration in central nervous system (Sutoo and Akiyama, 1996). Dopamine is a inhibitory component in the brain (Bear et al., 2007), and would increase the cognitive demand necessary to perform a task due its' presence. Indeed, MI is a particularly demanding cognitive process. Gentili et al. (2010) reported that MI practice decoupled from actual training was enough to increase perceived fatigue and decrease concentration (see also, Rozand et al., 2014). MI activates cortical and subcortical networks of the brain motor system comparable to those controlling the actual motor preparation and execution, including the primary motor cortex (Munzert et al., 2009; Hetu et al., 2013; Guillot et al., 2014). This particular area can be divided into an anterior part, of executive nature, and a posterior part, subserving primary cognitive functions such as motor planning (Sanes and Donoghue, 2000). Interestingly, Sharma et al. (2008) reported in a functional magnetic resonance imaging study a smaller cluster distribution within the anterior executive part of the primary motor cortex during MI (compared to physical practice), whereas the cluster distribution within the posterior part of the

primary motor cortex was identical. These neurophysiological findings corroborate the early statements of the motor simulation theory of MI (Jeannerod, 1994; Jeannerod, 2001; O'Shea and Moran, 2017). This theory postulates that MI represents a conscious access to the content of the implicit content of the motor preparation:

"Motor preparation is an entirely non-conscious process, which escapes the subject's awareness (...). If motor preparation, which normally lasts for a very brief period of time, could be prolonged, then the intention to act would become progressively a motor image of the same action". Jeannerod (1994), p. 7.

Interestingly, psychometric measures confirmed the selective impairment of MI ability according to the exercise type. Participants reported decreased MI vividness ratings after the intermittent exercise, but not after the continuous exercise (Figure 3B). This adds to previous findings in support of a relationship between psychometric and behavioral and neurophysiological indexes of MI ability (Di Rienzo et al., 2014). An absence of MI ability impairment consecutive to the continuous exercise seems contradictory with the reports by Di Rienzo et al. (2012), who recorded that a continuous and incremental swimming exercise yielded decreased MI ability of the somersault turn, as revealed by psychometric, behavioral and neurophysiological measures. However, the fatiguing exercise was performed until exhaustion in this experiment, with the final stages of the incremental exercise performed at maximal oxygen uptake. The participants were thus in an exercise scenario requiring an important contribution of the anaerobic pathways to energy expenditure to sustain exercise intensity as the contribution

of aerobic pathways had plateaued. In other words, the exercise paradigm in the study by Di Rienzo et al. (2012) elicited an fatigue state more comparable to that elicited by the intermittent exercise than the continuous exercise of the present experiment.

Furthermore, exercise impaired the MI ability selectively depending on the task type administered during the MI ability evaluation. Both intermittent and continuous exercise affected isochrony for the walking task, whereas isochrony was preserved for the pointing task. During and immediately after a fatiguing exercise, our sensorial systems tend to allocate more attentional resources to the effort perception than to external/environmental factors (Bigliassi, 2015). The amount of information retrieved from the environment is negatively related to the exercise-induced increase in perceived exertion (Bigliassi, 2015; McMorris et al., 2018). This was formalized in the theoretical framework of parallel processing (Rejeski, 1985). MI engages common cognitive motor processes as physical practice. The increase in effort perception in the present experiment (i.e., 5-6 on the Borg scale) may interfere with the allocation of cognitive resources to the MI, irrespective of the task type. In support to this claim, we recorded a marginal increase in perceived difficulty to preform MI for both walking and pointing tasks administered during MI ability evaluation. Yet, walking represents a developmental motor coordination, automated and consolidated by experience in the subcortical centers of motor memory (Collet, 2001). Self-paced walking thus requires a limited amount of cognitive control, limb coordination being primarily controlled by the spinal structures of the central nervous system, which were shown to constantly integrate and process proprioceptive afferents from the lower limbs (Egstrom, 1964; MacKay-Lyons, 2002; Zehr and Duysens, 2004; Courtine,

2012). Upper limb visuo-motor coordinations also represent a developmental and automated motor coordination (Collet, 2001). However, pointing requires a higher degree of attentional focus due to the presence of a target. There is strong evidence of the increased allocation of cognitive resources during pointing tasks, as attested by increased activations of cortical structures within the brain motor system (Astafiev et al., 2003; Cavina-Pratesi et al., 2018). We postulate that MI ability of pointing task was more susceptible to be hampered, due to reduced attentional focus on external/environmental factors associated with the increase in perceived exertion yielded by the continuous and intermittent exercises. An alternative hypothesis relates to the fact that both continuous and intermittent exercises were performed on a cycle ergometer. The exercise protocols thus mainly engaged lower limb muscles, similarly as the walking task. Demougeot and Papaxanthis (2011) insisted that after an isometric exercise recruiting shoulder muscles the isochrony of pointing movements was altered due to changes in sensorial inputs to the motor system in the fatigue state (see also Di Rienzo et al., 2012). This eventually altered motor predictions, which are computed form the current state of the motor system (i.e., forward modeling; Wolpert and Flanagan, 2001; Grush, 2004). Indeed, the authors observed that isochrony changes were restricted to MI of pointing movements with the fatigued upper limb. Also, short amounts of physical practice in a non-fatigued state restored the baseline levels of isochrony. Here, isochrony impairment restricted to the walking task could originate from the central integration of proprioceptive afferents in a fatigued state impacting, in turn, motor predictions of actions involving the lower limbs. This might also explain why isochrony was preserved during MI of the pointing task, which involved the upper limb.

In conclusion, the present study extends current knowledge on the relationship between MI and exercise. Present findings corroborate existing literature data supporting that prolonged exercises eliciting a fatigued body state might hamper MI ability (Demougeot and Papaxanthis, 2011; Di Rienzo et al., 2012). MI frameworks and guidelines for an optimal and efficient practice in both sports and rehabilitation settings should differentiate MI uses in relation to participant's perceived exertion (e.g., Holmes and Collins, 2001; Guillot and Collet, 2008). Specially in sport domain, coachs should build their MI practice program based on programed training cycle, especially knowing that intermittent training sessions might impair MI ability. Further understanding of how MI of motor skills engaging distinct motor cognition process, e.g., highly automated actions controlled by top-down processes or less automated actions relying to a greater on bottom up processes, may be altered by exercise is required. The use of semi-ambulatory central nervous system recordings such as electroencephalography, would bring important information regarding the interdependent relationships between MI ability and exercise.

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II) EFFECT OF MOTOR IMAGERY DURING PRACTICE ON FATIGUE

EXPERIMENTAL CONTRIBUTION #5 : Thiago FERREIRA DIAS KANTHACK, Aymeric GUILLOT, Leandro RICARDO ALTIMARI, Susana NUNEZ NAGY, Franck DI RIENZO. *"Selective efficacy of static and dynamic imagery in different states of physical fatigue"*. PLoS ONE, 11(3), 1-14, 2016.

MI practice has extensively proved to enhance sports performance (Feltz and Landers, 1983, Driskell et al., 1994, Schuster et al., 2011) due behavioral and functional similarities with actual practice leading to activity-dependent neuroplasticity (Debarnot et al., 2014, Di Rienzo et al., 2014a, Ruffino et al., 2017). MI usefulness if correlated with the ability to mentally represent the task (Lebon et al., 2012a), which can be measured by behavioral, physiological and psychological parameters (Collet et al., 2011). Recent findings showed that MI ability can be impaired by local (Demougeot and Papaxanthis, 2011) and general fatigue (Di Rienzo et al., 2012) elicited by one exercise session. Since MI practice is usually recommended to be embedded into actual training (Holmes and Collins, 2001, Guillot and Collet, 2008), to know the effects of fatigue on MI ability, and if MI practice remains useful for performance improvement after exercise is crucial for practical applications. So far, only Guillot et al. (2015) applied MI practice with the intention to control fatigue impairments on performance. Also, dynamic imagery, where low amplitude body movements sufficient to embody tasks' temporal invariants, has demonstrated to not only enhance performance but also induce better mental representation (Callow et al., 2006, Guillot et al., 2013b, Fusco et al., 2014). Thus, in experimental contribution #5 we aimed first to add

more information on the use of dynamic imagery for sports performance, and secondly to test the efficacy of MI and dynamic imagery under fatigue elicited by exercise.



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RESEARCH ARTICLE

Selective Efficacy of Static and Dynamic Imagery in Different States of Physical Fatigue

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Abstract

There is compelling evidence that motor imagery contributes to improved motor performance, and recent work showed that dynamic motor imagery (dMI) might provide additional benefits by comparison with traditional MI practice. However, the efficacy of motor imagery in different states of physical fatigue remains largely unknown, especially as imagery accuracy may be hampered by the physical fatigue states elicited by training. We investigated the effect of static motor imagery (sMI) and dMI on free-throw accuracy in 10 high-level basketball athletes, both in a non-fatigued state (Experiment 1) and immediately after an incremental running test completed until exhaustion (20m shuttle run-test–Experiment 2). We collected perceived exhaustion and heart rate to quantify the subjective experience of fatigue and energy expenditure. We found that dMI brought better shooting performance than sMI, except when athletes were physically exhausted. These findings shed light on the conditions eliciting optimal use of sMI and dMI. In particular, considering that the current physical state affects body representation, performing dMI under fatigue may result in mismatches between actual and predicted body states.

Introduction

Motor imagery is the mental representation of an action without physical execution of the corresponding movement. Experimental data provides ample evidence that motor imagery contributes to enhanced motor performance in both sporting and everyday life motor skills [1-3]. Likewise, motor imagery has been shown to promote motor recovery in injured athletes and in patients suffering from motor disorders [4-7]. Motor imagery further positively affects psychological factors involved in high-level sport performance, e.g. motivation and focus [8, 9]. Due to structural and functional similarities with physical practice (PP), motor imagery can operate on neurophysiological processes mediating motor learning, i.e., activity-dependent

neuroplasticity [7, 10]. Additionally, MI can be used to control non-invasive brain-computer interfaces ([11], for a recent overview). Typically, brain signals recorded during various MI tasks are classified and transduced into electric commands to control a robotic device (e.g., [12, 13]). These technologies emphasizes that brain activity during MI embeds relevant components of the corresponding motor tasks [14, 15].

Nonetheless, imagery guidelines and instructions for effective interventions vary to a great extent across disciplines (sports, music, education, medicine and psychology) (for a review, see [3]). While most training frameworks recommend to directly combine motor imagery with PP during actual training sessions [16, 17], little is known about the optimal guidelines of motor imagery practice, particularly considering that PP may elicit physical fatigue. The effect of fatigue upon motor imagery might change athletes' dispositions towards mental rehearsal. So far, physical fatigue is known to impair motor performance, but recent work suggested that it might also impair imagery accuracy [18, 19], although this deleterious effect is not systematically observed [20]. Recently, Rozand, Lebon [21] reported that mental fatigue has sufficient potential to alter the temporal organization of motor imagery, without necessarily impairing muscle performance (see [22, 23]). Interestingly, there is yet no experimental data comparing the respective effects of different MI content upon different states of physical fatigue.

Several theoretical frameworks were proposed to determine the optimal way to perform imagery and develop effective interventions [16, 17, 24, 25]. Practically, motor imagery should match the spatial and temporal parameters of the corresponding action to achieve optimal transfer from mental representation to actual performance [26, 27]. However, whether adequately embedding motor imagery into actual training sessions—where physical fatigue can be prevalent—has been far less considered. According to its classical definition, MI should be performed without concomitant body movements. Yet, recent modes of MI practice combine MI with actual body movements (e.g., [28]). Such body movements are of limited amplitude, i.e., insufficient to fully mimic the imagined action, but nonetheless sufficient to embody its temporal invariants (e.g., skiers reproducing with hands movements the timing of their slalom according to the curves of the ski slope, while concomitantly imagining their own performance). Guillot, Moschberger [29] investigated the efficacy of dynamic motor imagery (dMI) practice matching the patterns of the high jump. The dMI intervention improved both imagery quality and motor performance. This experiment directly addressed, through dMI, the interrelationships between mental and motor processes to boost the outcome of imagery interventions. Other experimental studies had showed that dMI might contribute to improve motor performance, vividness and confidence of athletes [28], as well as the temporal congruence between actual and imagined actions [30]. While the effects of fatigue on static MI (sMI) mentioned earlier have already been explored, little is known about its effect on dMI and subsequent consequences on motor performance. A related issue of interest is therefore to investigate whether high loads of physical exercise eliciting a physical fatigue state might interfere with both sMI and dMI quality and thus motor performance. Practically, physical fatigue could limit the efficacy of sMI and dMI due to interference between actual and predicted body states [18, 19].

Free-throw is a basketball skill of specific importance due to its complexity and its crucial role on final result, particularly when the score is tight. This role is exacerbated during the last minutes of the match, when players are exhausted [31]. sMI has extensively been shown to improve performance in basketball free-throw shooting [32–34]. The immediate effects of both sMI and dMI on free-throw performance (e.g., during matches) have not yet been investigated. Past protocols foremost implemented sMI practice periods from 1 day (with free-throw performance the next day [32]) to 3 weeks [35], but the effect of practicing sMI and dMI under fatigued states has never been considered. As previously mentioned, physical fatigue is known

to alter physical performance, but might interfere with the capacity of imagining oneself performing an action as well [18, 19]. Fatigue presumably elicits erroneous updates of the internal representation of the action due to the central integration of proprioceptive feedback under altered body state [19, 36, 37]. In the first experiment, we investigated whether sMI and dMI might elicit short-term effects on free-throw shooting accuracy in non-fatigued athletes. Then, we tested the efficacy of sMI and dMI in the same sample of athletes, under a state of physical fatigue corresponding to the last minutes of basketball games.

Experiment 1

Material and Methods

Participants. Ten state-level male basketball players (M = 18.4 years, SD = 0.5; M = 7.3 years of practice, SD = 2.3; 6 hours/day of training, 5 days per week) voluntarily participated in the study. They provided an informed written consent in agreement with the terms of the Declaration of Helsinki (1982). The study was approved by the ethical committee of Londrina State University (Brazil).

Experimental design. The study took place in an indoor court meeting the international standards for line distance, hoop height and ball weight. Each experimental session occurred at the same time of the day for each condition (9 am \pm 1 hour).

Before taking part in the experiment, athletes completed a 4 week sMI program for familiarization, including 2 sessions of 5 min per week embedded in the classical course of regular training. We delivered a limited amount of sMI practice to meet the purpose of familiarization without interfering with the classical course of training. We basically wanted athletes to have basic knowledge of sMI before engaging in the main experiment, hence preventing novelty bias. We intended to familiarize athletes with the different modalities of sMI practice of basketball skills. Athletes were requested to mentally rehearse strategic schemata of their teammates, shooting and passing actions using the first or third person perspective. They only used the first person visual perspective during the first week, combined first person visual perspective and kinesthetic information during the second and third weeks, and only kinesthetic MI during the last week of familiarization. Athletes were systematically instructed to match the spatial and temporal characteristics of the sequences.

Procedure. After familiarization to sMI, athletes went through three experimental conditions (i.e., one time each). Experimental sessions were scheduled within a span of 10 days: i) sMI condition where athletes performed five MI trials of the shooting task using the first-person perspective, before performing five actual free-throws; ii) dMI condition where athletes completed five imagery trials while performing concurrently slight body movements matching the pattern of the shooting task (i.e., limited body movements which do not result in the completion of the task during its imagination, but sufficient to allow an embodiment of the temporal invariants of the task such as the durations of the preparatory/shooting phases of free throw shooting), using the first-person perspective. dMI was followed by five actual free-throws; iii) control condition without any imagery intervention (CONTROL), where athletes remained motionless, discussing their daily training with one of the experimenters for an amount of time corresponding to that allocated to sMI and dMI. This control condition was followed by five actual free-throws. The purpose of having five free-throws for each condition was twofold. First, we wanted to limit the learning/habituation effect. The repeated performance of this closed skill in athletes might have produced ceiling effects which would interfere with the possible gains originating from a preliminary practice of sMI/dMI [33]. Second, we wanted athletes to feel a context which met as much as possible the demands of the free-throws performed during actual basketball games. Usually, players have two consecutive free-throws, sometimes



three according to the type of defensive foul, and must immediately perform at a high level of accuracy. In the present experimental design, we increased this number to 5 to increase sample size. The experimental conditions were provided in a counterbalanced order across participants to control carryover effects. To quantify the perceived carryover training load from one experimental session to another, athletes were presented before each session the modified Borg Scale [38] (Fig 1). Finally, each condition was separated from the 2 others by exactly 72 hours. Each started by a warm-up of five minutes involving running and dribbling with a ball between cones at own self pace.

Imagery interventions. During sMI and dMI, athletes were instructed to imagine as accurately as possible, the free-throw sequence from receiving the ball up to the final phase of shooting. During dMI, they were required to perform slight arm movements and semi-flexion of the legs thus miming the temporal invariants of the actual task. Athletes were positioned in the context of actual free-throw, i.e. on the line in front of the hoop. This was expected to facilitate mental simulation [39]. As indices of both sMI and dMI quality, participants self-reported the level of perceived vividness on a Likert scale ranging from 1 ("*Unclear and inaccurate mental representation*") to 6 ("*Perfectly clear and vivid mental representation*"). They also held a manual timer in the non-dominant hand measuring the time needed to imagine a free-throw sequence, from receiving the ball up to the final shooting phase. We then calculated the delta between actual and imagined free-throw durations as an index of temporal congruence [40].

Shooting accuracy. All trials were recorded with a video camera, to evaluate the number of successful trials and the duration of each free-throw through the number of images between the two action boundaries. Performance was evaluated in terms of converted free-throws (from 0 to 5).

Heart Rate and Exertion Perception. During each experimental session, athletes held a cardiac monitor (Polar $FT2^{\mathbb{R}}$) measuring the heart rate (HR) in beats per minute (bpm). HR was collected immediately after warm-up and sMI/dMI/CONTROL trials, under each condition. We used the OMNI Scale to measure fatigue perception after the warm-up, and after intervention of each experimental session [41].

Statistical Analyses. We used R [42] and *lme4* [43, 44] to build a mixed linear model for each dependent variable (*i.e.*, shooting accuracy, heart rate and OMNI ratings). We entered the experimental conditions as fixed effect, (*i.e.*, dMI, sMI and CONTROL). As a random effect, we had intercepts by participants (i.e., intra-subject analysis). We applied a rank transformation to the dependent variables of interest, in order to increase statistical power [45]. For corrected post-hoc comparisons [46], we iterated the mixed linear model on datasets from which classes of the factor considered were removed to allow dual comparisons. For HR and OMNI data, the recording moment was added as factor of the model (pre- and post-intervention) (Fig 1). The alpha threshold was settled at 5%. Considering the stringent statistical model implemented for data analysis, trends were investigated using the Smallest Worthwhile Change (SWC) [47]. SWC was developed to assess performance changes in sports, and specifically the percentage of chance that a given measure is considered Superior/Trivial/Inferior under two conditions. SWC provides a probability for each class according the following ranges: < 1% for "almost impossible"; 1–5% for "very unlikely", 5–25% for "unlikely", 25–75% for "possible", 75–95% for "probably", 95–99% for "very likely" and >99% for "certain".

Results

Physical fatigue. Data from one participant was not included due to technical failure. All athletes reported similar levels ($M \pm$ SD) of perceived fatigue before each experimental session on the Borg Scale (4.2 ± 2.5, $\chi^2(2) = 0.039$, p = 0.98). OMNI ratings after warm-up and intervention were comparable across conditions without time effect (pre = 2.2 ± 1.9, post = 1.1 ± 1.8, p = 0.79). Mixed linear models yielded a CONDITION * TEST interaction for HR ($\chi^2(2) = 0.019$, p = 0.01). HR values were similar across conditions before intervention (131 ± 15 bpm, p = 0.22). However, HR values after dMI (114 ± 14 bpm) were higher compared to both sMI and CONTROL (96 ± 12 bpm and 93 ± 10 bpm, respectively; p = 0.02).

sMI/dMI accuracy. No difference was found when comparing sMI and dMI vividness (4.5 ± 1.2) and the delta between actual and imagined free-throw durations (Fig 2). At the group level, athletes underestimated actual durations during both sMI and dMI by 0.61 ± 1.2 s (p < 0.01).

Shooting accuracy. Mixed linear modeling yielded a main effect of experimental conditions on shooting accuracy ($\chi^2(2) = 12.01$, p = 0.002). Shooting accuracy was higher following dMI (3.3 ± 1.4 free-throws converted) compared to both sMI (2.3 ± 1.2, p<0.05) and CON-TROL (1.6 ± 1.2, p<0.001) (Fig 2). A trend towards higher shooting accuracy during sMI compared to CONTROL was also observed (p = 0.06). This was confirmed by the SWC analyses, which supported a probable beneficial effect of sMI over CONTROL (i.e., 79% Superior, 17% Trivial, and 4% Inferior).

Experiment 2

Material and Methods

Participants. The same participants as in experiment 1 took part in experiment 2 (18.4 ± 0.5 years; 7.3 ± 2.3 years of practice, 6 hours/day of training 5 days per week). They provided a new informed written consent in agreement with the terms of the Declaration of Helsinki (1982). The study was approved by the ethical committee of Londrina State University (Brazil).

Experimental design. Experiment 2 took also place in the same indoor court as during experiment 1. The experimental intervention occurred at the same time of day for each condition (9 am \pm 1 hour) to avoid circadian effects. We implemented a counterbalanced design in order to control carryover effects between the experiments and conditions of the paradigm.



Fig 2. A. Self-reports of imagery vividness. B. Delta time between actual and imagined durations for sMI and dMI. C. Free-throw shooting accuracy for each athlete under each experimental condition. * p<0.05; ** p<0.01; # Different from 0, p<0.05, & Statistical trend (0.05<p<0.1).

Experimental conditions. The design involved three experimental sessions, which athletes went through once. Experimental sessions were scheduled within a span of 10 days and separated from each other by exactly 72 h. There was therefore a total intervention time of 20 days for experiments 1–2. Immediately after the warm-up (same content as in Experiment 1), the participants completed an incremental running test until exhaustion [48]. They were then subjected to one of the 3 following conditions: *i*) sMI under fatigue (sMI_f) where imagery trials (*n* = 5) preceding the 5 shooting trials were completed immediately after exhaustion; *ii*) dMI under fatigue (dMI_f), allowing slight movements related to the real task during motor imagery where imagery trials (*n* = 5) preceding the 5 free throws were also performed immediately after exhaustion; *iii*) control under fatigue (CONTROL_f) where athletes remained motionless and talked with the experimental sessions were delivered in a counterbalanced order to prevent carryover effects. Participants rated their perceived exertion before each experimental session on the modified Borg Scale [38] for each experimental session.

Exhaustion Test. Athletes performed a shuttle test requesting running between two cones separated from each other by 20 m [48]. Athletes ran from one cone to the other according to the auditory pace of a metronome. The metronome first paced a running speed of 8 km/h, and increased every minute by 0.5 km/h. The test ended in case of complete exhaustion, or if when a participant failed to match the metronome pace 3 times in a row, the test was over and he



Fig 3. Experimental paradigm for Experiment 2 and dependent variables. $CON = Control, sMI_f = Static Motor Imagery under fatigue, dMI_f = Dynamic Motor Imagery under fatigue, HR = Heart Rate, OMNI = Self-exhaustion perception, TL = Training Load from previous day. sMI_f, dMI_f and Shooting times were measured in each condition.$

was considered under fatigue. This test is known as closely reproducing efforts encountered during basketball games.

 sMI_f/dMI_f intervention. For sMI_f and dMI_f , athletes were positioned on the free-throw line for better mental simulation [39]. They were instructed to combine first-person visual imagery with kinesthetic imagery during sMI_f . For dMI_f , slight arm movements as well as semi-flexions were allowed. Immediately after the intervention, we collected the perceived vividness of sMI_f/dMI_f on a Likert scale ranging from 1 ("*Unclear and inaccurate mental representation*") to 6 ("*Perfectly clear and vivid mental representation*"). We also collected sMI_f/dMI_f durations, and calculated the delta between actual and imagined durations, a reliable index of temporal congruence [40].

Heart Rate and Exertion perception. Athletes held a cardiac monitor (Polar FT2[®]). HR (bpm) was collected after warm-up, after the exhaustion test, and immediately after the experimental intervention. Participants rated their perceived level of fatigue on the OMNI Scale after warm-up, after the exhaustion test and after the experimental intervention (Fig 3).

Free-throw performance. Actual shooting times (from the moment participants received the ball up to the final phase of shooting), as well as the number of converted free throws (from 0 to 5), were collected to evaluate shooting accuracy.

Statistical analyses. We implemented the same statistical procedure as in Experiment 1, based on mixed linear models. For HR and OMNI data, we included the recording moment (post warm-up, pre- and post-intervention) as a factor of the model, in addition to the experimental condition factor (sMI_f and CONTROL_f). The alpha threshold was settled at 5%. We also applied the SWC approach [47] as in Experiment 1.

Results

Physical fatigue. All players reported similar levels of perceived fatigue before each experimental session on the Borg Scale ($\chi^2(2) = 0.061$, p = 0.96; sMI_f: 4.3 ± 2.5, dMI_f: 4.2 ± 1.5, CON-TROL_f: 4.4 ± 1.5). We observed no difference among conditions related to HR and OMNI after the warm-up (HR: $\chi^2(2) = 3.91$, p = 0.14, OMNI: $\chi^2(2) = 0.91$, p = 0.93) and post-exhaustion test (HR: $\chi^2(2) = 5.29$, p = 0.07, OMNI: $\chi^2(2) = 4.43$, p = 0.10). As well, OMNI revealed no



Fig 4. HR values and OMNI score after warm-up, pre-intervention and post-experimental intervention. * p<0.05, ** p<0.01, *** p<0.001, [#] Statistical trend (0.05 < p < 0.1).

difference between post-intervention conditions ($\chi^2(2) = 1.14$, p = 0.56) (Fig.4). Lower HR values were recorded ($\chi^2(2) = 7.54$, p = 0.02) after the sMI_f session (131 ± 18 bpm) as compared to those monitored under CONTROL_f and dMI_f sessions (141 ± 17 bpm and 135 ± 15 bpm, respectively, p < 0.05). Values of HR in dMI_f tended to be lower compared to CONTROL_f (p = 0.09) (Fig.4).

Both HR and OMNI values significantly increased between the warm-up and the end of the exhaustion test preceding the experimental intervention (HR: $\chi^2(1) = 83.25$, p < 0.001, OMNI: ($\chi^2(1) = 67.70$, p < 0.001; Warm-up HR: 123 ± 17 bpm, OMNI: 2.2 ± 1.9; Pre-intervention HR: 178 ± 13 bpm, Pre-intervention OMNI: 7.5 ± 1.4). A significant decrease after the experimental intervention was then recorded (HR: $\chi^2(1) = 65.86$, p < 0.001, OMNI: $\chi^2(1) = 27.37$,

p < 0.001; Post-intervention HR: 136 ± 15 bpm, Post-intervention OMNI: 5.7 ± 1.5) (Fig 4).

Shooting accuracy. Self-reports of imagery vividness (sMI_f: 4.4 ± 1.2, dMI_f: 4.1 ± 0.7) and the delta between actual and imagined durations were similar across conditions ($\chi^2(1) = 0.62$,





p = 0.43, and $\chi^2(1) = 0.29$, p = 0.58 respectively, Fig 5). As in Experiment 1, participants overall underestimated actual durations by 1.1 ± 1.3 s (p < 0.01).

Mixed linear modeling yielded a trend for experimental conditions on the free-throw accuracy (sMI_f: 3.5 ± 0.7, dMI_f: 2.6 ± 1.5, CONTROL_f: 2.5 ± 1.5 free-throws converted, $\chi^2(2) = 2.78$, p = 0.09, Fig 5). Shooting accuracy tended to be higher during sMI_f as compared to CONTROL_f (*p* = 0.08). The SWC analysis revealed that sMI_f presented a higher percentage of chance to yield greater shooting accuracy values as compared to those recorded during both dMI_f (88% Superior, 10% Trivial, and 2% Inferior) and CONTROL_f (83% Superior, 14% Trivial, and 3% Inferior).

Discussion

The present study was designed to evaluate the selective efficacy of sMI and dMI under different states of fatigue. Overall, dMI was found to have the most beneficial effect on free-throw performance (Experiment 1), except when athletes were physically exhausted (Experiment 2), a physical state making sMI more efficient.

First, OMNI data showed that participants were in a similar state of perceived exhaustion before engaging in the different conditions for both Experiments 1 and 2. On average, the participants perceived a "moderate" level of fatigue. HR data further revealed that they adequately complied with the experimental instructions, particularly during Experiment 2 where a neat HR increase attested high energy expenditure following the shuttle test. HR data also showed that before completing the experimental conditions, participants were in a similar state of physiological arousal. During Experiment 1, we recorded higher HR values immediately after dMI as compared to both sMI and CONTROL. Indeed, dMI included slight body movements simultaneously with mental representation. This brings an added amount of physical activity potentially contributing to higher levels of cardiac activity. During Experiment 2, we recorded lower HR values under sMIf as compared to both CONTROLf and dMIf. Motor imagery practice is known to temporarily reduce cardiac activity due to the involvement of attentional resources (see [49]). However, the intake-rejection theory early postulated different HR changes according to the focus of attention [50]. Briefly, the authors reported decreased HR when the participants were requested to process external information, whereas they observed increased HR when the participants focused their attention on internal cues. Our results may seem different from what the theory postulated. Yet, although MI is considered an internal process, the content of mental representation is externally and spatially oriented. This suggests that the HR decrease under sMI_c may reflect the focus of attentional resources on the environmental context of the free-throw. This effect might have been emphasized compared to experiment 1 as players exhibited increased levels of cardiac activity immediately after the maximal incremental test. Such MI-related effects occurred to a lesser extent under dMI_f since they were possibly counterbalanced by overt body movement concomitant to motor imagery. From a physiological level of analysis, changes in HR attest to concurrent effects of the parasympathetic and orthosympathetic branches of the autonomic nervous system. We can thus consider that both systems were co-activated when high concentration level was associated with high energy expenditure. Although we did not record physiological data in the present study, recent findings related to autonomic nervous system functioning have demonstrated that the parasympathetic branch could be activated through the nucleus ambiguus which was demonstrated to specifically reduce heart rate activity in case of high cognitive demand (see [51, 52]). This remains a working hypothesis, awaiting further experimental investigation.

An important issue addressed in the present study is whether practicing sMI or dMI was likely to elicit short-term effects on shooting accuracy. In a study involving high-level junior race standard skiers, Callow, Roberts [28] reported higher levels of vividness during dMI than during sMI, hence supporting the potential benefits of dMI in applied sport settings. The positive effects of dMI on motor performance were recently confirmed by Guillot, Moschberger [29] in a sample of high jumpers, while Fusco, Iosa [30] later reported higher levels of temporal congruence between PP and dMI rather than between PP and sMI while imagining locomotors sequences.

Data from Experiments 1 and 2 provided evidence that no deleterious effects occurred under sMI or dMI. Interestingly, higher shooting accuracy was recorded in the dMI condition for Experiment 1 and the sMI_f condition for Experiment 2. Although we support that sMI contributed to increase basketball performance [33], findings from Experiment 1 confirmed better efficacy from dMI [28, 29], and further demonstrated that dMI can improve immediate subsequent motor performance when players are not physically fatigued. Jackson, Lafleur [53] underlined three key components involved in motor performance improvement over time: *i*) declarative knowledge, which refers to the explicit information about the skill available to the participant, *ii*) infra-conscious processes referring to implicit knowledge (procedural memory) related to the skill that participants are able to implement during motor processing but cannot verbally describe (e.g., complex muscle synergies, etc.), and *iii*) the feedback loop of actual skill execution which participants use to correct and stabilize motor programs. Based on this theoretical framework, sMI involves the two first aspects (i.e., declarative knowledge and infra-conscious processes), whereas dMI might involve the three aspects of the model, hence providing additional benefits.

Experiment 2 demonstrated that physical fatigue strongly altered these beneficial effects of dMI, as sMIf further impacted performance, while dMIf did not (as compared to the CONTROL condition). This result first supports the sMI efficacy on shooting tasks [54-57], and more specifically in free-throw shooting [32]. The superiority of sMI_f over dMI_f might be explained by the interference between actual and predicted body states in exhausted participants. Previous experiments showed that imagery ability could be degraded by physical fatigue [18, 19]. The authors inferred a possible erroneous update of the internal representation of the action due to fatigue. In our experiments, fatigue was elicited by a running test and athletes had to imagine a shooting task. However, as action representation was embodied and integrated the current state of the motor system [19], physical fatigue might have led to inappropriate state estimation provided by the forward model during dMI_f. Physiological body state is known to affect body representation through subtle changes in proprioceptive inputs to the central nervous system [58]. In other words, physiological body state plays an indirect role during central processing of imagined actions, since these involve predictive models derived from the current state of the motor system [15]. Hence, combining body movements during dMI as athletes were fatigued possibly increased mismatches between actual and predictive body states. Practically, under fatigue, dMI may be assimilated to a form of incongruence between imagery task and body state [59].

One of the major finding of our experiments is that MI selectively contributed to enhance motor performance, with the optimal use of sMI under fatigue, concurrently with dMI being linked to exhaustion/energy expenditure. dMI might have higher abilities than sMI to improve movement accuracy when athletes are not fatigued, whereas under physical fatigue, sMI would be more efficient. Although the present study remains a pilot experiment with a limited sample size including only young athletes, it provides fruitful new insights about the optimal use of sMI and dMI. As preliminary recommendations, we argue that dMI may be prioritized in activities which do not lead to extreme effort and fatigue or in the early phases of the game, i.e. when athletes are not fatigued. In contrast, although dMI is not harmful or debilitative, this is not the most relevant alternative in a fatigued state or when athletes are exhausted. Conversely, sMI should thus be preferred in activities where accuracy is crucial and where fatigue can concurrently impair performance. To overcome the potential issue of the limited number of shooting trials in the present pilot experiment, future studies testing the effect of sMI/dMI practice before each free-throw may afford a greater number of trials, while concomitantly controlling ceiling effects due to the repeated practice of the skill. However, such experimental design would not match the demands of an actual basketball game where the number of consecutive shooting trials remains limited. An interesting perspective of the present work would be testing whether sMI and dMI might selectively impact recovery processes in a rehabilitation context according to different fatigue/functional levels.

Supporting Information

S1 Dataset. Raw data collected during the experiment. (CSV)

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Author Contributions

Conceived and designed the experiments: TFDK AG LRA FDR. Performed the experiments: TFDK LRA. Analyzed the data: TFDK FDR AG. Contributed reagents/materials/analysis tools: TFDK AG LRA SNN CC FDR. Wrote the paper: TFDK AG SNN CC FDR.

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EXPERIMENTAL CONTRIBUTION #6 : Franck DI RIENZO, Yoann BLACHE, **Thiago FERREIRA DIAS KANTHACK**, Karine MONTEIL, Aymeric GUILLOT. *"Short-term effects of integrated motor imagery practice on muscle activation and force performance"*. Neuroscience, 305, 146-156, 2015.

The beneficial effect of MI practice on force enhancement is welldocumented in the literature (Yue and Cole, 1992, Ranganathan et al., 2004, Wright and Smith, 2009, Lebon et al., 2010, Yao et al., 2013). In general, strength gains relative to MI practice are explained by an amelioration in cognitive pathways, ie., coordination between against and antagonist muscles involved in the movement (Yao et al., 2013). Considering that MI practice is recommended to be combined with actual practice (Holmes and Collins, 2001, Guillot et al., 2005a, Wright and Smith, 2009),, it is surprising that so far only a few studies investigate MI practice included in actual training (Lebon et al., 2010), and none investigated the immediate effects of MI practice on force development. Thus, in experimental contribution #6 we verified whether MI practice applied in rest periods of a training session improved maximal isometric contraction force.

SHORT-TERM EFFECTS OF INTEGRATED MOTOR IMAGERY PRACTICE ON MUSCLE ACTIVATION AND FORCE PERFORMANCE

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Abstract-The effect of motor imagery (MI) practice on isometric force development is well-documented. However, whether practicing MI during rest periods of physical training improves the forthcoming performance remains unexplored. We involved 18 athletes in a counterbalanced design including three physical training sessions scheduled over five consecutive days. Training involved 10 maximal isometric contractions against a force plate, with the elbow at 90°. During two sessions, we integrated MI practice (focusing on either muscle activation or relaxation) during the inter-trial rest periods. We measured muscle performance from force plate and electromyograms of the biceps brachii and anterior deltoideus. We continuously monitored electrodermal activity (EDA) to control sympathetic nervous system activity. MI of muscle activation resulted in higher isometric force as compared to both MI of muscle relaxation and passive recovery (respectively +2.1% and +3.5%). MI practice of muscle relaxation also outperformed the control condition (+1.9%). Increased activation of the biceps brachii was recorded under both MI practice conditions compared to control. Biceps brachii activation was similar between the two MI practice conditions, but electromyography revealed a marginal trend toward greater activation of the anterior deltoideus during MI practice of muscle activation. EDA and self-reports indicated that these effects were independent from physiological arousal and motivation. These results might account for priming effects of MI practice vielding to higher muscle activation and force performance. Present findings may be of interest for applications in sports training and neurologic rehabilitation. © 2015 IBRO. Published by Elsevier Ltd. All rights reserved.

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responses; EMG, electromyogram; iEMG, integrated electromyogram; MI, motor imagery.

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INTRODUCTION

Motor imagery (MI), i.e., the mental rehearsal of an action without any overt execution, is a cognitive operation involving executive parts of the brain motor system (for reviews, see Lotze and Halsband, 2006; Munzert et al., 2009). MI recruits cerebral substrates controlling the actual preparation and execution of the movement including primary somatosensory and motor cortices (Munzert et al., 2009). In several experiments, subliminal muscle activations were detected during MI. Neuromuscular activity was primarily recorded within the prime movers of the imagined movement (Bird, 1984; Boschker, 2001). Despite challenging data (e.g., Personnier et al., 2010), subliminal muscle activation was found to increase according to the intensity of the imagined contraction (Bonnet et al., 1997; Boschker, 2001). The psycho-neuromuscular theory early postulated that similar electromyographic patterns could occur during both physical practice (PP) and MI (Jacobson, 1930, 1932; Wehner et al., 1984), albeit with reduced magnitude (Gandevia et al., 1997). Subliminal muscle activity was even found to reflect the type of muscle contraction imagined by the participant (i.e., isometric, concentric and excentric; Guillot et al., 2007), while brain activations during MI appeared to covariate with the imagined force level (Mizuguchi et al., 2014). Taken together, these data support that subliminal muscle activation during MI might result from an incomplete inhibition of the somatic motor command (see Jeannerod, 1994 for a pioneering discussion).

Somatic motor commands addressed to muscles are paralleled by neurovegetative commands to internal organs and smooth muscles of blood vessels through the parasympathetic and sympathetic pathways. The autonomic nervous system permanently adjusts the metabolic activity to face forthcoming demands in energy. The autonomic correlates of PP are wellreproduced during MI. For instance, Decety et al. (1991) provided evidence that both heart and respiratory rates increased proportionally according to the imagined walking speed. Autonomic nervous system recordings can thus be used to monitor MI in real time (for a review, see Collet et al., 2013).

Due to structural and functional similarities with PP, MI practice has been used as a training method to enhance

motor performance (Jackson et al., 2001; Morris et al., 2005). MI practice can facilitate motor learning and improve motor recovery after injury (for an overview, see Guillot and Collet, 2008). A more limited number of studies investigated its effects on strength. The pioneering study addressing this issue provided evidence that a 30-min session of MI practice increased the isometric strength of the quadriceps by 16% as compared to a control group not subjected to any form of physical or mental training (Cornwall et al., 1991). Most subsequent experiments yielded positive effects of MI practice, primarily on the development of maximal isometric strength (Yue and Cole, 1992; Smith et al., 2003; Wright and Smith, 2009). Gains usually ranged from 10% to 30% on both distal and proximal muscles of the upper limb (Yue and Cole, 1992; Wright and Smith, 2009). There is a general consensus that strength gains were of central origin, and occurred in the absence of any peripheral change, e.g., muscle hypertrophy (Yue and Cole, 1992; Ranganathan et al., 2004). Improvements may be grounded in cortical neuroplasticity, i.e., the capacity of neurons to reorganize their connectivity in response to the behavioral demand, hence leading to more efficient drive of motor units (spatial recruitment and stimulation intensities). Ranganathan et al. (2004) earlier reported a direct relationship between changes in cortical motor output and muscle performance after MI practice. Yao et al. (2013) confirmed that kinesthetic MI practice of maximal isometric force increased the maximal isometric force of elbow flexors through cortical motor and pre-motor neuroadaptations.

To date, most studies delivered MI practice interventions alone (Cornwall et al., 1991; Yue and Cole, 1992; Ranganathan et al., 2004), or in addition to physical training (e.g., Wright and Smith, 2009; Reiser et al., 2011). Only few investigated the impact of embedding MI practice into actual training of strength (e.g., Lebon et al., 2010). The immediate effects of MI practice during inter-trial periods of strength training sessions has not yet been investigated. This is somehow surprising as MI practice frameworks usually recommend practicing in combination with PP, in a similar context to that of actual training (Holmes and Collins, 2001; Guillot et al., 2005; Wright and Smith, 2009). In the present experiment, we addressed whether MI practice during rest periods of physical training improved maximal isometric force. We tested the selective effects of MI practice focusing either on muscle activation or relaxation on force and muscle performance compared to a passive recovery condition. We hypothesized that activating MI practice would outperform both relaxing MI practice and passive recovery since it involved a specific focus on the voluntary drive addressed to the somatic effectors of the force task. MI practice focused on muscle relaxation was expected to control for attention/placebo effects. Passive recovery was finally considered the reference condition since it is the usual modality of recovery during inter-trial periods. We aimed to provide original insights into the rules of MI practice for future applications in sports and rehabilitation (e.g., Lebon et al., 2012). A fundamental guestion finally related to the potential "online" benefits of MI practice

on muscle activation, by contrast to *"offline"* adaptations obtained after extended periods of practice decoupled from the immediate context of training.

EXPERIMENTAL PROCEDURES

Participants

Participants (n = 18, mean age = 19.31 ± 1.25 years) were recruited from the Faculty of Sports Sciences of the University Claude Bernard Lyon 1 (F-69100, Villeurbanne). All were right-handed inter-regional male athletes in terrestrial sports (i.e., tennis, volleyball, handball and climbing). They had a background of 2 years in upper limb muscle training in their own competing activities. No information concerning the purpose of the study was provided until completion of the design. The local review board approved the experiment, and participants' written consent was obtained according to the statements of the Declaration of Helsinki (1982).

Experimental design

The design was scheduled over five consecutive days and included three physical training sessions involving 10 trials of maximal isometric contractions (see below). To avoid circadian effects, training sessions were performed at the same time of the day (12 am before lunch), lasted 30 min, and were separated from each other by 48 h (i.e., one entire day interposed between each recording day). Experimental conditions (n = 3)were delivered during inter-trial periods of the training session: (i) MI practice of muscle activation (activating MI), (ii) MI practice of muscle relaxation (relaxing MI), and (iii) Passive recovery where the participants listened passively to three blocks of information about the international sports news (12 s each; control). Relaxing MI was expected to control for placebo effects (e.g., athletes' expectations toward the efficacy of MI practice) since it involved a specific focus on the biceps brachii recovery between force trials. The control condition aimed to control for the attention paid to audio instructions during MI conditions. To overcome carryover effects (e.g., residual muscle fatigue from one training session to another), we implemented a fully counterbalanced design with three participants assigned to each of the six possible order conditions (block randomization).

Strength training sessions

Participants sat on a bench, warmed-up and familiarized with experimental instructions for 15 min (see Appendix A, "*Warm-up*" and "*Familiarization*" for further description). Then, they were requested to perform 10 successive maximal flexions of their dominant elbow against an immobile force platform placed in front of them (isometric contractions) (Fig. 1A). They sustained their effort during 12 s. We used an auditory stimulus (110 Hz–50 dB) to trigger each trial start and end. Hand position was rigorously controlled by measuring that the



Fig. 1. (a) Representation of the experimental settings including (1) an inverted force platform on which the participants exerted maximal isometric contractions (vertical arrow indicated by the participant), (2) electromyography recordings and (3) EDA recording. Body position was standardized to prevent compensatory movements of the trunk and isolate the performance of elbow flexors. (b) Surface muscle electrodes were placed on the *anterior deltoideus* (1) and *biceps brachii* (2) of the dominant hand. (c) EDA sensors were placed on the second phalanx of the second (1) and third digits (2) of the non-dominant hand. (d) The inter-trial periods of rest lasted 1 min during which experimental conditions were delivered.

wrist, hand palm and fingers were in *flat* contact with the force plate (Fig. 1A). Goniometers controlled that the required static position was respected across all trials (90° between the forearm and the arm). Experimenters visually controlled that the arm constantly kept contact with the trunk. Trunk position was normalized using a reclining seatback keeping permanent contact with the back of the head, thoracic vertebras and pelvis (Fig. 1A). Participants constantly fixed a cross mark placed on the wall at the height of their eyes.

The experiment aimed at studying the effect of three recovery conditions on isometric force performance. Inter-trial periods lasted 1 min during which participants remained motionless with the arms resting on their thighs. For activating MI and relaxing MI, each trial lasted 12 s and was triggered by an audio stimulus (240 Hz, 50 dB). Three MI trials were completed during each recovery period of 1 min (Fig. 1D). Participants were instructed to use kinesthetic and visual imagery concurrently (see Appendix B, "*MI scripts*"). Experimenters visually controlled the absence of overt motion during MI practice.

Measurements

Force performance. The elbow flexion force was measured with a force platform (AMTI, model OR6-7-2000, Watertown, Massachusetts, USA, Fig. 1A).

Signals were sampled at 1000 Hz. After performing a frequency and residual analysis on raw signals, data were smoothed with a zero-lag 4th-order low-pass Butterworth filter with a cut-off frequency of 20 Hz. For each trial, the sudden force increase in response to auditory stimulus was determined with a threshold detection function (Matlab[®]). The total force was calculated by integrating the force slope with respect to the 12 s of each trial (trapezoid rules). Total force data were finally normalized in percentage of the maximal isometric force trial completed during the warm-up (see Appendix A).

Electromvography. We recor-Physiological data. ded electromyograms (EMGs) from agonist muscles during the force trials. EMG recordings were expected to bring complementary data to that from the force platform. Both dependent variables respectively addressed the effect of MI practice at the physiological and behavioral levels. We recorded the EMG of the biceps brachii using pairs of surface electrodes (EMG Triode, nickel-plated brass, 1 cm in diameter, inter-electrode distance = 2 cm, gain = 500, Thought Technology, Montreal, Canada, Fig. 1B). Pilot recordings revealed that the anterior deltoideus frequently assisted the elbow flexion task against the force platform at maximal intensities. Hence, we also recorded the EMG of the anterior deltoideus, considered a synergist muscle
(Fig. 1B). After shaving and cleaning the skin with alcohol, EMG sensors were positioned according to usual recommendations of the SENIAM project (Surface ElectroMyoGraphy for the Non-Invasive Assessment of Muscles) (Hermens et al., 2000). Electrode edges were outlined with a marker pen, and pictures were taken to ensure reproducible electrodes positioning across sessions. We collected EMG signals using the Flexcomp Infiniti system (Thought Technology, Montreal, Canada, 2048 Hz). Offline, EMG signals were rectified and smoothed with a band-pass of 20-500 Hz (Butterworth filter). The integrated EMG (iEMG) was calculated from the smoothed rectified EMG with respect to the 12 s of sustained maximal isometric contractions. iEMG data were finally normalized in percentage of the maximal isometric force trial completed during warm-up (see Appendix A).

Autonomic nervous system recordings. We continuously recorded electrodermal activity (EDA) as an index of sympathetic activation during physical training. Changes in EDA result from the activity of eccrine sweat glands (for an exhaustive review, see Collet et al., 2013). These are under the unique control of the sympathetic branch of the autonomic nervous system through acetylcholine release, and represent an exception to the principle of dual innervation (Shields et al., 1987). We recorded EDA using two 50-mm² unpolarizable Ag/AgCI electrodes (Clark Electromedical Instruments, Ref. E243) placed on the second phalanx of the second and third digits of the non-dominant hand (Fig. 1C), held by adhesive tape. We also used a 5-µA constant current to limit current density (10 µA/cm²). Isotonic conductive paste improved skin/electrode contact.

EDA recordings were expected to bring reliable information about general physiological arousal, but were not used as an index of force output. Indeed, the sympathetic pathways innervating eccrine sweat glands and blood vessels of the skeletal muscles are anatomically and functionally segregated (Wallin and Fagius, 1986, 1988; Jänig and Häbler, 1999). EDA recordings thus controlled physiological arousal across sessions of the counterbalanced paradigm (Collet et al., 2011). We expressed EDA in the form of skin resistance. With reference to basal level, skin resistance tonic values should decrease - or at least remain constant - as participants sustain their engagement/motivation toward task completion. By contrast, boredom or mental strain should result in increased skin resistance attesting reduced sympathetic activity (Collet et al., 2011). Skin resistance phasic values, i.e., electrodermal responses (EDR) to various stimuli, are characterized by a sudden drop of the EDA slope, followed by a slower and steady return to the baseline (for a more exhaustive description, see Vernet-Maury et al., 1995). EDR amplitude was standardized, i.e., reported to the basal level of the session.

Self-reports. After training, participants' compliance to experimental instructions was assessed through semistructured interviews. After each session, they reported the perceived level of motivation to complete the experimental paradigm on a 10-point Likert scale (0: no motivation, 10: very high motivation). When the training session involved MI practice, MI vividness was also measured on a 10-point Likert scale (0: no image at all, 10: vivid and accurate MI).

After completion of the paradigm (including the three experimental sessions), each participant was requested to indicate the training session during which he thought he performed at the highest level of force if the performance from the 10 successive trials of each session were pooled.

Statistical analyses

We used R (R Core Team, 2014) and Ime4 (Bates et al., 2014) to perform a linear mixed effects analysis of force platform and physiological data (i.e., EMG and EDA). As fixed effect, we entered the factor RECOVERY CONDITION (i.e., control, activating MI and relaxing MI). As random effects, we had intercepts for subjects and TRIALS (1 to 10). A neat force decrease was expected from trials 1 to 10, particularly marked during the first trials considering the patterns of force decreases elicited by maximal isometric contractions (Kroll, 1968; Camic et al., 2013; for human and animal data). Mixed linear models enabled to account for the amount of variance due to inter-day variations at the participant level when testing the RECOVERY CONDITION effect at the group level (in addition to the counterbalanced design). Inspection of residual plots did not reveal any obvious deviation from homoscedasticity or normality. The p-values were obtained by likelihood ratio tests of the full model against the model without the effect in question (Winter, 2013). For post-hoc investigations, mixed linear models were iterated on datasets from which classes of the factor considered were removed to allow dual comparisons. We applied Holms' sequential Bonferroni corrections. The alpha threshold was settled at $\alpha = .05$.

Self-reports were obtained using ordinal scales. Due to assumption of non-Gaussian distribution, we used non parametric tests. Friedman's test allowed comparing the levels of self-reported motivation and MI vividness across experimental sessions.

RESULTS

Force data

Raw total force data are provided in Appendix C. Total force was affected by the RECOVERY CONDITION ($\chi^2(2) = 24.99$, p < .001). Random effect coefficients for TRIALS confirmed the decrease in performance from trials 1 to 10, and particularly between trials 1 and 2 ($\simeq 15\%$; Fig. 2). We recorded higher isometric force during activating MI vs. both relaxing MI [2.1 ± .01% of fitted difference (standard error)] and control (3.5 ± .01% of fitted difference; Fig. 2). Total force was also 1.9 ± .01% higher (p = .02) during relaxing MI as compared to control (Fig. 2).

Electromyography data

Raw iEMG data are provided in Appendix C. iEMG from the *biceps brachii* was affected by the RECOVERY CONDITION ($\chi^2(2) = 31.51$, p < .001) (Fig. 3a).



Fig. 2. Integrated elbow flexion force (group level) from force trials 1 to 10 of physical training for experimental condition (see also Appendix C, "Data table").

Random effect coefficients for TRIALS for the *biceps brachii* iEMGs revealed a decrease in muscle activation from trials 1 to 10, which paralleled force data. This was particularly pronounced between trials 1 and 2 (\simeq 15%; see Appendix C, "*Data table*"). For the RECOVERY CONDITION, post-hoc analyses yielded higher EMG activity within the *biceps brachii* during both activating MI and relaxing MI as compared to control (p = .02 and p < .001, respectively, corresponding to a fitted difference of $8.2 \pm 2.0\%$ and $10.7 \pm 1.6\%$). The difference between activating and relaxing MI was not significant (p = .23).

The linear mixed effect analysis revealed that the RECOVERY CONDITION did not affect iEMG from the *anterior deltoïdeus*, even though the effect approached the statistical threshold ($\chi^2(2) = 4.19$, p = .12) (Fig. 3b). Fixed effect coefficients showed that this marginal effect originated from a trend toward higher iEMG values during activating MI as compared to both relaxing MI and control condition (p = .08 and p = .16, respectively, corresponding to a fitted difference of $3.6 \pm 2.0\%$ and $3.8 \pm 2.7\%$).

EDA

Tonic EDA presented a regular decrease throughout physical training from 110% to 90% of the basal value, for all experimental conditions (Fig. 4). Standard deviation was reduced during trials 1-4 as compared to trials 5-10 (Fig. 4). Higher variability in EDA during the first trials might reflect adjustments of the autonomic nervous system to task demand to reach regular and adjusted autonomic response patterns (trials 4-7). Higher variability in EDR during trials 7-10 might reflect inter-individual variability in autonomic adaptations to physical fatigue. We also observed that basal EDA was higher under the relaxing MI condition (291.47 \pm 114.99 k Ω) than during both activating MI and control (247.04 k Ω ± 112.46 and 278.18 k Ω ± 85.80, respectively).

For phasic EDA (i.e., EDR), mixed linear modeling revealed that RECOVERY CONDITION affected the response amplitude evoked by the force trials $(\chi^2(2) = 57.92, p < .001, R^2 = .56)$. Post-hoc analyses yielded higher EDR amplitudes during both relaxing and activating MI as compared to control (48.38 k Ω ± 28.8 34.78 k Ω ± 23.6 vs. 29.44 k Ω ± 18.4, both and p < .001; Fig. 4). Relaxing MI was also associated to slightly higher EDR amplitudes than activating MI $(1.4\% \pm 0.4 \text{ of difference}, p = .005)$. EDR amplitudes presented a moderate decrease from trials 1 to 10, particularly during the last trials of the session (see Fig. 4; Appendix C, "Data table"). We found no statistically significant relationship between EDR amplitude and total force decrement across trials and conditions ($\chi^2(2) = 1.94, p = .38$).

Self-reports

Participants reported a strong adherence to experimental instructions, particularly concerning the requested maximal training intensities during the force trials. They reported high and constant levels of motivation throughout sessions (median self-reports ranging from 8.0 to 8.5 across experimental conditions on the 10-point scale; Friedman's Chi-squared = 2.07; p = .35). MI ratings of vividness were comparable between activating MI and relaxing MI (median = 7 for both on the 10-point Likert scale; Friedman's Chi-squared = 0; p = .99).

Finally, participants felt more efficient during activating MI (69%) than during both relaxing MI and the control condition (i.e., respectively 25% and 6% of self-reports; $\chi^2 = 9.87$; p = .007).

DISCUSSION

The present study was designed to address the possibility of achieving short-term strength gains by embedding MI practice during the rest periods interposed between maximal isometric force trials. Self-reports associated with polynomial patterns of motor performance and



Fig. 3. (a) Integrated electromyogram (iEMG) from *biceps brachii* across the 10 trials of physical training, for each experimental condition (Appendix C, "*Data table*"). (b) iEMG from the *anterior deltoideus* across the 10 trials of physical training, for each experimental condition (Appendix C).



Fig. 4. Averaged standardized skin resistance values (plain line) recorded during physical training with standard deviation (dotted line). Trials (from 1 to 10) are indicated by the vertical dotted lines.

muscle activation decrease across trials provided reliable evidence that participants engaged in a maximal isometric effort (Kroll, 1968; Babault et al., 2006; Camic et al., 2013). This was somehow expected since we selected experienced athletes in upper limb force training. MI practice focused on muscle activation was expected to improve performance as compared to a passive recovery condition, while MI practice of muscle relaxation was considered a placebo control condition (i.e., several participants believed that it could facilitate recovery processes and limit inter-trial strength loss).¹ Experimental results

¹ This could be an interesting research hypothesis, yet we did not find experimental data supporting such possible effects.

Integrated vertical force (I	/ s)									
ACTIVE MI RELAXING MI PASSIVE RECOVERY Integrated electromyogran	2593.88 ± 130.83 2505.44 ± 127.48 2493.77 ± 145.69 1 form the biceps bra	2343.76 ± 131.03 2268.20 ± 135.15 2264.47 ± 138.77 <i>chii (mV s</i>)	2272.58 ± 119.87 2233.19 ± 126.34 2187.06 ± 121.85	2178.07 ± 98.15 2155.57 ± 112.38 2165.48 ± 126.50	2197.62 ± 104.76 2167.29 ± 113.38 2167.41 ± 118.86	2134.62 ± 110.59 2103.68 ± 125.50 2079.72 ± 108.82	2124.83 ± 107.95 2083.92 ± 103.12 2042.44 ± 114.98	2101.69 ± 100.07 2053.15 ± 105.36 2058.82 ± 107.15	2053.90 ± 99.20 2035.74 ± 107.20 2037.26 ± 117.97	2067.68 ± 109.00 2021.60 ± 111.43 1996.35 ± 117.05
ACTIVE MI RELAXING MI CONTROL Integrated electromyogram	0224.19 ± 1306.25 0534.59 ± 1348.80 9046.59 ± 1101.95 <i>i form the anterior de</i>	8661.81 ± 1136.45 8428.22 ± 1096.86 7741.13 ± 1062.00 <i>itoideus</i> (<i>mV s</i>)	8902.61 ± 1211.06 8536.71 ± 1030.31 7606.86 ± 1078.12	8165.28 ± 1157.32 8148.78 ± 1008.04 7371.68 ± 1026.61	8545.57 ± 1244.94 8442.42 ± 946.07 7476.69 ± 963.80	8359.78 ± 1128.36 8470.13 ± 1035.62 7254.75 ± 1019.41	8246.47 ± 1057.12 8267.26 ± 995.90 7203.22 ± 1004.62	8343.33 ± 1026.25 8518.53 ± 1033.00 7501.92 ± 1044.83	8134.30 ± 1084.06 8333.97 ± 1027.06 7108.99 ± 1151.68	8291.81 ± 1106.34 8566.31 ± 1147.80 7098.26 ± 1124.74
ACTIVE MI RELAXING MI CONTROL Skin resistance response.	5473.06 ± 824.05 4794.81 ± 884.55 4302.07 ± 729.18 amplitudes (% of bas	4265.51 ± 629.30 3968.74 ± 674.84 3759.08 ± 626.76 el value in $k\Omega$	4368.87 ± 619.05 4154.92 ± 666.24 3585.48 ± 611.66	4169.68 ± 567.03 3798.13 ± 657.59 3526.39 ± 616.35	3903.86 ± 639.45 3726.92 ± 680.92 3241.84 ± 623.71	4025.32 ± 626.88 3506.55 ± 593.83 3524.32 ± 618.78	3863.32 ± 609.04 4140.94 ± 647.40 3461.35 ± 653.06	3955.31 ± 628.63 3762.62 ± 685.03 3765.74 ± 691.72	4070.78 ± 666.16 3672.60 ± 660.89 3248.52 ± 589.96	3809.05 ± 668.73 3446.63 ± 562.40 2759.84 ± 454.64
ACTIVE MI RELAXING MI CONTROL	15.48 ± 2.72 17.63 ± 3.88 16.08 ± 2.43	15.23 ± 2.92 19.40 ± 3.67 11.06 ± 1.88	13.84 ± 2.59 17.49 ± 2.41 12.45 ± 1.57	12.71 ± 2.29 15.58 ± 2.13 10.05 ± 1.40	13.85 ± 2.48 17.22 ± 2.44 9.35 ± 1.41	13.92 ± 2.36 16.83 ± 2.11 10.33 ± 1.23	14.13 ± 2.33 16.65 ± 1.98 9.81 ± 1.24	1.40 ± 2.40 15.74 ± 1.74 7.03 ± 1.16	13.80 ± 2.42 14.09 ± 1.79 8.91 ± 1.52	13.63 ± 1.85 14.29 ± 1.68 10.28 ± 1.79

Table 1. Group mean ± standard errors recorded for each dependent variable of interest (see Experimental procedures), during each of the ten trials of physical training (from left to right). MI: Motor imagery

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confirmed this hypothesis. We ruled out order effects since we implemented a fully counterbalanced design. Data analysis was performed with mixed linear models. This accounted for the inter-day variations at the participants' level when testing the effect of recovery condition at the group level.

Isometric strength and surface iEMG are highly correlated variables (Moritani and deVries, 1978). During isometric force development, muscle performance is limited by central inhibition factors limiting motor units recruitment during the early stages of training (Babault et al., 2006). Rapid improvements in maximal isometric strength are due to neural adaptations, particularly a breakdown in central inhibition improving motor units recruitment and synchronization. Compared to both control and relaxing MI, activating MI yielded higher total force values. We received no feedback supporting that participants expected this condition to be more efficient than the two others. iEMG from the biceps brachii recorded during activating MI was higher than during control. However, while force performance was higher during activating MI as compared to relaxing MI, iEMGs from the biceps brachii were similar. This result somehow challenges the assumption that activating MI improved force performance through changes in muscle activation. Nonetheless, the mixed linear effects analysis yielded a statistical trend toward higher iEMG values from the anterior deltoideus during activating MI compared to both relaxing MI and control. This possibly reflects a greater synergy between the biceps brachii and the anterior deltoideus under activating MI. Indeed, compared to relaxing MI where the MI practice only focused on the biceps brachii, activating MI involved mental rehearsal of the whole upper limb coordination at maximal intensities. MI is known to replicate muscle synergies through specific patterns of corticospinal facilitation (Stinear, 2010). EMG recordings also revealed that agonist and synergist muscles coordination was adequately reproduced during MI (Guillot et al., 2007; Lebon et al., 2008). Gandevia et al. (1997) argued that such subliminal muscle activities could trigger a feedback loop promoting more efficient neural drive during future executions of the mentally rehearsed task. The postulates of the psycho-neuromuscular theory were elegantly synthesized by Jackson et al. (2001):

"The (...) theory proposes that micronerve impulses (...) facilitate[e] (...) future performance by priming specific "mental nodes" or "patterns of movement" necessary to execute a motor task", p. 1137.

Albeit this remains a working hypothesis (since iEMG was only measured during the force trials), central processing during activating MI could have "*primed*" neural excitability within task-specific somatic pathways, leading to increased muscle activation and intermuscular coordination through a more efficient recruitment of motor units (i.e., with reference to psycho-neuromuscular theory). "*Priming*" refers to a learning process where a given stimulus triggers a rapid change in behavior (for further description and a review

of applications to motor learning and rehabilitation, please see Stoykov and Madhavan, 2015). Integrative neuroscience underlined that actions may be organized according to hierarchical models (Schack, 2004; Zentgraf et al., 2009; Schack et al., 2014). These involve cognitive and sensorimotor levels of action control, assuming both representational and regulation functions (Jeannerod and Decety, 1995; Schack, 2004). At the cognitive level, MI practice is likely to reinforce the structure of motor representations, hence mediating increased expertise (Frank et al., 2014). More precisely, the authors argued that MI practice, by emphasizing the cognitive control of action, contributed to better structure procedural memory. Here, activating MI possibly primed performance through the structuration of recent memorial information, since it involved a conscious access to the efference copy of the somatic command addressed to the peripheral effectors (Jeannerod and Decety, 1995). Studies addressing the issue of priming through MI practice remain scarce. Ramsey et al. (2010) observed that incongruent, but not congruent, MI practice, hampered motor performance. This demonstrates that priming effects of MI practice require a tight congruence between the mental rehearsal content and the expected transfer to performance. Overall, in addition to the psycho-neuromuscular theory, hierarchical models of action organization provide an integrated rationale for priming effects of MI practice on performance. The relaxing MI condition was also associated with increased biceps brachii activation as compared to control. This might account for focused attention paid to this muscle during MI practice, or purely reflect a placebo effect. Focused attention alone may facilitate corticospinal activation toward the relevant muscles (Stinear, 2010; Hiraoka et al., 2013). Yet, we did not find scientific data reporting that attention-related facilitation could be prolonged over time up to facilitate an upcoming force trial.

We recorded larger EDR during activating MI than during control, attesting higher sympathetic discharges. Tonic level of skin resistance was higher under the relaxing MI condition. This is congruent with literature data reporting reduced sympathetic activation in response to relaxation practice (Vempati and Telles, 2002). However, the largest EDR were recorded during relaxing MI. This finding is rather surprising and somehow difficult to interpret. EDR amplitude is dependent on the initial state of autonomic arousal (see also Wilder, 1957, concerning the law of initial value, Vernet-Maury et al., 1995), which is why EDR amplitudes were normalized. Nonetheless, EDR could have been amplified during relaxing MI in order to compensate a more relaxed pretrial body state (relaxing MI practice involved a specific focus on muscle relaxation) as compared to both activating MI (involving MI practice of muscle activation at maximal intensities) and control (requiring sustained attention). Yet, no relationship was found between EDR amplitudes and force across trials and conditions.

Lebon et al. (2010) investigated the effect of MI practice during rest periods of physical training on the long-term development of dynamic muscle performance (i.e., 6 weeks of training including 12 sessions). They reported up to 20% of force gains, but did not record

any physiological data. They attributed performance gains to skill improvement, presumably due to greater task focus, self-confidence and motivation. In the present experiment, the psychological factors likely to affect performance were rigorously controlled. Self-reports and physiological recordings revealed that participants' commitment and motivation during experimental measures remained constant throughout sessions. Indeed, we observed a regular decrease of about 20% in baseline EDA. Tonic sympathetic activity thus tended to increase on a trial-to-trial basis, potentially to compensate the occurrence of both accumulated mental strain and physical fatigue. Contrary to Lebon et al. (2010), performance gains could not result from technical improvements, since the task did not involve dynamic but isometric contractions. The reference position was rigorously controlled, thus ruling out possible skill adjustments. We advocate that higher training intensities, particularly during activating MI, could reflect priming effects of MI practice on central motor processes. Such short-term adaptations potentially improved muscle activation and isometric force.

While some studies which tested the effects of MI practice over several weeks did not report a positive effect on force (e.g., Herbert et al., 1998, see also Graham et al., 2014 for absence of short-term effects on muscle endurance), the long-term positive effects of MI practice on isometric force are well-established. Authors argued that MI practice induced, over several weeks, "neuroplastic" adaptations including increased cortical activation during voluntary isometric contractions at maximal intensities (Yue and Cole, 1992; Ranganathan et al., 2004; Yao et al., 2013). Here, "online" force gain between 2.1% and 3.5% were measured compared to the other conditions. These were associated with 8.2% of increase in biceps brachii activation compared to the control condition. Present results show an immediate influence of mental rehearsal on maximal isometric force. Present data support that activating MI yielded to priming effects on performance. Such improvements may be grounded in short-term neuroplastic adaptations, possibly excitability changes in the motor cortex leading to more efficient drive of motor units. Indeed, as underlined by Stoykov and Madhavan (2015):

"(...) priming of the motor cortex is associated with changes in neuroplasticity that are associated with improvements in motor performance.", p. 33.

These gains remain however weaker than those reported by Yao et al. (2013) after 6 weeks of kinesthetic MI training (i.e., about 11% increase in maximal elbow flexion).

CONCLUSIONS

Embedding MI practice during rest periods is congruent with theoretical frameworks supporting that MI should be practiced under conditions close to those of physical training (Holmes and Collins, 2001; Guillot and Collet, 2008). Athletes' reports of self-efficacy corroborated both force and physiological data: they felt more efficient during activating MI. MI of muscle activation may be relevantly practiced during rest periods of training or physiotherapy sessions (see also Rozand et al., 2014). However, physiotherapy sessions foremost involve submaximal contractions. The extent to which MI practice is likely to impact performance hence remains to be more thoroughly studied. As short-term effects were measured on maximal isometric performance, testing the immediate effects of MI practice on submaximal force tasks is a perspective of the present experiment.

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APPENDIX A

Warm-up and familiarization to physical training.

Warm-up

Experiments took part in a quiet room. Participants first completed a 10 min of warm-up, which started with 4 min of physical arousal exercises. Participants then seated on the bench and adopted the standardized position of the experiment (Fig. 1). They were told to perform five incremental isometric contraction with a 90° of elbow flexion against the force plate sustained 10 s each, and separated by rest periods of 50 s. They completed warm-up by two maximal isometric flexions sustained 12 s each and separated by 1.5-min rest

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periods. Experimenters visually controlled on the force plate signal the strength increase.

Familiarization

Immediately after the warm-up, participants received the experimental instructions for the forthcoming physical training session. They were carefully explained the organization of rest periods. For the training session involving passive recovery, participants were instructed to remain motionless and listen to audio instructions during rest periods. Immediately before the first force trial of the physical training, they were broadcasted a 1-min audio sequence involving three sequences of 12 s of information concerning international sports news. When rest periods involved MI training, participants were carefully instructed to perform either activating or relaxing MI as accurately as possible. Immediately before the first trial of physical training, they were requested to complete three MI trials of 12 s over a period of 1 min, using a similar audio soundtrack to that used during rest periods of the physical training session.

APPENDIX B

MI scripts

For the activating MI condition, the following script was broadcasted to participants:

"Mentally represent yourself in the standardized experimental position. Perceive the intense contraction of your biceps in response to the auditory tone. Feel the maximal muscle activation, and focus on the contraction of all muscle fibers. Visualize your arm sustaining this maximal effort."

For relaxing MI, the following script was broadcasted to participants:

"Mentally represent yourself in the standardized experimental position. Perceive the profound relaxation of your biceps after trial completion. You feel complete muscle easing and calmness accompanying relaxation of all muscle fibers. Visualize your arm sustaining this relaxed state."

APPENDIX C

Data table

(Accepted 30 July 2015) (Available online 1 August 2015)

Due to overlapping neural substrates between MI and PP, the mental representation of an action represents a cognitive demanding task, with particular demand upon the brain motor system (Munzert et al., 2009, Guillot et al., 2014). MI thus represents a relevant approach to achieve peak performance through activity-dependent neuroplasticity (for a review, see Malouin et al., 2013, Di Rienzo et al., 2016). Embedding MI into training programs nonetheless requires participant's capacity to recreate as accurately as possible motor representations. Indeed, previous research emphasized that i) greater MI ability elicits greater recruitment of the brain motor system (Guillot et al., 2008, Lorey et al., 2011, Meulen et al., 2014), and *ii*) better imagers benefit to a greater extent of MI when compared with to imagers with reduced MI capacities (e.g., Martin et al., 1999, Roure et al., 1999). MI frameworks suggest that MI should be coupled with actual training (Holmes and Collins, 2001, Guillot and Collet, 2008). Yet, practical aspects regarding the relevant approach to embed MI into training programs remain uncertain. Classically, MI is performed decoupled from the actual training context, or during the recovery periods interposed between blocks of actual training (e.g., Weinberg et al., 1981, Lamirand and Rainey, 1994, Lerner et al., 1996, Dijkerman et al., 2004, Callow et al., 2006, Post et al., 2010, Seif-Barghi et al., 2012, Guillot et al., 2013a, Guillot et al., 2013b, Yao et al., 2013, Kanthack et al., 2014, Guillot et al., 2015). Schuster et al. (2011) underlined, in their systematic review, that MI administered after actual training elicited greater performance gains. However, recent findings showed that actual training context

might affect MI ability, particularly through physical fatigue processes (Demougeot and Papaxanthis, 2011, Di Rienzo et al., 2012). This doctoral dissertation aimed at filling two main literature gaps: *i*) investigating the efficacy of embedded forms of MI practice to actual training, and *ii*) investigating the influence of fatigue processes elicited by actual training on MI ability.

I) <u>MI PRACTICE CONCOMITANT TO ACTUAL TRAINING TO IMPROVE</u> <u>PERFORMANCE</u>

Vergeer and Roberts (2006) pioneered the use of embodied form of MI practice, embedded within actual practice sessions. In their longitudinal approach to flexibility improvement, the embodied MI practice intervention failed to significantly improve performance. Yet, an increase in the perceived comfort during actual training was observed during this experimental condition. The authors argued that embodied MI positively impacted psychological factors, but had few/no effect on physiological factors mediating performance. Practically, this remains an unexpected result as MI practice focused on the physiological process of stretching, even though they primarily asked participants to perform visual imagery of muscle fibers elongation, rather than kinesthetic imagery including feeling of the body position and sensations related to the movement. Accordingly, Guillot et al. (2010) later reported that flexibility might be enhanced by MI practice without concomitant body movements, but they did not incorporate an experimental condition including pure embedded MI practice. In the experimental contribution #1, we found that MI practice of muscle relaxation while stretching was likely to facilitate subsequent motor performance. This specific

form of MI yielded reduced muscle activation. Grosprêtre et al. (2015), investigating the amplitude of Hoffman (H) reflex, reported reduced H-reflex after a conditioning stimulation of the antagonist nerve, which activates presynaptic inhibitory interneurons. However, during MI H-reflex, values remained the same despite antagonist nerve stimulation, hence supporting that MI might act on peripheral level by activating low-threshold interneurons. We postulate that comparable neurophysiological mechanisms might account for the beneficial effects of MI practice on subsequent motor performance, while performed concomitantly to actual stretching.

In a second experiment dealing with the embedded form of practice (i.e., experimental contribution #2), we investigated the efficacy of performing MI concomitantly to actual breath-holding performance. Breath-holding represents a unique model of performance since the sparing of energy expenditure paradoxically represents one of the main determinants of performance (Ferretti et al., 1991). For the first time, we investigated whether the content of MI, i.e., either congruent or incongruent relative to the effort required by breath-holding, might influence its efficacy on the corresponding performance. MI frameworks and guidelines for optimal practice usually advocate that the MI content should focus relevant features of the expert performance (Short et al., 2002, Taylor and Shaw, 2002, Nordin and Cumming, 2005, Ramsey et al., 2008). Surprisingly, performing MI practice concomitantly to breath-holding by focusing on ventilatory movements and sensations (i.e., incongruent MI) elicited a greater performance compared to a more usual form of MI practice based on the muscle contractions required to maintain a breath-holding state (i.e., congruent MI). However, improvements consecutive to the incongruent MI practice was not associated

with physiological changes which could be linked with increased energy sparing. It is thus suggested that MI might have influenced the autonomic nervous system response patterns to breath-holding. MI is known to induce the autonomic nervous system responses patterns associated with the actual content of the mental rehearsal (Collet and Guillot, 2010, Collet et al., 2013). It is thus suggested that incongruent MI practice delayed central breath reflex due the internal stimulation of a breathing body state, hence improving the maximal breath-holding breakpoint (Javorka et al., 2001, Heusser et al., 2009).

Overall, the present doctoral dissertation demonstrates that MI performed in conjunction to actual training exercises is a relevant approach to improve performance. We chose unique sporting situations putting a specific emphasis on the central nervous system control over somatic and autonomic effectors to achieve high levels of performance. Those results support the use of MI for daily needs in both rehabilitation and sports domain. MI practice in conjunction to actual training exercise represents a particularly cost-effective strategy considering the human and material costs associated with most training programs (Skempes et al., 2018). For instance, physiotherapy session aiming to recover flexibility might strongly benefit from a concomitant MI practice on the relaxation of the concerned muscles. Yet, it could also be considered that MI also interferes with central system adaptive responses mediating defense mechanisms (e.g., artificial delay of the breath-holding breakpoint). For instance, distress tolerance, known as the "behavioral act of withstanding distressing internal states elicited by some type of stressor" (Zvolensky et al., 2010), is frequently measured by means of breath-holding tasks (Eke and McNally, 1996, Eifert et al., 1999, Brown et al., 2002, Leyro et al., 2010, Johnson et al., 2012).

Our results clearly demonstrate that the capacity to sustain a breath-holding task increased. Thus, future studies should focus on MI practice influencing distress tolerance and the psychological and physiological processes behind MI practice and concomitant with actual training, although we postulate that during action, the autonomic nervous system further responds to the action being performed, and might thus not be totally influenced by MI.

II) THE EFFECTS OF FATIGUE PROCESSES ELICITED BY EXERCISE ON MI ABILITY

Only a limited number of studies investigated the relationships between fatigue processes elicited by exercise and MI ability/accuracy, and most provided contradictory results. Guillot et al. (2005) first reported that after a fatiguing exercise for lower limbs, MI ability of a jumping task was not affected. It was assumed that MI ability represented a primarily cognitive process, which was not impacted by homeostatic perturbations elicited by a local muscular fatiguing exercise. Later, Demougeot and Papaxanthis (2011) observed that maximal isometric contractions of shoulder flexor muscles impaired MI of a pointing task. MI ability impairment was restricted to the exercised arm, and a small amount of actual training easily restored the MI ability. Such findings supported that mental representation accounts for current state of the complete motor system. Also, since MI time of non-fatigued arm remained the same after exercise, these authors argued that this could be explained by an sensorimotor state estimation of the task (Fadiga et al., 1998). The results of our experimental contribution #4 corroborates this hypothesis. After a cycling exercise, we observed that MI

isochrony of a walking task was altered as well. Interestingly, time distortion was not recorded during the pointing task, which involved other muscles not required during the fatiguing protocol. The effect of fatigue elicited by a continuous exercise was recently investigated by Di Rienzo et al. (2012). They reported that the exercise protocol involving the whole body and completed until exhaustion hampered internal, but not external, visual MI. Imagining a movement through the first-person perspective therefore requires more recall of the actual body configurations, possibly altered by the sensation of physical fatigue. Overall, looking at the experiments preceding the present doctoral dissertation revealed that authors administered very distinct fatiguing protocols, which primarily varied in terms of duration and intensity. Also, they only carried on MI ability measures from tasks involving fatigued peripheral somatic effectors. For these reasons, it appears difficult to draw final conclusions about the effect of physical fatigue on MI ability.

In an original experimental design (i.e., experimental contribution #3), we measured how MI ability of developmental skills consolidated by long-term experience, i.e., locomotion, might be altered by local muscle fatigue. Surprisingly, we recorded that MI ability, evaluated by mental chronometry, improved after the exercise. Interestingly, fatigue protocols intended to elicit a local fatigue from lower and upper limbs muscles (i.e. respectively a congruent and incongruent conditions in regards to the experimental walking task) both affected MI temporal constraints in a comparable fashion. In addition, congruent fatigue improved vividness to higher level than incongruent. These results were not expected, and might suggest that the presence of fatigue was likely to increase the attentional focus during the locomotion task, hence positively

affecting the forthcoming mental rehearsal, especially for congruent local fatigue. This unexpected finding nonetheless confirmed that local muscle fatigue may not be necessarily detrimental to MI ability of tasks involving the whole body (Guillot et al., 2005). In another experiment (i.e., experimental contribution #4), we investigated the effect of a prolonged continuous and intermittent exercise of moderate intensity on MI ability of two distinct developmental coordinations consolidated by long-term experience, i.e., locomotion and prehensile movements. Continuous and intermittent exercises were designed to prioritize the anaerobic and aerobic metabolic pathways to meet the demand in energy expenditure. So far, all experiments aiming to investigate the effect of an exercise session on MI ability implemented physical training with high training load or until exhaustion. However, actual training are performed with different workloads across sessions, ranging from micro- to macro-cycles. Those approaches with maximal effort demand makes it difficult to draw a line to determine at what point the development of fatigue is harmful or fruitful for MI ability. After both types of fatiguing exercises, we observed that participants experienced a marginally greater difficulty to perform MI of both tasks. However, only intermittent exercise impaired vividness and isochrony. MI is known to engage a large amount of cognitive process (O'Shea and Moran, 2017), and it has been extensively demonstrated that a session of anaerobic exercise (e.g., the intermittent approach applied in our work) might impair cognitive task performance (Chmura et al., 1997, Fery et al., 1997, Brisswalter et al., 2002). However, the exact nature of the processes behind such cognitive impairment are not resolved and remain in discussion.

MI ability of automated coordinations may be altered by the fatigue body states elicited by prolonged exercise involving whole body movements (Di Rienzo et al., 2012). By contrast, MI ability of automated coordinations appeared preserved (or even improved as in the present work) in the case of shorter exercise durations eliciting a more local muscle fatigue. By altering muscle functions, local muscle fatigue possibly induces a greater degree of attentional focus during the physical performance of automated skills, i.e. a greater degree of bottom-up processing and input to the motor memory facilitating the forthcoming mental rehearsal. Meanwhile, prolonged continuous exercise of moderate intensity may not elicit a sufficient degree of muscle function impairment to yield increased attentional focus. Noteworthy, local muscle fatigue was shown to alter MI ability of isolated limb movements with a strong focus on the fatigued somatic effectors (Demougeot and Papaxanthis, 2011). Finally, prolonged intermittent exercise of moderate intensity appeared likely to impair MI ability. Coaches and health professionals should thus pay attention to the type of actual training before delivering MI practice interventions. In Figure 22 we propose an illustration of the expected outcomes in MI ability and performance when performing conventional MI (i.e., motionless MI) as well as dynamic MI in both rested and fatigued states.

III) USING MOTOR IMAGERY TO CONTROL DELETERIOUS EFFECTS OF FATIGUE ON PERFORMANCE

During fatigue development process (See Figure 15), the central nervous system modulates both excitatory and inhibitory mechanisms. For instance, when

a great amount of force production is required to be sustained, an increase in the amount of motor units can be observed (Kayser et al., 1994), followed by a decrease in the amount and frequency of efferent signals (Tucker et al., 2004, Crewe et al., 2008). Increased motor-evoked potentials (MEP), as revealed by transcranial magnetic stimulation paradigms, indicate that a strength training session enhances the corticospinal excitability (Ruotsalainen et al., 2014, Nuzzo et al., 2016, Latella et al., 2017). However, decreases in corticospinal excitability in response to a strength training session has also been reported (Latella et al., 2016). This was particularly the case when fatiguing exercise protocols elicited high levels of exertion (Sacco et al., 2000, Gruet et al., 2014). In addition to the decrease in corticospinal excitability, increases in the silent period of voluntary muscle contraction consecutive to MEP was further observed (Gandevia et al., 1994, Sacco et al., 1997, Gruet et al., 2014). Central nervous system adaptations in the presence of fatigue are expected to protect the system to achieve a chaotic state that may lead to severe injuries (McMorris et al., 2018). MI is a motor cognition process, known to be related to the motor planning stage of action control (Jeannerod, 1994, 2001, Munzert et al., 2009). MI engages executive parts of the motor system and incorporates the current body state to engage motor stimulation (Jeannerod, 1994, 2001, Grush, 2004, Hanakawa et al., 2008). Thus, homeostatic perturbations elicited by fatigue might affect MI times by the proactive anticipatory adjustment of motor predictions to the current functioning state of the motor system. In addition, during MI, there is an absence of afferent signals related to peripheral somatic effectors involved in the task. Compared to the actual performance, this might delay MI temporal constraints recovery to basal level (Demougeot and Papaxanthis, 2011). Recently, Ruffino et al. (2017)

reviewed how MI practice might elicit performance gains through its capacity to induce corticospinal plasticity. The authors considered distinct learning stages, ranging from initial phase, where MI practice could, for instance, increase cortical organization related to the task with more precise cortical activation, to automatic phases where MI practice might decrease cortical activity and increase corticostriatal influence over the task. MI practice could play an adjunctive role facilitating learning processes at each learning stage, due to its effect on the reorganization of corticospinal pathways. For everyday automatized tasks such as walking, MI practice might prompt a more refined and circumscribed recruitment of cortical structures (Sakai et al., 1998, Miyai et al., 2001, Lafleur et al., 2002, Jahn et al., 2004, Lacourse et al., 2005). This participates to increase the neural efficiency within corticospinal pathways, due to i) enhanced synaptic gain within task-specific corticospinal circuits, and ii) the concomitant decrease of residual resting state activity within irrelevant corticospinal circuits through recruitment of spinal interneurons (see Ruffino et al., 2017). Our findings extend current knowledge by providing new insights on possible uses of MI under fatigued states elicited by exercise. For instance, since MI increases the corticospinal excitability, we might hypothesize cumulative rather than detrimental effects on the cortical neuroplasticity elicited by actual strength training sessions. Qualitative investigations of dose-response relationships between MI and performance under various fatigue states elicited by exercise surely represents an overall exciting research avenue.

A) Practical relevance of MI practice in the presence of fatigue

MI practice is known to improve motor performance when performed in addition to actual training. There is a general consensus that MI yields additional benefits on performance than actual training performed alone (Driskell et al., 1994, Yágüez et al., 1998, Jackson et al., 2004, Allami et al., 2008, Guillot et al., 2010). MI practice is a particularly relevant approach to facilitate learning of new and intra-muscular coordinations (Pascual-Leone et al., 1995, inter-Ranganathan et al., 2004, Gentili et al., 2006, Gentili et al., 2010, Lebon et al., 2010, Yao et al., 2013, Grosprêtre et al., 2017, Ruffino et al., 2017). However, gains linked with MI practice may be related to the individual ability to build accurate motor representations of the task (Martin et al., 1999). Little research sought to delineate the effects of fatigue states elicited by actual training on the individual MI ability. In this doctoral dissertation, we specifically addressed whether distinct actual training frameworks might impact the individual MI ability. We specifically tested in experimental contributions #5 and #6 if MI used after or during a training session could still be useful to increase performance for sport skill and force production.

First, our results are in agreement with Guillot et al. (2015) and support that MI practice is a valuable technique to control deleterious effect of fatigue on motor performance. In addition, we showed for the first time, that dynamic MI, i.e., a form of MI practice know to increase MI ability (Callow et al., 2006, Guillot et al., 2013b, Fusco et al., 2014), might lose its potential benefits on performance when practiced in a fatigued state. However, MI practice without any concomitant body movements, which represents the classical approach, remained a relevant

approach to improve the shooting accuracy under a fatigued state. Another interesting data comes from experimental contribution #6. During inter-trial periods, participants where requested to recreate the sensation of maximal muscle contraction as well as sensations of a rested muscle in two distinct experimental conditions. This second condition was expected to control for placebo effects, and indeed performance increased compared to control condition when participants recreated the sensation of a rested muscle. One possible explanation is the that MI practice inhibited central mechanisms responsible for organism protection, such as a decrease in efferent commands to avoid muscle injurie (Gibson et al., 2001, Tucker et al., 2004, Crewe et al., 2008). We already previously observed that MI practice might influence defensive mechanisms in experimental contribution #2, where mental recreation of breathing increased maximal breath-holding performance. Overall, our results contribute to existing MI frameworks advocating MI practice in conjunction with actual training (Holmes and Collins, 2001, Guillot and Collet, 2008). Specifically, dynamic MI should be used in conditions of optimal body state, and focusing on a congruent content with the demands of actual training may not always be the most appropriate approach. While this remains crucial when increased activation of peripheral effectors is required, incongruent MI practice could also punctually yield performance improvements in some circumstances, by delaying autonomic nervous system response patterns or modulating central defensive mechanisms that could interfere with high-level performance.

A final critical point to investigate is the possible modulations caused by exercise on MI practice mechanisms responsible for performance enhancement. For instance, what are the cortical activation differences of performing MI

concomitantly with action when compared to MI or action alone? By applying simple tasks such as prehensile hand movements to induce fatigue, laboratorial analyses with EEG and magnetoencephalography could provide interesting insights. In addition, ecological field studies within longitudinal approaches should be considered having groups performing MI either before or after actual training, with a constant control of physical workload, both physiologically and subjectively.



Figure 22. Expected outcomes on motor imagery ability and motor performance. Outcomes in red represent findings exclusively extracted from the present doctoral manuscript. Outcomes in blue are findings from this manuscript supported by previous existing literature. Outcomes in black were either not an object of study of this manuscript or impossible to add information based on our findings.

CONCLUSION

This doctoral manuscript aimed to extend current knowledge regarding the guidelines of efficient MI practice in both sports sciences and rehabilitation settings by investigating the interdependent relationships between MI and the psychophysiological correlates of the corresponding action. Sport coaches and health professionals should thus benefit from the avenues and guidelines underlined by the present work, when building or delivering MI interventions in the presence of fatigue states elicited by exercise. Experimental contributions overall support that embodied forms of MI practice performed in actual training contexts represent relevant approaches to enhance motor performance, even when fatigue is present.

APPENDICES

APPENDICE N°1: VIVIDNESS OF MOVEMENT IMAGERY QUESTIONNAIRE-2 (VMIQ-2)

APPENDICE N°2: 10 point Borg scale

APPENDICES N°1

Motor imagery is imagining a movement. The aim of this questionnaire is to determine you imagery quality (vividness). You will need to imagine the following actions and assign your mental representation quality using a scale of 5 levels. For each item, circulate the note you would like to attribute. In the first column, you will need to imagine as seeing the action from outside (spectator, camera), which means, with an **external visual Imagery**. On second column, you must imagine as you had a camera in your eyes, recording the visual information from the activity while you perform them (internal visual imagery). For last, in third column, you must try to fell the movement that those actions would create (body sensations, muscles, stretching) (Kinesthetic imagery). Try to make each column separately. Complete all items from external visual imagery, after return to the top of the questionnaire and start again with internal visual imagery. Once again, return to the top of the questionnaire to complete the kinesthetic imagery. Attention, the notes for the same task must be different between the 3 columns. Please, close your eyes every time you try to complete a task.

Self-evaluation scale (For all itens):

Perfect clear and vivid mental representation	 1
Somehow clear and vivid mental representation	 2
Moderately clear and vivid mental representation	 3
Unclear and diffuse mental representation	 4
No mental representation, I just thought about the movement	 5

	E) (imag	kternal gine you	Visual Im	agery outside)	Int (imagine	terval what y perfo	Visual Ima ou see whe rm the task	agery en you re <)	ally		Kinesth (Feel the	e tic Imag moveme	ery ent)	
Item	Perfect clear and vivid mental representation	Somehow clear and vivid mental representation	Moderately clear and vivid mental representation	Unclear and diffuse mental representation	No images	Perfect clear and vivid mental representation	Somehow clear and vivid mental representation	Moderately clear and vivid mental representation	Unclear and diffuse mental representation	No images	Perfect clear and vivid mental representation	Somehow clear and vivid mental representation	Moderately clear and vivid mental representation	Unclear and diffuse mental representation	No images
1. Wark	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
2. Running	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
3. Stumble on a rock	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
4. To crouch to pick up a coin	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
5. Run in the stairs	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
6. Side jump	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
7. Throw a rock in the water	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
8. Hit a ballon in the air	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
9. Run in the downward	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
10. Ride a bicycle	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
11. Swing yourself in a rope	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
12. Jump from a high wall	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
					-		-		-	-	-			-	

APPENDICES N°2

1 - Perce	10 Borg Rating of eived Exertion Scale
0	Rest
1	Really Easy
2	Easy
3	Moderate
4	Sort of Hard
5	Hard
6	
7	Really Hard
8	
9	Really, Really, Hard
10	Maximal: Just like my hardest race

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