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# Interdependent relationships between the mental representation and psychophysiological correlates of action

Thiago Ferreira Dias Kanthack

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**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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---

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me erguido tanto nas derrotas. Eu amo vocês, e isso é muito fácil de se fazer. I also thanks my sister Carol and my brother André, for all the support and for showing that my happiness was a matter of high value to them at all time.

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## RÉSUMÉ

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L'objectif de ce travail était d'apporter des données encore inconnues 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 réalisée 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 peut-être bénéfique pour la capacité d'imagerie motrice d'une habileté 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, entraînement intégrée, imagerie motrice.

## **ABSTRACT**

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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

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

## FIGURE LIST

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## GENERAL INTRODUCTION

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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 Einstein: An Interview by George Sylvester Viereck” in *The Saturday Evening Post* p. 17 (October 26<sup>th</sup>, 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 19<sup>th</sup>, 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:

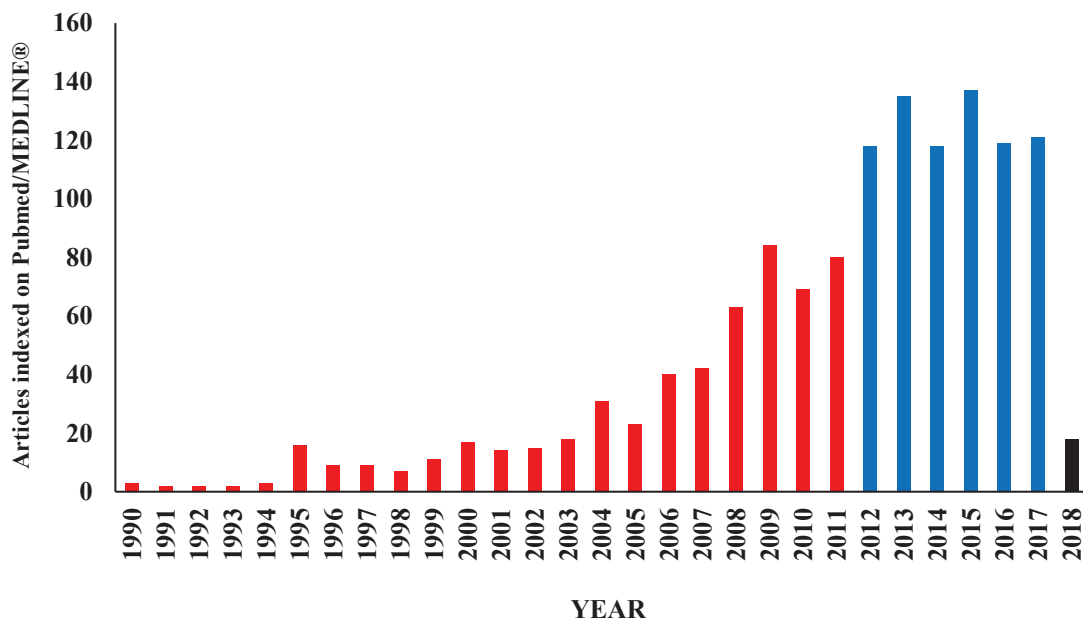
*“(...) imagery and execution are on a continuum, with imagined movements inadvertently generating muscle activity when facilitation of corticospinal excitability crosses a threshold for activating the alpha motor neuron pool” (Stinear, 2010 in Guillot and Collet, The Neurophysiological Foundations of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

Early postulates from the first half of the 20<sup>th</sup> 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 draw 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 led 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 below one hundred (Red columns). From 2012 until 2017, the exponential growth 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 3<sup>rd</sup> 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 meta-analysis 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 were 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.

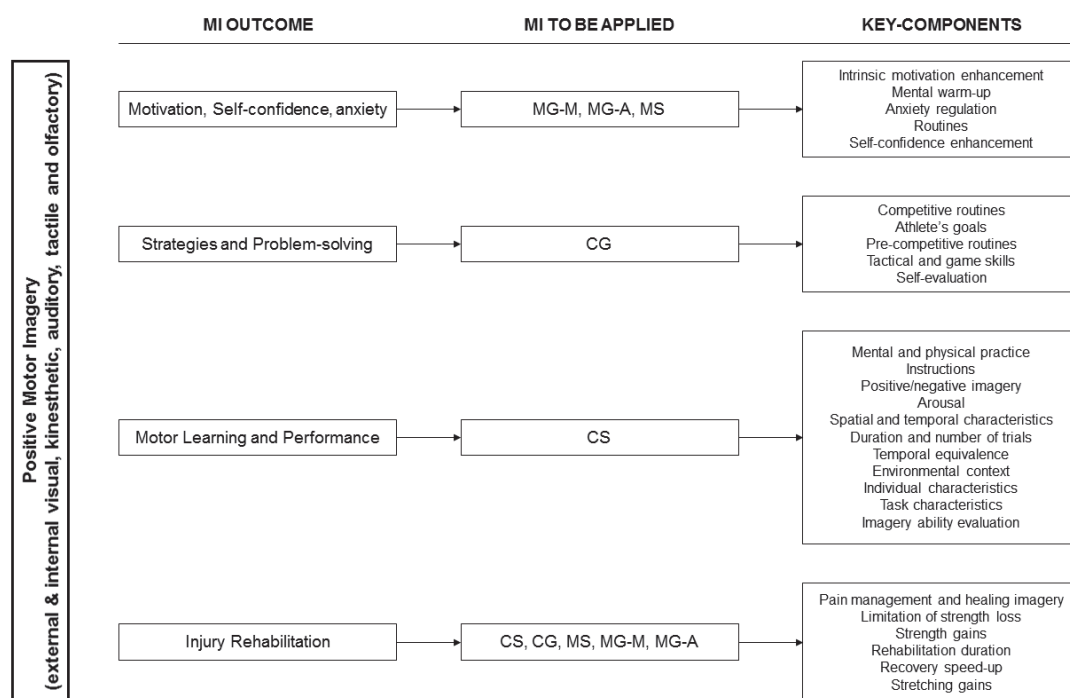
Learning – Since task knowledge evolves with training, so should MI sessions be reviewed to match functional equivalence of performers current state.

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.

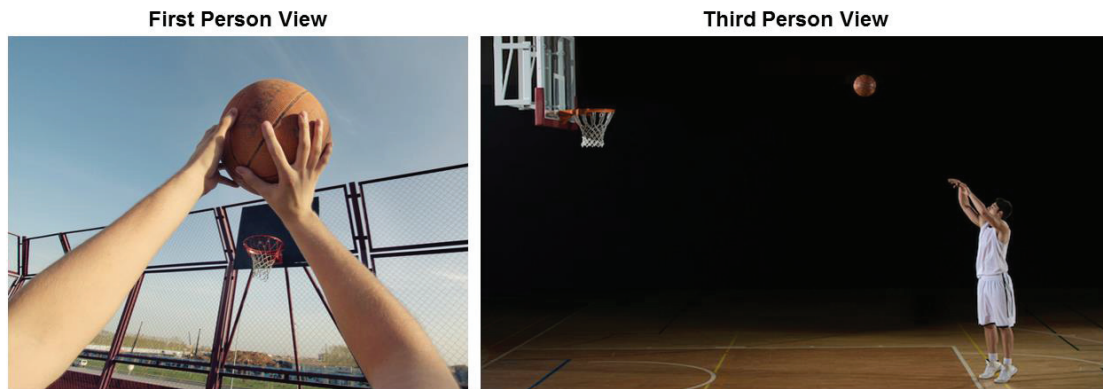
# THEORETICAL FRAMEWORK I

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## 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 person 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).

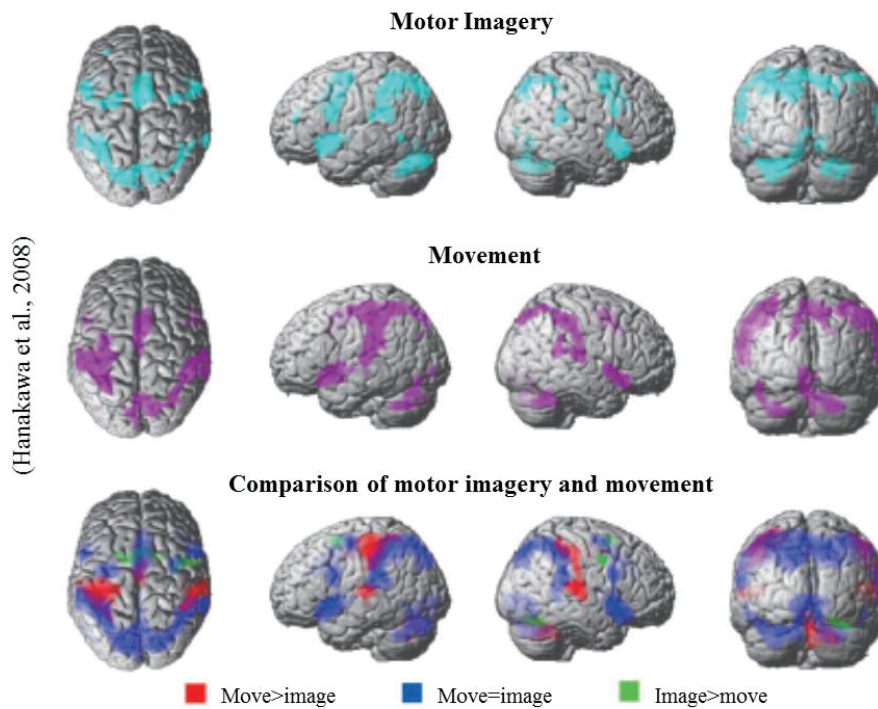
Here, we discuss to which extent MI and PP share overlapping neural substrates. Firstly, we will focus on the shared cortical and spinal activations between the two tasks.

## **(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 upper-limb 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 ( $M_1$ ) has been widely 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 Héту et al., 2013). A pioneering study from Roland et al. (1980) using fMRI did not report activation of the contralateral  $M_1$  during MI. This finding was further supported by other studies which did not report  $M_1$  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, M<sub>1</sub> 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 M<sub>1</sub> 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 M<sub>1</sub> 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 M<sub>1</sub> 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 M<sub>1</sub> 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 M<sub>1</sub> activation during mental representation. Despite such early controversial studies, the debate is somewhat resolved and there is now a growing consensus that M<sub>1</sub> 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).

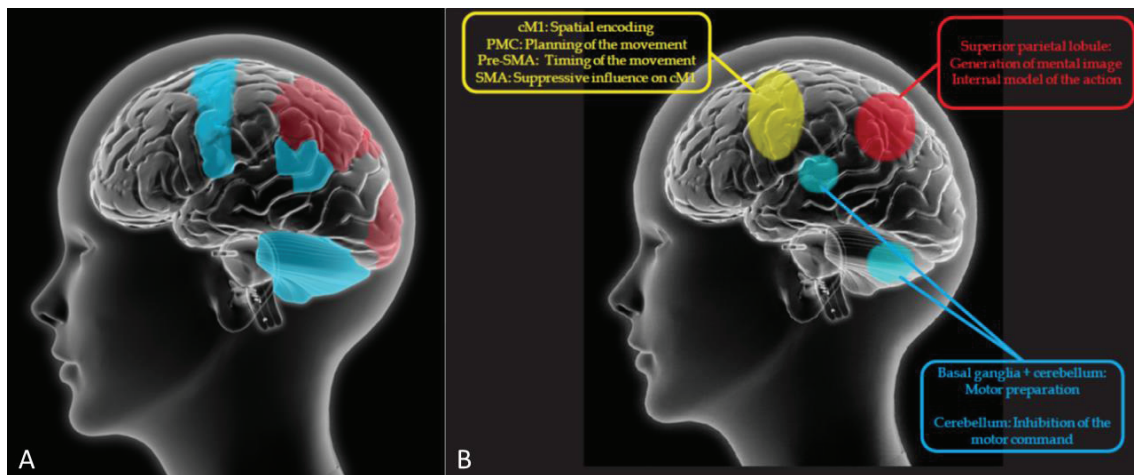
**Supplementary Motor Area:** This region is anatomically divided in three functional parts: *i)* the pre-SMA, involved in movement control, *ii)* the rostral part, involved in motor imagination, and *iii)* the caudal part, highly connected with motor execution (Vorobiev et al., 1998, Gerardin et al., 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 M<sub>1</sub> 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 these 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 M<sub>1</sub>, 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

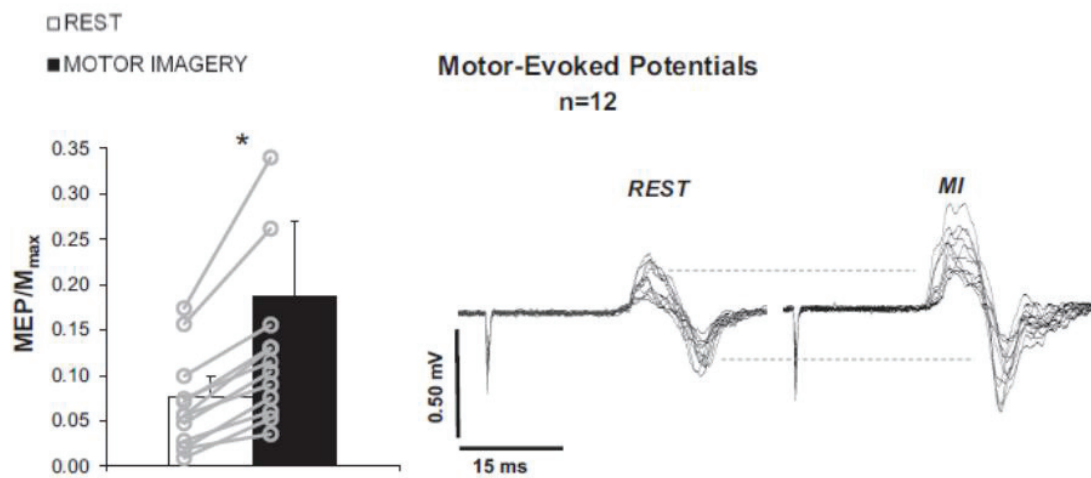
coupled with kinesthetic induced greater muscle activation (see also, Jacobson, 1932, Lang, 1979). Internal visual imagery alone further produced greater muscle activity compared to external MI (Hale, 1982).

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 M<sub>1</sub> 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 carpi 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) **SPECIFICITY OF CORTICOSPINAL RECRUITMENT DURING MI**

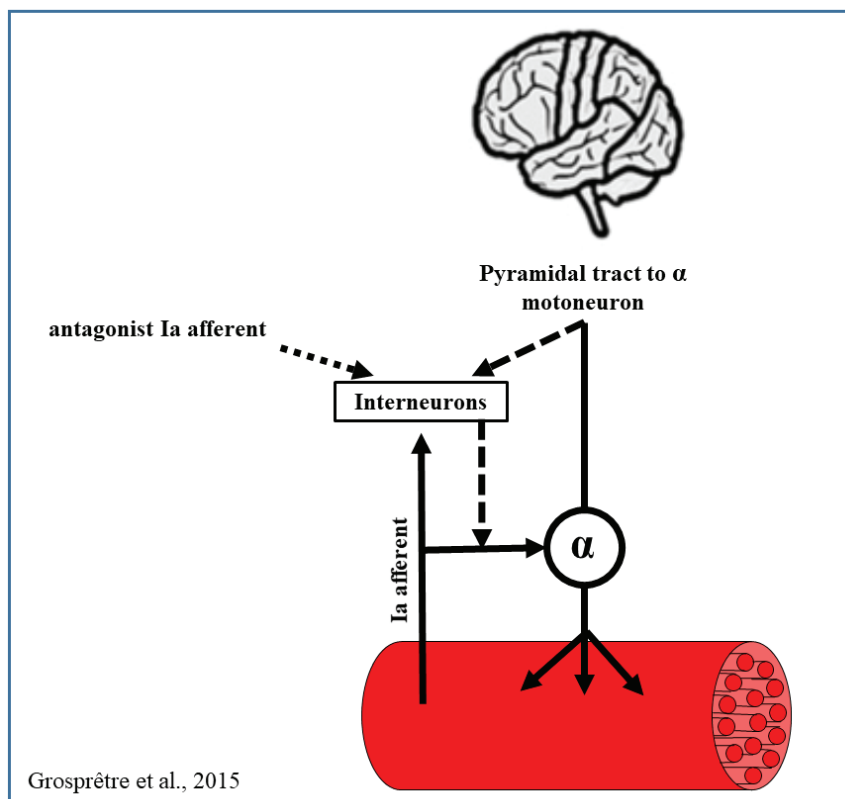
According to Stinear (2010), “*Imagery and execution are on a continuum, with imagined movements inadvertently generating muscle activity when facilitation of corticospinal excitability crosses a threshold for activating the alpha motor neuron pool*”. This claim is supported by a large amount of TMS data attesting the high degree of specificity of M<sub>1</sub> facilitation during MI, which closely parallels that observed during the physical performance of the task. MI does not only induce synaptic modifications in M<sub>1</sub>, 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) **CORTICOSPINAL ACTIVATION THROUGH A PARALLEL PATH**

For years, researchers looked for spinal facilitation induced by MI. A reliable approach is the recording of the H-reflex, a reflexory reaction from muscle after electrical stimulation of Ia 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 Ia afferents modulating their activity (See Figure 7).



**Figure 7.** Illustrated representation of motor imagery parallel path into corticospinal excitability. Corticospinal 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 afferent signals from agonist and antagonist muscles, and regulate  $\alpha$  motoneuron signal transmission.

### **(3) MOTOR INHIBITION DURING MOTOR IMAGERY**

The absence of movement during MI is somewhat intriguing considering the activation of M<sub>1</sub> 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 M<sub>1</sub>, 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 M<sub>1</sub> inhibition, reported that during MI of muscle contraction the cerebellum contributed to the facilitatory control of M<sub>1</sub> 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 M<sub>1</sub> 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 M<sub>1</sub> during MI. Several authors have further shown that reduced M<sub>1</sub> 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) (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 M<sub>1</sub>. 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).

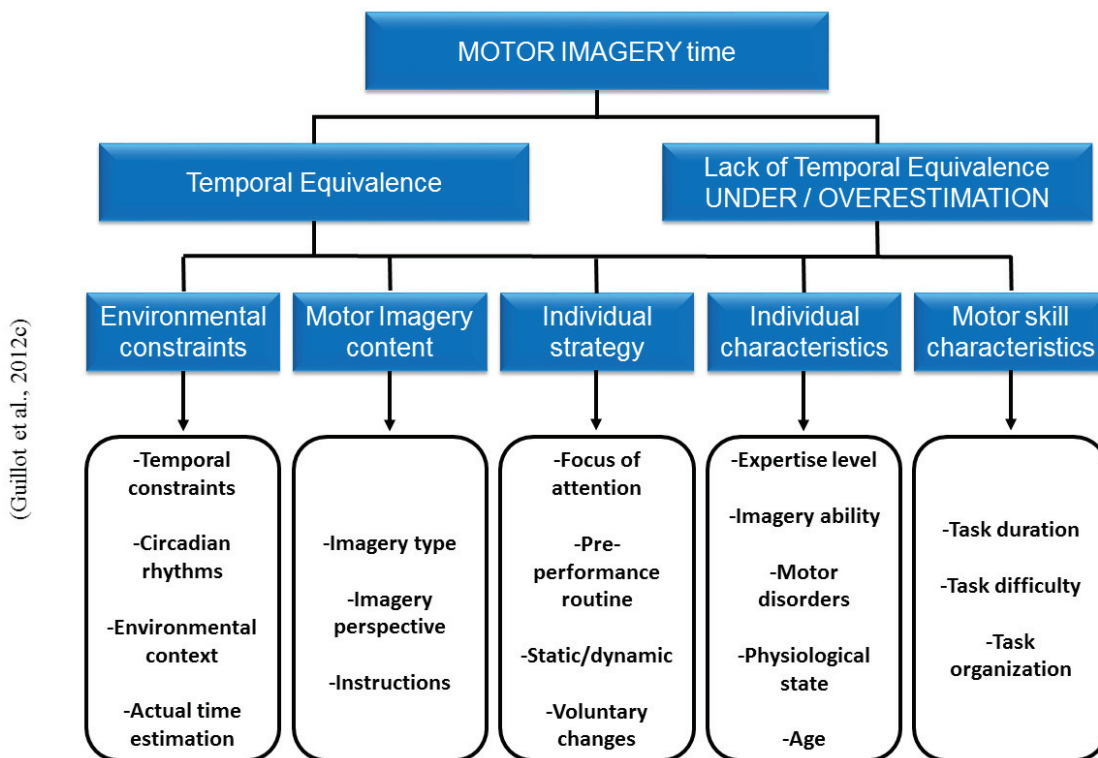
### **(1) BEHAVIORAL MEASURES**

#### **(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) **VIVIDNESS OF MOVEMENT IMAGERY QUESTIONNAIRE**

**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 further development on the topic).

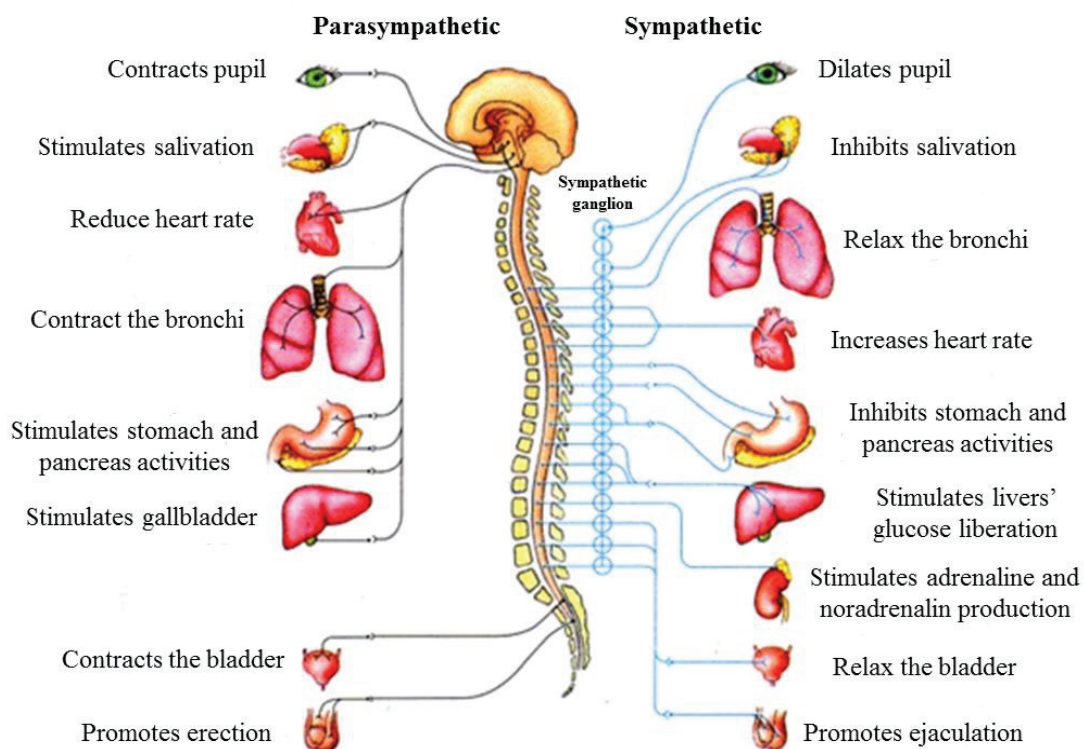
### (iii) **PHYSIOLOGICAL MEASURES**

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 branches. This is the case of

eccrine sweat glands, 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 with a high density in the fingers' skin (Wilke et al., 2004. Figure 10).

### Concentration of eccrine glands per cm<sup>2</sup>

<b>Palms - 644</b>
<b>Forearms - 134</b>
<b>Abdomen - 127</b>
<b>Upper arm - 90</b>
<b>Underarm - 68</b>
<b>Face - 59</b>
<b>Thigh - 57</b>
<b>Chest - 20</b>
<b>Back - &lt;20</b>

**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 project 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 led 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.

- **ELECTRODERMAL ACTIVITY**

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 XIX<sup>th</sup> 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 sweat is present, due to sympathetic activity over sweat glands, fillings the sweat channels. Sweat release increases skin conductance and, therefore, reduces skin resistance. Skin specificity in terms of sympathetic activation represents an exception to the

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 duration”, a robust temporal index of sympathetic system activation (Figure 11). An electric current (15  $\mu\text{A}$ , with  $0.2 \mu\text{A}\cdot\text{mm}^{-2}$  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 learning (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 eye-body 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 been 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**

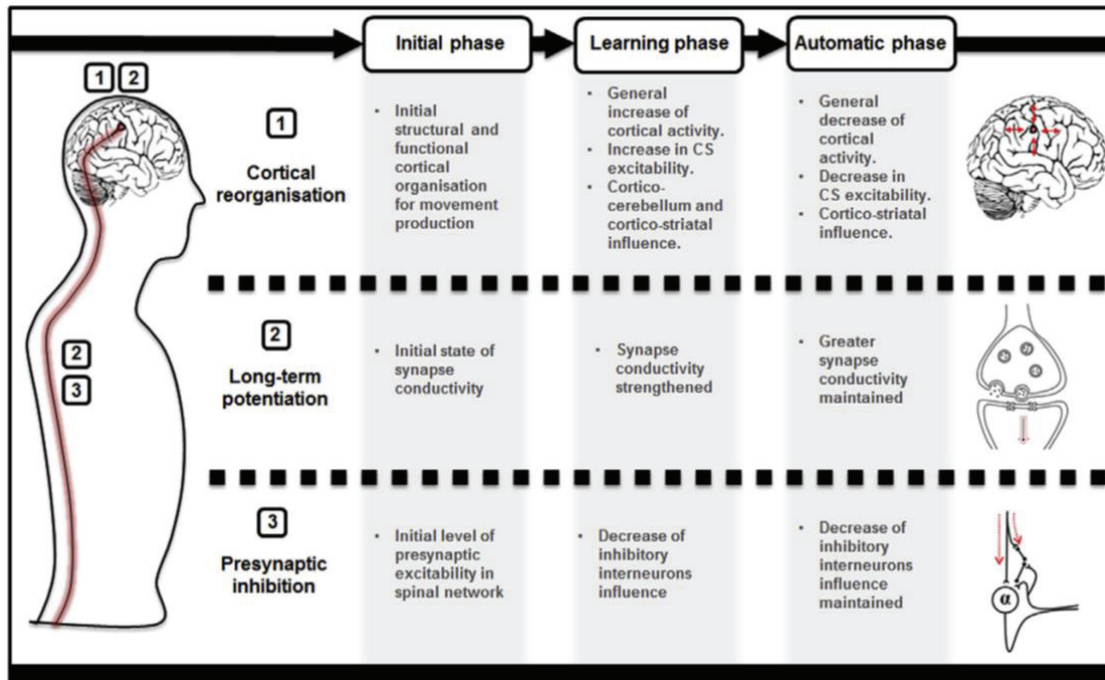
Controlling the movement to achieve a perfect speed-accuracy trade-off is of critical importance. To our knowledge, Boschker et al. (2000) were the first to report that MI practice is likely to alter PP durations, specifically by accelerating/reducing the speed of the actual execution. Participants were 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).



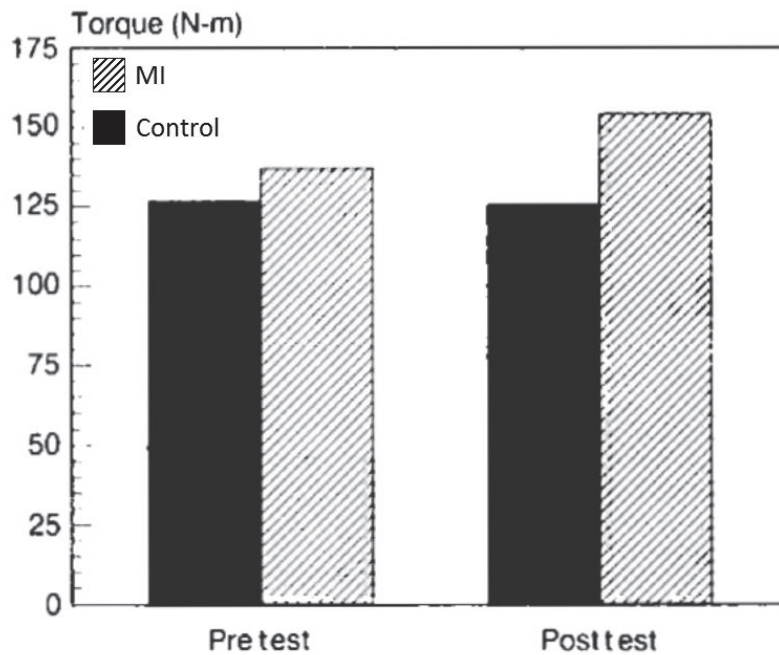
**Figure 12.** Neural adaptation model of mental practice with motor imagery (Ruffino et al., 2017). 1) During the first phases of learning, corticospinal excitability would increase and gradually decrease as learning approaches the automated phases. 2) At cortical and spinal levels, the low motor command 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 were 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 led 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 ± 27.6 Nm, Post – 154.4 ± 20.5 Nm) significantly increased performance while no change was observed in Control (Pre – 127.1 ± 16.6 Nm, Post – 125.9 ± 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 plateau. 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) **SPECIFICITIES OF MOTOR IMAGERY ON STRENGTH 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 II - B. 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.

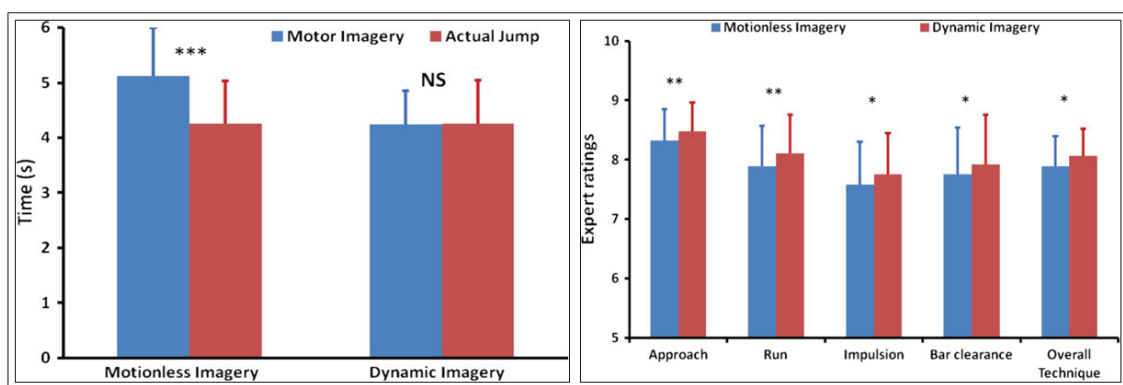
## **(2) MENTAL REPRESENTATION INCLUDING ACTION**

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 is 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.

## EXPERIMENTAL PROCEDURES I

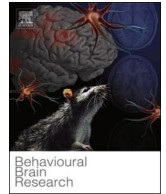
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### I) EFFECT OF MOTOR IMAGERY COMBINED WITH PRACTICE ON PERFORMANCE

**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.



## 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 stretching during B2 trials in the MI practice group. We recorded electromyography from the *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 ( $p < 0.05$ ). Participants in the MI practice group exhibited reduced hamstring activation during both B2 part 1 ( $p < 0.001$ ) 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, Bruscatto and Barry [21], several experi-

ments 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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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-sessions-stretching 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 ( $22.6 \pm 3.2$  years;  $178.3 \pm 5.3$  cm;  $72.8 \pm 9.8$  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.,  $3 \times 10$  squats,  $4 \times 5$  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 sit-and-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

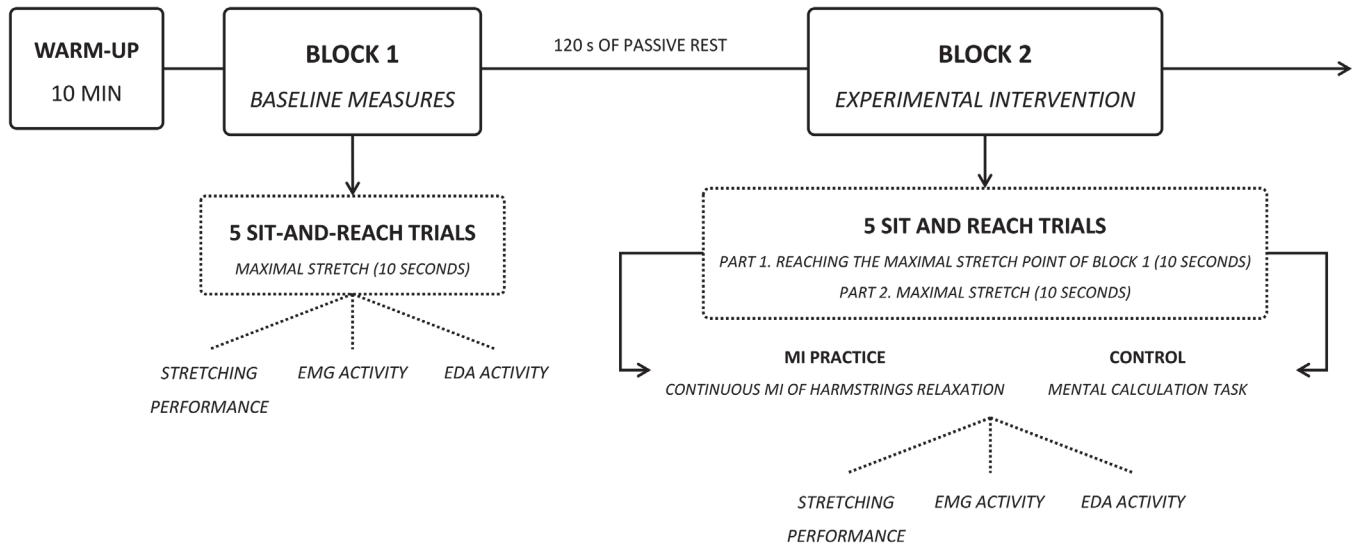


Fig. 1. Flowchart of the experimental design. EMG: Electromyography, EDA: Electrodermal activity, MI: Motor Imagery.

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.

#### 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: > 0.95), but also exercise power output (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-

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”).

##### 2.4.2. 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:

$$\frac{\text{Stretchingperformance}(B1\text{trials}, B2\text{part}2\text{trials}) - \text{Stretchingperformance}(\text{maximum}B1\text{trial})}{\text{Stretchingperformance}(\text{maximum}B1\text{trial})}$$

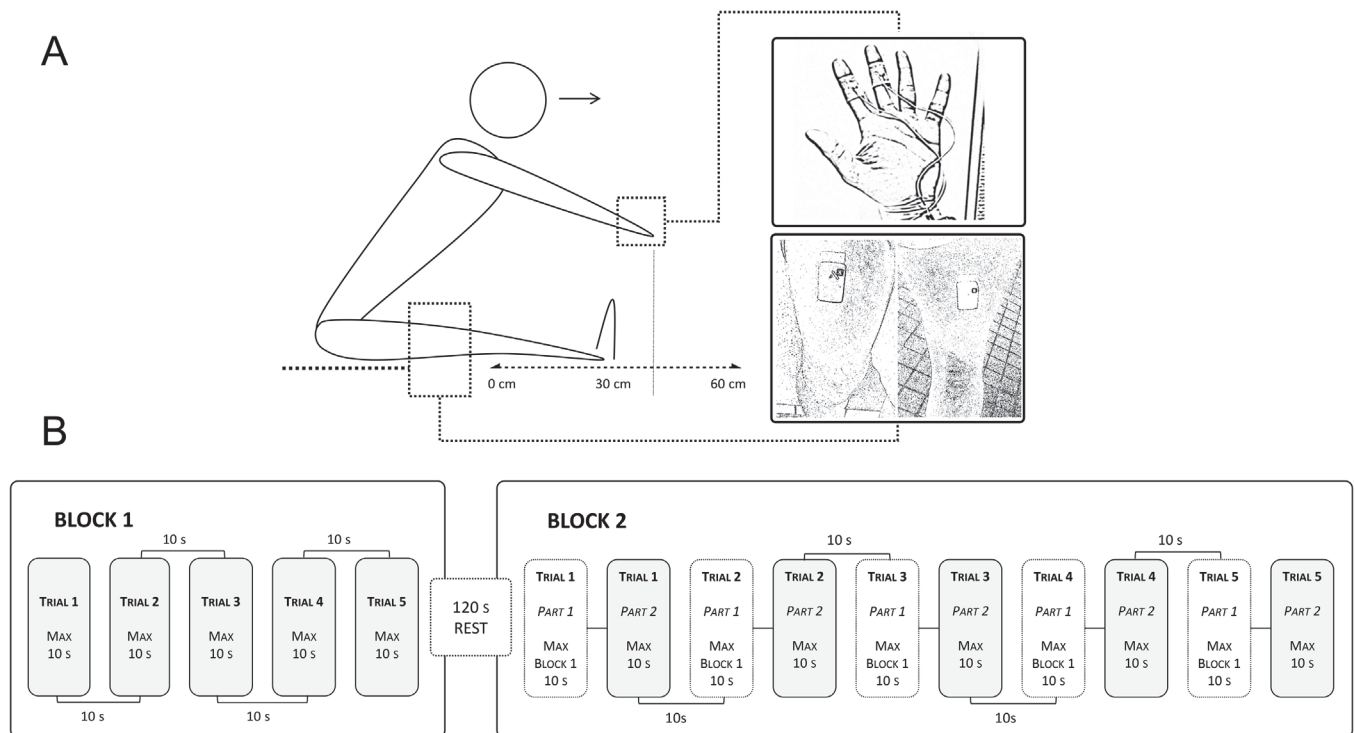
Participants were instructed to maintain a 180° knee extension throughout the sit-and-reach trials (including the 10 s rest). During the 120 s between B1 and B2, participants folded their legs in a comfortable position.

##### 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 thigh 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:

$$\frac{sEMG(B1\text{trials}, B2\text{part1trials}, B2\text{part2trials}) - sEMG(\text{maximumB1trial})}{sEMG(\text{maximumB1trial})}$$

**2.4.3.2. Electrodermal activity.** We continuously measured electrodermal activity through skin conductance ( $\mu\text{S}$ , i.e.,  $1 \text{ m}^{-2} \cdot \text{kg}^{-1} \cdot \text{s}^3 \cdot \text{A}^2 \cdot 10^{-6}$ ) using two unpolarizable  $50 \text{ mm}^2$  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:

$$\frac{EDR(B1\text{trials}, B2\text{part1trials}, B2\text{part2trials}) - EDR(\text{maximumB1trial})}{EDR(\text{maximumB1trial})}$$

## 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

**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 <sup>-2</sup> )	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 first-person 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 (± standard deviation) stretching performance across groups are provided in Appendix A. The stretching performance was 29.95 cm ± 8.13 in the MI practice group and 33.14 cm ± 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% ± 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% ± 0.08,  $p < 0.001$ ) was greater than that in the Control group (8.62% ± 0.06,  $p < 0.001$ ) (Figure 3).

### 3.4. Physiological data

#### 3.4.1. Electromyography

Raw averages (± standard deviation) sEMG across groups are provided in Appendix A. The raw sEMG of the HT during B1 was 102.21 mV ± 20.84 in the MI practice and 104.68 mV ± 34.36 in the Control group. The raw sEMG of the RF during B1 was 102.49 mV ± 33.45 in the MI practice and 106.42 mV ± 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

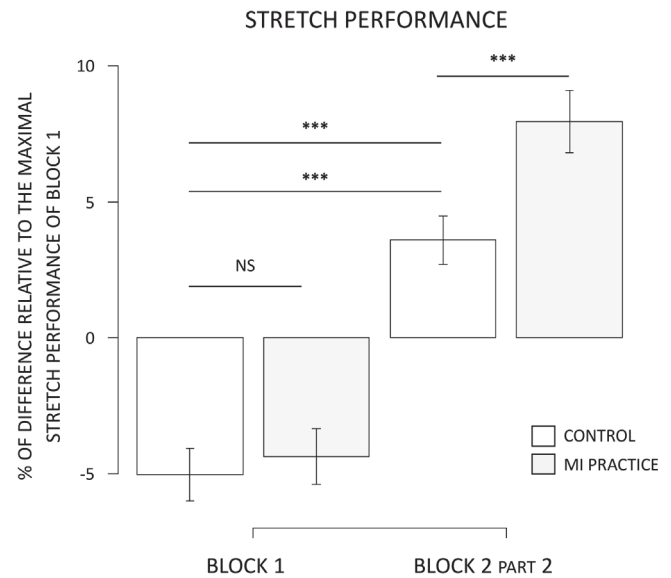


Fig. 3. Stretching performance during B1 and B2 part 2 for MI practice and Control groups. \*\*\* =  $p < 0.001$ , NS=No statistically significant difference.

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

#### 3.4.2. Electrodermal activity

Raw averages (± 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  $\mu\text{S}$  ± 9.51 in the MI practice and 4.33  $\mu\text{S}$  ± 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



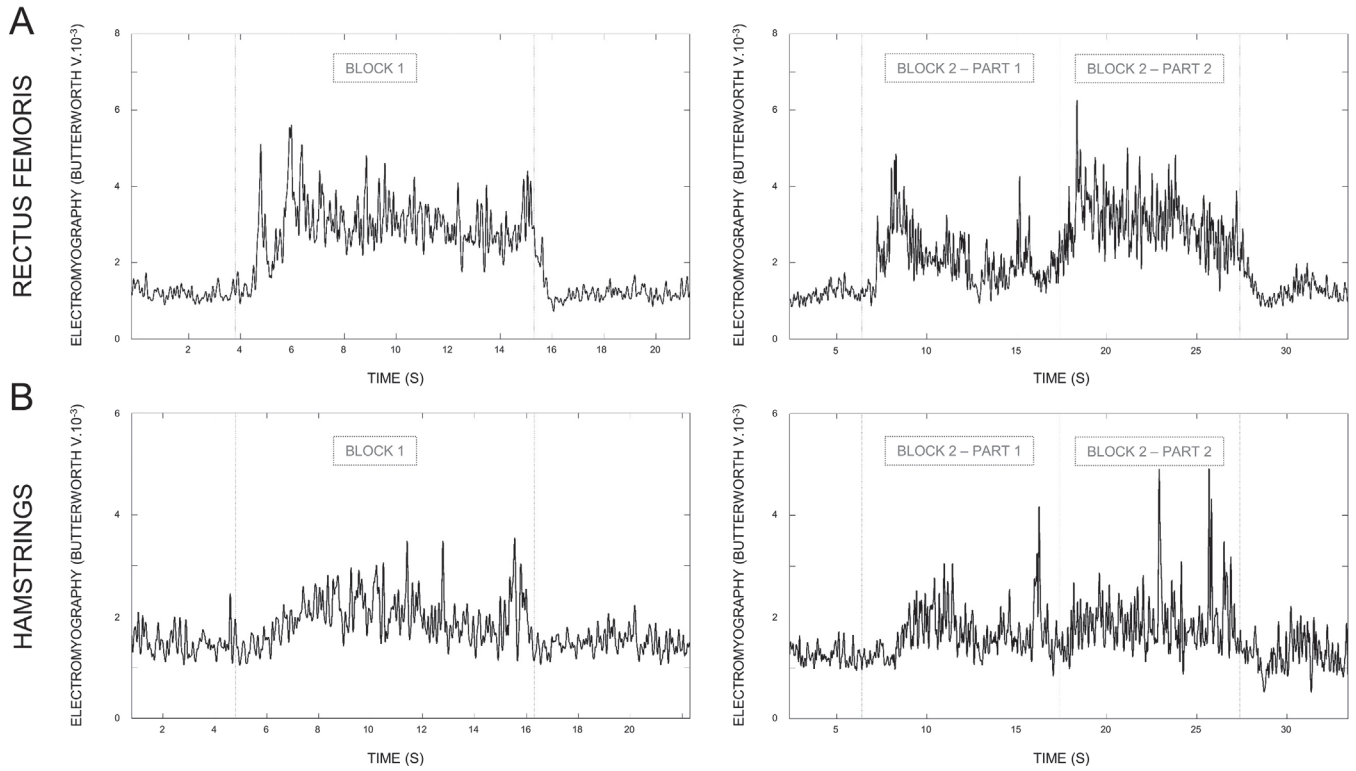


Fig. 4. A. Electromyography (Butterworth filter 20–450 Hz, 4th order) of the rectus femoris during B1 (left panel) and B2 part 1 and 2 (right panel). B. Electromyography (Butterworth filter 20–450 Hz, 4th order) of the hamstring during B1 and B2 part 1 and 2. Data were extracted from a representative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

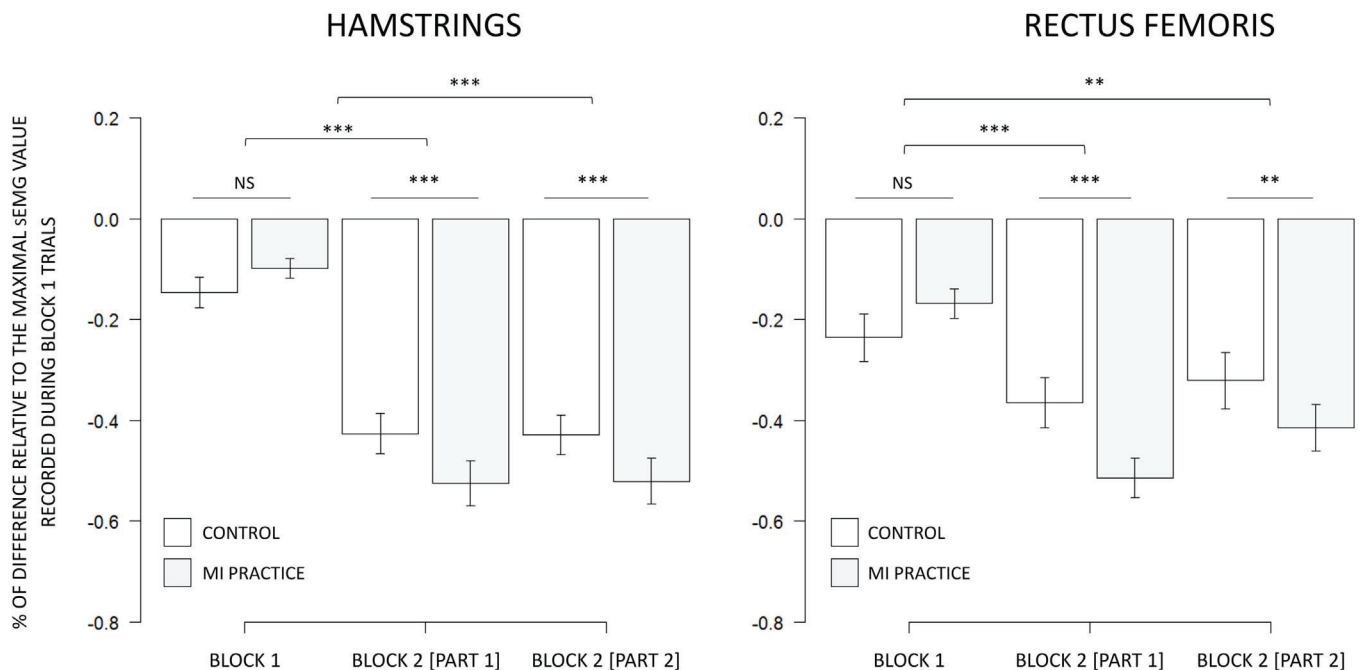
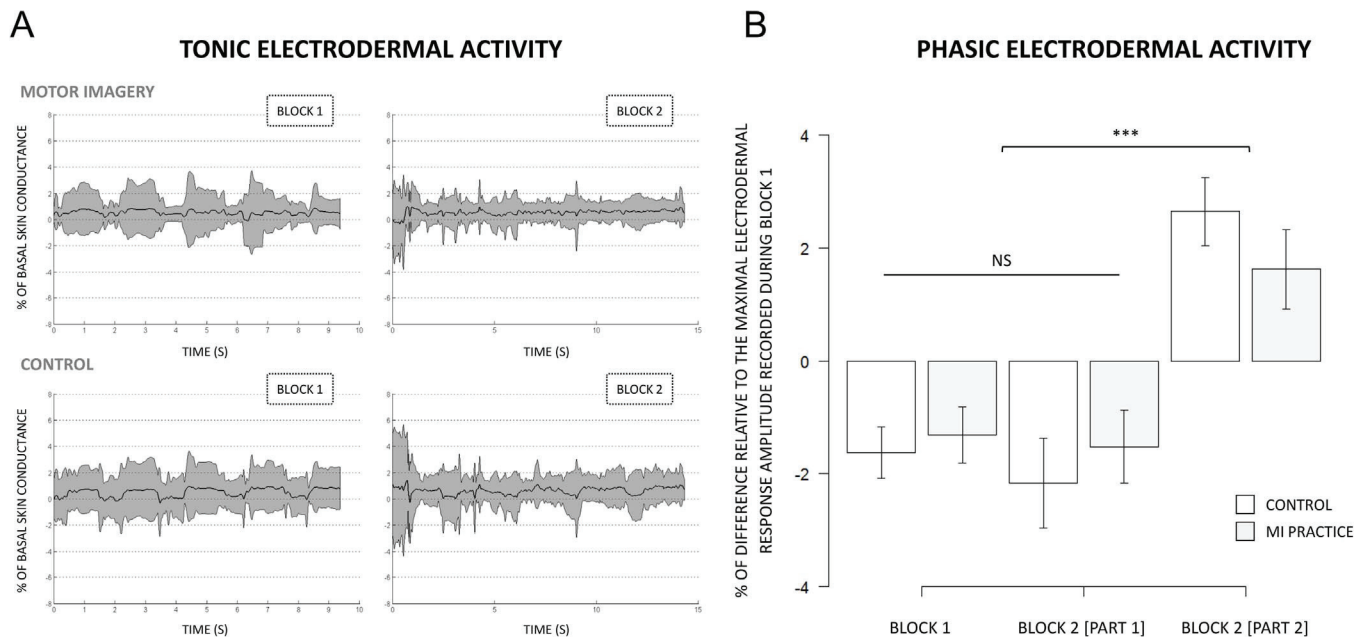


Fig. 5. Standardized smoothed EMG in hamstring (left panel) and rectus femoris (right panel) muscles during the sit-and-reach paradigm in MI practice and Control groups. \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ , NS=No statistically significant difference.



**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 difficult 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 led 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 effector-specific [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 ± standard deviation) electromyography (mV), electrodermal activity (µS) and performance (cm) data in MI practice and Control groups for Block 1 and Block 2 (part 1 and 2).

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

References

[1] J. Munzert, B. Lorey, K. Zentgraf, Cognitive motor processes: the role of motor imagery in the study of motor representations, *Brain Res. Rev.* 60 (2) (2009) 306–326.

[2] M. Jeannerod, Neural simulation of action: a unifying mechanism for motor cognition, *Neuroimage* 14 (1) (2001) S103–S109.

[3] J. Decety, D. Perani, M. Jeannerod, V. Bettinardi, B. Tadary, R. Woods, J.C. Mazziotta, F. Fazio, Mapping Motor Representations with Positron Emission Tomography, (1994).

[4] M. Lotze, P. Montoya, M. Erb, E. Hülsmann, H. Flor, U. Klose, N. Birbaumer, W. Grodd, Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study, *J. Cogn. Neurosci.* 11 (5) (1999) 491–501.

[5] M. Roth, J. Decety, M. Raybaudi, R. Massarelli, C. Delon-Martin, C. Segebarth, S. Morand, A. Gemignani, M. Décorps, M. Jeannerod, Possible involvement of primary motor cortex in mentally simulated movement: a functional magnetic resonance imaging study, *Neuroreport* 7 (7) (1996) 1280–1284.

[6] F. Di Rienzo, U. Debarnot, S. Daligault, E. Saruco, C. Delpuech, J. Doyon, C. Collet, A. Guillot, Online and offline performance gains following motor imagery practice: a comprehensive review of behavioral and neuroimaging studies, *Front. Hum. Neurosci.* 10 (2016) 315.

[7] M. Lotze, U. Halsband, Motor imagery, *J. Physiol. -Paris* 99 (4) (2006) 386–395.

[8] L.K. Case, J. Pineda, V.S. Ramachandran, Common coding and dynamic interactions between observed, imagined, and experienced motor and somatosensory activity, *Neuropsychologia* 79 (2015) 233–245.

[9] S. Hetu, M. Gregoire, A. Saimpont, M.P. Coll, F. Eugene, P.E. Michon, P.L. Jackson, The neural network of motor imagery: an ALE meta-analysis, *Neurosci. Biobehav. Rev.* 37 (5) (2013) 930–949.

[10] J. Munzert, B. Lorey, K. Zentgraf, Cognitive motor processes: the role of motor imagery in the study of motor representations, *Brain Res. Rev.* 60 (2) (2009) 306–326.

[11] V.K. Ranganathan, V. Siemionow, J.Z. Liu, V. Sahgal, G.H. Yue, From mental power to muscle power—gaining strength by using the mind, *Neuropsychologia* 42 (7) (2004) 944–956.

[12] P. Personnier, C. Paizis, Y. Ballay, C. Papaxanthis, Mentally represented motor actions in normal aging II. The influence of the gravito-inertial context on the duration of overt and covert arm movements, *Behav. Brain Res.* 186 (2) (2008) 273–283.

[13] R. Hashimoto, J.C. Rothwell, Dynamic changes in corticospinal excitability during motor imagery, *Exp. Brain Res.* 125 (1) (1999) 75–81.

[14] S.C. Gandevia, L.R. Wilson, J.T. Inglis, D. Burke, Mental rehearsal of motor tasks recruits  $\alpha$ -motoneurons but fails to recruit human fusiform motor neurons selectively, *J. Physiol.* 505 (1) (1997) 259–266.

[15] M.S.J. Boschker, Action-based Imagery: On the Nature of Mentally Imagined Motor Actions, (2001).

[16] M. Bonnet, J. Decety, M. Jeannerod, J. Requin, Mental simulation of an action modulates the excitability of spinal reflex pathways in man, *Cognit. Brain Res.* 5 (3) (1997) 221–228.

[17] A. Guillot, F. Lebon, D. Rouffet, S. Champely, J. Doyon, C. Collet, Muscular responses during motor imagery as a function of muscle contraction types, *Int. J. Psychophysiol.* 66 (1) (2007) 18–27.

[18] F. Lebon, A. Guillot, D. Rouffet, C. Collet, EMG correlates different types of muscular contraction during motor imagery, *Neurosci. Lett.* 435 (2008) 181–185.

[19] A. Guillot, C. Collet, Construction of the motor imagery integrative model in sport: a review and theoretical investigation of motor imagery use, *Int. Rev. Sport Exerc. Psychol.* 1 (1) (2008) 31–44.

[20] C. Schuster, R. Hilfiker, O. Amft, A. Scheidhauer, B. Andrews, J. Butler, U. Kischka, T. Ettlin, Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines, *BMC Med.* 9 (1) (2011) 75.

[21] M.W. Cornwall, M.P. Bruscatto, S. Barry, Effect of mental practice on isometric muscular strength 1, *J. Orthop. Sports Phys. Ther.* 13 (5) (1991) 231–234.

[22] G. Yue, K.J. Cole, Strength increases from the motor program: comparison of training with maximal voluntary and imagined muscle contractions, *J. Neurophysiol.* 67 (5) (1992) 1114–1123.

[23] D. Smith, D. Collins, P. Holmes, Impact and mechanism of mental practice effects on strength, *Int. J. Sport Exerc. Psychol.* 1 (3) (2003) 293–306.

[24] V.K. Ranganathan, V. Siemionow, J.Z. Liu, V. Sahgal, G.H. Yue, From mental power to muscle power—gaining strength by using the mind, *Neuropsychologia* 42 (7) (2004) 944–956.

[25] C.J. Wright, D. Smith, The effect of PETTLEP imagery on strength performance, *Int. J. Sport Exerc. Psychol.* 7 (1) (2009) 18–31.

[26] F. Di Rienzo, Y. Blache, T. Kanthack, K. Monteil, C. Collet, A. Guillot, Short-term effects of integrated motor imagery practice on muscle activation and force performance, *Neuroscience* 305 (2015) 146–156.

[27] W.X. Yao, V.K. Ranganathan, D. Alexandre, V. Siemionow, G.H. Yue, Kinesthetic imagery training of forceful muscle contractions increases brain signal and muscle strength, *Front. Hum. Neurosci.* 7 (2013) 561.

[28] E. Jacobson, Electrophysiology of mental activities, *Am. J. Psychol.* 44 (4) (1932)

- 677–694.
- [29] E. Jacobson, Electrical measurements of neuromuscular states during mental activities, *Am. J. Physiol.-Legacy Content* 91 (2) (1930) 567–608.
- [30] A. Guillot, F. Di Rienzo, T. MacIntyre, A.P. Moran, C. Collet, Imagining Is Not Doing but Involves Specific Motor Commands: a Review of Experimental Data Related to Motor Inhibition, (2012).
- [31] J.C. Rothwell, Physiological studies of electric and magnetic stimulation of the human brain, *Electroencephalogr. Clin. Neurophysiol.* 43 (1991) 29–35 Supplement.
- [32] J. Reis, O.B. Swayne, Y. Vandermeeren, M. Camus, M.A. Dimyan, M. Harris-Love, M.A. Perez, P. Ragert, J.C. Rothwell, L.G. Cohen, Contribution of transcranial magnetic stimulation to the understanding of cortical mechanisms involved in motor control, *The J. Physiol.* 586 (2) (2008) 325–351.
- [33] E. Dayan, N. Censor, E.R. Buch, M. Sandrini, L.G. Cohen, Noninvasive brain stimulation: from physiology to network dynamics and back, *Nat. Neurosci.* 16 (7) (2013) 838–844.
- [34] M. Takemi, Y. Masakado, M. Liu, J. Ushiba, Event-related desynchronization reflects down-regulation of intracortical inhibition in human primary motor cortex, *J. Neurophysiol.* (2013).
- [35] C.M. Stinear, W.D. Byblow, Motor imagery of phasic thumb abduction temporally and spatially modulates corticospinal excitability, *Clin. Neurophysiol.* 114 (5) (2003) 909–914.
- [36] C.M. Stinear, Corticospinal facilitation during motor imagery, in: A. Guillot, C. Collet (Eds.), *The Neurophysiological Foundations of Mental and Motor Imagery*, Oxford University Press, New York, NY, 2010, pp. 47–61.
- [37] G. Abbruzzese, C. Trompetto, M. Schieppati, The excitability of the human motor cortex increases during execution and mental imagination of sequential but not repetitive finger movements, *Exp. Brain Res.* 111 (3) (1996) 465–472.
- [38] R. Hashimoto, J.C. Rothwell, Dynamic changes in corticospinal excitability during motor imagery, *Exp. Brain Res.* 125 (1) (1999) 75–81.
- [39] T. Kasai, S. Kawai, M. Kawanishi, S. Yahagi, Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery, *Brain Res.* 744 (1) (1997) 147–150.
- [40] P.M. Cowley, B.C. Clark, L.L. Ploutz-Snyder, Kinesthetic motor imagery and spinal excitability: the effect of contraction intensity and spatial localization, *Clin. Neurophysiol.* 119 (8) (2008) 1849–1856.
- [41] J. Fujisawa, H. Touyama, M. Hirose, Extracting alpha band modulation during visual spatial attention without flickering stimuli using common spatial pattern, Conference proceedings: ... Annual International Conference of the IEEE Engineering in Medicine and Biology Society, IEEE Eng. Med. Biol. Soc. Conf. 2008 (2008) 620–623.
- [42] M. Hara, J. Kimura, D.D. Walker, S. Taniguchi, H. Ichikawa, R. Fujisawa, H. Shimizu, T. Abe, T. Yamada, R. Kayamori, T. Mizutani, Effect of motor imagery and voluntary muscle contraction on the F wave, *Muscle Nerve* 42 (2) (2010) 208–212.
- [43] H. Ichikawa, J. Kimura, S. Taniguchi, M. Hara, R. Fujisawa, H. Shimizu, T. Yamada, M. Kawamura, Motor imagery facilitates the spinal motor neurons without hemispheric asymmetry, *J. Clin. Neurophysiol.* 26 (5) (2009) 358–365.
- [44] S. Grosprêtre, F. Lebon, C. Papaxanthis, A. Martin, New evidence of cortico-spinal network modulation induced by motor imagery, *J. Neurophysiol.* (2015) jn.00952.2015.
- [45] A. Guillot, F. Di Rienzo, T. MacIntyre, A. Moran, C. Collet, Imagining is not doing but involves specific motor commands: a review of experimental data related to motor inhibition, *Front. Hum. Neurosci.* 6 (2012) 1–22.
- [46] J.G. Williams, J.L. Odley, M. Callaghan, Motor imagery boosts proprioceptive neuromuscular facilitation in the attainment and retention of range-of-motion at the hip joint, *J. Sports Sci. Med.* 3 (3) (2004) 160.
- [47] I. Vergeer, J. Roberts, Movement and stretching imagery during flexibility training, *J. Sports Sci.* 24 (2) (2006) 197–208.
- [48] A. Guillot, C. Tolleron, C. Collet, Does motor imagery enhance stretching and flexibility? *J. Sports Sci.* 28 (3) (2010) 291–298.
- [49] A. Paivio, Cognitive and motivational functions of imagery in human performance: Canadian journal of applied sport sciences, *J. Can. Des. Sci. Appl. Au Sport* 10 (4) (1985) 22S–28S.
- [50] C.R. Hall, D.E. Mack, A. Paivio, H.A. Hausenblas, Imagery use by athletes: development of the sport imagery questionnaire, *Int. J. Sport Psychol.* 29 (1998) 73–89.
- [51] A. Guillot, C. Collet, Construction of the Motor Imagery Integrative Model in Sport: a review and theoretical investigation of motor imagery use, *Int. Rev. Sport Exerc. Psychol.* 1 (1) (2008) 31–44.
- [52] P.S. Holmes, D.J. Collins, The PETTLEP approach to motor imagery: a functional equivalence model for sport psychologists, *J. Appl. Sport Psychol.* 13 (1) (2001) 60–83.
- [53] T.F.D. Kanthack, A. Guillot, L.R. Altamari, S. Nunez Nagy, C. Collet, F. Di Rienzo, Selective efficacy of static and dynamic imagery in different states of physical fatigue, *PLoS One* (2016) in revisions.
- [54] A. Guillot, F. Di Rienzo, V. Pialoux, G. Simon, S. Skinner, I. Rogowski, Implementation of motor imagery during specific aerobic training session in young tennis players, *PLoS One* 10 (11) (2015) e0143331.
- [55] F. Di Rienzo, Y. Blache, T.F. Kanthack, K. Monteil, C. Collet, A. Guillot, Short-term effects of integrated motor imagery practice on muscle activation and force performance, *Neuroscience* 305 (2015) 146–156.
- [56] N. Callow, R. Roberts, J.Z. Fawkes, Effects of dynamic and static imagery on vividness of imagery, skiing performance, and confidence, *J. Imag. Res. Sport Phys. Act.* 1 (2006) 1–15.
- [57] I. Vergeer, J. Roberts, Movement and stretching imagery during flexibility training, *J. Sport Sci.* 24 (2) (2006) 197–208.
- [58] S. Grosprêtre, C. Ruffino, F. Lebon, Motor imagery and cortico-spinal excitability: a review, *Eur. J. Sport Sci.* (2015) 1–8.
- [59] K.F. Wells, E.K. Dillon, The sit and reach—a test of back and leg flexibility, *Research Quarterly, Am. Assoc. Health Phys. Educ. Recreat.* 23 (1) (1952) 115–118.
- [60] G.A. Borg, Psychophysical bases of perceived exertion, *Med. Sci. Sports Exerc.* 14 (5) (1982) 377–381.
- [61] G. Borg, G. Ljunggren, R. Ceci, The increase of perceived exertion, aches and pain in the legs, heart rate and blood lactate during exercise on a bicycle ergometer, *Eur. J. Appl. Physiol. Occup. Physiol.* 54 (4) (1985) 343–349.
- [62] G.A. Borg, B.J. Noble, Perceived exertion, *Exerc. Sport Sci. Rev.* 2 (1) (1974) 131–154.
- [63] R. Roberts, N. Callow, L. Hardy, D. Markland, J. Bringer, Movement imagery ability: development and assessment of a revised version of the vividness of movement imagery questionnaire, *J. Sport Exerc. Psychol.* 30 (2008) 200–221.
- [64] H.J. Hermens, B. Freriks, C. Disselhorst-Klug, G. Rau, Development of recommendations for SEMG sensors and sensor placement procedures, *J. Electromyogr. Kinesiol.* 10 (5) (2000) 361–374.
- [65] T. Hokfelt, O. Johansson, A. Ljungdahl, J.M. Lundberg, M. Schultzberg, Peptidergic neurones, *Nature* 284 (5756) (1980) 515–521.
- [66] C. Collet, F. Di Rienzo, N. El Hoyek, A. Guillot, Autonomic nervous system correlates in movement observation and motor imagery, *Front. Hum. Neurosci.* 7 (2013) 415.
- [67] E. Vernet-Maury, O. Robin, A. Dittmar, The ohmic perturbation duration, an original temporal index to quantify electrodermal responses, *Behav. Brain Res.* 67 (1) (1995) 103–107.
- [68] R.C. Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2012, p. 2014 (ISBN 3–900051–07–0).
- [69] D. Bates, M. Maechler, B. Bolker, S. Walker, lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–7, This is computer program (R package). The URL of the package is: <http://CRAN.R-project.org/package=lme4> (2014).
- [70] B. Winter, Linear Models and Linear Mixed Effects Models in R with Linguistic Applications, (2013) arXiv:1308.5499. [<http://arxiv.org/pdf/1308.5499.pdf>] (2013).
- [71] S. Holm, A simple sequentially rejective multiple test procedure, *Scand. J. Stat.* (1979) 65–70.
- [72] W.J. Rejeski, Perceived exertion: an active or passive process, *J. Sport Psychol.* 7 (4) (1985) 371–378.
- [73] W.J. Rejeski, The perception of exertion: a social psychophysiological integration, *J. Sport Psychol.* (1981).
- [74] S. Magnusson, E. Simonsen, P. Aagaard, G. Gleim, M. McHugh, M. Kjaer, Viscoelastic response to repeated static stretching in the human hamstring muscle, *Scand. J. Med. Sci. Sports* 5 (6) (1995) 342–347.
- [75] S. Magnusson, E. Simonsen, P. Dyhre-Poulsen, P. Aagaard, T. Mohr, M. Kjaer, Viscoelastic stress relaxation during static stretch in human skeletal muscle in the absence of EMG activity, *Scand. J. Med. Sci. Sports* 6 (6) (1996) 323–328.
- [76] P. Lew, C. Briggs, Relationship between the cervical component of the slump test and change in hamstring muscle tension, *Man. Ther.* 2 (2) (1997) 98–105.
- [77] J. Fowles, D. Sale, J. MacDougall, Reduced strength after passive stretch of the human plantarflexors, *J. Appl. Physiol.* 89 (3) (2000) 1179–1188.
- [78] A.D. Kay, A.J. Blazeovich, Moderate-duration static stretch reduces active and passive plantar flexor moment but not Achilles tendon stiffness or active muscle length, *J. Appl. Physiol.* 106 (4) (2009) 1249–1256.
- [79] G.S. Trajano, L.B. Seitz, K. Nosaka, A.J. Blazeovich, Can passive stretch inhibit motoneuron facilitation in the human plantar flexors? *J. Appl. Physiol.* 117 (12) (2014) 1486–1492.
- [80] J. Avela, H. Kyröläinen, P.V. Komi, Altered reflex sensitivity after repeated and prolonged passive muscle stretching, *J. Appl. Physiol.* 86 (4) (1999) 1283–1291.
- [81] A.S. Hyngstrom, M.D. Johnson, J.F. Miller, C. Heckman, Intrinsic electrical properties of spinal motoneurons vary with joint angle, *Nat. Neurosci.* 10 (3) (2007) 363–369.
- [82] M. Dimitriou, Human muscle spindle sensitivity reflects the balance of activity between antagonistic muscles, *J. Neurosci.* 34 (41) (2014) 13644–13655.
- [83] A. Konrad, M. Tilp, Increased range of motion after static stretching is not due to changes in muscle and tendon structures, *Clin. Biomech.* 29 (6) (2014) 636–642.
- [84] M.J. Alter, Science of flexibility, *Hum. Kinet.* (2004).
- [85] V. Rozand, F. Lebon, C. Papaxanthis, R. Lepers, Does a mental training session induce neuromuscular fatigue, *Med. Sci. Sports Exerc.* 46 (10) (2014) 1981–1989.
- [86] S. Li, M.L. Latash, V.M. Zatsiorsky, Effects of motor imagery on finger force responses to transcranial magnetic stimulation, *Cognit. Brain Res.* 20 (2) (2004) 273–280.
- [87] C.M. Stinear, W.D. Byblow, Motor imagery of phasic thumb abduction temporally and spatially modulates corticospinal excitability, *Clin. Neurophysiol.* 114 (5) (2003) 909–914.
- [88] C.M. Stinear, W.D. Byblow, M. Steyvers, O. Levin, S.P. Swinnen, Kinesthetic, but not visual, motor imagery modulates corticomotor excitability, *Exp. Brain Res.* 168 (1–2) (2006) 157–164.
- [89] A. Guillot, C. Tolleron, C. Collet, Does motor imagery enhance stretching and flexibility? *J. Sport Sci.* 28 (3) (2010) 291–298.
- [90] J.G. Williams, J.L. Odley, M. Callaghan, Motor imagery boosts proprioceptive neuromuscular facilitation in the attainment and retention of range-of—motion at the hip joint, *J. Sports Sci. Med.* 3 (3) (2004) 160–166.
- [91] M.W. Cornwall, M.P. Bruscatto, S. Barry, Effect of mental practice on isometric

- muscular strength, *J. Orthop. Sports Phys. Ther.* 13 (5) (1991) 231–234.
- [92] G. Yue, K.J. Cole, Strength increases from the motor program: comparison of training with maximal voluntary and imagined muscle contractions, *J. Neurophysiol.* 67 (5) (1992) 1114–1123.
- [93] M. Reiser, D. Busch, J. Munzert, Strength gains by motor imagery with different ratios of physical to mental practice, *Front. Psychol.* 2 (2011) 194.
- [94] M. Jeannerod, The representing brain: neural correlates of motor intention and imagery, *Behav. Brain Sci.* 17 (02) (1994) 187–202.
- [95] D.G. Mackay, The problem of rehearsal or mental practice, *J. Mot. Behav.* 13 (4) (1981) 274–285.
- [96] S.C. Gandevia, L.R. Wilson, J.T. Inglis, D. Burke, Mental rehearsal of motor tasks recruits alpha-motoneurons but fails to recruit human fusimotor neurons selectively, *J. Physiol.* 505 (Pt 1) (1997) 259–266.
- [97] S.P. Magnusson, Passive properties of human skeletal muscle during stretch maneuvers, A review, *Scand. J. Med. Sci. Sports* 8 (2) (1998) 65–77.
- [98] C. Schuster, R. Hilfiker, O. Amft, A. Scheidhauer, B. Andrews, J. Butler, U. Kischka, T. Ettlin, Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines, *BMC Med.* 9 (2011) 75.
- [99] A. Guillot, N. Hoyek, M. Louis, C. Collet, Understanding the timing of motor imagery: recent findings and future directions, *Int. Rev. Sport Exerc. Psychol.* 5 (1) (2012) 3–22.
- [100] M. Louis, C. Collet, A. Guillot, Differences in motor imagery times during aroused and relaxed conditions, *J. Cognit. Psychol.* 23 (3) (2011) 374–382.
- [101] L. Fadiga, G. Buccino, L. Craighero, L. Fogassi, V. Gallese, G. Pavesi, Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study, *Neuropsychologia* 37 (2) (1998) 147–158.

**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 breath-holding trials while concomitantly practicing i) MI of breathing, ii) MI of breath-holding. 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 breath-holding 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 interval) 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., MI<sub>INCONGRUENT</sub>), ii) MI practice focused on the proprioceptive information of holding breath (i.e., MI<sub>CONGRUENT</sub>) and finally, iii) focus on a cross fixed in front of them 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**

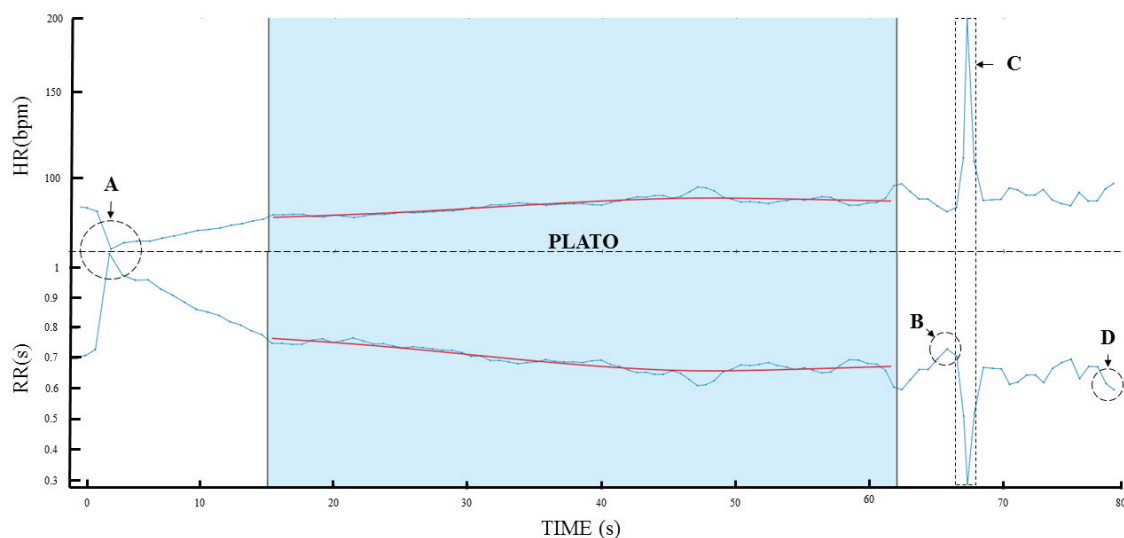
Fifteen seconds before each trial, participants were warned of prepare themselves and to perform a maximal inspiration before starting. Participants were instructed to hold their breath after completion of the ventilation routine for the as long as possible. breath-holding performance was quantified 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 ( $SO_2$ ) 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, SO<sub>2</sub> was checked for return of basal values.

### C) Psychometric recordings

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

After completion of MI<sub>CONGRUENT</sub>, MI<sub>INCONGRUENT</sub> 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<sub>CONGRUENT</sub> and MI<sub>INCONGRUENT</sub> 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 thought 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.,

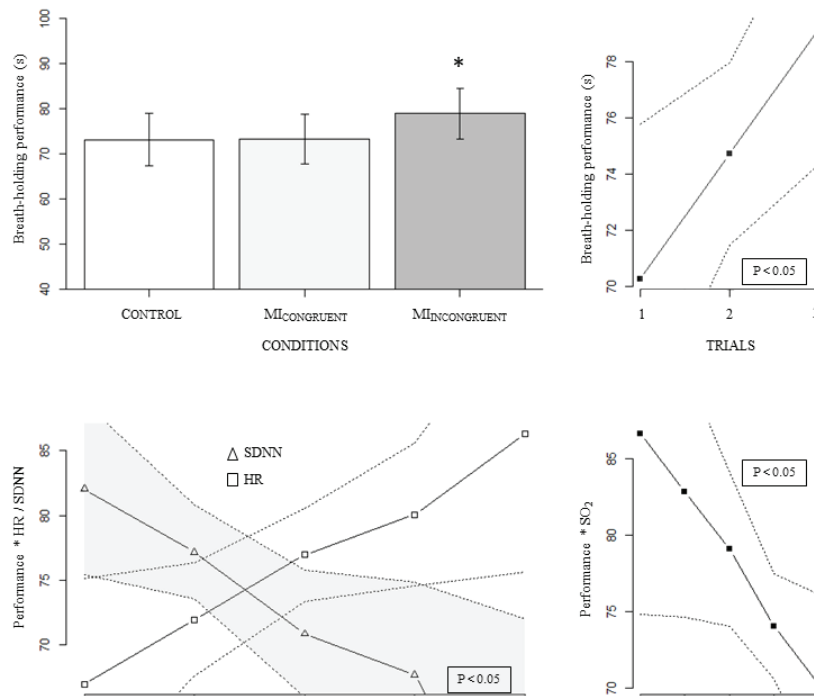
MI<sub>CONGRUENT</sub>, MI<sub>INCONGRUENT</sub> CONTROL), TRIAL (i.e., TRIALS 1-3), with interaction term. We also included SO<sub>2</sub>, HR, RMSSD and SDNN (without interaction term). TRIAL was included as numeric regressor in the model since we expected an habituation to breath-holding from trials 1-3. For the analysis of psychometric variables, we used the EXPERIMENTAL CONDITION (i.e., MI<sub>CONGRUENT</sub>, MI<sub>INCONGRUENT</sub>, CONTROL) as fixed effect. A backward stepwise procedure was used to fit the random-coefficient 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  $\Omega_0^2$  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<sub>NORM</sub>, SDNN<sub>NORM</sub> and SO<sub>2</sub> ( $\Omega_0^2 = 0.29$ ). 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<sub>INCONGRUENT</sub> outperformed that during both MI<sub>CONGRUENT</sub>

( $+5.58 \pm 2.42$ ,  $p = 0.05$ ) and CONTROL ( $+5.78 \pm 2.53$ ,  $p = 0.05$ ) (Figure 2). There was no difference between MI<sub>CONGRUENT</sub> 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:  $+4.46 \text{ s} \pm 1.26$ ;  $\chi^2(1) = 12.54$ ,  $p < 0.001$ ), HR<sub>NORM</sub> (fitted estimate:  $+0.31 \text{ s} \pm 0.11$ ;  $\chi^2(1) = 7.56$ ,  $p < 0.01$ ), SDNN<sub>NORM</sub> (fitted estimate:  $-0.16 \text{ s} \pm 0.05$ ;  $\chi^2(1) = 8.58$ ,  $p < 0.01$ ) and SO<sub>2</sub> (fitted estimate:  $-1.26 \text{ s} \pm 0.55$ ;  $\chi^2(1) = 5.28$ ,  $p < 0.01$ ). breath-holding performance was not predicted by RMSSD<sub>NORM</sub> ( $p > 0.05$ ) (Figure 2).

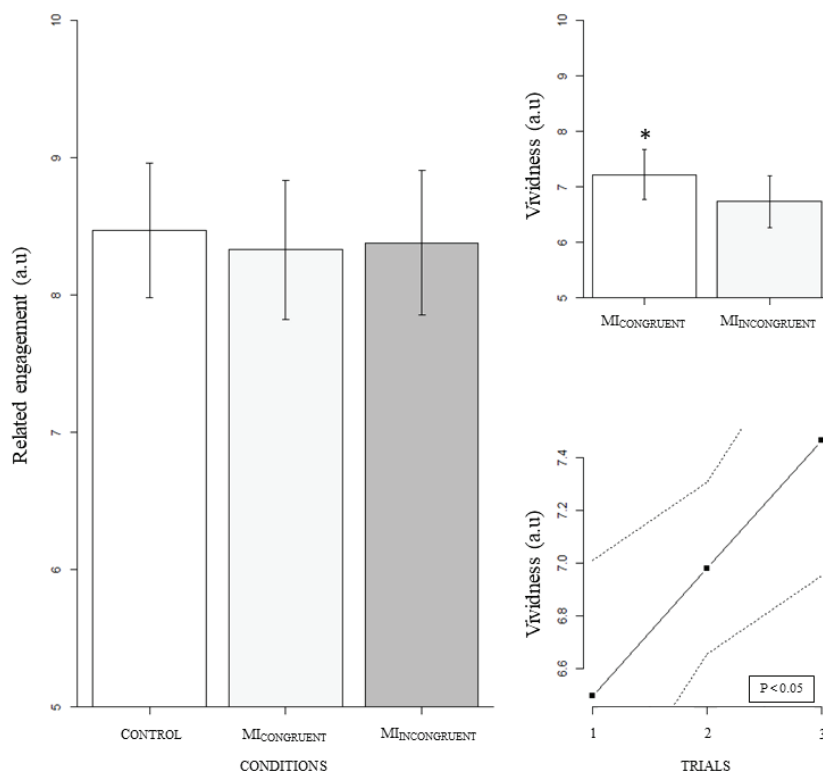
## V) Analysis of the psychometric data

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<sub>INCONGRUENT</sub> (38 %) and MI<sub>CONGRUENT</sub> (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  $8.40 \pm 0.20$  on the 10-points Likert scale.



**Figure 3.** Effect influencing self-report of motor imagery vividness and task engagement. \* Significant difference across experimental conditions ( $p < 0.05$ ).

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<sub>CONGRUENT</sub> than during MI<sub>INCONGRUENT</sub> ( $+0.48 \pm 0.24$ ,  $p = 0.04$ ). TRIAL positively predicted the self-reports of perceived MI vividness ( $+0.48 \pm 0.15$ ,  $p < 0.001$ ) (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 factors involved in maximal breath-holding performance (Parkes, 2006). Throughout conditions, participants reported identical levels of commitment to achieve a maximal breath-holding performance. Yet, we found that MI<sub>INCONGRUENT</sub>, i.e., where participants mentally recreated the sensations of breathing, but not MI<sub>CONGRUENT</sub>, 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 breath-

holding 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., self-talk and relaxation) significantly increased breath-holding durations in cold water immersion, without altering breath-holding performance in normal, non-threatening 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<sub>INCONGRUENT</sub> is the generation through the *Motivational* function of MI of a more sustainable mental state during the breath-holding 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 motoneurons, 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) MI<sub>INCONGRUENT</sub>, but not MI<sub>CONGRUENT</sub>, 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 SO<sub>2</sub>. 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 breath-holding 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<sub>2</sub> deprivation, 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 O<sub>2</sub> supply to the tissues, hence facilitating the forthcoming breath-hold performance.

Participants reported higher levels of vividness during MI<sub>CONGRUENT</sub>. 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 performance 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 perceived that their breath-holding performance during MI<sub>INCONGRUENT</sub> outperformed that during MI<sub>CONGRUENT</sub>. It is thus suggested that the beneficial effects of MI<sub>INCONGRUENT</sub>, 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 efficacy. Nonetheless, embedding mental practice possibly 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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## **REFERENCES**

- Bain AR, Drvis I, Dujic Z, MacLeod DB, Ainslie PN (2018) Physiology of static breath holding in elite apneists. *Experimental Physiology*.
- Balkowiec A, Katz DM (1998) Brain-derived neurotrophic factor is required for normal development of the central respiratory rhythm in mice. *The Journal of physiology* 510:527-533.
- Bartoli A, Bystrzycka E, Guz A, Jain S, Noble M, Trenchard D (1973) Studies of the pulmonary vagal control of central respiratory rhythm in the absence of breathing movements. *The Journal of physiology* 230:449-465.
- Barwood MJ, Dalzell J, Datta AK, Thelwell RC, Tipton MJ (2006) Breath-hold performance during cold water immersion: effects of psychological skills training. *Aviation, space, and environmental medicine* 77:1136-1142.
- Brandt CP, Johnson KA, Schmidt NB, Zvolensky MJ (2012) Main and interactive effects of emotion dysregulation and breath-holding duration in relation to panic-relevant fear and expectancies about anxiety-related sensations among adult daily smokers. *Journal of anxiety disorders* 26:173-181.

- Collet C, Deschaumes-Molinaro C, Delhomme G, Dittmar A, Vernet-Maury E (1994) Autonomic responses correlate to motor anticipation. *Behavioural brain research* 63:71-79.
- Collet C, Di Rienzo F, El Hoyek N, Guillot A (2013) Autonomic nervous system correlates in movement observation and motor imagery. *Frontiers in human neuroscience* 7:415.
- Collet C, Guillot A (2009) Peripheral responses elicited by motor imagery: a window on central and peripheral nervous system relationships through motor commands inhibition. In: *Cognitive Psychology Research Developments*(Weingarten, S. P. and Penat, H. O., eds), pp 1-17 United States: Nova Science Publishers.
- Collet C, Guillot A, Lebon F, MacIntyre T, Moran A (2011) Measuring motor imagery using psychometric, behavioral, and psychophysiological tools. *Exercise and Sport Science Reviews* 39:85-92.
- Decety J (1996) The neurophysiological basis of motor imagery. *Behavioural brain research* 77:45-52.
- Decety J, Jeannerod M, Durozard D, Baverel G (1993) Central activation of autonomic effectors during mental simulation of motor actions in man. *The Journal of physiology* 461:549-563.
- Decety J, Jeannerod M, Germain M, Pastene J (1991) Vegetative response during imagined movement is proportional to mental effort. *Behavioural brain research* 42:1-5.
- Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor



Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. *Frontiers in human neuroscience* 10:315.

Di Rienzo F, Hoyek N, Collet C, Guillot A (2014) Physiological changes in response to apnea impact the timing of motor representations: a preliminary study. *Behavioral and Brain Functions* 10:15.

Draper NR, Smith H (2014) *Applied regression analysis*: John Wiley & Sons.

Eifert GH, Zvolensky MJ, Sorrell JT, Hopko DR, Lejuez C (1999) Predictors of self-reported anxiety and panic symptoms: An evaluation of anxiety sensitivity, suffocation fear, heart-focused anxiety, and breath-holding duration. *Journal of Psychopathology and Behavioral Assessment* 21:293-305.

Eke M, McNally RJ (1996) Anxiety sensitivity, suffocation fear, trait anxiety, and breath-holding duration as predictors of response to carbon dioxide challenge. *Behaviour Research and Therapy* 34:603-607.

Feldman JL (1986) Neurophysiology of breathing in mammals. *Comprehensive Physiology*.

Ferrigno M, Hickey DD, Liner M, Lundgren C (1986) Cardiac performance in humans during breath holding. *Journal of Applied Physiology* 60:1871-1877.

Foster G, Sheel A (2005) The human diving response, its function, and its control. *Scandinavian journal of medicine & science in sports* 15:3-12.

Fusi S, Cutuli D, Valente M, Bergonzi P, Porro C, Di Prampero P (2005) Cardioventilatory responses during real or imagined walking at low speed. *Archives Italiennes de Biologie* 143:223-228.

- Guillot A, Collet C (2008) Construction of the motor imagery integrative model in sport: a review and theoretical investigation of motor imagery use. *International Review of Sport and Exercise Psychology* 1:31-44.
- Guillot A, Collet C, Dittmar A (2005) Influence of environmental context on motor imagery quality: an autonomic nervous system study. *Biology of sport* 22:215.
- Guillot A, Di Rienzo F, Collet C (2014) The neurofunctional architecture of motor imagery. In: *Advanced Brain Neuroimaging Topics in Health and Disease- Methods and Applications: InTech*.
- Hetu S, Gregoire M, Saimpont A, Coll MP, Eugene F, Michon PE, Jackson PL (2013) The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and biobehavioral reviews* 37:930-949.
- Heusser K, Dzamonja G, Tank J, Palada I, Valic Z, Bakovic D, Obad A, Ivancev V, Breskovic T, Diedrich A (2009) Cardiovascular regulation during apnea in elite divers. *Hypertension* 53:719-724.
- Hocking RR (1976) A Biometrics invited paper. The analysis and selection of variables in linear regression. *Biometrics* 32:1-49.
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics* 65-70.
- Holmes PS, Collins DJ (2001) The PETTLEP approach to motor imagery: A functional equivalence model for sport psychologists. *Journal of Applied Sport Psychology* 13:60-83.
- Javorka M, Zila I, Javorka K, Calkovska A (2002) Do oscillations of cardiovascular parameters persist during voluntary apnea in humans? *Physiological research* 51:227-238.

- Javorka M, Žila I, Javorka K, Čalkovská A (2001) 'Respiratory' oscillations of cardiovascular parameters during voluntary apnea. *Respiration physiology* 126:251-254.
- Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14:S103-S109.
- Klocke F, Rahn H (1959) Breath holding after breathing of oxygen. *Journal of Applied Physiology* 14:689-693.
- Kreider M (1967) Death and survival during water immersion: account of plane crashes near Cape Cod and Hamilton Bay. *Aerospace medicine* 38:1060-1062.
- Malik M, Bigger JT, Camm AJ, Kleiger RE, Malliani A, Moss AJ, Schwartz PJ (1996) Heart rate variability: Standards of measurement, physiological interpretation, and clinical use. *European heart journal* 17:354-381.
- Martin KA, Moritz SE, Hall CR (1999) Imagery use in sport: A literature review and applied model. *The Sport Psychologist* 13:245-268.
- Moore T, Lin Y, Lally D, Hong S (1972) Effects of temperature, immersion, and ambient pressure on human apneic bradycardia. *Journal of Applied Physiology* 33:36-41.
- Munzert J, Lorey B, Zentgraf K (2009) Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain research reviews* 60:306-326.
- Noble M, Eisele J, Frankel H, Else W, Guz A (1971) The role of the diaphragm in the sensation of holding the breath. *Clinical science* 41:275-283.
- Overgaard K, Friis S, Pedersen RB, Lykkeboe G (2006) Influence of lung volume, glossopharyngeal inhalation and PET O<sub>2</sub> and PET CO<sub>2</sub> on apnea

performance in trained breath-hold divers. *European journal of applied physiology* 97:158-164.

Paivio A (1985) Cognitive and motivational functions of imagery in human performance. *Canadian journal of applied sport sciences Journal canadien des sciences appliquees au sport* 10:22S-28S.

Parkes M (2006) Breath-holding and its breakpoint. *Experimental Physiology* 91:1-15.

Pinheiro J, Bates D, DebRoy S, Sarkar D (2011) R Development Core Team. NLME: linear and nonlinear mixed effects models. R package version 3.1-109 <http://cran.r-project.org/web/packages/nlme/index.html>.

R Core Team (2015) R: A language and environment for statistical computing. Vienna, Austria. R Foundation for Statistical Computing.

Ratmanova P, Semenyuk R, Popov D, Kuznetsov S, Zelenkova I, Napalkov D, Vinogradova O (2016) Prolonged dry apnoea: effects on brain activity and physiological functions in breath-hold divers and non-divers. *European journal of applied physiology* 116:1367-1377.

Roth WT, Wilhelm FH, Trabert W (1998) Voluntary breath holding in panic and generalized anxiety disorders. *Psychosomatic Medicine* 60:671-679.

Shykoff B, Naqvi S, Menon A, Slutsky A (1991) Respiratory sinus arrhythmia in dogs. Effects of phasic afferents and chemostimulation. *Journal of Clinical Investigation* 87:1621.

Snow G (2013) blockrand: Randomization for block random clinical trials. R package version 1.

- Tipton M (1992) The concept of an 'Integrated Survival System' for protection against the responses associated with immersion in cold water. *Journal of the Royal Naval Medical Service* 79:11-14.
- Trzebski A, Śmietanowski M (1996) Cardiovascular periodicities in healthy humans in the absence of breathing and under reduced chemical drive of respiration. *Journal of the autonomic nervous system* 57:144-148.
- Vanderlei LCM, Pastre CM, Hoshi RA, Carvalho TDd, Godoy MFd (2009) Basic notions of heart rate variability and its clinical applicability. *Brazilian Journal of Cardiovascular Surgery* 24:205-217.
- Xu R (2003) Measuring explained variation in linear mixed effects models. *Statistics in Medicine* 22:3527-3541.

## THEORETICAL FRAMEWORK II

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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

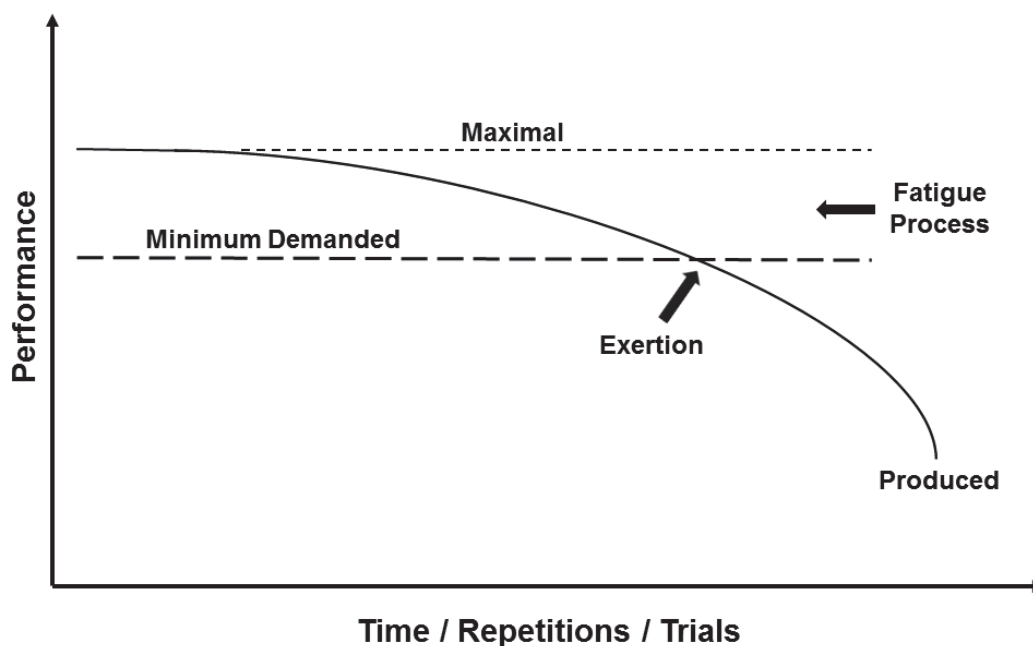
Homeostatic imbalance elicited by fatigue represents a unitary process triggering adaptive psychophysiological responses. This corresponds to the central process involved in performance gains. Hence, physical fatigue is expectedly the focus of most training interventions. The concept of fatigue has been 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 O<sub>2</sub> 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).



**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).

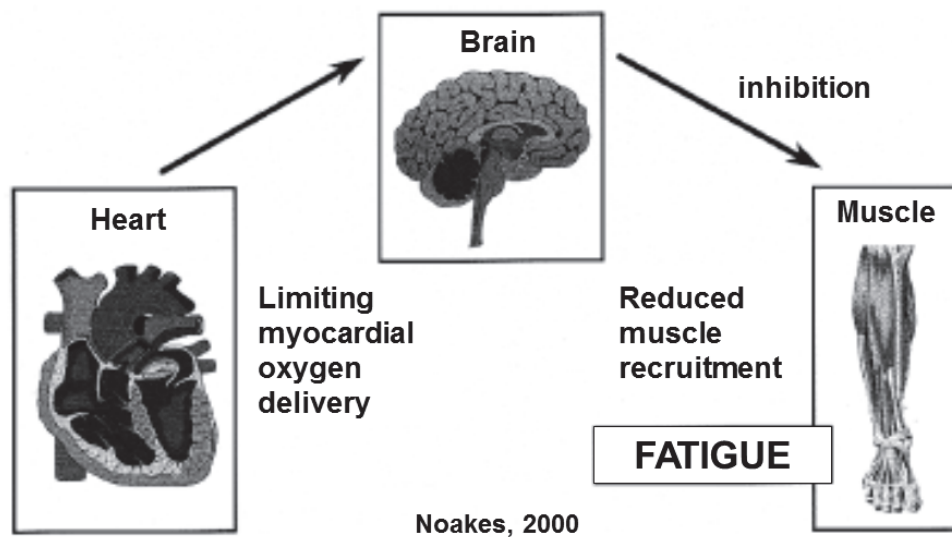
However, according to Noakes (2000), these were largely ignored (for a short critic on the catastrophic model, see Noakes and Gibson, 2004).

## **(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 administered. 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© (license 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 factors:

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

- II) Energy depletion: Carbohydrate, 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

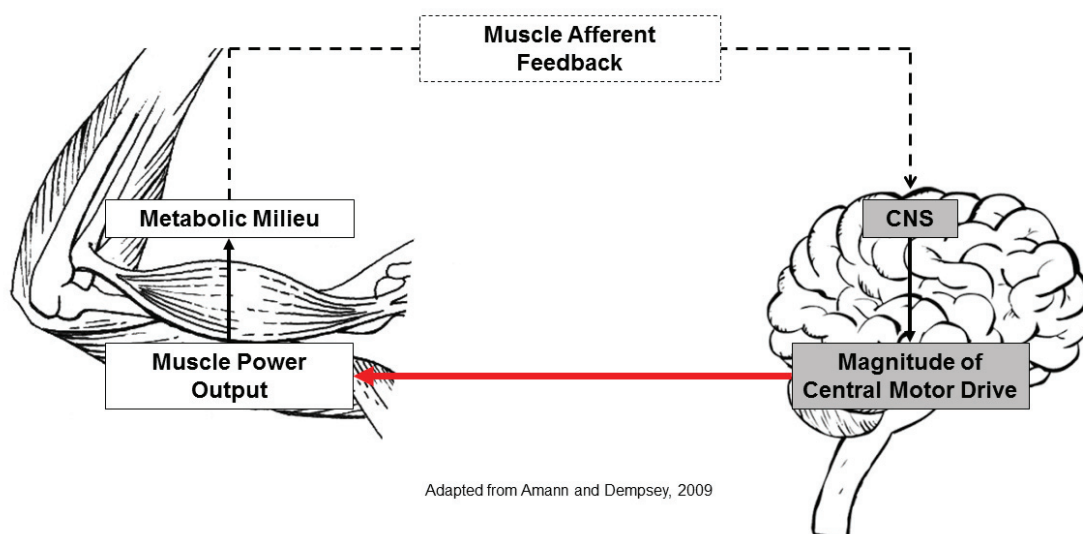
Altogether, these factors would be constantly controlled by the central governor and could be responsible for increasing fatigue until exhaustion point. Overall, the “central governor” seems to play an important role in the fatigue processes. Central governor models nonetheless fail to fully account 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-threatening 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 the 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 supports 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).



Adapted from Amann and Dempsey, 2009

**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 O<sub>2</sub> 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 O<sub>2</sub> 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 time-trial. 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.

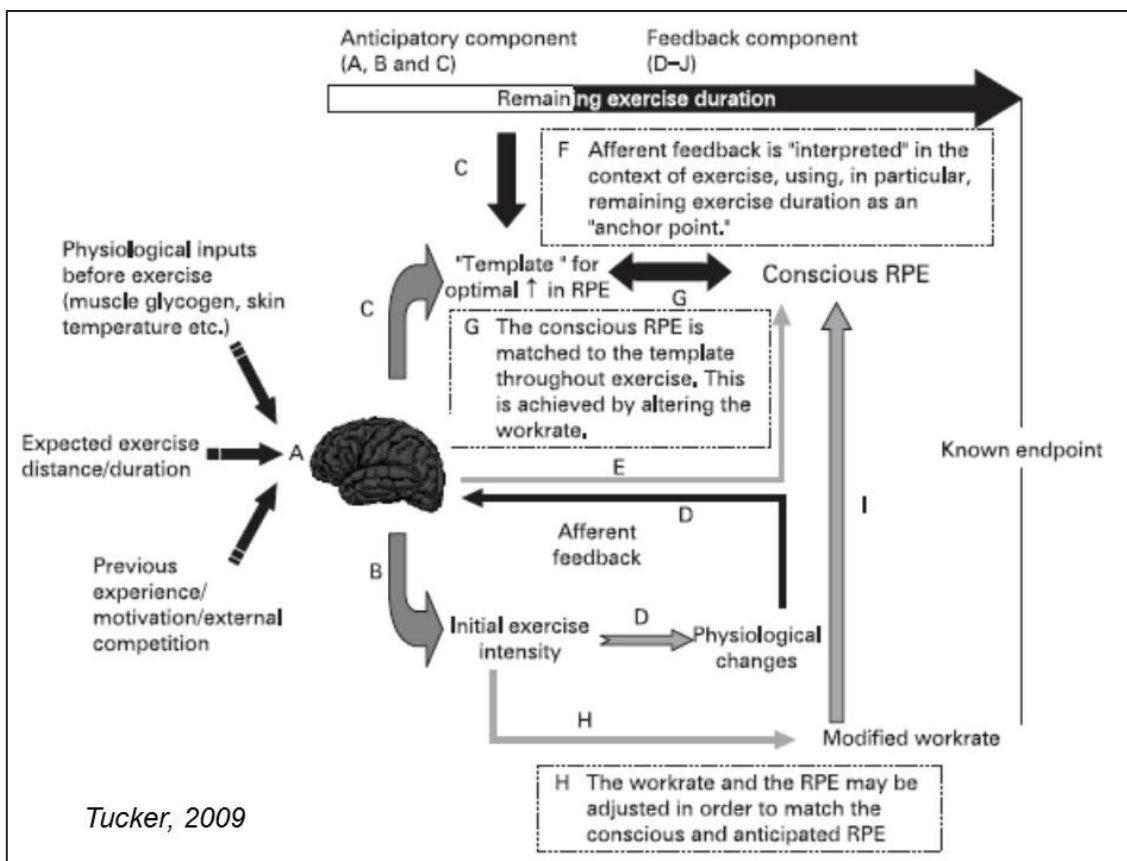
Later, researchers argued that the Central Governor model was somehow incomplete due to its focus on physiological systems, without considering



psychological components (Gibson et al., 2001). Baden et al. (2005) analyzed VO<sub>2</sub>, 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

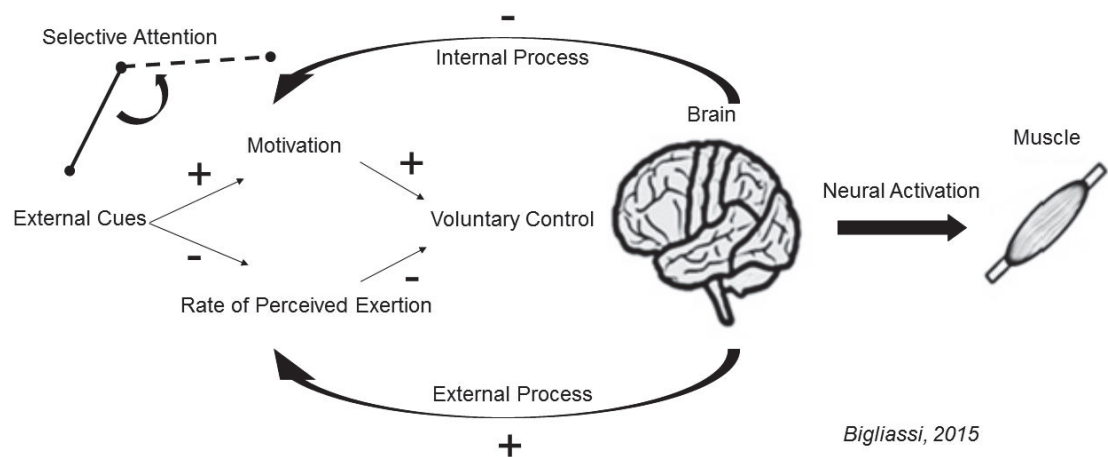
intervention during a cycling exercise, i.e., hypnosis was used to suggest a downhill and uphill condition for the last 5 min on a 15 min constant load exercise. Downhill suggestion through hypnosis yielded decreased RPE and blood flow in the left insular cortex and anterior cingulate cortex, as attested 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 administered 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 known that a drop in muscle pH caused by the presence of free H<sup>+</sup> impairs muscle functionality (Fuchs et al., 1970). In conjunction to other 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) PSYCHOPHYSIOLOGICAL MEASURES OF PHYSICAL FATIGUE**

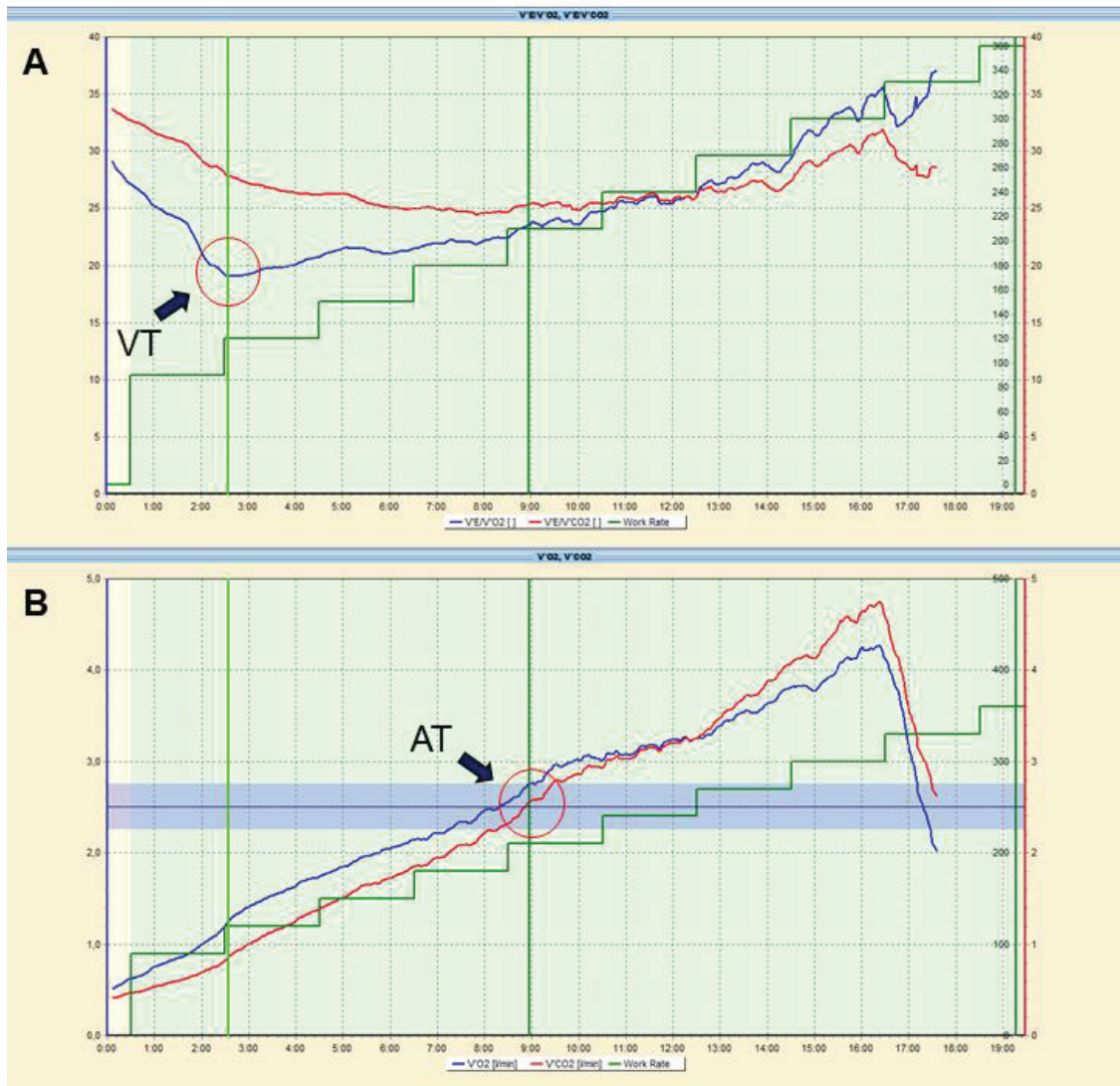
### **(1) CARDIORESPIRATORY MEASURES**

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 CO<sub>2</sub> production.

#### **(i) VENTILATORY AND ANAEROBIC THRESHOLD**

The relationship between oxygen consumption and CO<sub>2</sub> release via cardiopulmonary system can be used to determine the ventilatory threshold. The ventilatory threshold is marked by a first sudden increase in the O<sub>2</sub> 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 CO<sub>2</sub> 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<sup>+</sup> 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 O<sub>2</sub> for ATP production is called VO<sub>2</sub>max.



**Figure 20.** Visual representation of O<sub>2</sub> (Blue line) and CO<sub>2</sub> (Red line) during an ergocycle incremental test (Green line). A. Ventilatory equivalent (V'E) for O<sub>2</sub> and CO<sub>2</sub>. Ventilatory threshold (VT) is represented by a sudden deflection on O<sub>2</sub> consumption curve, due a greater percentage of the breathed O<sub>2</sub> being used for energy production. B. Volume of used O<sub>2</sub> and CO<sub>2</sub> expired. Increase on anaerobic metabolism and blood pH is countered by stimulation of ventilation to increase CO<sub>2</sub> excretion. Thus, Anaerobic Threshold (AT) is represented by a sudden deflection on CO<sub>2</sub> volume curve.

## (ii) VO<sub>2</sub>max measure

In order to measure VO<sub>2</sub>max 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, O<sub>2</sub> consumption and CO<sub>2</sub> 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 VO<sub>2</sub> and heart rate are strongly correlated physiological variables. In particular, the slope from HR-VO<sub>2</sub> curve represents an individual parameter of aerobic fitness. The capacity to achieve higher levels of VO<sub>2</sub> (until VO<sub>2max</sub>) with lower HR represents a better cardiovascular efficiency (McArdle et al., 2010). Therefore, measuring heart rate during VO<sub>2max</sub> analyses is advisable (Achten and Jeukendrup, 2003).

However, classical incremental tests to determine the VO<sub>2max</sub> 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 VO<sub>2max</sub> 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:

$$P = F \cdot v$$

$P$  = Power (Watts)

$F$  = Force (Newtons)

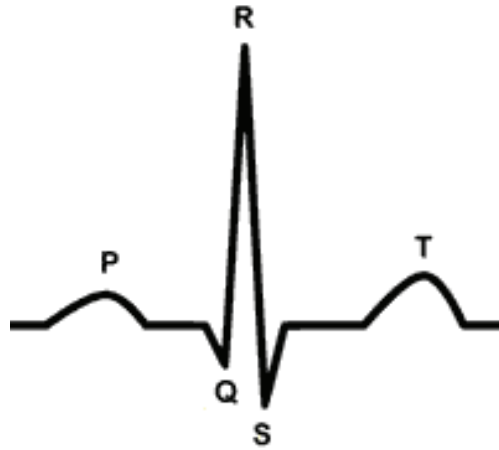
$v$  = Speed (m/s)

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) HEART RATE

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 20<sup>th</sup> 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  $VO_2$ , 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 VO<sub>2</sub> consumption.

## **(2) SUBJECTIVE MEASURES**

### **(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 VO<sub>2</sub> modulation (Jakicic et al., 1995, Ueda and Kurokawa, 1995). Thus, represents a good measure that combines both central and peripheral modulations during exercise.

## EXPERIMENTAL PROCEDURES II

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### 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 through 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 not 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

specifically performing 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.

Table 1. Participant's characteristics (M  $\pm$  SD)

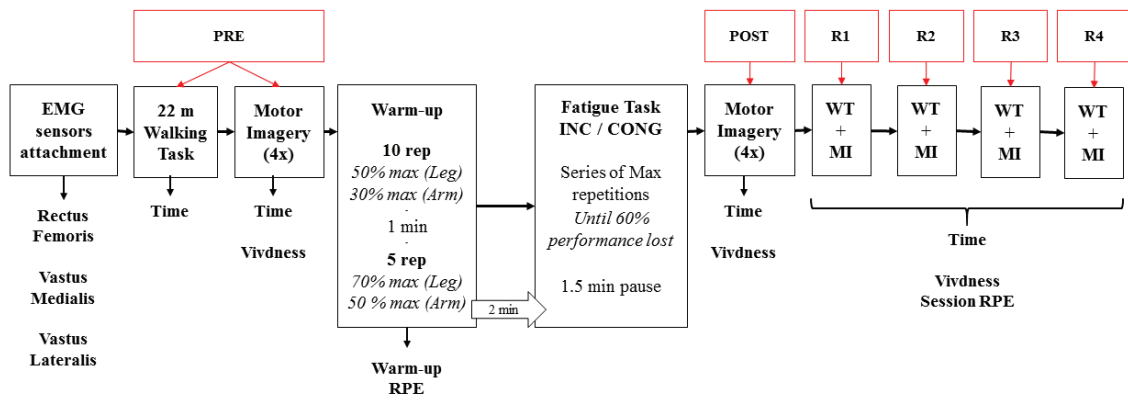
	Age (years)	Height (cm)	Weight (kg)	IMC (kg/m <sup>2</sup> )	Leg Extension Load (kg)	Arm Curl Load (kg)
Men (n = 9)	25.0 $\pm$ 4.4	180.1 $\pm$ 5.2	74.6 $\pm$ 7.4	23.0 $\pm$ 2.4	33.9 $\pm$ 3.4	28.7 $\pm$ 2.8
Women (n = 5)	26.8 $\pm$ 2.8	164.8 $\pm$ 4.6	57.2 $\pm$ 6.2	21.0 $\pm$ 2.1	22.0 $\pm$ 2.3	15.2 $\pm$ 1.6

## 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., machine leg extension; CONGRUENT FATIGUE).





**Figure 1.** Flowchart of the experimental design. Sequence: WT followed by four MI trials (Pre) → Experimental condition → Four MI trials (Post) → 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 TRIALS<sub>1-4</sub>).

### (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):

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

For RECOVERY TRIALS<sub>1-4</sub>, 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*”)

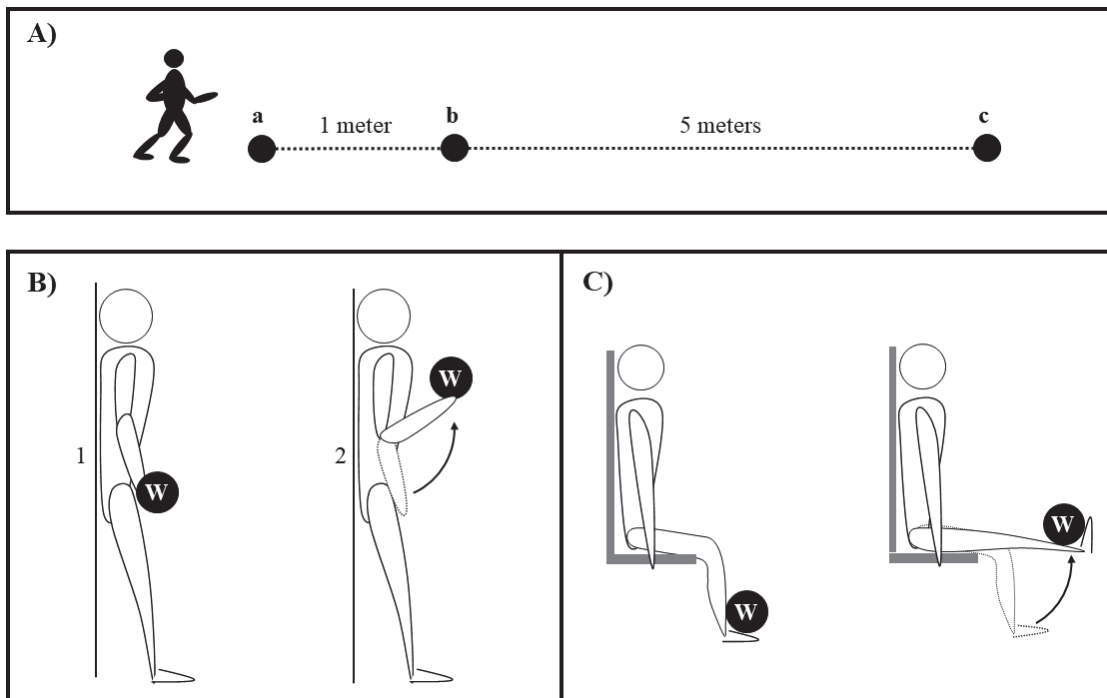
to 10 (i.e., “*Perfectly vivid image, as if I was physically performing the movement*”).

#### 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 Trigno™ 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<sub>RMS</sub>). EMG<sub>RMS</sub> data was finally normalized with reference to the first trial of the fatigue task (i.e., %EMG<sub>RMS</sub>).

## 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<sub>RMS</sub>), 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,

CONGRUENT FATIGUE) the fixed effect of the MEASURE (i.e., POST WARM-UP, POST EXERCISE). For the %EMG<sub>RMS</sub>, we entered the fixed effects of the EXPERIMENTAL CONDITION (i.e., INCONGRUENT FATIGUE, CONGRUENT FATIGUE), TEST (i.e., PRETEST, POSTTEST, RECOVERY TRIALS<sub>1-4</sub>) 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<sub>RMS</sub>. 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 TRIALS<sub>1-4</sub>), with interaction term. TEST was included as a numeric regressor to account for the effect of the successive repetition of the physical practice and MI walking trials on isochrony.

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  $\alpha = 5\%$ . As effect sizes, we calculated the amount of explained variance, i.e., partial coefficients of determination ( $R_p^2$ ). 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 ( $6.93 \pm 1.83$ ) compared to INCONGRUENT FATIGUE ( $4.64 \pm 1.78$ ) (fitted difference:  $2.28 \pm 0.61$  s.e.,  $p < 0.001$ ).

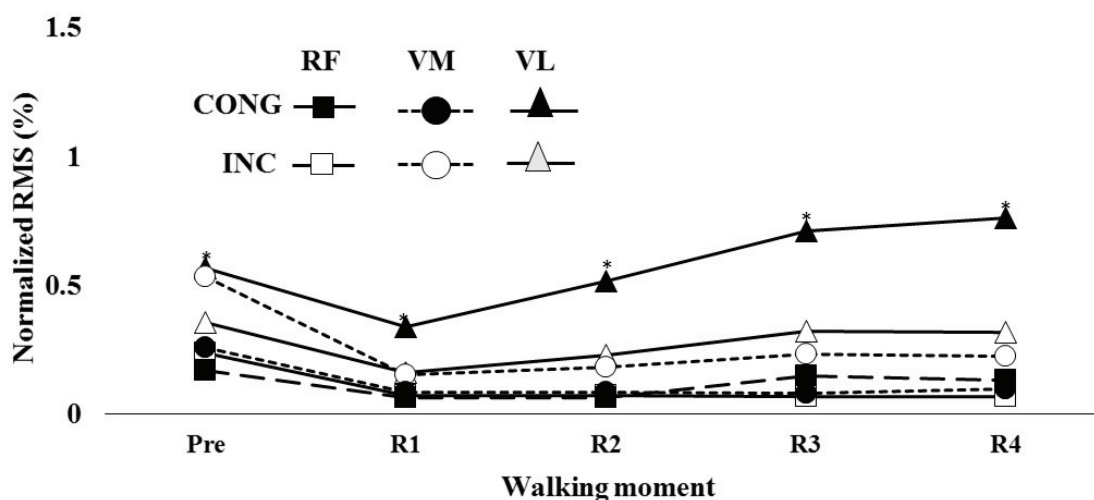
#### B) RPE scores

The two-way EXPERIMENTAL CONDITION  $\times$  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 ( $Rp^2 = 0.17$ ,  $\chi^2(1) = 4.47$ ,  $p = 0.03$ ) and MEASURE ( $Rp^2 = 0.62$ ,  $\chi^2(1) = 140.26$ ,  $p < 0.001$ ). Indeed, participants reported greater RPE scores after the CONGRUENT FATIGUE ( $6.32 \pm 2.52$ ) compared to INCONGRUENT FATIGUE ( $5.60 \pm 2.42$ ) (fitted difference:  $0.71 \pm 0.34$  s.e.,  $p < 0.001$ ). Also, participants reported greater RPE scores POST WARM UP ( $3.96 \pm 1.69$  s.d.) compared to POST EXERCISE ( $7.96 \pm 1.17$ ) (fitted difference:  $4.00 \pm 0.34$  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 ( $Rp^2 = 0.07$ ,  $\chi^2(2) = 53.52$ ,  $p < 0.001$ ) and TEST ( $Rp^2 = 0.04$ ,  $\chi^2(1) = 53.52$ ,  $p < 0.001$ ) on %EMGRMS. The %EMGRMS 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 %EMGRMS 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).



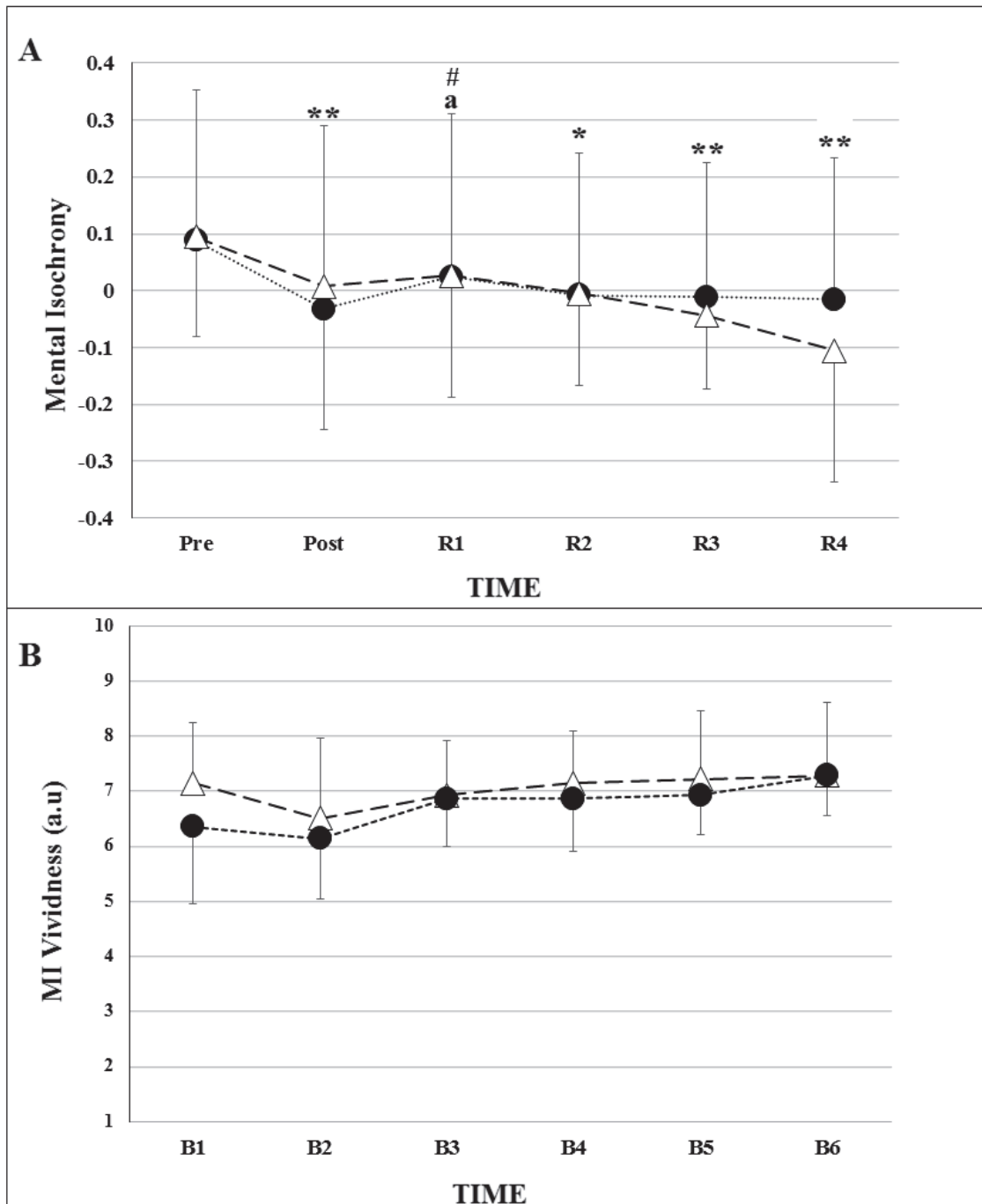
**Figure 3.** Normalized RMS values for each WT across time. \* Significant difference in VL between conditions ( $P < 0.05$ ). Notes: RMS – Root Mean Square; REL – Leg exertion condition; INC – Arm exertion condition; RF – Rectus

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 ( $R_p^2 = 0.11, \chi^2(2) = 12.64, p < 0.001$ ). There was indeed a negative relationships between the repeated measures from the PRETEST to RECOVERY TRIAL<sub>4</sub> and isochrony (PRETEST:  $9.14 \% \pm 21.94$ , POSTTEST:  $-1.25 \% \pm 28.45$ , RECOVERY TRIAL<sub>1</sub>:  $2.49 \% \pm 24.76$ , RECOVERY TRIAL<sub>2</sub>:  $-0.07 \% \pm 20.65$ , RECOVERY TRIAL<sub>3</sub>:  $-2.78 \% \pm 18.81$ , RECOVERY TRIAL<sub>4</sub>:  $-6.08 \% \pm 24.01$ ; fitted estimate:  $-2.40 \pm 0.67$  S.E.,  $p < 0.01$ ). Noteworthy, from the PRETEST up to RECOVERY TRIAL<sub>2</sub>, 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 ( $p < 0.01$ ); a Significant difference with R4 ( $p < 0.05$ ); # 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 ( $R_p^2 = 0.05$ ,  $\chi^2(2) = 5.72$ ,  $p < 0.05$ ) and TRIAL ( $R_p^2 = 0.13$ ,  $\chi^2(1) = 15.59$ ,  $p < 0.001$ ) on MI vividness scores. Participants reported higher MI vividness scores during CONGRUENT FATIGUE ( $7.04 \pm 1.19$ ) compared to INCONGRUENT FATIGUE ( $6.74 \pm 1.03$ ) (fitted estimate:  $0.29 \pm 0.12$ ,  $p < 0.05$ ). Also, there was a positive relationship between the successive trials of TEST (PRETEST:  $6.75 \pm 1.29$ , POSTTEST:  $6.32 \pm 1.28$ , RECOVERY TRIAL<sub>1</sub>:  $6.89 \pm 0.91$ , RECOVERY TRIAL<sub>2</sub>:  $7.00 \pm 0.92$ , RECOVERY TRIAL<sub>3</sub>:  $7.07 \pm 1.02$ , RECOVERY TRIAL<sub>4</sub>:  $7.28 \pm 1.05$ ) and MI vividness scores (fitted estimate:  $0.14 \pm 0.04$ ,  $p < 0.001$ ) (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 established 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 self-paced 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 well-established 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 state 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 attention-demanding coordinations.

## REFERENCES

- Bates DM (2010) lme4: Mixed-effects modeling with R. URL <http://lme4.r-forge.r-project.org/book>.
- Beauchet O, Annweiler C, Assal F, Bridenbaugh S, Herrmann FR, Kressig RW, Allali G (2010) Imagined Timed Up & Go test: a new tool to assess higher-level gait and balance disorders in older adults? *Journal of the neurological sciences* 294:102-106.
- Borg GA (1982) Psychophysical bases of perceived exertion. *Med sci sports exerc* 14:377-381.
- Bril B, Brenière Y (1993) Posture and independent locomotion in early childhood: learning to walk or learning dynamic postural control? In: *Advances in psychology*, vol. 97, pp 337-358: Elsevier.
- Callow N, Roberts R, Fawkes JZ (2006) Effects of dynamic and static imagery on vividness of imagery, skiing performance, and confidence. *Journal of Imagery Research in Sport and Physical Activity* 1.

- Church RM (1984) Properties of the internal clock. *Annals of the New York Academy of Sciences* 423:566-582.
- Decety J, Jeannerod M, Germain M, Pastene J (1991) Vegetative response during imagined movement is proportional to mental effort. *Behavioural brain research* 42:1-5.
- Decety J, Jeannerod M, Prablanc C (1989) The timing of mentally represented actions. *Behavioural brain research* 34:35-42.
- Decety J, Perani D, Jeannerod M, Bettinardi V, Tadary B, Woods R, Mazziotta JC, Fazio F (1994) Mapping motor representations with positron emission tomography.
- Demougeot L, Papaxanthis C (2011) Muscle fatigue affects mental simulation of action. *The Journal of Neuroscience* 31:10712-10720.
- Di Rienzo F, Collet C, Hoyek N, Guillot A (2012) Selective effect of physical fatigue on motor imagery accuracy. *PloS one* 7:e47207.
- Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. *Frontiers in human neuroscience* 10.
- Di Rienzo F, Hoyek N, Collet C, Guillot A (2014) Physiological changes in response to apnea impact the timing of motor representations: a preliminary study. *Behavioral and Brain Functions* 10:15.
- Dosseville F, Moussay S, Larue J, Gauthier A, Davenne D (2002) Physical exercise and time of day: influences on spontaneous motor tempo. *Perceptual and motor skills* 95:965-972.

- Driskell JE, Copper C, Moran A (1994) Does mental practice enhance performance? *Journal of Applied Psychology* 79:481.
- Ehrsson HH, Geyer S, Naito E (2003) Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of neurophysiology* 90:3304-3316.
- Enoka RM, Stuart DG (1992) Neurobiology of muscle fatigue. *Journal of Applied Physiology* 72:1631-1648.
- Feeney D, Jelaska I, Uygur M, Jaric S (2015) Effects of unilateral muscle fatigue on performance and force coordination in bimanual manipulation tasks. *Motor control*.
- Feltz DL, Landers DM (1983) The effects of mental practice on motor skill learning and performance: A meta-analysis. *Journal of sport psychology*.
- Figueiredo T, Menezes P, Kattenbraker M, Polito M, Reis V, Simão R (2013) Influence of exercise order on blood pressure and heart rate variability after a strength training session. *J Sports Med Phys Fitness* 53:12-17.
- Figueiredo T, Rhea MR, Peterson M, Miranda H, Bentes CM, dos Reis VMdR, Simão R (2015) Influence of number of sets on blood pressure and heart rate variability after a strength training session. *The Journal of Strength & Conditioning Research* 29:1556-1563.
- Fleck SJ (2003) Cardiovascular responses to strength training. *Strength and power in sport* 2:387-406.
- Fraisse P (1982) Rhythm and tempo. *The psychology of music* 1:149-180.
- Fukuyama H, Ouchi Y, Matsuzaki S, Nagahama Y, Yamauchi H, Ogawa M, Kimura J, Shibasaki H (1997) Brain functional activity during gait in normal subjects: a SPECT study. *Neuroscience Letters* 228:183-186.

- Fusco A, Iosa M, Gallotta MC, Paolucci S, Baldari C, Guidetti L (2014) Different performances in static and dynamic imagery and real locomotion. An exploratory trial. *Frontiers in human neuroscience* 8.
- Gandevia S (2001) Spinal and supraspinal factors in human muscle fatigue. *Physiological reviews* 81:1725-1789.
- Gao Q, Duan X, Chen H (2011) Evaluation of effective connectivity of motor areas during motor imagery and execution using conditional Granger causality. *NeuroImage* 54:1280-1288.
- Grillner S (1985) Neurobiological bases of rhythmic motor acts in vertebrates. *Science* 228:143-149.
- Grosprêtre S, Lebon F, Papaxanthis C, Martin A (2015) New evidence of cortico-spinal network modulation induced by motor imagery. *Journal of neurophysiology* jn. 00952.02015.
- Guillot A, Collet C (2008) Construction of the motor imagery integrative model in sport: a review and theoretical investigation of motor imagery use. *International Review of Sport and Exercise Psychology* 1:31-44.
- Guillot A, Di Rienzo F, MacIntyre T, Moran AP, Collet C (2012a) Imagining is not doing but involves specific motor commands: a review of experimental data related to motor inhibition.
- Guillot A, Haguenaer M, Dittmar A, Collet C (2005) Effect of a fatiguing protocol on motor imagery accuracy. *European journal of applied physiology* 95:186-190.
- Guillot A, Hoyek N, Louis M, Collet C (2012b) Understanding the timing of motor imagery: recent findings and future directions. *International Review of Sport and Exercise Psychology* 5:3-22.

- Guillot A, Moschberger K, Collet C (2013) Coupling movement with imagery as a new perspective for motor imagery practice. *Behav Brain Funct* 9.
- Hanakawa T, Katsumi Y, Fukuyama H, Honda M, Hayashi T, Kimura J, Shibasaki H (1999) Mechanisms underlying gait disturbance in Parkinson's disease: a single photon emission computed tomography study. *Brain* 122:1271-1282.
- Harada T, Miyai I, Suzuki M, Kubota K (2009) Gait capacity affects cortical activation patterns related to speed control in the elderly. *Experimental Brain Research* 193:445-454.
- Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G (2000) Development of recommendations for SEMG sensors and sensor placement procedures. *Journal of electromyography and Kinesiology* 10:361-374.
- Hetu S, Gregoire M, Saimpont A, Coll MP, Eugene F, Michon PE, Jackson PL (2013) The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and biobehavioral reviews* 37:930-949.
- Heyward VH, Gibson A (2014) *Advanced fitness assessment and exercise prescription 7th edition: Human kinetics.*
- Hoagland H (1933) The physiological control of judgments of duration: Evidence for a chemical clock. *The Journal of general psychology* 9:267-287.
- Holmes PS, Collins DJ (2001) The PETTLEP approach to motor imagery: A functional equivalence model for sport psychologists. *Journal of Applied Sport Psychology* 13:60-83.
- Jamin T, Joulia F, Fontanari P, Giacomoni M, Bonnon M, Vidal F, Cremieux J (2004) Apnea-induced changes in time estimation and its relation to bradycardia. *Aviation, space, and environmental medicine* 75:876-880.

- Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14:S103-S109.
- Jordan LM (1998) Initiation of locomotion in mammals. *Annals of the New York Academy of Sciences* 860:83-93.
- Jordan LM, Liu J, Hedlund PB, Akay T, Pearson KG (2008) Descending command systems for the initiation of locomotion in mammals. *Brain research reviews* 57:183-191.
- Kanthack TFD, Guillot A, Altimari LR, Nagy SN, Collet C, Di Rienzo F (2016) Selective efficacy of static and dynamic imagery in different states of physical fatigue. *PloS one* 11:e0149654.
- Kawato M (1999) Internal models for motor control and trajectory planning. *Current opinion in neurobiology* 9:718-727.
- Koren Y, Raanan Y, Parmet Y, Bar-Haim S (2018) Treading on the unknown—the feasibility of a novel approach to investigating the motor control of walking. *Physiological measurement* 39:04NT01.
- Lorey B, Bischoff M, Pilgramm S, Stark R, Munzert J, Zentgraf K (2009) The embodied nature of motor imagery: the influence of posture and perspective. *Experimental brain research* 194:233-243.
- Lorey B, Pilgramm S, Bischoff M, Stark R, Vaitl D, Kindermann S, Munzert J, Zentgraf K (2011) Activation of the parieto-premotor network is associated with vivid motor imagery—a parametric fMRI study. *PloS one* 6:e20368.
- Lotze M, Montoya P, Erb M, Hülsmann E, Flor H, Klose U, Birbaumer N, Grodd W (1999) Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal of cognitive neuroscience* 11:491-501.

- Louis M, Collet C, Guillot A (2011) Differences in motor imagery times during aroused and relaxed conditions. *Journal of Cognitive Psychology* 23:374-382.
- Lundberg A (1979) Multisensory control of spinal reflex pathways. In: *Progress in brain research*, vol. 50, pp 11-28: Elsevier.
- MacKay-Lyons M (2002) Central pattern generation of locomotion: a review of the evidence. *Physical therapy* 82:69.
- Malouin F, Jackson PL, Richards CL (2013) Towards the integration of mental practice in rehabilitation programs. A critical review. *Frontiers in human neuroscience* 7.
- McMorris T, Barwood M, Corbett J (2018) Central fatigue theory and endurance exercise: toward an interoceptive model. *Neuroscience & Biobehavioral Reviews*.
- Meck WH, Church RM (1984) Simultaneous temporal processing. *Journal of experimental psychology Animal behavior processes* 10:1-29.
- Mihara M, Miyai I, Hatakenaka M, Kubota K, Sakoda S (2007) Sustained prefrontal activation during ataxic gait: a compensatory mechanism for ataxic stroke? *Neuroimage* 37:1338-1345.
- Mishima J (1968) On the measurement of the mental tempo. *Journal of Child Development*.
- Miyai I, Tanabe HC, Sase I, Eda H, Oda I, Konishi I, Tsunazawa Y, Suzuki T, Yanagida T, Kubota K (2001) Cortical mapping of gait in humans: a near-infrared spectroscopic topography study. *Neuroimage* 14:1186-1192.

- Munzert J, Lorey B, Zentgraf K (2009) Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain research reviews* 60:306-326.
- Pageaux B (2014) The psychobiological model of endurance performance: an effort-based decision-making theory to explain self-paced endurance performance. *Sports Medicine* 44:1319-1320.
- Rejeski WJ (1985) Perceived exertion: An active or passive process? *Journal of sport psychology* 7:371-378.
- Rezk C, Marrache R, Tinucci T, Mion D, Forjaz C (2006) Post-resistance exercise hypotension, hemodynamics, and heart rate variability: influence of exercise intensity. *European journal of applied physiology* 98:105-112.
- Rossignol S (2000) Locomotion and its recovery after spinal injury. *Current opinion in neurobiology* 10:708-716.
- Roth M, Decety J, Raybaudi M, Massarelli R, Delon-Martin C, Segebarth C, Morand S, Gemignani A, Décorps M, Jeannerod M (1996) Possible involvement of primary motor cortex in mentally simulated movement: a functional magnetic resonance imaging study. *Neuroreport* 7:1280-1284.
- Rozand V, Lebon F, Papaxanthis C, Lepers R (2014a) Does a mental training session induce neuromuscular fatigue. *Med Sci Sports Exerc* 46:1981-1989.
- Rozand V, Lebon F, Papaxanthis C, Lepers R (2015) Effect of mental fatigue on speed–accuracy trade-off. *Neuroscience* 297:219-230.
- Rozand V, Lebon F, Stapley PJ, Papaxanthis C, Lepers R (2016) A prolonged motor imagery session alter imagined and actual movement durations:



- potential implications for neurorehabilitation. *Behavioural brain research* 297:67-75.
- Rozand V, Pageaux B, Marcora SM, Papaxanthis C, Lepers R (2014b) Does mental exertion alter maximal muscle activation? *Frontiers in human neuroscience* 8.
- Ruffino C, Papaxanthis C, Lebon F (2017) Neural plasticity during motor learning with motor imagery practice: Review and perspectives. *Neuroscience* 341:61-78.
- Schmid M, Schieppati M, Pozzo T (2006) Effect of fatigue on the precision of a whole-body pointing task. *Neuroscience* 139:909-920.
- Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, Kischka U, Ettl T (2011) Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. *BMC medicine* 9:75.
- Shik ML, Orlovsky GN (1976) Neurophysiology of locomotor automatism. *Physiological reviews* 56:465-501.
- Stinear CM (2010) Corticospinal facilitation during motor imagery. In: *The neurophysiological foundations of mental and motor imagery*(Guillot, A. and Collet, C., eds), pp 47-61 New York, NY: Oxford University Press.
- Team RC (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2012. ISBN 3-900051-07-0.
- Temperley NM (1963) Personal tempo and subjective accentuation. *The Journal of general psychology* 68:267-287.

- Treisman M (1963) Temporal discrimination and the indifference interval: Implications for a model of the "internal clock". *Psychological Monographs: General and Applied* 77:1.
- van der Meulen M, Allali G, Rieger SW, Assal F, Vuilleumier P (2012) The influence of individual motor imagery ability on cerebral recruitment during gait imagery. *Hum Brain Mapp.*
- Winter DA (2009) *Biomechanics and motor control of human movement*: John Wiley & Sons.
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269:1880.
- Zehr EP, Duysens J (2004) Regulation of arm and leg movement during human locomotion. *The Neuroscientist* 10:347-361.

**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 well-established 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). Indeed, 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 half-squat 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 controlled 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.,  $1.\text{kg}.\text{m}^2.\text{s}^{-3}$ ) 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:

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

Heart rate (HR) and the volume of oxygen uptake ( $\text{VO}_2$ ) were continually monitored. The maximal  $\text{VO}_2$  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 were 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 an 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% O<sub>2</sub>, 5% CO<sub>2</sub> balanced with N<sub>2</sub>) and volume prior to each recording. No data recordings were performed during warm-up to avoid excessive time with the VO<sub>2</sub> mask, which might cause discomfort. We first measured participant's VO<sub>2</sub>. The spiroergometer also afforded recordings of heart rate (HR) and ventilatory rate. The latter was used to calculate VT<sub>2</sub>. 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 VO<sub>2</sub> kinematics differences due the accumulated O<sub>2</sub> 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 task was adapted from the paradigm by Demougeot and Papaxanthis (2011). Three targets were set according to each participant's height. The line between the head of the humerus and the point A, located at participant's 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 be excluded from the forthcoming analyses (7% of trials excluded overall). An illustration of the walking and pointing

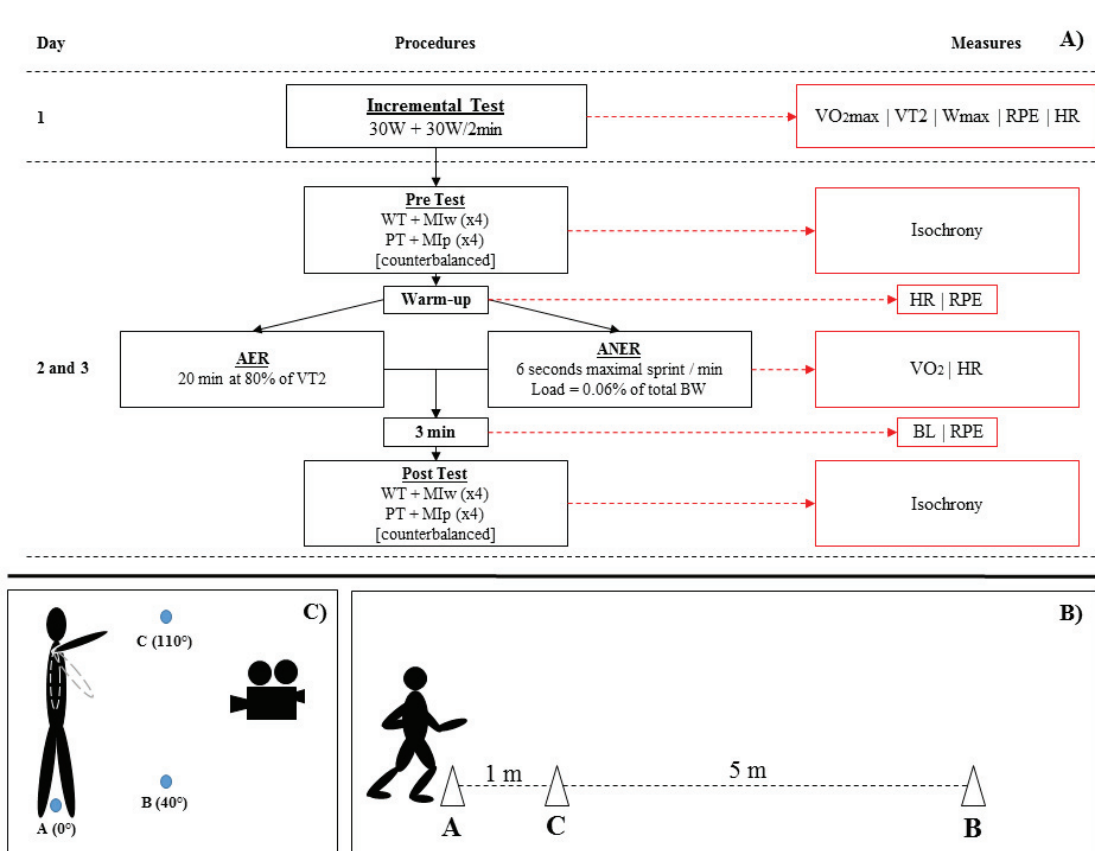
tasks is provided in Figure 1C. Participants first performed the tasks physically, followed by MI. Participants completed MI from an identical standardized body position to that during the physical practice. Indeed, previous experiments underlined that an incongruent body posture could bias the ease 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):

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

#### (ii) Self-reports

After completion of the MI ability evaluations, participants provided a self-report 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 self-reported 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 VO<sub>2</sub>max, 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  $\alpha = 5\%$ . As effect sizes, we calculated the amount of explained variance, i.e., partial coefficients of determination ( $R_p^2$ ) 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 from 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 ( $M \pm SD$ ) 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, VO<sub>2</sub>max: Maximal oxygen uptake, VT<sub>2</sub>: Second ventilatory threshold.

	Body mass Index (kg/m <sup>2</sup> )	Age (years)	Cycle ergometer load at exhaustion (W)	VO <sub>2</sub> max (ml/kg/min <sup>-1</sup> )	VT <sub>2</sub> (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., VO<sub>2</sub>, 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 ± SD). VO<sub>2</sub>: Oxygen uptake, HR: Heart rate, RPE: Rate of perceived exertion.

	CONTINUOUS EXERCISE	INTERMITTENT EXERCISE	R <sup>2</sup>	χ <sup>2</sup>	P
VO <sub>2</sub> (% of VO <sub>2</sub> max)	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 VO<sub>2</sub> and HR measures, recordings during CONTINUOUS EXERCISE outperformed

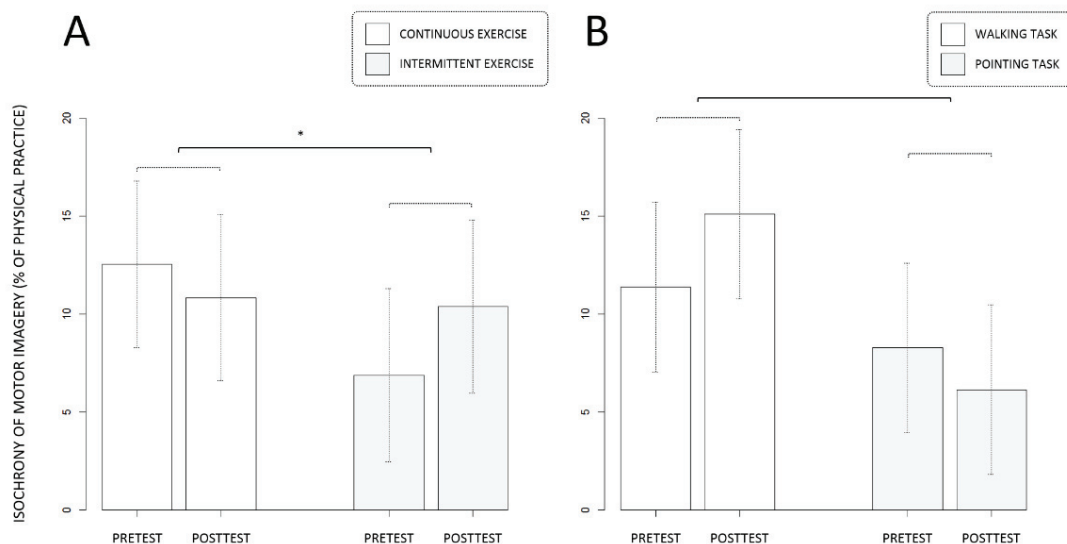
that during INTERMITTENT EXERCISE (fitted difference: 21.92 %  $\pm$  3.70,  $p < 0.001$ ; 21.59 bpm  $\pm$  6.83,  $p < 0.01$ , respectively). There was also a main EXPERIMENTAL CONDITION effect for blood lactate concentration, which was higher during INTERMITTENT EXERCISE compared to CONTINUOUS EXERCISE (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 two-way interaction between EXPERIMENTAL CONDITION and TEST, and ii) a two-way 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 %  $\pm$  19.55) versus POSTTEST (11.09 %  $\pm$  23.50) difference for INTERMITTENT EXERCISE was higher than the PRETEST (12.55 %  $\pm$  22.83) versus POSTTEST (10.84 %  $\pm$  22.70) difference recorded for the CONTINUOUS EXERCISE (fitted difference: 5.21 %  $\pm$  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 ( $11.72 \% \pm 23.37$ ) versus POSTTEST ( $15.43 \% \pm 25.75$ ) difference for the WALKING TASK was higher than the PRETEST ( $8.61 \% \pm 19.24$ ) versus POSTTEST ( $6.48 \% \pm 19.04$ ) difference recorded for the POINTING TASK (fitted difference:  $5.85 \% \pm 2.82$ ,  $p = 0.03$ ).

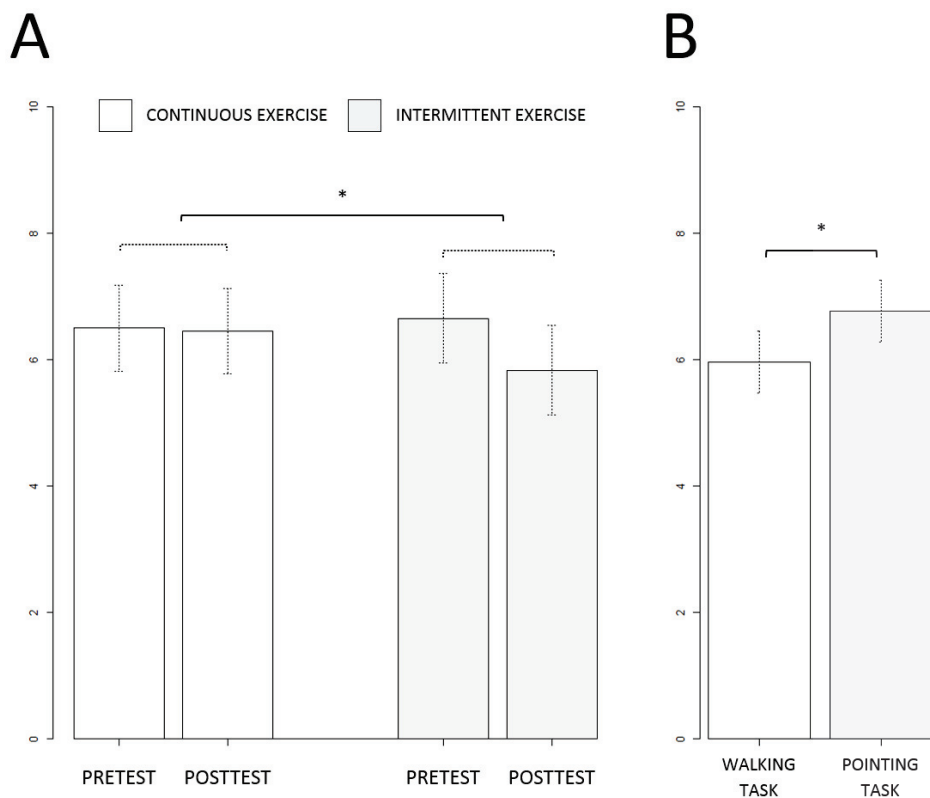


**Figure 2.** Linear mixed effects analysis of isochrony data (i.e., fitted estimates). A. EXPERIMENTAL CONDITION by TEST interaction effect from isochrony measures. B. TASK by TEST interactions from isochrony measures. \* $p < 0.05$ ; \*\*\*  $p < 0.01$ .

### 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.  $\pm$  1.59) versus POSTTEST (5.77 a.u.  $\pm$  1.93) difference for INTERMITTENT EXERCISE was higher than the PRETEST (6.50 a.u.  $\pm$  1.64) versus POSTTEST (6.46 a.u.  $\pm$  1.67) difference for CONTINUOUS EXERCISE (fitted difference: 0.78 a.u.  $\pm$  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.  $\pm$  1.76) compared to the WALKING TASK (5.93 a.u.  $\pm$  1.58) (fitted difference: 0.80 a.u.  $\pm$  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.  $\pm$  1.87) were higher than those recorded for the POINTING TASK (3.80 a.u.  $\pm$  2.15) (fitted difference: 0.37 a.u.  $\pm$  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.  $\pm$  1.96) were indeed marginally lower compared to the POSTTEST (4.17 a.u.  $\pm$  2.06) (fitted difference: 0.37  $\pm$  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 an 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  $VO_2$  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 Krueel, 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 from 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, coaches should build their MI practice program based on programmed 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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## REFERENCES

- Astafiev SV, Shulman GL, Stanley CM, Snyder AZ, Van Essen DC, Corbetta M (2003) Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *Journal of Neuroscience* 23:4689-4699.
- Bear MF, Connors BW, Paradiso MA (2007) *Neuroscience*: Lippincott Williams & Wilkins.
- Beauchet O, Annweiler C, Assal F, Bridenbaugh S, Herrmann FR, Kressig RW, Allali G (2010) Imagined Timed Up & Go test: a new tool to assess higher-level gait and balance disorders in older adults? *Journal of the neurological sciences* 294:102-106.
- Bigliassi M (2015) Corollary discharges and fatigue-related symptoms: the role of attentional focus. *Frontiers in psychology* 6:1002.
- Borg GA (1982) Psychophysical bases of perceived exertion. *Med sci sports exerc* 14:377-381.
- Brentano M, Martins Kruehl L (2011) A review on strength exercise-induced muscle damage: applications, adaptation mechanisms and limitations. *J Sports Med Phys Fitness* 51:1-10.
- Bretz F, Westfall P, Hothorn T (2016) *Multiple comparisons using R*: Chapman and Hall/CRC.
- Brisswalter J, Collardeau M, René A (2002) Effects of acute physical exercise characteristics on cognitive performance. *Sports Medicine* 32:555-566.
- Cavina-Pratesi C, Connolly JD, Monaco S, Figley TD, Milner AD, Schenk T, Culham JC (2018) Human neuroimaging reveals the subcomponents of grasping, reaching and pointing actions. *Cortex* 98:128-148.

- Chen T, Nosaka K (2006) Effects of number of eccentric muscle actions on first and second bouts of eccentric exercise of the elbow flexors. *Journal of Science and Medicine in Sport* 9:57-66.
- Chen TC, Hsieh SS (2001) Effects of a 7-day eccentric training period on muscle damage and inflammation. *Medicine and science in sports and exercise* 33:1732-1738.
- Collet C (2001) *Mouvements et cerveau: neurophysiologie des activités physiques et sportives: De Boeck Université.*
- Collet C, Deschaumes-Molinario C, Delhomme G, Dittmar A, Vernet-Maury E (1994) Autonomic responses correlate to motor anticipation. *Behavioural brain research* 63:71-79.
- Collet C, Guillot A, Lebon F, MacIntyre T, Moran A (2011a) Measuring motor imagery using psychometric, behavioral, and psychophysiological tools. *Exercise and Sport Science Reviews* 39:85-92.
- Collet C, Guillot A, Lebon F, MacIntyre T, Moran A (2011b) Measuring motor imagery using psychometric, behavioral, and psychophysiological tools. *Exercise and sport sciences reviews* 39:85-92.
- Courtine G (2012) Inspiring new thinking to restore motor functions after spinal cord injury. In: 51th annual scientific meeting of the international spinal cord society(Society, I. S. C., ed), p 107 London.
- Demougeot L, Papaxanthis C (2011) Muscle fatigue affects mental simulation of action. *The Journal of Neuroscience* 31:10712-10720.
- Di Rienzo F, Blache Y, Kanthack T, Monteil K, Collet C, Guillot A (2015) Short-term effects of integrated motor imagery practice on muscle activation and force performance. *Neuroscience* 305:146-156.

- Di Rienzo F, Collet C, Hoyek N, Guillot A (2012) Selective effect of physical fatigue on motor imagery accuracy. *PloS one* 7:e47207.
- Di Rienzo F, Collet C, Hoyek N, Guillot A (2014) Impact of neurologic deficits on motor imagery: A systematic review of clinical evaluations. *Neuropsychology review*.
- Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. *Frontiers in human neuroscience* 10:315.
- Draper NR, Smith H (2014) *Applied regression analysis*: John Wiley & Sons.
- Driskell JE, Copper C, Moran A (1994) Does mental practice enhance performance? *Journal of Applied Psychology* 79:481.
- Edwards LJ, Muller KE, Wolfinger RD, Qaqish BF, Schabenberger O (2008) An R(2) Statistic for Fixed Effects in the Linear Mixed Model. *Statistics in Medicine* 27:6137-6157.
- Egstrom GH (1964) Effects of an emphasis on conceptualizing techniques during early learning of a gross motor skill. *Research Quarterly American Association for Health, Physical Education and Recreation* 35:472-481.
- Enoka RM, Stuart DG (1992) Neurobiology of muscle fatigue. *Journal of Applied Physiology* 72:1631-1648.
- Feltz DL, Landers DM (1983) The effects of mental practice on motor skill learning and performance: A meta-analysis. *Journal of sport psychology*.
- Fusco A, Iosa M, Gallotta MC, Paolucci S, Baldari C, Guidetti L (2014) Different performances in static and dynamic imagery and real locomotion. An exploratory trial. *Frontiers in human neuroscience* 8.

- Gentili R, Han CE, Schweighofer N, Papaxanthis C (2010) Motor learning without doing: trial-by-trial improvement in motor performance during mental training. *Journal of neurophysiology* 104:774-783.
- Grush R (2004) The emulation theory of representation: motor control, imagery, and perception. *Behavioral and Brain Sciences* 27:377-396; discussion 396-442.
- Guillot A, Collet C (2005) Contribution from neurophysiological and psychological methods to the study of motor imagery. *Brain research reviews* 50:387-397.
- Guillot A, Collet C (2008) Construction of the Motor Imagery Integrative Model in Sport: a review and theoretical investigation of motor imagery use. *Int Rev Sport Exerc Psychol* 1:31-44.
- Guillot A, Collet C, Nguyen VA, Malouin F, Richards C, Doyon J (2008) Functional neuroanatomical networks associated with expertise in motor imagery. *Neuroimage* 41:1471-1483.
- Guillot A, Di Rienzo F, Collet C (2014) The neurofunctional architecture of motor imagery. In: *Advanced Brain Neuroimaging Topics in Health and Disease- Methods and Applications: InTech*.
- Guillot A, Di Rienzo F, Pialoux V, Simon G, Skinner S, Rogowski I (2015) Implementation of motor imagery during specific aerobic training session in young tennis players. *PLoS one* 10:e0143331.
- Guillot A, Haguenaer M, Dittmar A, Collet C (2005) Effect of a fatiguing protocol on motor imagery accuracy. *European journal of applied physiology* 95:186-190.

- Guillot A, Hoyek N, Louis M, Collet C (2012) Understanding the timing of motor imagery: recent findings and future directions. *International Review of Sport and Exercise Psychology* 5:3-22.
- Guillot A, Moschberger K, Collet C (2013) Coupling movement with imagery as a new perspective for motor imagery practice. *Behav Brain Funct* 9.
- Guillot A, Tolleran C, Collet C (2010) Does motor imagery enhance stretching and flexibility? *Journal of sports sciences* 28:291-298.
- Hetu S, Gregoire M, Saimpont A, Coll MP, Eugene F, Michon PE, Jackson PL (2013) The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and biobehavioral reviews* 37:930-949.
- Hocking RR (1976) A Biometrics invited paper. The analysis and selection of variables in linear regression. *Biometrics* 32:1-49.
- Holmes PS, Collins DJ (2001) The PETTLEP approach to motor imagery: A functional equivalence model for sport psychologists. *Journal of Applied Sport Psychology* 13:60-83.
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical journal* 50:346-363.
- Jackson PL, Doyon J, Richards CL, Malouin F (2004) The efficacy of combined physical and mental practice in the learning of a foot-sequence task after stroke: a case report. *Neurorehabilitation and Neural repair* 18:106-111.
- Jackson PL, Lafleur MF, Malouin F, Richards C, Doyon J (2001) Potential role of mental practice using motor imagery in neurologic rehabilitation. *Archives of physical medicine and rehabilitation* 82:1133-1141.



- Jaeger BC, Edwards LJ, Das K, Sen PK (2017) An R2 statistic for fixed effects in the generalized linear mixed model. *Journal of Applied Statistics* 44:1086-1105.
- Jeannerod M (1994) The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain sciences* 17:187-202.
- Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage* 14:S103-109.
- Kanthack TFD, Bigliassi M, Altimari LR (2013) Equal prefrontal cortex activation between males and females in a motor tasks and different visual imagery perspectives: a functional near-infrared spectroscopy (fNIRS) study. *Motriz: Revista de Educação Física* 19:627-632.
- Lebon F, Byblow WD, Collet C, Guillot A, Stinear CM (2012) The modulation of motor cortex excitability during motor imagery depends on imagery quality. *European Journal of Neuroscience* 35:323-331.
- Lorey B, Pilgramm S, Bischoff M, Stark R, Vaitl D, Kindermann S, Munzert J, Zentgraf K (2011) Activation of the parieto-premotor network is associated with vivid motor imagery—a parametric fMRI study. *PloS one* 6:e20368.
- Louis M, Guillot A, Maton S, Doyon J, Collet C (2008) Effect of imagined movement speed on subsequent motor performance. *Journal of motor behavior* 40:117-132.
- Mackay-Lyons M (2002) Central pattern generation of locomotion: a review of the evidence. *Physical therapy* 82:69.
- Malouin F, Richards CL, Durand A, Doyon J (2008) Reliability of mental chronometry for assessing motor imagery ability after stroke. *Archives of physical medicine and rehabilitation* 89:311-319.

- Martin KA, Moritz SE, Hall CR (1999) Imagery use in sport: A literature review and applied model. *The Sport Psychologist* 13:245-268.
- McMorris T, Barwood M, Corbett J (2018) Central fatigue theory and endurance exercise: toward an interoceptive model. *Neuroscience & Biobehavioral Reviews*.
- Medbo JI, Mohn A-C, Tabata I, Bahr R, Vaage O, Sejersted OM (1988) Anaerobic capacity determined by maximal accumulated O<sub>2</sub> deficit. *Journal of Applied Physiology* 64:50-60.
- Meulen M, Allali G, Rieger SW, Assal F, Vuilleumier P (2014) The influence of individual motor imagery ability on cerebral recruitment during gait imagery. *Human brain mapping* 35:455-470.
- Munzert J, Lorey B, Zentgraf K (2009) Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain research reviews* 60:306-326.
- O'Shea H, Moran A (2017) Does motor simulation theory explain the cognitive mechanisms underlying motor imagery? A critical review. *Frontiers in human neuroscience* 11.
- Pinheiro J, Bates D, DebRoy S, Sarkar D (2011) R Development Core Team. NLME: linear and nonlinear mixed effects models. R package version 3.1-109 <http://cran.r-project.org/web/packages/nlme/index.html>.
- Posner MI (1978) *Chronometric explorations of mind*. Hillsdale, NJ: Erlbaum.
- R Core Team (2015) *R: A language and environment for statistical computing*. Vienna, Austria. R Foundation for Statistical Computing.
- Rejeski WJ (1985) Perceived exertion: An active or passive process? *Journal of sport psychology* 7:371-378.

- Roure R, Collet C, Deschaumes-Molinaro C, Delhomme G, Dittmar A, Vernet-Maury E (1999) Imagery quality estimated by autonomic response is correlated to sporting performance enhancement. *Physiology & Behavior* 66:63-72.
- Rozand V, Lebon F, Papaxanthis C, Lepers R (2014) Does a mental training session induce neuromuscular fatigue. *Med Sci Sports Exerc* 46:1981-1989.
- Ruffino C, Papaxanthis C, Lebon F (2017) Neural plasticity during motor learning with motor imagery practice: Review and perspectives. *Neuroscience* 341:61-78.
- Sanes JN, Donoghue JP (2000) Plasticity and primary motor cortex. *Annual review of neuroscience* 23:393-415.
- Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, Kischka U, Ettl T (2011) Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. *BMC medicine* 9:75.
- Sharma N, Jones PS, Carpenter T, Baron J-C (2008) Mapping the involvement of BA 4a and 4p during motor imagery. *Neuroimage* 41:92-99.
- Sirigu A, Duhamel J (2001) Motor and visual imagery as two complementary but neurally dissociable mental processes. *Journal of cognitive neuroscience* 13:910-919.
- Sutoo De, Akiyama K (1996) The mechanism by which exercise modifies brain function. *Physiology & Behavior* 60:177-181.
- Sutoo De, Akiyama K (2003) Regulation of brain function by exercise. *Neurobiology of disease* 13:1-14.

- Van Praag H (2009) Exercise and the brain: something to chew on. *Trends in neurosciences* 32:283-290.
- Vargas C, Olivier E, Craighero L, Fadiga L, Duhamel J, Sirigu A (2004) The influence of hand posture on corticospinal excitability during motor imagery: a transcranial magnetic stimulation study. *Cerebral cortex* 14:1200-1206.
- Wolpert DM, Flanagan JR (2001) Motor prediction. *Current biology : CB* 11:R729-732.
- Yágüez L, Nagel D, Hoffman H, Canavan A, Wist E, Hömberg V (1998) A mental route to motor learning: improving trajectorial kinematics through imagery training. *Behavioural brain research* 90:95-106.
- Zehr EP, Duysens J (2004) Regulation of arm and leg movement during human locomotion. *The Neuroscientist* 10:347-361.

## 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 is 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.

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 emphasize 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

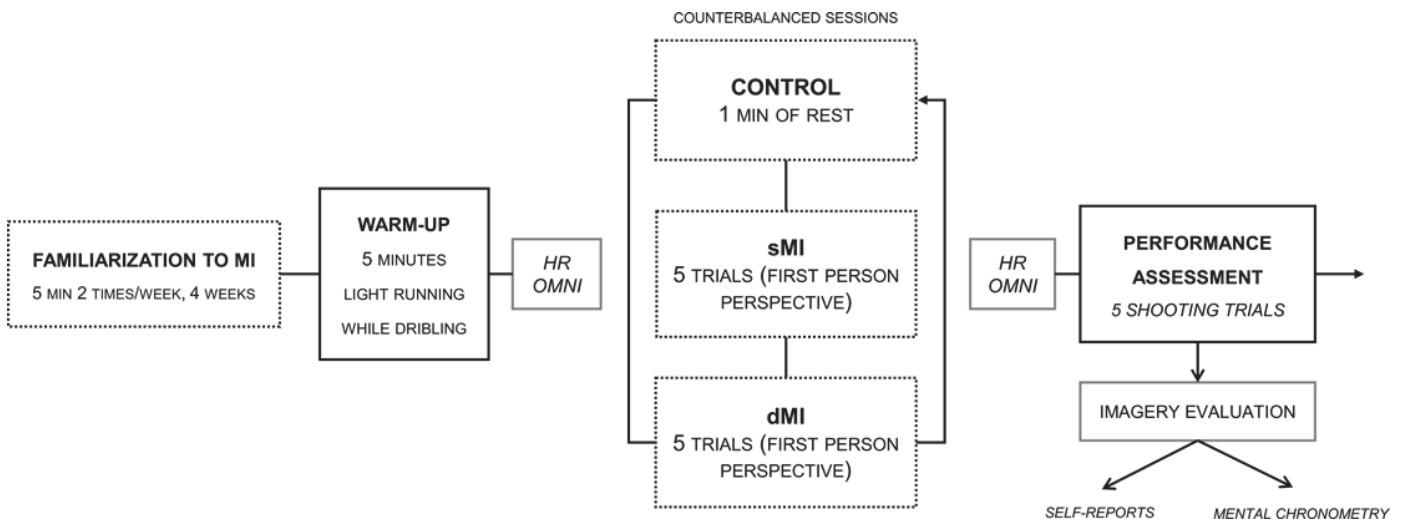
### Material and Methods

**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



**Fig 1. Flowchart of the experimental design.** sMI = Static Motor Imagery, dMI = Dynamic Motor Imagery, HR = Heart Rate, OMNI = Self-exhaustion perception, TL = Training Load from previous day. sMI, dMI and Shooting time measured in each condition.

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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<sup>®</sup>) 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 ( $4.2 \pm 2.5$ ,  $\chi^2(2) = 0.039$ ,  $p = 0.98$ ). OMNI ratings after warm-up and intervention were comparable across conditions without time effect (pre =  $2.2 \pm 1.9$ , post =  $1.1 \pm 1.8$ ,  $p = 0.79$ ). 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 ( $131 \pm 15$  bpm,  $p = 0.22$ ). However, HR values after dMI ( $114 \pm 14$  bpm) were higher compared to both sMI and CONTROL ( $96 \pm 12$  bpm and  $93 \pm 10$  bpm, respectively;  $p = 0.02$ ).

**sMI/dMI accuracy.** No difference was found when comparing sMI and dMI vividness ( $4.5 \pm 1.2$ ) 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  $0.61 \pm 1.2$  s ( $p < 0.01$ ).

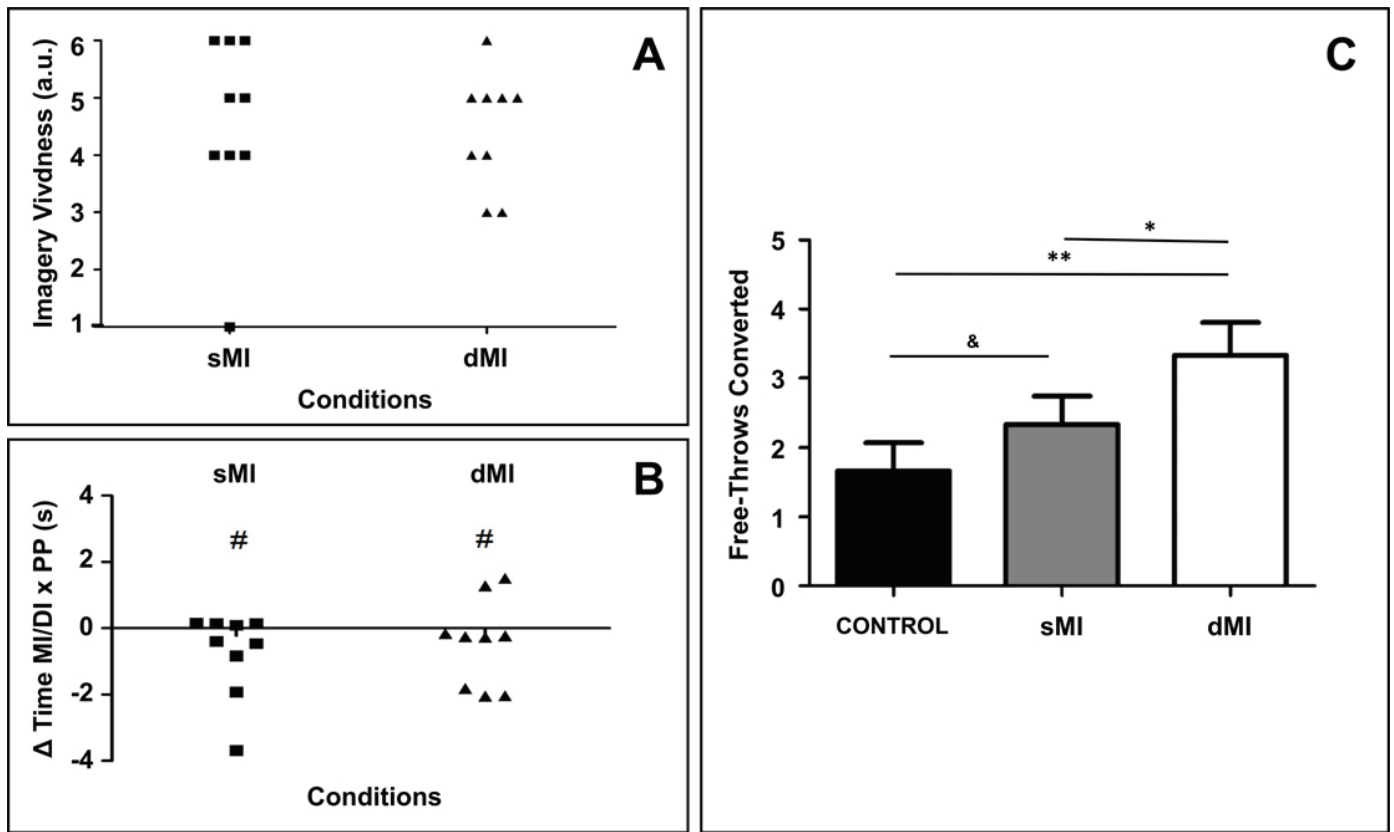
**Shooting accuracy.** Mixed linear modeling yielded a main effect of experimental conditions on shooting accuracy ( $\chi^2(2) = 12.01$ ,  $p = 0.002$ ). Shooting accuracy was higher following dMI ( $3.3 \pm 1.4$  free-throws converted) compared to both sMI ( $2.3 \pm 1.2$ ,  $p < 0.05$ ) and CONTROL ( $1.6 \pm 1.2$ ,  $p < 0.001$ ) (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 ( $18.4 \pm 0.5$  years;  $7.3 \pm 2.3$  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 ( $9 \text{ am} \pm 1 \text{ hour}$ ) to avoid circadian effects. We implemented a counterbalanced design in order to control carryover effects between the experiments and conditions of the paradigm.

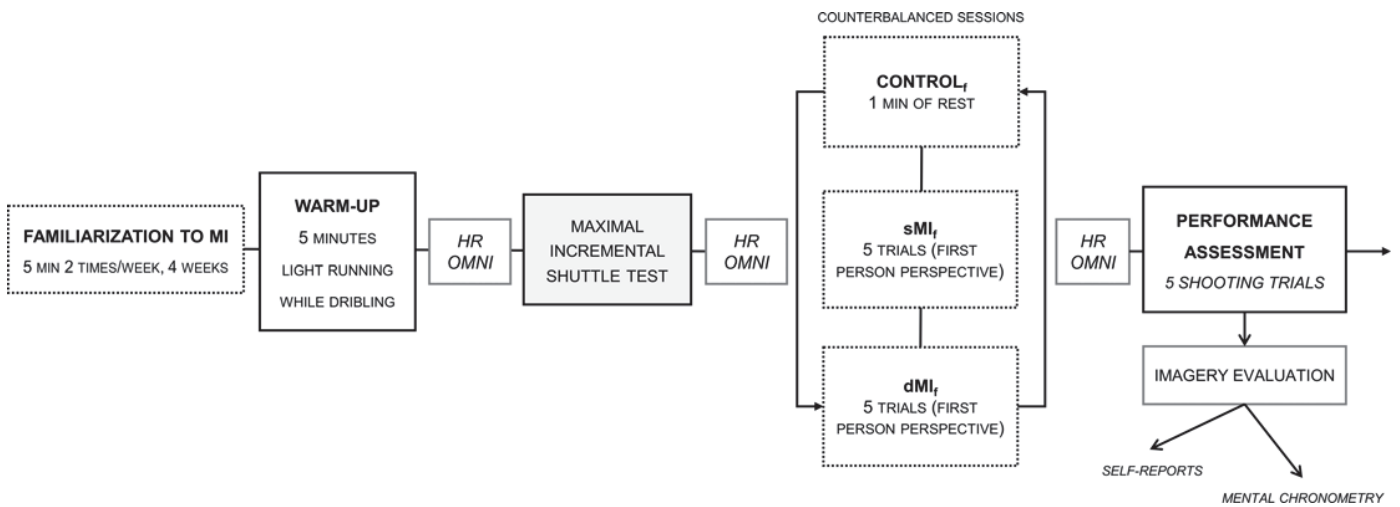


**Fig 2.** A. Self-reports of imagery vividness. B. Delta time between actual and imagined durations for sMI and dMI. C. Free-throw shooting accuracy for each athlete under each experimental condition. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; # Different from 0,  $p < 0.05$ , & Statistical trend ( $0.05 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

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**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 experimenter about their daily training during an equivalent amount of time, after exhaustion. 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<sub>f</sub> = Static Motor Imagery under fatigue, dMI<sub>f</sub> = Dynamic Motor Imagery under fatigue, HR = Heart Rate, OMNI = Self-exhaustion perception, TL = Training Load from previous day. sMI<sub>f</sub>, dMI<sub>f</sub> and Shooting times were measured in each condition.

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

**sMI<sub>f</sub>/dMI<sub>f</sub> intervention.** For sMI<sub>f</sub> and dMI<sub>f</sub>, 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<sub>f</sub>. For dMI<sub>f</sub>, slight arm movements as well as semi-flexions were allowed. Immediately after the intervention, we collected the perceived vividness of sMI<sub>f</sub>/dMI<sub>f</sub> on a Likert scale ranging from 1 (“Unclear and inaccurate mental representation”) to 6 (“Perfectly clear and vivid mental representation”). We also collected sMI<sub>f</sub>/dMI<sub>f</sub> durations, and calculated the delta between actual and imagined durations, a reliable index of temporal congruence [40].

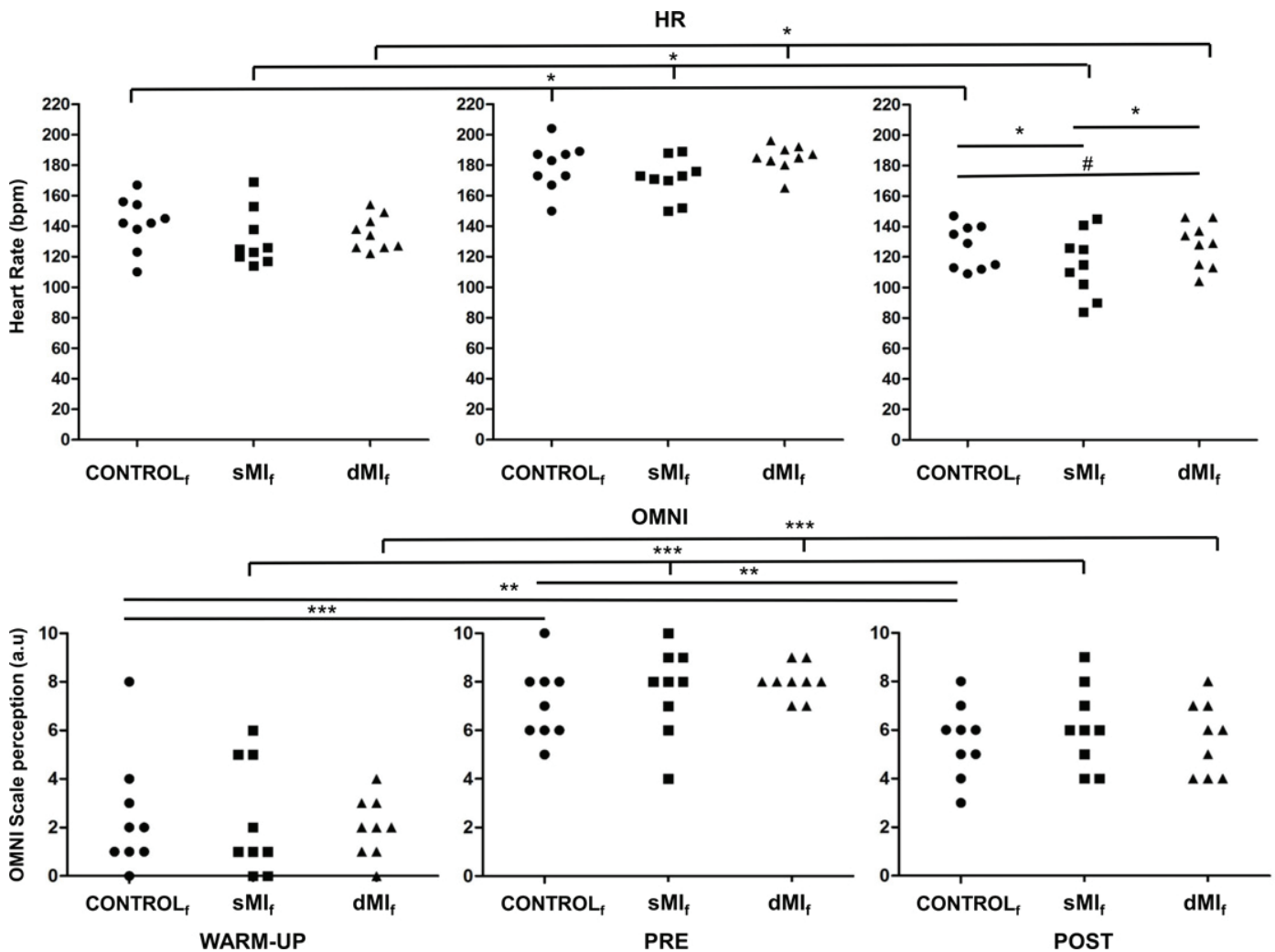
**Heart Rate and Exertion perception.** Athletes held a cardiac monitor (Polar FT2<sup>®</sup>). HR (bpm) was collected after warm-up, after the exhaustion test, and immediately after the experimental intervention. Participants rated their perceived level of fatigue on the OMNI Scale after warm-up, after 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<sub>f</sub>, dMI<sub>f</sub> and CONTROL<sub>f</sub>). 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<sub>f</sub>:  $4.3 \pm 2.5$ , dMI<sub>f</sub>:  $4.2 \pm 1.5$ , CONTROL<sub>f</sub>:  $4.4 \pm 1.5$ ). 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



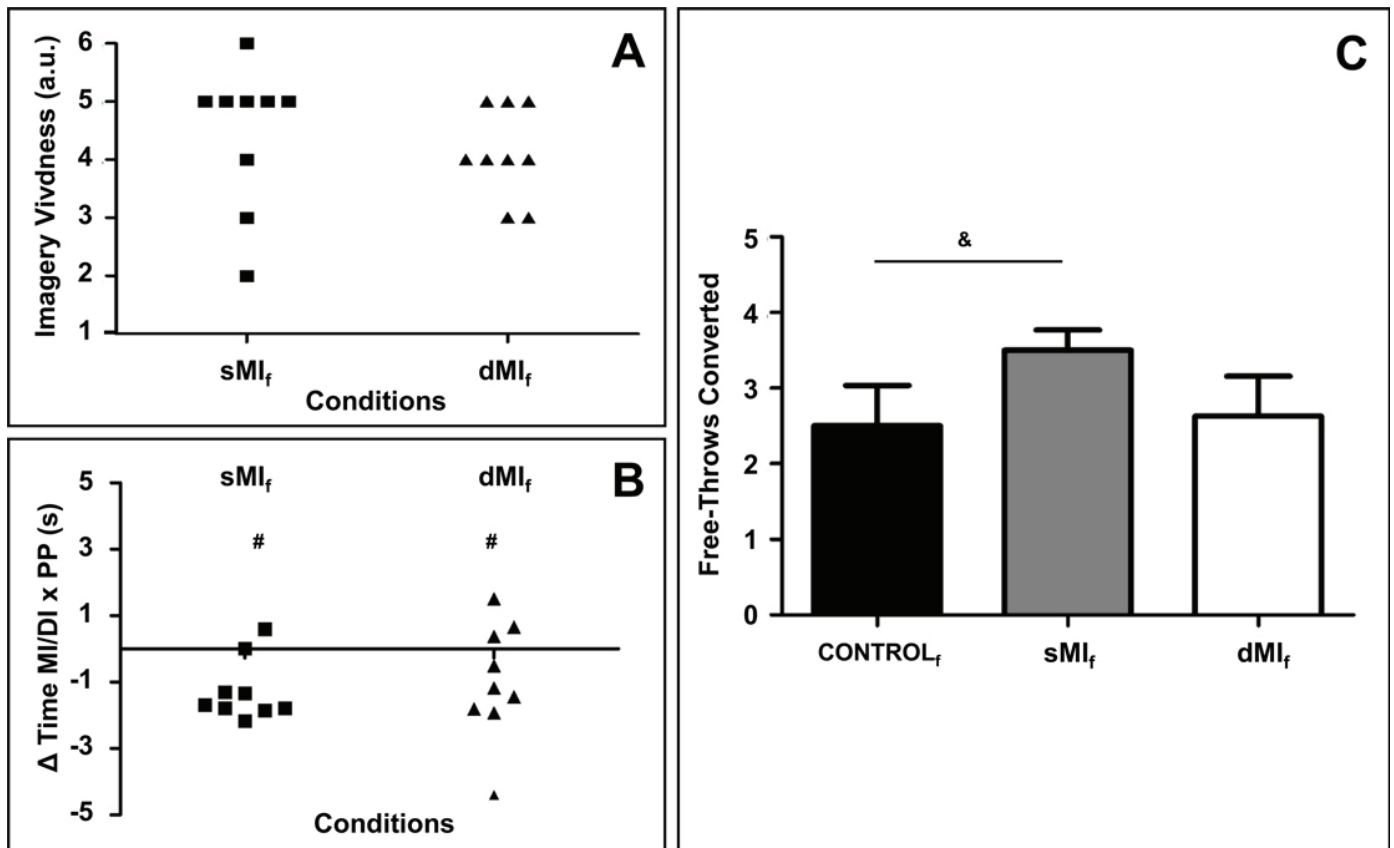
**Fig 4.** HR values and OMNI score after warm-up, pre-intervention and post-experimental intervention. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ , # Statistical trend ( $0.05 < p < 0.1$ ).

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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<sub>f</sub> session ( $131 \pm 18$  bpm) as compared to those monitored under CONTROL<sub>f</sub> and dMI<sub>f</sub> sessions ( $141 \pm 17$  bpm and  $135 \pm 15$  bpm, respectively,  $p < 0.05$ ). Values of HR in dMI<sub>f</sub> tended to be lower compared to CONTROL<sub>f</sub> ( $p = 0.09$ ) (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:  $123 \pm 17$  bpm, OMNI:  $2.2 \pm 1.9$ ; Pre-intervention HR:  $178 \pm 13$  bpm, Pre-intervention OMNI:  $7.5 \pm 1.4$ ). 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:  $136 \pm 15$  bpm, Post-intervention OMNI:  $5.7 \pm 1.5$ ) (Fig 4).

**Shooting accuracy.** Self-reports of imagery vividness (sMI<sub>f</sub>:  $4.4 \pm 1.2$ , dMI<sub>f</sub>:  $4.1 \pm 0.7$ ) and the delta between actual and imagined durations were similar across conditions ( $\chi^2(1) = 0.62$ ,



**Fig 5.** A. Self-reports of imagery vividness. B. Delta between actual and imagined free-throw durations during sMI<sub>f</sub> and dMI<sub>f</sub> conditions. C. Free-throw accuracy across conditions. # Different from 0 ( $p < 0.05$ ), & Statistical trend ( $0.05 < p < 0.1$ ).

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

Mixed linear modeling yielded a trend for experimental conditions on the free-throw accuracy (sMI<sub>f</sub>:  $3.5 \pm 0.7$ , dMI<sub>f</sub>:  $2.6 \pm 1.5$ , CONTROL<sub>f</sub>:  $2.5 \pm 1.5$  free-throws converted,  $\chi^2(2) = 2.78$ ,  $p = 0.09$ , Fig 5). Shooting accuracy tended to be higher during sMI<sub>f</sub> as compared to CONTROL<sub>f</sub> ( $p = 0.08$ ). The SWC analysis revealed that sMI<sub>f</sub> presented a higher percentage of chance to yield greater shooting accuracy values as compared to those recorded during both dMI<sub>f</sub> (88% Superior, 10% Trivial, and 2% Inferior) and CONTROL<sub>f</sub> (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 sMI<sub>f</sub> as compared to both CONTROL<sub>f</sub> and dMI<sub>f</sub>. 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<sub>f</sub> 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<sub>f</sub> 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 locomotor 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<sub>f</sub> 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 sMI<sub>f</sub> further impacted performance, while dMI<sub>f</sub> did not (as compared to the CONTROL<sub>f</sub> 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<sub>f</sub> over dMI<sub>f</sub> 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<sub>f</sub>. 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 debilitating, 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)

## Acknowledgments

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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.

## References

1. Feltz DL, Landers DM. The effects of mental practice on motor skill learning and performance: a meta-analysis. *Journal of Sport & Exercise Psychology*. 1983; 5:25–57.
2. Driskell JE, Copper C, Moran A. Does mental practice enhance performance? *The Journal of applied psychology*. 1994; 79:481–92.
3. Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, et al. Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. *BMC medicine*. 2011; 9:75. Epub 2011/06/21. doi: [10.1186/1741-7015-9-75](https://doi.org/10.1186/1741-7015-9-75) PMID: [21682867](https://pubmed.ncbi.nlm.nih.gov/21682867/); PubMed Central PMCID: PMC3141540.
4. Dijkerman HC, Ietswaart M, Johnston M, MacWalter RS. Does motor imagery training improve hand function in chronic stroke patients? A pilot study. *Clinical rehabilitation*. 2004; 18(5):538–49. Epub 2004/08/06. PMID: [15293488](https://pubmed.ncbi.nlm.nih.gov/15293488/).
5. Driediger M, Hall C, Callow N. Imagery use by injured athletes: a qualitative analysis. *Journal of Sport Sciences*. 2006; 24(3):261–71. Epub 2005/12/22. doi: [10.1080/02640410500128221](https://doi.org/10.1080/02640410500128221) PMID: [16368636](https://pubmed.ncbi.nlm.nih.gov/16368636/).
6. Langhorne P, Coupar F, Pollock A. Motor recovery after stroke: a systematic review. *Lancet neurology*. 2009; 8(8):741–54. Epub 2009/07/18. doi: [10.1016/S1474-4422\(09\)70150-4](https://doi.org/10.1016/S1474-4422(09)70150-4) PMID: [19608100](https://pubmed.ncbi.nlm.nih.gov/19608100/).
7. Di Rienzo F, Collet C, Hoyek N, Guillot A. Impact of neurologic deficits on motor imagery: A systematic review of clinical evaluations. *Neuropsychology review*. 2014. Epub 2014/04/05. doi: [10.1007/s11065-014-9257-6](https://doi.org/10.1007/s11065-014-9257-6) PMID: [24700315](https://pubmed.ncbi.nlm.nih.gov/24700315/).
8. Williams SE, Cumming J, Balanos GM. The use of imagery to manipulate challenge and threat appraisal States in athletes. *Journal of Sport & Exercise Psychology*. 2010; 32(3):339–58. Epub 2010/07/01. PMID: [20587822](https://pubmed.ncbi.nlm.nih.gov/20587822/).
9. Williams SE, Cumming J. Sport imagery ability predicts trait confidence, and challenge and threat appraisal tendencies. *European journal of sport science*. 2012; 12(6):499–508. doi: [10.1080/17461391.2011.630102](https://doi.org/10.1080/17461391.2011.630102)
10. Debarnot U, Sperduti M, Di Rienzo F, Guillot A. Experts bodies, experts minds: How physical and mental training shape the brain. *Frontiers in human neuroscience*. 2014; 8:280. Epub 2014/05/23. doi: [10.3389/fnhum.2014.00280](https://doi.org/10.3389/fnhum.2014.00280) PMID: [24847236](https://pubmed.ncbi.nlm.nih.gov/24847236/); PubMed Central PMCID: PMC4019873.
11. He B, Baxter B, Edelman BJ, Cline CC, Ye WW. Noninvasive brain-computer interfaces based on sensorimotor rhythms. *Proceedings of the IEEE*. 2015; 103(6):907–25.
12. Doud AJ, Lucas JP, Pisansky MT, He B. Continuous three-dimensional control of a virtual helicopter using a motor imagery based brain-computer interface. *PloS one*. 2011; 6(10):e26322. Epub 2011/11/03. doi: [10.1371/journal.pone.0026322](https://doi.org/10.1371/journal.pone.0026322) PMID: [22046274](https://pubmed.ncbi.nlm.nih.gov/22046274/); PubMed Central PMCID: PMC3202533.
13. Laffleur K, Cassady K, Doud A, Shades K, Rogin E, He B. Quadcopter control in three-dimensional space using a noninvasive motor imagery-based brain-computer interface. *Journal of neural engineering*. 2013; 10(4):046003. Epub 2013/06/06. doi: [10.1088/1741-2560/10/4/046003](https://doi.org/10.1088/1741-2560/10/4/046003) PMID: [23735712](https://pubmed.ncbi.nlm.nih.gov/23735712/).
14. Yuan H, Liu T, Szarkowski R, Rios C, Ashe J, He B. Negative covariation between task-related responses in alpha/beta-band activity and BOLD in human sensorimotor cortex: an EEG and fMRI study of motor imagery and movements. *NeuroImage*. 2010; 49(3):2596–606. Epub 2009/10/24. doi: [10.1016/j.neuroimage.2009.10.028](https://doi.org/10.1016/j.neuroimage.2009.10.028) PMID: [19850134](https://pubmed.ncbi.nlm.nih.gov/19850134/); PubMed Central PMCID: PMC2818527.
15. Edelman B, Baxter B, He B. EEG Source Imaging Enhances the Decoding of Complex Right Hand Motor Imagery Tasks. *IEEE transactions on bio-medical engineering*. 2015. Epub 2015/08/16. doi: [10.1109/TBME.2015.2467312](https://doi.org/10.1109/TBME.2015.2467312) PMID: [26276986](https://pubmed.ncbi.nlm.nih.gov/26276986/).
16. Holmes PS, Collins DJ. The PETTLEP approach to motor imagery: A functional equivalence model for sport psychologists. *Journal of Applied Sport Psychology*. 2001; 13(1):60–83. doi: [10.1080/10413200109339004](https://doi.org/10.1080/10413200109339004)
17. Guillot A, Collet C. Construction of the Motor Imagery Integrative Model in Sport: a review and theoretical investigation of motor imagery use. *Int Rev Sport Exerc Psychol*. 2008; 1(1):31–44.
18. Di Rienzo F, Collet C, Hoyek N, Guillot A. Selective effect of physical fatigue on motor imagery accuracy. *PloS one*. 2012; 7(10):e47207. doi: [10.1371/journal.pone.0047207](https://doi.org/10.1371/journal.pone.0047207) PMID: [23082148](https://pubmed.ncbi.nlm.nih.gov/23082148/)
19. Demougeot L, Papaxanthis C. Muscle fatigue affects mental simulation of action. *Journal of Neuroscience*. 2011; 31(29):10712–20. Epub 2011/07/22. doi: [10.1523/JNEUROSCI.6032-10.2011](https://doi.org/10.1523/JNEUROSCI.6032-10.2011) PMID: [21775614](https://pubmed.ncbi.nlm.nih.gov/21775614/).
20. Guillot A, Haguenaer M, Dittmar A, Collet C. Effect of a fatiguing protocol on motor imagery accuracy. *European journal of applied physiology*. 2005; 95(2–3):186–90. Epub 2005/07/09. doi: [10.1007/s00421-005-1400-x](https://doi.org/10.1007/s00421-005-1400-x) PMID: [16003536](https://pubmed.ncbi.nlm.nih.gov/16003536/).

21. Rozand V, Lebon F, Papaxanthis C, Lepers R. Effect of mental fatigue on speed–accuracy trade-off. *Neuroscience*. 2015; 297:219–30. doi: <http://dx.doi.org/10.1016/j.neuroscience.2015.03.066>. PMID: [25849613](https://pubmed.ncbi.nlm.nih.gov/25849613/)
22. Rozand V, Pageaux B, Marcora SM, Papaxanthis C, Lepers R. Does mental exertion alter maximal muscle activation? *Frontiers in human neuroscience*. 2014; 8:755. Epub 2014/10/14. doi: [10.3389/fnhum.2014.00755](https://doi.org/10.3389/fnhum.2014.00755) PMID: [25309404](https://pubmed.ncbi.nlm.nih.gov/25309404/); PubMed Central PMCID: PMC4176059.
23. Martin K, Thompson KG, Keegan R, Ball N, Rattray B. Mental fatigue does not affect maximal anaerobic exercise performance. *European journal of applied physiology*. 2015; 115(4):715–25. Epub 2014/11/27. doi: [10.1007/s00421-014-3052-1](https://doi.org/10.1007/s00421-014-3052-1) PMID: [25425259](https://pubmed.ncbi.nlm.nih.gov/25425259/).
24. Macintyre TE, Moran AP, Collet C, Guillot A. An emerging paradigm: a strength-based approach to exploring mental imagery. *Frontiers in human neuroscience*. 2013; 7:104. Epub 2013/04/05. doi: [10.3389/fnhum.2013.00104](https://doi.org/10.3389/fnhum.2013.00104) PMID: [23554591](https://pubmed.ncbi.nlm.nih.gov/23554591/); PubMed Central PMCID: PMC3612690.
25. Cumming J, Williams SE. Introducing the revised applied model of deliberate imagery use for sport, dance, exercise, and rehabilitation. *Movement & Sport Sciences*. 2013; 82(4):69–81.
26. Louis M, Guillot A, Maton S, Doyon J, Collet C. Effect of imagined movement speed on subsequent motor performance. *Journal of motor behavior*. 2008; 40(2):117–32. Epub 2008/04/11. doi: [10.3200/JMBR.40.2.117-132](https://doi.org/10.3200/JMBR.40.2.117-132) PMID: [18400678](https://pubmed.ncbi.nlm.nih.gov/18400678/).
27. Olsson CJ, Nyberg L. Motor imagery: if you can't do it, you won't think it. *Scandinavian journal of medicine & science in sports*. 2010; 20(5):711–5. Epub 2010/03/27. doi: [10.1111/j.1600-0838.2010.01101.x](https://doi.org/10.1111/j.1600-0838.2010.01101.x) PMID: [20338003](https://pubmed.ncbi.nlm.nih.gov/20338003/).
28. Callow N, Roberts R, Fawkes JZ. Effects of dynamic and static imagery on vividness of imagery, skiing performance, and confidence. *Journal of Imagery Research in Sport and Physical Activity*. 2006; 1:1–15.
29. Guillot A, Moschberger K, Collet C. Coupling movement with imagery as a new perspective for motor imagery practice. *Behavioral and Brain Functions*. 2013; 9:8. Epub 2013/02/22. doi: [10.1186/1744-9081-9-8](https://doi.org/10.1186/1744-9081-9-8) PMID: [23425312](https://pubmed.ncbi.nlm.nih.gov/23425312/); PubMed Central PMCID: PMC3599464.
30. Fusco A, Iosa M, Gallotta MC, Paolucci S, Baldari C, Guidetti L. Different performances in static and dynamic imagery and real locomotion. An exploratory trial. *Frontiers in human neuroscience*. 2014; 8:760. Epub 2014/10/18. doi: [10.3389/fnhum.2014.00760](https://doi.org/10.3389/fnhum.2014.00760) PMID: [25324758](https://pubmed.ncbi.nlm.nih.gov/25324758/); PubMed Central PMCID: PMC4183108.
31. Csataljaj G, O'Donoghue P, Hughes M, Dancs H. Performance indicators that distinguish winning and losing teams in basketball. *International Journal of Performance Analysis in Sport*. 2009; 9(1):60–6.
32. Wrisberg CA, Anshel MH. The effect of cognitive strategies on the free throw shooting performance of young athletes. *The Sport Psychologist*. 1989; 3:95–104.
33. Kanthack TFD, Bigliassi M, Vieira LF, Altimari LR. Acute effect of motor imagery on basketball players' free throw performance and self-efficacy. *Revista Brasileira de Cineantropometria & Desempenho Humano*. 2014; 16(1):47–57.
34. Post PG, Wrisberg CA, Mullins S. A field test of the influence of pre-game imagery on basketball free throw shooting. *Journal of Imagery Research in Sport and Physical Activity*. 2010; 5(1).
35. Lamirand M, Rainey D. Mental imagery, relaxation, and accuracy of basketball foul shooting. *Perceptual and motor skills*. 1994; 78(3 Pt 2):1229–30. Epub 1994/06/01. doi: [10.2466/pms.1994.78.3c.1229](https://doi.org/10.2466/pms.1994.78.3c.1229) PMID: [7936947](https://pubmed.ncbi.nlm.nih.gov/7936947/).
36. Maruff P, Velakoulis D. The voluntary control of motor imagery. Imagined movements in individuals with feigned motor impairment and conversion disorder. *Neuropsychologia*. 2000; 38(9):1251–60. PMID: [10865101](https://pubmed.ncbi.nlm.nih.gov/10865101/)
37. Kanekar N, Santos MJ, Aruin AS. Anticipatory postural control following fatigue of postural and focal muscles. *Clinical Neurophysiology*. 2008; 119(10):2304–13. Epub 2008/08/30. doi: [10.1016/j.clinph.2008.06.015](https://doi.org/10.1016/j.clinph.2008.06.015) PMID: [18752990](https://pubmed.ncbi.nlm.nih.gov/18752990/).
38. Borg GA. Psychophysical bases of perceived exertion. *Medicine and science in sports and exercise*. 1982; 14(5):377–81. Epub 1982/01/01. PMID: [7154893](https://pubmed.ncbi.nlm.nih.gov/7154893/).
39. Guillot A, Collet C, Dittmar A. Influence of environmental context on motor imagery quality. *Biology of Sport*. 2005; 22:215–26.
40. Guillot A, Hoyek N, Louis M, Collet C. Understanding the timing of motor imagery: recent findings and future directions. *International Review of Sport and Exercise Psychology*. 2012; 5(1):3–22. doi: [10.1080/1750984x.2011.623787](https://doi.org/10.1080/1750984x.2011.623787)
41. Utter AC, Robertson RJ, Green JM, Suminski RR, McAnulty SR, Nieman DC. Validation of the Adult OMNI Scale of perceived exertion for walking/running exercise. *Medicine and science in sports and exercise*. 2004; 36(10):1776–80. PMID: [15595300](https://pubmed.ncbi.nlm.nih.gov/15595300/)

42. R-Core-Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, 2014.
43. Bates D, Maechler M, Bolker B, Walker S. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0–6. <http://CRAN.R-project.org/package=lme4>. 2014.
44. Winter B. Linear models and linear mixed effects models in R with linguistic applications. arXiv:13085499 [<http://arxiv.org/pdf/13085499pdf>]. 2013.
45. Baguley T. Serious stats: A guide to advanced statistics for the behavioral sciences: Palgrave Macmillan; 2012.
46. Holm S. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*. 1979; 6:65–70. doi: [10.2307/4615733](https://doi.org/10.2307/4615733)
47. Hopkins W, Marshall S, Batterham A, Hanin J. Progressive statistics for studies in sports medicine and exercise science. *Medicine and science in sports and exercise*. 2009; 41(1):3. doi: [10.1249/MSS.0b013e31818cb278](https://doi.org/10.1249/MSS.0b013e31818cb278) PMID: [19092709](https://pubmed.ncbi.nlm.nih.gov/19092709/)
48. Leger L, Mercier D, Gadoury C, Lambert J. The multistage 20 metre shuttle run test for aerobic fitness. *Journal of Sport Sciences*. 1988; 6(2):93–101.
49. Collet C, Guillot A, Lebon F, MacIntyre T, Moran A. Measuring motor imagery using psychometric, behavioral, and psychophysiological tools. *Exercise and Sport Science Reviews*. 2011; 39(2):85–92. Epub 2011/01/06. doi: [10.1097/JES.0b013e31820ac5e0](https://doi.org/10.1097/JES.0b013e31820ac5e0) PMID: [21206282](https://pubmed.ncbi.nlm.nih.gov/21206282/).
50. Lacey J, Lacey B. The specific role of heart rate in sensorimotor integration. *Neural mechanisms of goal-directed behavior and learning*: Academic Press New York; 1980. p. 495–509.
51. Porges SW. The Polyvagal Perspective. *Biological psychology*. 2007; 74(2):116–43. doi: [10.1016/j.biopsycho.2006.06.009](https://doi.org/10.1016/j.biopsycho.2006.06.009) PMID: [PMC1868418](https://pubmed.ncbi.nlm.nih.gov/PMC1868418/).
52. Collet C, Di Rienzo F, El Hoyek N, Guillot A. Autonomic nervous system correlates in movement observation and motor imagery. *Frontiers in human neuroscience*. 2013; 7:415. Epub 2013/08/03. doi: [10.3389/fnhum.2013.00415](https://doi.org/10.3389/fnhum.2013.00415) PMID: [23908623](https://pubmed.ncbi.nlm.nih.gov/23908623/); PubMed Central PMCID: [PMC3726866](https://pubmed.ncbi.nlm.nih.gov/PMC3726866/).
53. Jackson PL, Lafleur MF, Malouin F, Richards C, Doyon J. Potential role of mental practice using motor imagery in neurologic rehabilitation. *Archives of Physical Medicine and Rehabilitation*. 2001; 82(8):1133–41. Epub 2001/08/09. doi: [10.1053/apmr.2001.24286](https://doi.org/10.1053/apmr.2001.24286) PMID: [11494195](https://pubmed.ncbi.nlm.nih.gov/11494195/).
54. Guillot A, Genevois C, Desliens S, Saieb S, Rogowski I. Motor imagery and 'placebo-racket effects' in tennis serve performance. *Psychology of Sport and Exercise*. 2012; 13(5):533–40. <http://dx.doi.org/10.1016/j.psychsport.2012.03.002>.
55. Guillot A, Desliens S, Rouyer C, Rogowski I. Motor imagery and tennis serve performance: the external focus efficacy. *J Sports Sci Med*. 2013; 12(2):332–8. Epub 2013/10/24. PMID: [24149813](https://pubmed.ncbi.nlm.nih.gov/24149813/); PubMed Central PMCID: [PMC3761826](https://pubmed.ncbi.nlm.nih.gov/PMC3761826/).
56. Peynircioglu ZF, Thompson JL, Tanielian TB. Improvement strategies in free-throw shooting and grip-strength tasks. *J Gen Psychol*. 2000; 127(2):145–56. Epub 2000/06/08. doi: [10.1080/00221300009598574](https://doi.org/10.1080/00221300009598574) PMID: [10843257](https://pubmed.ncbi.nlm.nih.gov/10843257/).
57. Coelho CJ, Nusbaum HC, Rosenbaum DA, Fenn KM. Imagined actions aren't just weak actions: task variability promotes skill learning in physical practice but not in mental practice. *Journal of experimental psychology Learning, memory, and cognition*. 2012; 38(6):1759–64. Epub 2012/05/02. doi: [10.1037/a0028065](https://doi.org/10.1037/a0028065) PMID: [22545613](https://pubmed.ncbi.nlm.nih.gov/22545613/).
58. Gibson ASC, Noakes T. Evidence for complex system integration and dynamic neural regulation of skeletal muscle recruitment during exercise in humans. *British journal of sports medicine*. 2004; 38(6):797–806. PMID: [15562183](https://pubmed.ncbi.nlm.nih.gov/15562183/)
59. Vogt S, Di Rienzo F, Collet C, Collins A, Guillot A. Multiple roles of motor imagery during action observation. *Frontiers in human neuroscience*. 2013; 7. doi: [10.3389/fnhum.2013.00807](https://doi.org/10.3389/fnhum.2013.00807)

**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 well-documented 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 agonist 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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**Key words:** mental practice, force development, training, rehabilitation.

### 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 well-reproduced 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

**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 yielding 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.

\*Corresponding author. Address: Centre de Recherche et d'Innovation sur le Sport, EA 647, Université Claude Bernard Lyon 1, 27-29 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France. Tel: +33-4-72-43-16-25; fax: +33-4-72-44-80-10. E-mail address: franck.di-rienzo@univ-lyon1.fr (F. Di Rienzo). Abbreviations: EDA, electrodermal activity; EDR, electrodermal responses; EMG, electromyogram; iEMG, integrated electromyogram; MI, motor imagery.

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 question 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

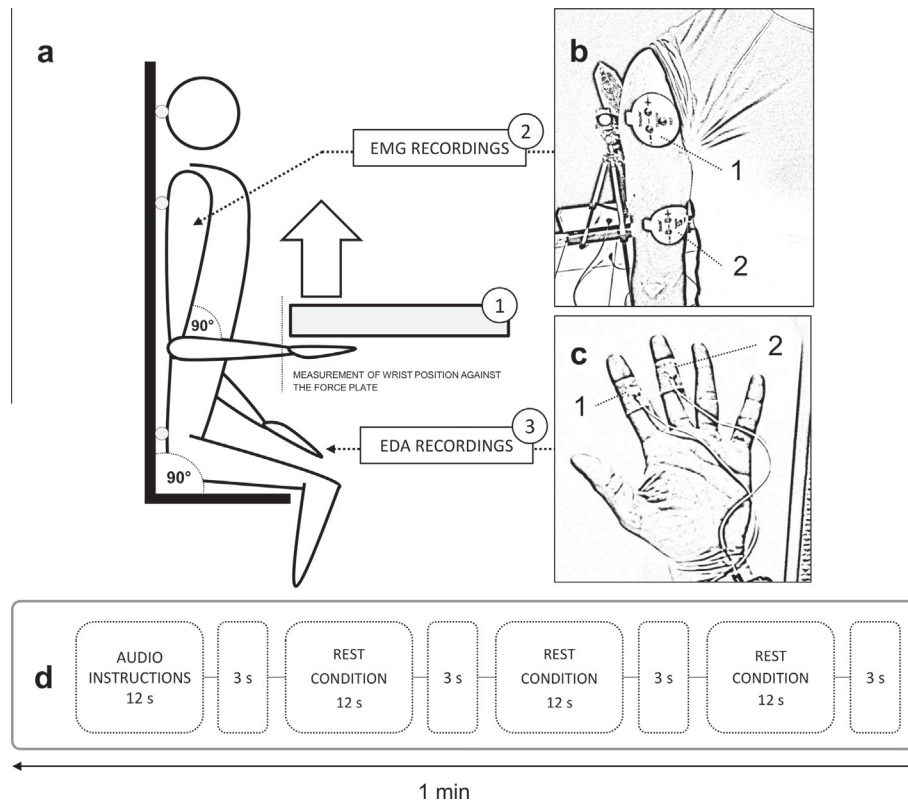
Participants ( $n = 18$ , mean age =  $19.31 \pm 1.25$  years) were recruited from the Faculty of Sports Sciences of the University Claude Bernard Lyon 1 (F-69100, Villeurbanne). All were right-handed inter-regional male athletes in terrestrial sports (i.e., tennis, volleyball, handball and climbing). 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 ( $90^\circ$  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 vertebrae 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 (AMT1, 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<sup>®</sup>). 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).

**Physiological data.** **Electromyography.** We recorded 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-mm<sup>2</sup> unpolarizable Ag/AgCl 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- $\mu$ A constant current to limit current density (10  $\mu$ A/cm<sup>2</sup>). 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 semi-structured 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 lme4 (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.

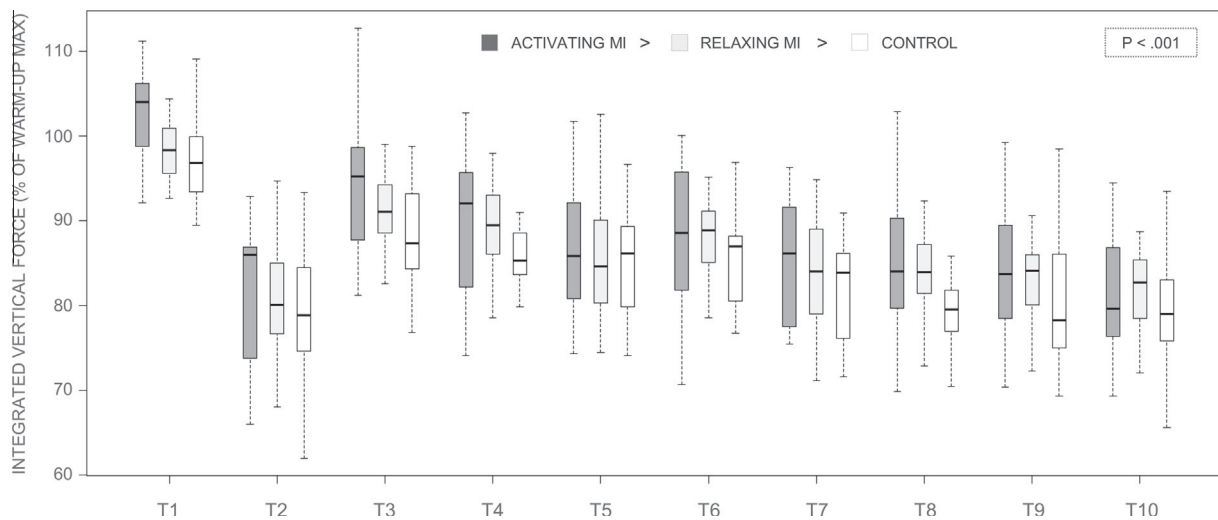
## RESULTS

### 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 ( $\approx 15\%$ ; Fig. 2). We recorded higher isometric force during activating MI vs. both relaxing MI [ $2.1 \pm .01\%$  of fitted difference (standard error)] and control ( $3.5 \pm .01\%$  of fitted difference; Fig. 2). Total force was also  $1.9 \pm .01\%$  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 ( $\approx 15\%$ ; 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 deltoideus*, 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 ( $291.47 \pm 114.99 \text{ k}\Omega$ ) than during both activating MI and control ( $247.04 \text{ k}\Omega \pm 112.46$  and  $278.18 \text{ k}\Omega \pm 85.80$ , 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 ( $48.38 \text{ k}\Omega \pm 28.8$  and  $34.78 \text{ k}\Omega \pm 23.6$  vs.  $29.44 \text{ k}\Omega \pm 18.4$ , both  $p < .001$ ; [Fig. 4](#)). Relaxing MI was also associated to slightly higher EDR amplitudes than activating MI ( $1.4\% \pm 0.4$  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 ( $\chi^2(2) = 1.94$ ,  $p = .38$ ).

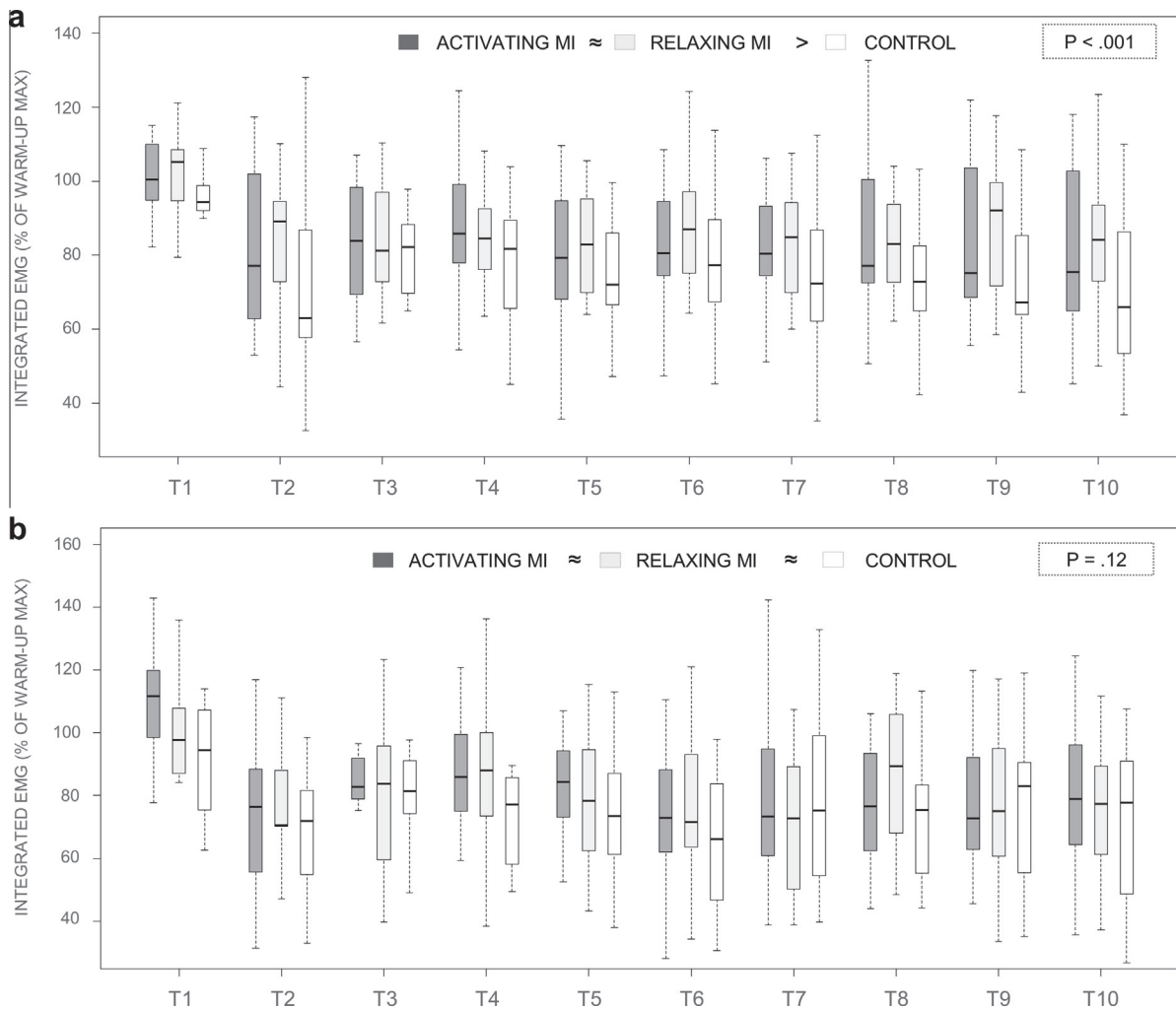
## Self-reports

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;  $p = .99$ ).

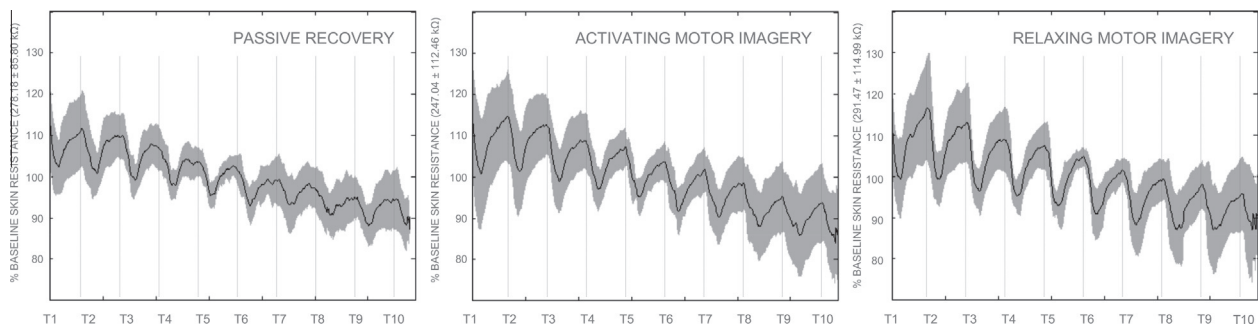
Finally, participants felt more efficient during activating MI (69%) than during both relaxing MI and the control condition (i.e., respectively 25% and 6% of self-reports;  $\chi^2 = 9.87$ ;  $p = .007$ ).

## 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).<sup>1</sup> Experimental results

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

**Table 1.** Group mean  $\pm$  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

<i>Integrated vertical force (N s)</i>										
ACTIVE MI	2593.88 $\pm$ 130.83	2343.76 $\pm$ 131.03	2272.58 $\pm$ 119.87	2178.07 $\pm$ 98.15	2197.62 $\pm$ 104.76	2134.62 $\pm$ 110.59	2124.83 $\pm$ 107.95	2101.69 $\pm$ 100.07	2053.90 $\pm$ 99.20	2067.68 $\pm$ 109.00
RELAXING MI	2505.44 $\pm$ 127.48	2268.20 $\pm$ 135.15	2233.19 $\pm$ 125.34	2155.57 $\pm$ 112.38	2167.29 $\pm$ 113.38	2103.68 $\pm$ 125.50	2083.92 $\pm$ 103.12	2053.15 $\pm$ 105.36	2035.74 $\pm$ 107.20	2021.60 $\pm$ 111.43
PASSIVE RECOVERY	2493.77 $\pm$ 145.69	2264.47 $\pm$ 138.77	2187.06 $\pm$ 121.85	2165.48 $\pm$ 126.50	2167.41 $\pm$ 118.86	2079.72 $\pm$ 108.82	2042.44 $\pm$ 114.98	2058.82 $\pm$ 107.15	2037.26 $\pm$ 117.97	1996.35 $\pm$ 117.05
<i>Integrated electromyogram from the biceps brachii (mV s)</i>										
ACTIVE MI	10224.19 $\pm$ 1306.25	8661.81 $\pm$ 1136.45	8902.61 $\pm$ 1211.06	8165.28 $\pm$ 1157.32	8545.57 $\pm$ 1244.94	8359.78 $\pm$ 1128.36	8246.47 $\pm$ 1057.12	8343.33 $\pm$ 1026.25	8134.30 $\pm$ 1084.06	8291.81 $\pm$ 1106.34
RELAXING MI	10534.59 $\pm$ 1348.80	8428.22 $\pm$ 1096.86	8536.71 $\pm$ 1030.31	8148.78 $\pm$ 1008.04	8442.42 $\pm$ 946.07	8470.13 $\pm$ 1035.62	8267.26 $\pm$ 985.90	8518.53 $\pm$ 1033.00	8333.97 $\pm$ 1027.06	8566.31 $\pm$ 1147.80
CONTROL	9046.59 $\pm$ 1101.95	7741.13 $\pm$ 1062.00	7606.86 $\pm$ 1078.12	7371.68 $\pm$ 1026.61	7476.69 $\pm$ 963.80	7254.75 $\pm$ 1019.41	7203.22 $\pm$ 1004.62	7501.92 $\pm$ 1044.83	7108.99 $\pm$ 1151.68	7098.26 $\pm$ 1124.74
<i>Integrated electromyogram from the anterior deltoideus (mV s)</i>										
ACTIVE MI	5473.06 $\pm$ 824.05	4265.51 $\pm$ 629.30	4368.87 $\pm$ 619.05	4169.68 $\pm$ 567.03	3903.86 $\pm$ 639.45	4025.32 $\pm$ 626.88	3863.32 $\pm$ 609.04	3955.31 $\pm$ 628.63	4070.78 $\pm$ 666.16	3809.05 $\pm$ 668.73
RELAXING MI	4794.81 $\pm$ 884.55	3968.74 $\pm$ 674.84	4154.92 $\pm$ 666.24	3798.13 $\pm$ 657.59	3726.92 $\pm$ 680.92	3506.55 $\pm$ 593.83	4140.94 $\pm$ 647.40	3762.62 $\pm$ 685.03	3672.60 $\pm$ 660.89	3446.63 $\pm$ 562.40
CONTROL	4302.07 $\pm$ 729.18	3759.08 $\pm$ 626.76	3585.48 $\pm$ 611.66	3526.39 $\pm$ 616.35	3241.84 $\pm$ 623.71	3524.32 $\pm$ 618.78	3461.35 $\pm$ 653.06	3765.74 $\pm$ 691.72	3248.52 $\pm$ 589.96	2759.84 $\pm$ 454.64
<i>Skin resistance response amplitudes (% of basal value in k<math>\Omega</math>)</i>										
ACTIVE MI	15.48 $\pm$ 2.72	15.23 $\pm$ 2.92	13.84 $\pm$ 2.59	12.71 $\pm$ 2.29	13.85 $\pm$ 2.48	13.92 $\pm$ 2.36	14.13 $\pm$ 2.33	1.40 $\pm$ 2.40	13.80 $\pm$ 2.42	13.63 $\pm$ 1.85
RELAXING MI	17.63 $\pm$ 3.88	19.40 $\pm$ 3.67	17.49 $\pm$ 2.41	15.58 $\pm$ 2.13	17.22 $\pm$ 2.44	16.83 $\pm$ 2.11	16.65 $\pm$ 1.98	15.74 $\pm$ 1.74	14.09 $\pm$ 1.79	14.29 $\pm$ 1.68
CONTROL	16.08 $\pm$ 2.43	11.06 $\pm$ 1.88	12.45 $\pm$ 1.57	10.05 $\pm$ 1.40	9.35 $\pm$ 1.41	10.33 $\pm$ 1.23	9.81 $\pm$ 1.24	7.03 $\pm$ 1.16	8.91 $\pm$ 1.52	10.28 $\pm$ 1.79

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 pre-trial 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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## REFERENCES

- [Babault N, Desbrosses K, Fabre M-S, Michaut A, Pousson M \(2006\) Neuromuscular fatigue development during maximal concentric and isometric knee extensions. J Appl Physiol 100:780–785.](#)
- [Bates D, Maechler M, Bolker B, Walker S \(2014\) lme4: linear mixed-effects models using Eigen and S4. R package version 1.0-6. <http://CRAN.R-project.org/package=lme4>.](#)
- [Bird EI \(1984\) EMG quantification of mental rehearsal. Percept Mot Skills 59:899–906.](#)
- [Bonnet M, Decety J, Jeannerod M, Requin J \(1997\) Mental simulation of an action modulates the excitability of spinal reflex pathways in man. Cognit Brain Res 5:221–228.](#)
- [Boschker MSJ \(2001\) Action-based imagery: on the nature of mentally imagined motor actions, p 165. University of Amsterdam.](#)
- [Camic CL, Housh TJ, Zuniga JM, Russell Hendrix C, Bergstrom HC, Traylor DA, Schmidt RJ, Johnson GO \(2013\) Electromyographic and mechanomyographic responses across repeated maximal isometric and concentric muscle actions of the leg extensors. J Electromyography Kinesiol 23:342–348.](#)
- [Collet C, Di Rienzo F, El Hoyek N, Guillot A \(2013\) Autonomic nervous system correlates in movement observation and motor imagery. Front Hum Neurosci 7:415.](#)
- [Collet C, Guillot A, Lebon F, MacIntyre T, Moran A \(2011\) Measuring motor imagery using psychometric, behavioral, and psychophysiological tools. Exercise Sport Sci Rev 39:85–92.](#)
- [Cornwall MW, Bruscatto MP, Barry S \(1991\) Effect of mental practice on isometric muscular strength. J Orthopaedic Sports Phys Ther 13:231–234.](#)
- [Decety J, Jeannerod M, Germain M, Pastene J \(1991\) Vegetative response during imagined movement is proportional to mental effort. Behav Brain Res 42:1–5.](#)
- [Frank C, Land WM, Popp C, Schack T \(2014\) Mental representation and mental practice: experimental investigation on the functional links between motor memory and motor imagery. PLoS One 9:e95175.](#)
- [Gandevia SC, Wilson LR, Inglis JT, Burke D \(1997\) Mental rehearsal of motor tasks recruits alpha-motoneurons but fails to recruit human fusimotor neurons selectively. J Physiol 505\(Pt 1\):259–266.](#)
- [Graham JD, Sonne MW, Bray SR \(2014\) It wears me out just imagining it! Mental imagery leads to muscle fatigue and diminished performance of isometric exercise. Biol Psychol 103C:1–6.](#)
- [Guillot A, Collet C \(2008\) Construction of the Motor Imagery Integrative Model in Sport: a review and theoretical investigation of motor imagery use. Int Rev Sport Exercise Psychol 1:31–44.](#)
- [Guillot A, Collet C, Dittmar A \(2005\) Influence of environmental context on motor imagery quality. Biol Sport 22:215–226.](#)
- [Guillot A, Lebon F, Rouffet D, Champely S, Doyon J, Collet C \(2007\) Muscular responses during motor imagery as a function of muscle contraction types. Int J Psychophysiol 66:18–27.](#)

- Herbert RD, Dean C, Gandevia SC (1998) Effects of real and imagined training on voluntary muscle activation during maximal isometric contractions. *Acta Physiol Scand* 163:361–368.
- Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G (2000) Development of recommendations for SEMG sensors and sensor placement procedures. *J Electromyography Kinesiol* 10:361–374.
- Hiraoka K, Mori N, Horino H (2013) Immediate effect of visual attention on corticospinal excitability in the upper trapezius muscle. *Percept Mot Skills* 117:1253–1256.
- Holmes PS, Collins DJ (2001) The PETTLEP approach to motor imagery: a functional equivalence model for sport psychologists. *J Appl Sport Psychol* 13:60–83.
- Jackson PL, Lafleur MF, Malouin F, Richards C, Doyon J (2001) Potential role of mental practice using motor imagery in neurologic rehabilitation. *Arch Phys Med Rehabil* 82:1133–1141.
- Jacobson E (1930) Electrical measurements of neuromuscular states during mental activities. *Am J Physiol* 91:567–608.
- Jacobson E (1932) Electrophysiology of mental activities. *Am J Psychol* 44:677–694.
- Jänig W, Häbler H-J (1999) Specificity in the organization of the autonomic nervous system: a basis for precise neural regulation of homeostatic and protective body functions. *Prog Brain Res* 122:351–367.
- Jeannerod M (1994) The representing brain: neural correlates of motor intention and imagery. *Behav Brain Sci* 17:187–202.
- Jeannerod M, Decety J (1995) Mental motor imagery: a window into the representational stages of action. *Curr Opin Neurobiol* 5:727–732.
- Kroll W (1968) Isometric fatigue curves under varied intertrial recuperation periods. *Res Q Am Assoc Health Phys Educ Recreation* 39:106–115.
- Lebon F, Collet C, Guillot A (2010) Benefits of motor imagery training on muscle strength. *J Strength Conditioning Res/National Strength Conditioning Assoc* 24:1680–1687.
- Lebon F, Guillot A, Collet C (2012) Increased muscle activation following motor imagery during the rehabilitation of the anterior cruciate ligament. *Appl Psychophysiol Biofeedback* 37:45–51.
- Lebon F, Rouffet D, Collet C, Guillot A (2008) Modulation of EMG power spectrum frequency during motor imagery. *Neurosci Lett* 435:181–185.
- Lotze M, Halsband U (2006) Motor imagery. *J Physiol, Paris* 99:386–395.
- Mizuguchi N, Nakata H, Kanosue K (2014) Activity of right premotor-parietal regions dependent upon imagined force level: an fMRI study. *Front Hum Neurosci* 8:1–8.
- Moritani T, deVries HA (1978) Reexamination of the relationship between the surface integrated electromyogram (IEMG) and force of isometric contraction. *Am J Phys Med* 57:263–277.
- Morris T, Spittle M, Watt AP (2005) *Imagery in sport*. Champaign, IL: Human Kinetics.
- Munzert J, Lorey B, Zentgraf K (2009) Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain Res Rev* 60:306–326.
- Personnier P, Ballay Y, Papaxanthis C (2010) Mentally represented motor actions in normal aging: III. Electromyographic features of imagined arm movements. *Behav Brain Res* 206:184–191.
- R Core Team (2014) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ramsey R, Cumming J, Eastough D, Edwards MG (2010) Incongruent imagery interferes with action initiation. *Brain Cogn* 74:249–254.
- Ranganathan VK, Siemionow V, Liu JZ, Sahgal V, Yue GH (2004) From mental power to muscle power—gaining strength by using the mind. *Neuropsychologia* 42:944–956.
- Reiser M, Busch D, Munzert J (2011) Strength gains by motor imagery with different ratios of physical to mental practice. *Front Psychol* 2:194.
- Rozand V, Lebon F, Papaxanthis C, Lepers R (2014) Does a mental training session induce neuromuscular fatigue? *Med Sci Sports Exercise* 46:1981–1989.
- Schack T (2004) The cognitive architecture of complex movement. *Int J Sport Exercise Psychol* 2:403–438.
- Schack T, Essig K, Frank C, Koester D (2014) Mental representation and motor imagery training. *Front Hum Neurosci* 8:328.
- Shields SA, MacDowell KA, Fairchild SB, Campbell ML (1987) Is mediation of sweating cholinergic, adrenergic, or both? A comment on the literature. *Psychophysiology* 24:312–319.
- Smith D, Collins D, Holmes P (2003) Impact and mechanism of mental practice effects on strength. *Int J Sport Exercise Psychol* 1:293–306.
- Stinear CM (2010) Corticospinal facilitation during motor imagery. In: *The neurophysiological foundations of mental and motor imagery* (Guillot A, Collet C, eds), pp 47–61. New York, NY: Oxford University Press.
- Stoykov ME, Madhavan S (2015) Motor priming in neurorehabilitation. *J Neurologic Phys Ther* 39:33–42.
- Vempati RP, Telles S (2002) Yoga-based guided relaxation reduces sympathetic activity judged from baseline levels. *Psychol Rep* 90:487–494.
- Vernet-Maury E, Robin O, Dittmar A (1995) The ohmic perturbation duration, an original temporal index to quantify electrodermal responses. *Behav Brain Res* 67:103–107.
- Wallin BG, Fagius J (1986) The sympathetic nervous system in man — aspects derived from microelectrode recordings. *Trends Neurosci* 9:63–67.
- Wallin BG, Fagius J (1988) Peripheral sympathetic neural activity in conscious humans. *Annu Rev Physiol* 50:565–576.
- Wehner T, Vogt S, Stadler M (1984) Task-specific EMG-characteristics during mental training. *Psychol Res* 46:389–401.
- Wilder J (1957) The law of initial value in neurology and psychiatry: facts and problems. *J Nerv Ment Dis* 125:73–86.
- Winter B (2013) Linear models and linear mixed effects models in R with linguistic applications. arXiv:13085499 (http://arxiv.org/pdf/13085499pdf).
- Wright CJ, Smith D (2009) The effect of PETTLEP imagery on strength performance. *Int J Sport Exercise Psychol* 7:18–31.
- Yao WX, Ranganathan VK, Allexandre D, Siemionow V, Yue GH (2013) Kinesthetic imagery training of forceful muscle contractions increases brain signal and muscle strength. *Front Hum Neurosci* 7:561.
- Yue G, Cole KJ (1992) Strength increases from the motor program: comparison of training with maximal voluntary and imagined muscle contractions. *J Neurophysiol* 67:1114–1123.
- Zentgraf K, Green N, Munzert J, Schack T, Tenenbaum G, Vickers JN, Weigelt M, Wolfensteller U, Heekeren HR (2009) How are actions physically implemented? *Prog Brain Res* 174:303–318.

## 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

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**

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## GENERAL DISCUSSION

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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) MI PRACTICE CONCOMITANT TO ACTUAL TRAINING TO IMPROVE PERFORMANCE**

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**

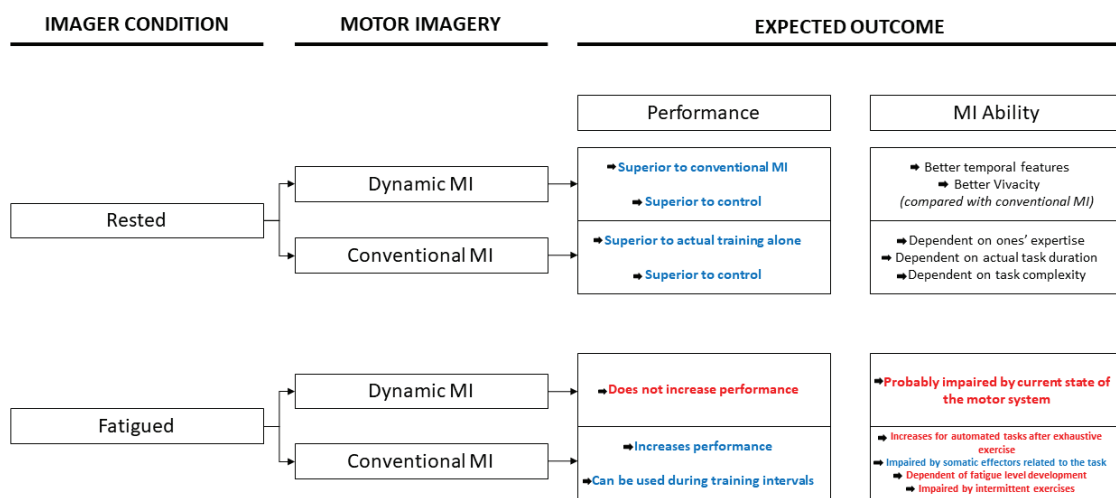
MI practice is known to improve motor performance when performed in addition to actual training. There is a general consensus that MI yields additional benefits on performance than actual training performed alone (Driskell et al., 1994, Yágüez et al., 1998, Jackson et al., 2004, Allami et al., 2008, Guillot et al., 2010). MI practice is a particularly relevant approach to facilitate learning of new inter- and intra-muscular coordinations (Pascual-Leone et al., 1995, 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 known 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 were 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 that MI practice inhibited central mechanisms responsible for organism protection, such as a decrease in efferent commands to avoid muscle injury (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

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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**

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**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 your 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 feel 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.**

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Self-evaluation scale (For all items):

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



Item	External Visual Imagery (imagine yourself from outside)					Interval Visual Imagery (imagine what you see when you really perform the task)					Kinesthetic Imagery (Feel the movement)				
	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. Walk	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 - 10 Borg Rating of Perceived 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

## BIBLIOGRAPHY

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- Abbruzzese G, Trompetto C, Schieppati M (1996) The excitability of the human motor cortex increases during execution and mental imagination of sequential but not repetitive finger movements. *Experimental Brain Research* 111:465-472.
- Achten J, Jeukendrup AE (2003) Heart rate monitoring. *Sports Medicine* 33:517-538.
- Adreani CM, Hill JM, Kaufman MP (1997) Responses of group III and IV muscle afferents to dynamic exercise. *Journal of Applied Physiology* 82:1811-1817.
- Afrouzeh M, Sohrabi E, Haghkhan A, Rowshani F, Goharrokhi S (2015) Effectiveness of PETTLEP imager on performance of passing skill in volleyball. *The Journal of sports medicine and physical fitness* 55:30-36.
- Ahmaidi S, Hardy J, Varray A, Collomp K, Mercier J, Prefaut C (1993) Respiratory gas exchange indices used to detect the blood lactate accumulation threshold during an incremental exercise test in young athletes. *European journal of applied physiology and occupational physiology* 66:31-36.
- Albertus Y, Tucker R, St Clair Gibson A, Lambert EV, Hampson DB, Noakes TD (2005) Effect of distance feedback on pacing strategy and perceived exertion during cycling. *Med sci sports exerc* 37:461-468.
- Albouy G, Ruby P, Phillips C, Luxen A, Peigneux P, Maquet P (2006) Implicit oculomotor sequence learning in humans: Time course of offline processing. *Brain research* 1090:163-171.

- Alexander GE, Crutcher MD (1990) Functional architecture of basal ganglia circuits: neural substrates of parallel processing. *Trends in neurosciences* 13:266-271.
- Allami N, Paulignan Y, Brovelli A, Boussaoud D (2008) Visuo-motor learning with combination of different rates of motor imagery and physical practice. *Experimental Brain Research* 184:105-113.
- Allen G, Gandevia S, McKenzie D (1995) Reliability of measurements of muscle strength and voluntary activation using twitch interpolation. *Muscle & nerve* 18:593-600.
- Amann M, Dempsey J (2009) When fatiguing cycling muscles complain, the brain insightfully responds! *Physiology News* 75:13-14.
- Amann M, Dempsey JA (2008) Locomotor muscle fatigue modifies central motor drive in healthy humans and imposes a limitation to exercise performance. *The Journal of physiology* 586:161-173.
- Amann M, Proctor LT, Sebranek JJ, Eldridge MW, Pegelow DF, Dempsey JA (2008) Somatosensory feedback from the limbs exerts inhibitory influences on central neural drive during whole body endurance exercise. *Journal of Applied Physiology* 105:1714-1724.
- Amann M, Proctor LT, Sebranek JJ, Pegelow DF, Dempsey JA (2009) Opioid-mediated muscle afferents inhibit central motor drive and limit peripheral muscle fatigue development in humans. *The Journal of physiology* 587:271-283.
- Anderson BJ, Li X, Alcantara AA, Isaacs KR, Black JE, Greenough WT (1994) Glial hypertrophy is associated with synaptogenesis following motor-skill learning, but not with angiogenesis following exercise. *Glia* 11:73-80.

- Appenzeller O, Oribe E (1997) The autonomic nervous system: an introduction to basic and clinical concepts: Elsevier Health Sciences.
- Åstrand P-O (2003) Textbook of work physiology: physiological bases of exercise: Human Kinetics.
- Avanzino L, Giannini A, Tacchino A, Pelosin E, Ruggeri P, Bove M (2009) Motor imagery influences the execution of repetitive finger opposition movements. *Neuroscience Letters* 466:11-15.
- Avanzino L, Gueugneau N, Bisio A, Ruggeri P, Papaxanthis C, Bove M (2015) Motor cortical plasticity induced by motor learning through mental practice. *Frontiers in behavioral neuroscience* 9:105.
- Baden D, McLean T, Tucker R, Noakes T, Gibson ASC (2005) Effect of anticipation during unknown or unexpected exercise duration on rating of perceived exertion, affect, and physiological function. *British journal of sports medicine* 39:742-746.
- Bakker M, De Lange F, Stevens J, Toni I, Bloem B (2007) Motor imagery of gait: a quantitative approach. *Experimental Brain Research* 179:497-504.
- Banister E (1991) Modeling elite athletic performance. *Physiological testing of elite athletes* 403-424.
- Barker AT, Jalinous R, Freeston IL (1985) Non-invasive magnetic stimulation of human motor cortex. *The Lancet* 325:1106-1107.
- Barr DP, Himwich HE (1923) Studies in the physiology of muscular exercise II. Comparison of arterial and venous blood following vigorous exercise. *Journal of Biological Chemistry* 55:525-537.

- Barr DP, Himwich HE, Green RP (1923) Studies in the physiology of muscular exercise I. Changes in acid-base equilibrium following short periods of vigorous muscular exercise. *Journal of Biological Chemistry* 55:495-523.
- Barry BK, Enoka RM (2007) The neurobiology of muscle fatigue: 15 years later. *Integrative and comparative biology* 47:465-473.
- Battaglia C, D'Artibale E, Fiorilli G, Piazza M, Tsopani D, Giombini A, Calcagno G, di Cagno A (2014) Use of video observation and motor imagery on jumping performance in national rhythmic gymnastics athletes. *Human movement science* 38:225-234.
- Bäumer T, Schippling S, Kroeger J, Zittel S, Koch G, Thomalla G, Rothwell J, Siebner H, Orth M, Münchau A (2009) Inhibitory and facilitatory connectivity from ventral premotor to primary motor cortex in healthy humans at rest—a bifocal TMS study. *Clinical Neurophysiology* 120:1724-1731.
- Bear MF, Connors BW, Paradiso MA (2007) *Neuroscience*: Lippincott Williams & Wilkins.
- Bigland-Ritchie B, Dawson N, Johansson R, Lippold O (1986) Reflex origin for the slowing of motoneurone firing rates in fatigue of human voluntary contractions. *The Journal of physiology* 379:451.
- Bigland-Ritchie B, Johansson R, Lippold O, Woods J (1983) Contractile speed and EMG changes during fatigue of sustained maximal voluntary contractions. *Journal of neurophysiology* 50:313-324.
- Bigland-Ritchie B, Woods J (1984) Changes in muscle contractile properties and neural control during human muscular fatigue. *Muscle & nerve* 7:691-699.
- Bigliassi M (2015) Corollary discharges and fatigue-related symptoms: the role of attentional focus. *Frontiers in psychology* 6:1002.

- Bigliassi M, Karageorghis CI, Wright MJ, Orgs G, Nowicky AV (2017) Effects of auditory stimuli on electrical activity in the brain during cycle ergometry. *Physiology & Behavior* 177:135-147.
- Bigliassi M, León-Domínguez U, Buzzachera CF, Barreto-Silva V, Altimari LR (2015) How does music aid 5 km of running? *The Journal of Strength & Conditioning Research* 29:305-314.
- Bigliassi M, Peruzollo AS, Kanthack TFD, da Silva VB, Pezarat-Correia P, Atimari L (2014) Effects of a sensory strategy in an isometric muscular endurance task. *Revista Andaluza de Medicina del Deporte* 7:55-59.
- Binkofski F, Amunts K, Stephan KM, Posse S, Schormann T, Freund HJ, Zilles K, Seitz RJ (2000) Broca's region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Human brain mapping* 11:273-285.
- Black JE, Isaacs KR, Anderson BJ, Alcantara AA, Greenough WT (1990) Learning causes synaptogenesis, whereas motor activity causes angiogenesis, in cerebellar cortex of adult rats. *Proceedings of the National Academy of Sciences* 87:5568-5572.
- Bodner ME, Rhodes EC (2000) A review of the concept of the heart rate deflection point. *Sports Medicine* 30:31-46.
- Bolliet O, Collet C, Dittmar A (2005) Actual versus simulated preparation in weight lifting: a neurovegetative study. *Appl Psychophysiol Biofeedback* 30:11-20.
- Bonnet M, Decety J, Jeannerod M, Requin J (1997) Mental simulation of an action modulates the excitability of spinal reflex pathways in man. *Cognitive Brain Research* 5:221-228.
- Borg GA (1982) Psychophysical bases of perceived exertion. *Med sci sports exerc* 14:377-381.

- Boschker MS, Bakker FC, Rietberg B (2000) Retroactive interference effects of mentally imagined movement speed. *Journal of sports sciences* 18:593-603.
- Boulay MR, Simoneau J-a, Lortie G, Bouchard C (1997) Monitoring high-intensity endurance exercise with heart rate and thresholds. *Medicine and science in sports and exercise* 29:125-132.
- Boutcher SH, Seip RL, Hetzler RK, Pierce EF, Snead D, Weltman A (1989) The effects of specificity of training on rating of perceived exertion at the lactate threshold. *European journal of applied physiology and occupational physiology* 59:365-369.
- Braith RW, Wood CE, Limacher MC, Pollock ML, Lowenthal DT, Phillips MI, Staples ED (1992) Abnormal neuroendocrine responses during exercise in heart transplant recipients. *Circulation* 86:1453-1463.
- Brehm JW, Self EA (1989) The intensity of motivation. *Annual review of psychology* 40:109-131.
- Brink-Elfegoun T, Kaijser L, Gustafsson T, Ekblom B (2007) Maximal oxygen uptake is not limited by a central nervous system governor. *Journal of Applied Physiology* 102:781-786.
- Brisswalter J, Collardeau M, René A (2002) Effects of acute physical exercise characteristics on cognitive performance. *Sports Medicine* 32:555-566.
- Brown RA, Lejuez C, Kahler CW, Strong DR (2002) Distress tolerance and duration of past smoking cessation attempts. *Journal of abnormal psychology* 111:180.
- Bruno V, Fossataro C, Garbarini F (2018) "Inhibition or facilitation? Modulation of corticospinal excitability during motor imagery". *Neuropsychologia*.



- Burianová H, Marstaller L, Sowman P, Tesan G, Rich AN, Williams M, Savage G, Johnson BW (2013) Multimodal functional imaging of motor imagery using a novel paradigm. *Neuroimage* 71:50-58.
- Callow N, Roberts R, Fawkes JZ (2006) Effects of dynamic and static imagery on vividness of imagery, skiing performance, and confidence. *Journal of Imagery Research in Sport and Physical Activity* 1.
- Cannon WB (1929) Bodily changes in pain, hunger, fear and rage.
- Case LK, Pineda J, Ramachandran VS (2015) Common coding and dynamic interactions between observed, imagined, and experienced motor and somatosensory activity. *Neuropsychologia* 79:233-245.
- Cengiz B, Boran HE (2016) The role of the cerebellum in motor imagery. *Neuroscience Letters* 617:156-159.
- Chmura J, Kryzstofiak H, Ziemia AW, Nazar K, Kaciuba-Uścilko H (1997) Psychomotor performance during prolonged exercise above and below the blood lactate threshold. *European journal of applied physiology and occupational physiology* 77:77-80.
- Collet C, Di Rienzo F, Hoyek N, Guillot A (2013) Autonomic nervous system correlates in movement observation and motor imagery. *Frontiers in human neuroscience* 7:415.
- Collet C, Guillot A (2010) Autonomic nervous system activities during imagined movements. *The neurophysiological foundations of mental and motor imagery* 95-108.
- Collet C, Guillot A, Lebon F, MacIntyre T, Moran A (2011) Measuring motor imagery using psychometric, behavioral, and psychophysiological tools. *Exercise and sport sciences reviews* 39:85-92.

- Collins D, Carson HJ (2017) The future for PETTLEP: A modern perspective on an effective and established tool. *Current opinion in psychology* 16:12-16.
- Conconi F, Ferrari M, Ziglio PG, Droghetti P, Codeca L (1982) Determination of the anaerobic threshold by a noninvasive field test in runners. *Journal of Applied Physiology* 52:869-873.
- Cornwall MW, Bruscatto MP, Barry S (1991) Effect of Mental Practice on Isometric Muscular Strength 1. *Journal of Orthopaedic & Sports Physical Therapy* 13:231-234.
- Crewe H, Tucker R, Noakes TD (2008) The rate of increase in rating of perceived exertion predicts the duration of exercise to fatigue at a fixed power output in different environmental conditions. *European journal of applied physiology* 103:569.
- Critchley HD (2002) Electrodermal responses: what happens in the brain. *The Neuroscientist* 8:132-142.
- Cumming J, Williams SE (2013) Introducing the revised applied model of deliberate imagery use for sport, dance, exercise, and rehabilitation. *Movement & Sport Sciences* 82:69-81.
- Curra A, Modugno N, Inghilleri M, Manfredi M, Hallett M, Berardelli A (2002) Transcranial magnetic stimulation techniques in clinical investigation. *Neurology* 59:1851-1859.
- Daniele CA, MacDermott AB (2009) Low-threshold primary afferent drive onto GABAergic interneurons in the superficial dorsal horn of the mouse. *Journal of Neuroscience* 29:686-695.

- Daskalakis ZJ, Paradiso GO, Christensen BK, Fitzgerald PB, Gunraj C, Chen R (2004) Exploring the connectivity between the cerebellum and motor cortex in humans. *The Journal of physiology* 557:689-700.
- Dayan E, Cohen LG (2011) Neuroplasticity subserving motor skill learning. *Neuron* 72:443-454.
- De Koning JJ, Foster C, Bakkum A, Kloppenburg S, Thiel C, Joseph T, Cohen J, Porcari JP (2011) Regulation of pacing strategy during athletic competition. *PloS one* 6:e15863.
- de Morree HM, Klein C, Marcora SM (2014) Cortical substrates of the effects of caffeine and time-on-task on perception of effort. *Journal of Applied Physiology* 117:1514-1523.
- Debarnot U, Louis M, Collet C, Guillot A (2011) How does motor imagery speed affect motor performance times? Evaluating the effects of task specificity. *Applied cognitive psychology* 25:536-540.
- Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: how physical and mental training shape the brain. *Frontiers in human neuroscience* 8.
- Decety J, Jeannerod M, Durozard D, Baverel G (1993) Central activation of autonomic effectors during mental simulation of motor actions in man. *The Journal of physiology* 461:549-563.
- Decety J, Jeannerod M, Prablanc C (1989) The timing of mentally represented actions. *Behavioural brain research* 34:35-42.
- Decety J, Michel F (1989) Comparative analysis of actual and mental movement times in two graphic tasks. *Brain and Cognition* 11:87-97.

- Dechent P, Merboldt K-D, Frahm J (2004) Is the human primary motor cortex involved in motor imagery? *Cognitive Brain Research* 19:138-144.
- Demello JJ, Cureton KJ, Boineau RE, Singh MM (1987) Ratings of perceived exertion at the lactate threshold in trained and untrained men and women. *Med sci sports exerc* 19:354-362.
- Demougeot L, Normand H, Denise P, Papaxanthis C (2009) Discrete and effortful imagined movements do not specifically activate the autonomic nervous system. *PloS one* 4:e6769.
- Demougeot L, Papaxanthis C (2011) Muscle fatigue affects mental simulation of action. *The Journal of Neuroscience* 31:10712-10720.
- Di Rienzo F, Collet C, Hoyek N, Guillot A (2012) Selective effect of physical fatigue on motor imagery accuracy. *PloS one* 7:e47207.
- Di Rienzo F, Collet C, Hoyek N, Guillot A (2014a) Impact of neurologic deficits on motor imagery: a systematic review of clinical evaluations. *Neuropsychology review* 24:116-147.
- Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. *Frontiers in human neuroscience* 10:315.
- Di Rienzo F, Hoyek N, Collet C, Guillot A (2014b) Physiological changes in response to apnea impact the timing of motor representations: a preliminary study. *Behavioral and Brain Functions* 10:15.
- Dijkerman HC, Ietswaart M, Johnston M, MacWalter RS (2004) Does motor imagery training improve hand function in chronic stroke patients? A pilot study. *Clinical rehabilitation* 18:538-549.

- Doyon J, Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor skills. *Current opinion in neurobiology* 15:161-167.
- Doyon J, Owen AM, Petrides M, Sziklas V, Evans AC (1996) Functional anatomy of visuomotor skill learning in human subjects examined with positron emission tomography. *European Journal of Neuroscience* 8:637-648.
- Doyon J, Song AW, Karni A, Lalonde F, Adams MM, Ungerleider LG (2002) Experience-dependent changes in cerebellar contributions to motor sequence learning. *Proceedings of the National Academy of Sciences* 99:1017-1022.
- Driskell JE, Copper C, Moran A (1994) Does mental practice enhance performance? *Journal of Applied Psychology* 79:481.
- Duclay J, Pasquet B, Martin A, Duchateau J (2011) Specific modulation of corticospinal and spinal excitabilities during maximal voluntary isometric, shortening and lengthening contractions in synergist muscles. *The Journal of physiology* 589:2901-2916.
- Edwards RH (1981) Human muscle function and fatigue. *Human muscle fatigue: physiological mechanisms* 1-18.
- Edwards RH (1983) Biochemical bases of fatigue in exercise performance: catastrophe theory of muscular fatigue. *Biochemistry of exercise* 13:3-28.
- Ehrsson HH, Geyer S, Naito E (2003) Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of neurophysiology* 90:3304-3316.
- Eifert GH, Zvolensky MJ, Sorrell JT, Hopko DR, Lejuez C (1999) Predictors of self-reported anxiety and panic symptoms: An evaluation of anxiety sensitivity, suffocation fear, heart-focused anxiety, and breath-holding

duration. *Journal of Psychopathology and Behavioral Assessment* 21:293-305.

Eke M, McNally RJ (1996) Anxiety sensitivity, suffocation fear, trait anxiety, and breath-holding duration as predictors of response to carbon dioxide challenge. *Behaviour Research and Therapy* 34:603-607.

Elbert T, Pantev C, Wienbruch C, Rockstroh B, Taub E (1995) Increased cortical representation of the fingers of the left hand in string players. *Science* 270:305-307.

Enoka RM (1988) Muscle strength and its development. *Sports Medicine* 6:146-168.

Enoka RM, Stuart DG (1992) Neurobiology of muscle fatigue. *Journal of Applied Physiology* 72:1631-1648.

Eton DT, Gilner FH, Munz DC (1998) The measurement of imagery vividness: A test of the reliability and validity of the Vividness of Visual Imagery Questionnaire and the Vividness of Movement Imagery Questionnaire. *Journal of Mental Imagery*.

Facchini S, Muellbacher W, Battaglia F, Boroojerdi B, Hallett M (2002) Focal enhancement of motor cortex excitability during motor imagery: a transcranial magnetic stimulation study. *Acta Neurologica Scandinavica* 105:146-151.

Fadiga L, Buccino G, Craighero L, Fogassi L, Gallese V, Pavesi G (1998) Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study. *Neuropsychologia* 37:147-158.

Feltz DL, Landers DM (1983) The effects of mental practice on motor skill learning and performance: A meta-analysis. *Journal of sport psychology*.

- Féré C (1888) Note about the modifications of electrical tension in the human body. CR Soc Biol 5-23.
- Fernandes A, Galbo H, Kjaer M, Mitchell J, Secher N, Thomas S (1990) Cardiovascular and ventilatory responses to dynamic exercise during epidural anaesthesia in man. The Journal of physiology 420:281.
- Ferretti G, Costa M, Ferrigno M, Grassi B, Marconi C, Lundgren C, Cerretelli P (1991) Alveolar gas composition and exchange during deep breath-hold diving and dry breath holds in elite divers. Journal of Applied Physiology 70:794-802.
- Fery Y, Ferry A, Hofe AV, Rieu M (1997) Effect of physical exhaustion on cognitive functioning. Perceptual and motor skills 84:291-298.
- Fitts PM (1954) The information capacity of the human motor system in controlling the amplitude of movement. Journal of experimental psychology 47:381.
- Fontani G, Migliorini S, Benocci R, Facchini A, Casini M, Corradeschi F (2007) Effect of mental imagery on the development of skilled motor actions. Perceptual and motor skills 105:803-826.
- Foster C, Florhaug JA, Franklin J, Gottschall L, Hrovatin LA, Parker S, Doleshal P, Dodge C (2001) A new approach to monitoring exercise training. The Journal of Strength & Conditioning Research 15:109-115.
- Friedman D, Brennum J, Sztuk F, Hansen O, Clifford PS, Bach F, Arendt-Nielsen L, Mitchell J, Secher N (1993) The effect of epidural anaesthesia with 1% lidocaine on the pressor response to dynamic exercise in man. The Journal of physiology 470:681.

- Fuchs F, Reddy Y, Briggs FN (1970) The interaction of cations with the calcium-binding site of troponin. *Biochimica et Biophysica Acta (BBA)-Protein Structure* 221:407-409.
- Fujisawa R, Kimura J, Taniguchi S, Ichikawa H, Hara M, Shimizu H, Iida H, Yamada T, Tani T (2011) Effect of volitional relaxation and motor imagery on F wave and MEP: do these tasks affect excitability of the spinal or cortical motor neurons? *Clinical Neurophysiology* 122:1405-1410.
- Fusco A, Iosa M, Gallotta MC, Paolucci S, Baldari C, Guidetti L (2014) Different performances in static and dynamic imagery and real locomotion. An exploratory trial. *Frontiers in human neuroscience* 8.
- Fusi S, Cutuli D, Valente M, Bergonzi P, Porro C, Di Prampero P (2005) Cardioventilatory responses during real or imagined walking at low speed. *Archives Italiennes de Biologie* 143:223-228.
- Gandevia S (1992) Some central and peripheral factors affecting human motoneuronal output in neuromuscular fatigue. *Sports Medicine* 13:93-98.
- Gandevia S (1998) Neural control in human muscle fatigue: changes in muscle afferents, motor neurones and motor cortical drive. *Acta Physiologica Scandinavica* 162:275-283.
- Gandevia S (2001) Spinal and supraspinal factors in human muscle fatigue. *Physiological reviews* 81:1725-1789.
- Gandevia S, Allen G, McKenzie D (1995) Central fatigue. In: *Fatigue*, pp 281-294: Springer.
- Gandevia S, Allen GM, Butler JE, Taylor JL (1996) Supraspinal factors in human muscle fatigue: evidence for suboptimal output from the motor cortex. *The Journal of physiology* 490:529.



- Gandevia S, Butler J, Allen G, Taylor J (1994) Prolongation of the silent period following transcranial magnetic stimulation during human muscle fatigue. In: JOURNAL OF PHYSIOLOGY-LONDON, vol. 480, pp P110-P110: CAMBRIDGE UNIV PRESS 40 WEST 20TH STREET, NEW YORK, NY 10011-4211.
- Gandevia SC, Wilson LR, Inglis JT, Burke D (1997) Mental rehearsal of motor tasks recruits  $\alpha$ -motoneurons but fails to recruit human fusimotor neurons selectively. *The Journal of physiology* 505:259-266.
- Ganguly K, Poo M-m (2013) Activity-dependent neural plasticity from bench to bedside. *Neuron* 80:729-741.
- Garland S, Kaufman M (1995) Role of muscle afferents in the inhibition of motoneurons during fatigue. In: *Fatigue*, pp 271-278: Springer.
- Gentili R, Han CE, Schweighofer N, Papaxanthis C (2010) Motor learning without doing: trial-by-trial improvement in motor performance during mental training. *Journal of neurophysiology* 104:774-783.
- Gentili R, Papaxanthis C, Pozzo T (2006) Improvement and generalization of arm motor performance through motor imagery practice. *Neuroscience* 137:761-772.
- Gerardin E, Sirigu A, Lehericy S, Poline J-B, Gaymard B, Marsault C, Agid Y, Le Bihan D (2000) Partially overlapping neural networks for real and imagined hand movements. *Cerebral cortex* 10:1093-1104.
- Gibson ASC, Lambert MI, Noakes TD (2001) Neural control of force output during maximal and submaximal exercise. *Sports Medicine* 31:637-650.

- Gibson ASC, Noakes T (2004) Evidence for complex system integration and dynamic neural regulation of skeletal muscle recruitment during exercise in humans. *British journal of sports medicine* 38:797-806.
- Girón EC, Mclsaac T, Nilsen D (2012) Effects of kinesthetic versus visual imagery practice on two technical dance movements: a pilot study. *Journal of Dance Medicine & Science* 16:36-38.
- Gould D, Damarjian N (1996) Imagery training for peak performance.
- Grafton ST, Hazeltine E, Ivry RB (1998) Abstract and effector-specific representations of motor sequences identified with PET. *Journal of Neuroscience* 18:9420-9428.
- Green H, Sutton J, Young P, Cymerman A, Houston C (1989) Operation Everest II: muscle energetics during maximal exhaustive exercise. *Journal of Applied Physiology* 66:142-150.
- Grosprêtre S, Jacquet T, Lebon F, Papaxanthis C, Martin A (2017) Neural mechanisms of strength increase after one-week motor imagery training. *European Journal of Sport Science* 1-10.
- Grosprêtre S, Lebon F, Papaxanthis C, Martin A (2015a) New evidence of cortico-spinal network modulation induced by motor imagery. *Journal of neurophysiology jn*. 00952.02015.
- Grosprêtre S, Ruffino C, Lebon F (2015b) Motor imagery and cortico-spinal excitability: A review. *European Journal of Sport Science* 1-8.
- Gruet M, Temesi J, Rupp T, Levy P, Verges S, Millet GY (2014) Dynamics of corticospinal changes during and after high-intensity quadriceps exercise. *Experimental Physiology* 99:1053-1064.

- Grush R (2004) The emulation theory of representation: Motor control, imagery, and perception. *Behavioral and Brain sciences* 27:377-396.
- Gueugneau N, Crognier L, Papaxanthis C (2008) The influence of eye movements on the temporal features of executed and imagined arm movements. *Brain research* 1187:95-102.
- Guillot A, Collet C (2008) Construction of the motor imagery integrative model in sport: a review and theoretical investigation of motor imagery use. *International Review of Sport and Exercise Psychology* 1:31-44.
- Guillot A, Collet C, Dittmar A (2005a) Influence of environmental context on motor imagery quality: an autonomic nervous system study. *Biology of sport* 22:215.
- Guillot A, Collet C, Nguyen VA, Malouin F, Richards C, Doyon J (2008) Functional neuroanatomical networks associated with expertise in motor imagery. *Neuroimage* 41:1471-1483.
- Guillot A, Collet C, Nguyen VA, Malouin F, Richards C, Doyon J (2009) Brain activity during visual versus kinesthetic imagery: an fMRI study. *Human brain mapping* 30:2157-2172.
- Guillot A, Desliens S, Rouyer C, Rogowski I (2013a) Motor imagery and tennis serve performance: the external focus efficacy. *Journal of sports science & medicine* 12:332.
- Guillot A, Di Rienzo F, Collet C (2014) The neurofunctional architecture of motor imagery. In: *Advanced Brain Neuroimaging Topics in Health and Disease- Methods and Applications: InTech*.

- Guillot A, Di Rienzo F, MacIntyre T, Moran AP, Collet C (2012a) Imagining is not doing but involves specific motor commands: a review of experimental data related to motor inhibition.
- Guillot A, Di Rienzo F, Pialoux V, Simon G, Skinner S, Rogowski I (2015) Implementation of motor imagery during specific aerobic training session in young tennis players. *PLoS one* 10:e0143331.
- Guillot A, Genevois C, Desliens S, Saieb S, Rogowski I (2012b) Motor imagery and 'placebo-racket effects' in tennis serve performance. *Psychology of Sport and Exercise* 13:533-540.
- Guillot A, Haguenaer M, Dittmar A, Collet C (2005b) Effect of a fatiguing protocol on motor imagery accuracy. *European journal of applied physiology* 95:186-190.
- Guillot A, Hoyek N, Louis M, Collet C (2012c) Understanding the timing of motor imagery: recent findings and future directions. *International Review of Sport and Exercise Psychology* 5:3-22.
- Guillot A, Moschberger K, Collet C (2013b) Coupling movement with imagery as a new perspective for motor imagery practice. *Behav Brain Funct* 9.
- Guillot A, Tolleran C, Collet C (2010) Does motor imagery enhance stretching and flexibility? *Journal of sports sciences* 28:291-298.
- Guo F, Sun Y-J, Zhang R-H (2017) Perceived exertion during muscle fatigue as reflected in movement-related cortical potentials: an event-related potential study. *Neuroreport* 28:115-122.
- Gustin SM, Wrigley PJ, Henderson LA, Siddall PJ (2010) Brain circuitry underlying pain in response to imagined movement in people with spinal cord injury. *PAIN®* 148:438-445.

- Hale BD (1982) The effects of internal and external imagery on muscular and ocular concomitants. *Journal of sport psychology* 4:379-387.
- Hall CR, Martin KA (1997) Measuring movement imagery abilities: a revision of the movement imagery questionnaire. *Journal of Mental Imagery*.
- Hall EG, Erffmeyer ES (1983) The effect of visuo-motor behavior rehearsal with videotaped modeling on free throw accuracy of intercollegiate female basketball players. *Journal of sport psychology* 5:343-346.
- Hampson DB, Gibson ASC, Lambert MI, Noakes TD (2001) The influence of sensory cues on the perception of exertion during exercise and central regulation of exercise performance. *Sports Medicine* 31:935-952.
- Hanakawa T, Dimyan MA, Hallett M (2008) Motor planning, imagery, and execution in the distributed motor network: a time-course study with functional MRI. *Cerebral cortex* 18:2775-2788.
- Hanakawa T, Goldfine AM, Hallett M (2017) A Common Function of Basal Ganglia-Cortical Circuits Subserving Speed in Both Motor and Cognitive Domains. *eNeuro* 4:ENEURO. 0200-0217.2017.
- Hanakawa T, Immisch I, Toma K, Dimyan MA, Van Gelderen P, Hallett M (2003) Functional properties of brain areas associated with motor execution and imagery. *Journal of neurophysiology* 89:989-1002.
- Hara M, Kimura J, Walker DD, Taniguchi S, Ichikawa H, Fujisawa R, Shimizu H, Abe T, Yamada T, Kayamori R (2010) Effect of motor imagery and voluntary muscle contraction on the F wave. *Muscle & nerve* 42:208-212.
- Hardy L, Callow N (1999) Efficacy of external and internal visual imagery perspectives for the enhancement of performance on tasks in which form is important. *Journal of Sport and Exercise Psychology* 21:95-112.

- Hartree W, Hill A (1923) The anaerobic processes involved in muscular activity. *The Journal of physiology* 58:127-137.
- Hasson SM, Williams J, Signorile J (1989) Fatigue-induced changes in myoelectric signal characteristics and perceived exertion. *Canadian journal of sport sciences= Journal canadien des sciences du sport* 14:99-102.
- Herbert R, Dean C, Gandevia S (1998) Effects of real and imagined training on voluntary muscle activation during maximal isometric contractions. *Acta Physiologica Scandinavica* 163:361-368.
- Herbert R, Gandevia S (1996) Muscle activation in unilateral and bilateral efforts assessed by motor nerve and cortical stimulation. *Journal of Applied Physiology* 80:1351-1356.
- Héту S, Grégoire M, Saimpont A, Coll M-P, Eugène F, Michon P-E, Jackson PL (2013) The neural network of motor imagery: an ALE meta-analysis. *Neuroscience & Biobehavioral Reviews* 37:930-949.
- Hetzler R, Seip R, Boutcher S, Pierce E, Snead D, Weltman A (1991) Effect of exercise modality on ratings of perceived exertion at various lactate concentrations. *Medicine and science in sports and exercise* 23:88-92.
- Heusser K, Dzamonja G, Tank J, Palada I, Valic Z, Bakovic D, Obad A, Ivancev V, Breskovic T, Diedrich A (2009) Cardiovascular regulation during apnea in elite divers. *Hypertension* 53:719-724.
- Hill AV (1924) Muscular activity and carbohydrate metabolism. *Science* 60:505-514.
- Hill AV, Long C, Lupton H (1924) Muscular exercise, lactic acid, and the supply and utilisation of oxygen. *Proceedings of the Royal Society of London Series B, Containing Papers of a Biological Character* 97:84-138.

- Holmes PS, Collins DJ (2001) The PETTLEP approach to motor imagery: A functional equivalence model for sport psychologists. *Journal of Applied Sport Psychology* 13:60-83.
- Ichikawa H, Kimura J, Taniguchi S, Hara M, Fujisawa R, Shimizu H, Yamada T, Kawamura M (2009) Motor imagery facilitates the spinal motor neurons without hemispheric asymmetry. *Journal of Clinical Neurophysiology* 26:358-365.
- Innes J, De Cort S, Evans P, Guz A (1992) Central command influences cardiorespiratory response to dynamic exercise in humans with unilateral weakness. *The Journal of physiology* 448:551.
- Isaac A, Marks DF, Russell DG (1986) An instrument for assessing imagery of movement: The Vividness of Movement Imagery Questionnaire (VMIQ). *Journal of Mental Imagery*.
- Isaac AR (1992) Mental practice—does it work in the field? *The Sport Psychologist* 6:192-198.
- Isaac AR, Marks DF (1994) Individual differences in mental imagery experience: developmental changes and specialization. *British Journal of Psychology* 85:479-500.
- Jackson PL, Doyon J, Richards CL, Malouin F (2004) The efficacy of combined physical and mental practice in the learning of a foot-sequence task after stroke: a case report. *Neurorehabilitation and Neural repair* 18:106-111.
- Jackson PL, Lafleur MF, Malouin F, Richards C, Doyon J (2001) Potential role of mental practice using motor imagery in neurologic rehabilitation. *Archives of physical medicine and rehabilitation* 82:1133-1141.

- Jackson PL, Lafleur MF, Malouin F, Richards CL, Doyon J (2003) Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. *Neuroimage* 20:1171-1180.
- Jacobson E (1930) Electrical measurements of neuromuscular states during mental activities. *American Journal of Physiology--Legacy Content* 91:567-608.
- Jacobson E (1932) Electrophysiology of mental activities. *The American Journal of Psychology* 44:677-694.
- Jahn K, Deutschländer A, Stephan T, Strupp M, Wiesmann M, Brandt T (2004) Brain activation patterns during imagined stance and locomotion in functional magnetic resonance imaging. *Neuroimage* 22:1722-1731.
- Jakicic J, Donnelly J, Pronk N, Jawad A, Jacobsen D (1995) Prescription of exercise intensity for the obese patient: the relationship between heart rate, VO<sub>2</sub> and perceived exertion. *International journal of obesity and related metabolic disorders: journal of the International Association for the Study of Obesity* 19:382-387.
- Javorka M, Žila I, Javorka K, Čalkovská A (2001) 'Respiratory' oscillations of cardiovascular parameters during voluntary apnea. *Respiration physiology* 126:251-254.
- Jeannerod M (1994) The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain sciences* 17:187-202.
- Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14:S103-S109.



- Jenkins I, Brooks D, Nixon P, Frackowiak R, Passingham R (1994) Motor sequence learning: a study with positron emission tomography. *Journal of Neuroscience* 14:3775-3790.
- Jenny O, Hall C (2009) A quantitative analysis of athletes' voluntary use of slow motion, real time, and fast motion images. *Journal of Applied Sport Psychology*.
- Jeukendrup A, Diemen AV (1998) Heart rate monitoring during training and competition in cyclists. *Journal of sports sciences* 16:91-99.
- Jeukendrup A, Hesselink M, Snyder A, Kuipers H, Keizer H (1992) Physiological changes in male competitive cyclists after two weeks of intensified training. *International journal of sports medicine* 13:534-541.
- Johnson KA, Berenz EC, Zvolensky MJ (2012) Nonclinical panic attack history and anxiety sensitivity: testing the differential moderating role of self-report and behavioral indices of distress tolerance. *Cognitive therapy and research* 36:603-611.
- Jones L, Karageorghis CI, Ekkekakis P (2014) Can high-intensity exercise be more pleasant?: attentional dissociation using music and video. *Journal of Sport and Exercise Psychology* 36:528-541.
- Joseph T, Johnson B, Battista R, Wright G, Dodge C, Porcari J, De Koning J, Foster C (2008) Perception of fatigue during simulated competition. *Medicine+ Science in Sports+ Exercise* 40:381.
- Jueptner M, Frith C, Brooks D, Frackowiak R, Passingham R (1997a) Anatomy of motor learning. II. Subcortical structures and learning by trial and error. *Journal of neurophysiology* 77:1325-1337.

- Jueptner M, Stephan KM, Frith CD, Brooks DJ, Frackowiak RS, Passingham RE (1997b) Anatomy of motor learning. I. Frontal cortex and attention to action. *Journal of neurophysiology* 77:1313-1324.
- Kami A, Meyer G, Jezzard P, Adams MM, Turner R, Ungerleider LG (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377:155.
- Kanthack TFD, Bigliassi M, Vieira LF, Altimari LR (2014) Acute effect of motor imagery on basketball players' free throw performance and self-efficacy. *Revista Brasileira de Cineantropometria & Desempenho Humano* 16:47-57.
- Kanthack TFD, Guillot A, Altimari LR, Nagy SN, Collet C, Di Rienzo F (2016) Selective efficacy of static and dynamic imagery in different states of physical fatigue. *PloS one* 11:e0149654.
- Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams MM, Turner R, Ungerleider LG (1998) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Sciences* 95:861-868.
- Kasai T, Kawai S, Kawanishi M, Yahagi S (1997) Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. *Brain research* 744:147-150.
- Kasess CH, Windischberger C, Cunnington R, Lanzenberger R, Pezawas L, Moser E (2008) The suppressive influence of SMA on M1 in motor imagery revealed by fMRI and dynamic causal modeling. *Neuroimage* 40:828-837.
- Kayser B, Narici M, Binzoni T, Grassi B, Cerretelli P (1994) Fatigue and exhaustion in chronic hypobaric hypoxia: influence of exercising muscle mass. *Journal of Applied Physiology* 76:634-640.

- Kincses ZT, Johansen-Berg H, Tomassini V, Bosnell R, Matthews PM, Beckmann CF (2008) Model-free characterization of brain functional networks for motor sequence learning using fMRI. *Neuroimage* 39:1950-1958.
- Kjær M, Hanel B, Worm L, Perko G, Lewis SF, Sahlin K, Galbo H, Secher NH (1999) Cardiovascular and neuroendocrine responses to exercise in hypoxia during impaired neural feedback from muscle. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 277:R76-R85.
- Kleim JA, Barbay S, Cooper NR, Hogg TM, Reidel CN, Remple MS, Nudo RJ (2002) Motor learning-dependent synaptogenesis is localized to functionally reorganized motor cortex. *Neurobiology of learning and memory* 77:63-77.
- Kleim JA, Lussnig E, Schwarz ER, Comery TA, Greenough WT (1996) Synaptogenesis and Fos expression in the motor cortex of the adult rat after motor skill learning. *Journal of Neuroscience* 16:4529-4535.
- Kraeutner SN, Keeler LT, Boe SG (2016) Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. *Experimental Brain Research* 234:397-407.
- Kuhtz-Buschbeck J, Mahnkopf C, Holzknecht C, Siebner H, Ulmer S, Jansen O (2003) Effector-independent representations of simple and complex imagined finger movements: a combined fMRI and TMS study. *European Journal of Neuroscience* 18:3375-3387.
- Kuipers H, Keizer H, De Vries T, Van Rijthoven P, Wijts M (1988) Comparison of heart rate as a non-invasive determinant of anaerobic threshold with the lactate threshold when cycling. *European journal of applied physiology and occupational physiology* 58:303-306.

- Lacourse MG, Orr EL, Cramer SC, Cohen MJ (2005) Brain activation during execution and motor imagery of novel and skilled sequential hand movements. *Neuroimage* 27:505-519.
- Lacourse MG, Turner JA, Randolph-Orr E, Schandler SL, Cohen MJ (2004) Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. *Journal of rehabilitation research and development* 41:505.
- Lafleur MF, Jackson PL, Malouin F, Richards CL, Evans AC, Doyon J (2002) Motor learning produces parallel dynamic functional changes during the execution and imagination of sequential foot movements. *Neuroimage* 16:142-157.
- Lamirand M, Rainey D (1994) Mental imagery, relaxation, and accuracy of basketball foul shooting. *Perceptual and motor skills* 78:1229-1230.
- Lang PJ (1979) A bio-informational theory of emotional imagery. *Psychophysiology* 16:495-512.
- Latella C, Hendy AM, Pearce AJ, VanderWesthuizen D, Teo W-P (2016) The time-course of acute changes in corticospinal excitability, intra-cortical inhibition and facilitation following a single-session heavy strength training of the biceps brachii. *Frontiers in human neuroscience* 10.
- Latella C, Teo W-P, Harris D, Major B, VanderWesthuizen D, Hendy AM (2017) Effects of acute resistance training modality on corticospinal excitability, intra-cortical and neuromuscular responses. *European journal of applied physiology* 1-14.

- Lebon F, Byblow WD, Collet C, Guillot A, Stinear CM (2012a) The modulation of motor cortex excitability during motor imagery depends on imagery quality. *European Journal of Neuroscience* 35:323-331.
- Lebon F, Collet C, Guillot A (2010) Benefits of motor imagery training on muscle strength. *The Journal of Strength & Conditioning Research* 24:1680-1687.
- Lebon F, Lotze M, Stinear CM, Byblow WD (2012b) Task-dependent interaction between parietal and contralateral primary motor cortex during explicit versus implicit motor imagery. *PloS one* 7:e37850.
- Leger L, Tokmakidis S (1988) Use of the heart rate deflection point to assess the anaerobic threshold. *Journal of Applied Physiology* 64:1758-1760.
- Lehmann M, Baumgartl P, Wiesenack C, Seidel A, Baumann H, Fischer S, Spöri U, Gendrisch G, Kaminski R, Keul J (1992) Training-overtraining: influence of a defined increase in training volume vs training intensity on performance, catecholamines and some metabolic parameters in experienced middle-and long-distance runners. *European journal of applied physiology and occupational physiology* 64:169-177.
- Leonardo M, Fieldman J, Sadato N, Campbell G, Ibañez V, Cohen L, Deiber MP, Jezzard P, Pons T, Turner R (1995) A functional magnetic resonance imaging study of cortical regions associated with motor task execution and motor ideation in humans. *Human brain mapping* 3:83-92.
- Lerner BS, Ostrow AC, Yura MT, Etzel EF (1996) The effects of goal-setting and imagery training programs on the free-throw performance of female collegiate basketball players. *Sport Psychologist* 10:382-397.

- Leyro TM, Zvolensky MJ, Bernstein A (2010) Distress tolerance and psychopathological symptoms and disorders: a review of the empirical literature among adults. *Psychological bulletin* 136:576.
- Li S, Latash ML, Zatsiorsky VM (2004) Effects of motor imagery on finger force responses to transcranial magnetic stimulation. *Cognitive Brain Research* 20:273-280.
- Loizou G, Karageorghis C (2015) Effects of psychological priming, video, and music on anaerobic exercise performance. *Scandinavian journal of medicine & science in sports* 25:909-920.
- Long C (1924) The lactic acid in the blood of a resting man. *The Journal of physiology* 58:455-460.
- Lorey B, Pilgramm S, Bischoff M, Stark R, Vaitl D, Kindermann S, Munzert J, Zentgraf K (2011) Activation of the parieto-premotor network is associated with vivid motor imagery—a parametric fMRI study. *PloS one* 6:e20368.
- Löscher W, Cresswell AG, Thorstensson A (1996) Central fatigue during a long-lasting submaximal contraction of the triceps surae. *Experimental Brain Research* 108:305-314.
- Lotze M, Flor H, Grodd W, Larbig W, Birbaumer N (2001) Phantom movements and pain An fMRI study in upper limb amputees. *Brain* 124:2268-2277.
- Lotze M, Halsband U (2006) Motor imagery. *Journal of Physiology-Paris* 99:386-395.
- Lotze M, Montoya P, Erb M, Hülsmann E, Flor H, Klose U, Birbaumer N, Grodd W (1999) Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal of cognitive neuroscience* 11:491-501.

- Lotze M, Zentgraf K (2010) Contribution of the primary motor cortex to motor imagery. The neurophysiological foundations of mental and motor imagery 31-45.
- Louis M, Guillot A, Maton S, Doyon J, Collet C (2008) Effect of imagined movement speed on subsequent motor performance. *Journal of motor behavior* 40:117-132.
- Machado AdC, Barbosa TC, Sales K, Robson A, de Souza MN, da Nóbrega ACL, Silva BM (2017) Adults with initial metabolic syndrome have altered muscle deoxygenation during incremental exercise. *Obesity*.
- Macuga KL, Frey SH (2012) Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *Neuroimage* 59:2798-2807.
- Mader A, Heck H (1986) A theory of the metabolic origin of “anaerobic threshold”. *International journal of sports medicine* 7:S45-S65.
- Malouin F, Belleville S, Richards CL, Desrosiers J, Doyon J (2004) Working memory and mental practice outcomes after stroke. *Archives of physical medicine and rehabilitation* 85:177-183.
- Malouin F, Jackson PL, Richards CL (2013) Towards the integration of mental practice in rehabilitation programs. A critical review. *Frontiers in human neuroscience* 7.
- Malouin F, Richards CL, Durand A, Doyon J (2008) Reliability of mental chronometry for assessing motor imagery ability after stroke. *Archives of physical medicine and rehabilitation* 89:311-319.

- Marconi B, Pecchioli C, Koch G, Caltagirone C (2007) Functional overlap between hand and forearm motor cortical representations during motor cognitive tasks. *Clinical Neurophysiology* 118:1767-1775.
- Marcora S (2009) Perception of effort during exercise is independent of afferent feedback from skeletal muscles, heart, and lungs. *Journal of Applied Physiology* 106:2060-2062.
- Marcora S (2010) Last word on point: counterpoint: afferent feedback from fatigued locomotor muscles is not an important determinant of endurance exercise performance. *Journal of Applied Physiology* 108:470-470.
- Marcora S (2014) The end-spurt does not require a subconscious intelligent system, just our conscious brain. *BJSM, BMJ Group Blogs [Internet]*; 2008.
- Marcora SM, Bosio A, de Morree HM (2008) Locomotor muscle fatigue increases cardiorespiratory responses and reduces performance during intense cycling exercise independently from metabolic stress. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 294:R874-R883.
- Marcora SM, Staiano W (2010) The limit to exercise tolerance in humans: mind over muscle? *European journal of applied physiology* 109:763-770.
- Marks DF (1973) Visual imagery differences in the recall of pictures. *British Journal of Psychology* 64:17-24.
- Marks DF, Isaac AR (1995) Topographical distribution of EEG activity accompanying visual and motor imagery in vivid and non-vivid imagers. *British Journal of Psychology* 86:271-282.
- Martin KA, Moritz SE, Hall CR (1999) Imagery use in sport: A literature review and applied model. *The Sport Psychologist* 13:245-268.



- McArdle WD, Katch FI, Katch VL (2010) Exercise physiology: nutrition, energy, and human performance: Lippincott Williams & Wilkins.
- McComas A, Miller R, Gandevia S (1995) Fatigue brought on by malfunction of the central and peripheral nervous systems. In: Fatigue, pp 495-512: Springer.
- McCorry LK (2007) Physiology of the autonomic nervous system. American journal of pharmaceutical education 71:78.
- McKenzie D, Gandevia S (1991) Recovery from fatigue of human diaphragm and limb muscles. Respiration physiology 84:49-60.
- McMorris T, Barwood M, Corbett J (2018) Central fatigue theory and endurance exercise: toward an interoceptive model. Neuroscience & Biobehavioral Reviews.
- Meeusen R, Watson P, Hasegawa H, Roelands B, Piacentini MF (2006) Central fatigue. Sports Medicine 36:881-909.
- Meulen M, Allali G, Rieger SW, Assal F, Vuilleumier P (2014) The influence of individual motor imagery ability on cerebral recruitment during gait imagery. Human brain mapping 35:455-470.
- Michelon P, Vettel JM, Zacks JM (2006) Lateral somatotopic organization during imagined and prepared movements. Journal of neurophysiology 95:811-822.
- Mitchell JH, Victor RG (1996) Neural control of the cardiovascular system: insights from muscle sympathetic nerve recordings in humans. Medicine and science in sports and exercise 28:S60-69.

- Miyai I, Tanabe HC, Sase I, Eda H, Oda I, Konishi I, Tsunazawa Y, Suzuki T, Yanagida T, Kubota K (2001) Cortical mapping of gait in humans: a near-infrared spectroscopic topography study. *Neuroimage* 14:1186-1192.
- Mizuguchi N, Nakata H, Kanosue K (2014) Activity of right premotor-parietal regions dependent upon imagined force level: an fMRI study. *Frontiers in human neuroscience* 8.
- Mizuguchi N, Umehara I, Nakata H, Kanosue K (2013) Modulation of corticospinal excitability dependent upon imagined force level. *Experimental Brain Research* 230:243-249.
- Mizuno Y, Tanaka R, Yanagisawa N (1971) Reciprocal group I inhibition on triceps surae motoneurons in man. *Journal of neurophysiology* 34:1010-1017.
- Moran A, Guillot A, MacIntyre T, Collet C (2012) Re-imagining motor imagery: Building bridges between cognitive neuroscience and sport psychology. *British Journal of Psychology* 103:224-247.
- Morree HM, Klein C, Marcora SM (2012) Perception of effort reflects central motor command during movement execution. *Psychophysiology* 49:1242-1253.
- Morris T, Spittle M, Watt AP (2005) *Imagery in sport: Human Kinetics.*
- Morrison JE (1991) *Training for performance: Principles of applied human learning: John Wiley & Sons.*
- Moseley GL (2007) Using visual illusion to reduce at-level neuropathic pain in paraplegia. *Pain* 130:294-298.

- Mouthon AA, Ruffieux J, Keller M, Taube W (2016) Age-related differences in corticospinal excitability during observation and motor imagery of balance tasks. *Frontiers in aging neuroscience* 8:317.
- Mulder T, de Vries S, Zijlstra S (2005) Observation, imagination and execution of an effortful movement: more evidence for a central explanation of motor imagery. *Experimental Brain Research* 163:344-351.
- Mulder T, Zijlstra S, Zijlstra W, Hochstenbach J (2004) The role of motor imagery in learning a totally novel movement. *Experimental Brain Research* 154:211-217.
- Munzert J, Lorey B, Zentgraf K (2009) Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain research reviews* 60:306-326.
- Nair DG, Purcott KL, Fuchs A, Steinberg F, Kelso JS (2003) Cortical and cerebellar activity of the human brain during imagined and executed unimanual and bimanual action sequences: a functional MRI study. *Cognitive Brain Research* 15:250-260.
- Nakagawa K, Masugi Y, Saito A, Obata H, Nakazawa K (2018) Influence of motor imagery on spinal reflex excitability of multiple muscles. *Neuroscience Letters*.
- Noakes T (2000) Physiological models to understand exercise fatigue and the adaptations that predict or enhance athletic performance. *Scandinavian journal of medicine & science in sports* 10:123-145.
- Noakes T, Gibson ASC (2004) Logical limitations to the “catastrophe” models of fatigue during exercise in humans. *British journal of sports medicine* 38:648-649.

- Noakes TD (2004) Physiological factors limiting exercise performance in CFS. *Medicine and science in sports and exercise* 36:1087-1087.
- Noakes TD (2006) Factors "limiting" exercise performance in hypoxia. *Medicine and science in sports and exercise* 38:191; author reply 192.
- Noakes TD (2008) Testing for maximum oxygen consumption has produced a brainless model of human exercise performance. *British journal of sports medicine* 42:551-555.
- Noakes TD, Peltonen JE, Rusko HK (2001) Evidence that a central governor regulates exercise performance during acute hypoxia and hyperoxia. *Journal of Experimental Biology* 204:3225-3234.
- Nordin SM, Cumming J (2005) More than meets the eye: Investigating imagery type, direction, and outcome. *The Sport Psychologist* 19:1-17.
- Nuzzo JL, Barry BK, Gandevia SC, Taylor JL (2016) Acute Strength Training Increases Responses to Stimulation of Corticospinal Axons. *Medicine and science in sports and exercise* 48:139-150.
- Nyberg L, Eriksson J, Larsson A, Marklund P (2006) Learning by doing versus learning by thinking: an fMRI study of motor and mental training. *Neuropsychologia* 44:711-717.
- Nybo L, Secher NH (2004) Cerebral perturbations provoked by prolonged exercise. *Progress in neurobiology* 72:223-261.
- O J, Munroe-Chandler KJ (2008) The effects of image speed on the performance of a soccer task. *The Sport Psychologist*.
- O'Shea H, Moran A (2017) Does motor simulation theory explain the cognitive mechanisms underlying motor imagery? A critical review. *Frontiers in human neuroscience* 11.

- Oishi K, Kasai T, Maeshima T (2000) Autonomic response specificity during motor imagery. *Journal of physiological anthropology and applied human science* 19:255-261.
- Oishi K, Maeshima T (2004) Autonomic nervous system activities during motor imagery in elite athletes. *Journal of Clinical Neurophysiology* 21:170-179.
- Okada TR, Bigliassi M, Bodnariuc FE, Altimari L, Dalla Pria BA, De Moares A (2015) Can information on remaining time modulate psychophysiological parameters during an intermittent exercise? *The Journal of sports medicine and physical fitness* 55:439-445.
- Okushima D, Poole DC, Barstow TJ, Rossiter HB, Kondo N, Bowen TS, Amano T, Koga S (2016) Greater O<sub>2</sub>peak is correlated with greater skeletal muscle deoxygenation amplitude and hemoglobin concentration within individual muscles during ramp-incremental cycle exercise. *Physiological Reports* 4:e13065.
- Olsson C-J, Jonsson B, Larsson A, Nyberg L (2008a) Motor representations and practice affect brain systems underlying imagery: an fMRI study of internal imagery in novices and active high jumpers. *The open neuroimaging journal* 2:5.
- Olsson CJ, Jonsson B, Nyberg L (2008b) Internal imagery training in active high jumpers. *Scandinavian journal of psychology* 49:133-140.
- Pageaux B (2014) The psychobiological model of endurance performance: an effort-based decision-making theory to explain self-paced endurance performance. *Sports Medicine* 44:1319-1320.

- Palmieri RM, Ingersoll CD, Hoffman MA (2004) The Hoffmann reflex: methodologic considerations and applications for use in sports medicine and athletic training research. *Journal of athletic training* 39:268.
- Papaxanthis C, Paizis C, White O, Pozzo T, Stucchi N (2012) The relation between geometry and time in mental actions. *PloS one* 7:e51191.
- Parent A, Hazrati L-N (1995) Functional anatomy of the basal ganglia. I. The cortico-basal ganglia-thalamo-cortical loop. *Brain research reviews* 20:91-127.
- Pascual-Leone A, Nguyet D, Cohen LG, Brasil-Neto JP, Cammarota A, Hallett M (1995) Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of neurophysiology* 74:1037-1045.
- Patuzzo S, Fiaschi A, Manganotti P (2003) Modulation of motor cortex excitability in the left hemisphere during action observation: a single-and paired-pulse transcranial magnetic stimulation study of self-and non-self-action observation. *Neuropsychologia* 41:1272-1278.
- Paulo Manochio J, Lattari E, Matta Mello Portugal E, Sobral Monteiro-Junior R, Paes F, Budde H, de Tarso Veras Farinatti P, Arias-Carrión O, Wegner M, Giovanni Carta M (2015) From mind to body: is mental practice effective on strength gains? A meta-analysis. *CNS & Neurological Disorders-Drug Targets (Formerly Current Drug Targets-CNS & Neurological Disorders)* 14:1145-1151.
- Pearce AJ, Thickbroom GW, Byrnes ML, Mastaglia FL (2000) Functional reorganisation of the corticomotor projection to the hand in skilled racquet players. *Experimental Brain Research* 130:238-243.

- Penhune VB, Doyon J (2002) Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. *Journal of Neuroscience* 22:1397-1406.
- Personnier P, Kubicki A, Laroche D, Papaxanthis C (2010) Temporal features of imagined locomotion in normal aging. *Neuroscience Letters* 476:146-149.
- Personnier P, Paizis C, Ballay Y, Papaxanthis C (2008) Mentally represented motor actions in normal aging: II. The influence of the gravito-inertial context on the duration of overt and covert arm movements. *Behavioural brain research* 186:273-283.
- Pialoux V, Genevois C, Capoen A, Forbes SC, Thomas J, Rogowski I (2015) Playing vs. nonplaying aerobic training in tennis: physiological and performance outcomes. *PloS one* 10:e0122718.
- Pinniger G, Nordlund M, Steele J, Cresswell AG (2001) H-reflex modulation during passive lengthening and shortening of the human triceps surae. *The Journal of physiology* 534:913-923.
- Pollak KA, Swenson JD, Vanhaitsma TA, Hughen RW, Jo D, Light KC, Schweinhardt P, Amann M, Light AR (2014) Exogenously applied muscle metabolites synergistically evoke sensations of muscle fatigue and pain in human subjects. *Experimental Physiology* 99:368-380.
- Porro CA, Cettolo V, Francescato MP, Baraldi P (2000) Ipsilateral involvement of primary motor cortex during motor imagery. *European Journal of Neuroscience* 12:3059-3063.
- Porro CA, Francescato MP, Cettolo V, Diamond ME, Baraldi P, Zuiani C, Bazzocchi M, Di Prampero PE (1996) Primary motor and sensory cortex

- activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *Journal of Neuroscience* 16:7688-7698.
- Posner MI (1978) *Chronometric explorations of mind*: Lawrence Erlbaum.
- Post PG, Wrisberg CA, Mullins S (2010) A field test of the influence of pre-game imagery on basketball free throw shooting. *Journal of Imagery Research in Sport and Physical Activity* 5.
- Ramsey R, Cumming J, Eastough D, Edwards MG (2010) Incongruent imagery interferes with action initiation. *Brain and Cognition* 74:249-254.
- Ramsey R, Cumming J, Edwards MG (2008) Exploring a modified conceptualization of imagery direction and golf putting performance. *International Journal of Sport and Exercise Psychology* 6:207-223.
- Ranganathan VK, Siemionow V, Liu JZ, Sahgal V, Yue GH (2004) From mental power to muscle power—gaining strength by using the mind. *Neuropsychologia* 42:944-956.
- Rauch H, Gibson ASC, Lambert E, Noakes T (2005) A signalling role for muscle glycogen in the regulation of pace during prolonged exercise. *British journal of sports medicine* 39:34-38.
- Reed CL (2002) Chronometric comparisons of imagery to action: Visualizing versus physically performing springboard dives. *Memory & Cognition* 30:1169-1178.
- Reis J, Swayne OB, Vandermeeren Y, Camus M, Dimyan MA, Harris-Love M, Perez MA, Ragert P, Rothwell JC, Cohen LG (2008) Contribution of transcranial magnetic stimulation to the understanding of cortical mechanisms involved in motor control. *The Journal of physiology* 586:325-351.



- Reiser M, Büsch D, Munzert J (2011) Strength gains by motor imagery with different ratios of physical to mental practice. *Frontiers in psychology* 2.
- Rejeski WJ (1985) Perceived exertion: An active or passive process? *Journal of sport psychology* 7:371-378.
- Rizzolatti G, Luppino G, Matelli M (1998) The organization of the cortical motor system: new concepts. *Clinical Neurophysiology* 106:283-296.
- Roberts R, Callow N, Hardy L, Markland D, Bringer J (2008) Movement imagery ability: development and assessment of a revised version of the vividness of movement imagery questionnaire. *Journal of Sport and Exercise Psychology* 30:200-221.
- Robertson EM, Pascual-Leone A, Miall RC (2004a) Current concepts in procedural consolidation. *Nature Reviews Neuroscience* 5:576-582.
- Robertson EM, Pascual-Leone A, Press DZ (2004b) Awareness modifies the skill-learning benefits of sleep. *Current biology* 14:208-212.
- Robin N, Dominique L, Toussaint L, Blandin Y, Guillot A, Her ML (2007) Effects of motor imagery training on service return accuracy in tennis: The role of imagery ability. *International Journal of Sport and Exercise Psychology* 5:175-186.
- Roland PE, Larsen B, Lassen NA, Skinhoj E (1980) Supplementary motor area and other cortical areas in organization of voluntary movements in man. *Journal of neurophysiology* 43:118-136.
- Ross EZ, Middleton N, Shave R, George K, Nowicky A (2007) Corticomotor excitability contributes to neuromuscular fatigue following marathon running in man. *Experimental Physiology* 92:417-426.

- Rossi S, Rossini PM (2004) TMS in cognitive plasticity and the potential for rehabilitation. *Trends in cognitive sciences* 8:273-279.
- Rossini PM, Rossi S, Pasqualetti P, Tecchio F (1999) Corticospinal excitability modulation to hand muscles during movement imagery. *Cerebral cortex* 9:161-167.
- Roth M, Decety J, Raybaudi M, Massarelli R, Delon-Martin C, Segebarth C, Morand S, Gemignani A, Décorps M, Jeannerod M (1996) Possible involvement of primary motor cortex in mentally simulated movement: a functional magnetic resonance imaging study. *Neuroreport* 7:1280-1284.
- Rothwell J (1991) Physiological studies of electric and magnetic stimulation of the human brain. *Electroencephalography and clinical neurophysiology Supplement* 43:29-35.
- Rotstein A, Inbar O, Berginsky T, Meckel Y (2005) Preferred transition speed between walking and running: effects of training status. *Medicine and science in sports and exercise* 37:1864.
- Roure R, Collet C, Deschaumes-Molinaro C, Delhomme G, Dittmar A, Vernet-Maury E (1999) Imagery quality estimated by autonomic response is correlated to sporting performance enhancement. *Physiology & Behavior* 66:63-72.
- Ruffino C, Papaxanthis C, Lebon F (2017) Neural plasticity during motor learning with motor imagery practice: Review and perspectives. *Neuroscience* 341:61-78.
- Ruotsalainen I, Ahtiainen JP, Kidgell DJ, Avela J (2014) Changes in corticospinal excitability during an acute bout of resistance exercise in the elbow flexors. *European journal of applied physiology* 114:1545-1553.

- Sabaté M, González B, Rodríguez M (2007) Adapting movement planning to motor impairments: the motor-scanning system. *Neuropsychologia* 45:378-386.
- Sabbah P, Simond G, Levrier O, Habib M, Trabaud V, Murayama N, Mazoyer B, Briant J, Raybaud C, Salamon G (1995) Functional magnetic resonance imaging at 1.5 T during sensorimotor and cognitive task. *European neurology* 35:131-136.
- Sacco P, Thickbroom GW, Byrnes ML, Mastaglia FL (2000) Changes in corticomotor excitability after fatiguing muscle contractions. *Muscle & nerve* 23:1840-1846.
- Sacco P, Thickbroom GW, Thompson ML, Mastaglia FL (1997) Changes in corticomotor excitation and inhibition during prolonged submaximal muscle contractions. *Muscle & nerve* 20:1158-1166.
- Sackett RS (1934) The influence of symbolic rehearsal upon the retention of a maze habit. *The Journal of general psychology* 10:376-398.
- Sackett RS (1935) The relationship between amount of symbolic rehearsal and retention of a maze habit. *The Journal of general psychology* 13:113-130.
- Sakai K, Hikosaka O, Miyauchi S, Takino R, Sasaki Y, Pütz B (1998) Transition of brain activation from frontal to parietal areas in visuomotor sequence learning. *Journal of Neuroscience* 18:1827-1840.
- Sale DG (2008) Neural adaptation to strength training. *Strength and Power in Sport, Second Edition* 281-314.
- Sanes JN, Donoghue JP (2000) Plasticity and primary motor cortex. *Annual review of neuroscience* 23:393-415.

- Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, Kischka U, Ettl T (2011) Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. *BMC medicine* 9:75.
- Schwoebel J, Boronat CB, Coslett HB (2002) The man who executed “imagined” movements: evidence for dissociable components of the body schema. *Brain and Cognition* 50:1-16.
- Seidler R, Purushotham A, Kim S-G, Uğurbil K, Willingham D, Ashe J (2002) Cerebellum activation associated with performance change but not motor learning. *Science* 296:2043-2046.
- Seif-Barghi T, Kordi R, Memari A-H, Mansournia M-A, Jalali-Ghomi M (2012) The effect of an ecological imagery program on soccer performance of elite players. *Asian journal of sports medicine* 3:81.
- Shadmehr R, Smith MA, Krakauer JW (2010) Error correction, sensory prediction, and adaptation in motor control. *Annual review of neuroscience* 33:89-108.
- Sharma N, Jones PS, Carpenter T, Baron J-C (2008) Mapping the involvement of BA 4a and 4p during motor imagery. *Neuroimage* 41:92-99.
- Shick J (1970) Effects of mental practice on selected volleyball skills for college women. *Research Quarterly American Association for Health, Physical Education and Recreation* 41:88-94.
- Shields SA, MacDowell KA, Fairchild SB, Campbell ML (1987) Is mediation of sweating cholinergic, adrenergic, or both? A comment on the literature. *Psychophysiology* 24:312-319.
- Short SE, Bruggeman JM, Engel SG, Marback TL, Wang LJ, Willadsen A, Short MW (2002) The effect of imagery function and imagery direction on self-

efficacy and performance on a golf-putting task. *The Sport Psychologist* 16:48-67.

Sirigu A, Duhamel J-R, Cohen L, Pillon B, Dubois B, Agid Y (1996) The mental representation of hand movements after parietal cortex damage. *Science-AAAS-Weekly Paper Edition* 273:1564-1570.

Skempes D, Melvin J, Von Groote P, Stucki G, Bickenbach J (2018) Using Concept Mapping to Develop a Human Rights Based Indicator Framework to Assess Country Efforts to Strengthen Rehabilitation Provision and Policy: The Rehabilitation System Diagnosis and Dialogue (RESYST) Framework.

Smith D, Wright C, Allsopp A, Westhead H (2007) It's all in the mind: PETTLEP-based imagery and sports performance. *Journal of Applied Sport Psychology* 19:80-92.

Solodkin A, Hlustik P, Chen EE, Small SL (2004) Fine modulation in network activation during motor execution and motor imagery. *Cerebral cortex* 14:1246-1255.

Stand AP (1990) The recommended quantity and quality of exercise for developing and maintaining cardiorespiratory and muscular fitness in healthy adults. *Medicine & Science in Sports & Exercise* 22:265-274.

Stephan K, Frackowiak R (1996) Motor imagery—anatomical representation and electrophysiological characteristics. *Neurochemical research* 21:1105-1116.

Stinear CM (2010) Corticospinal facilitation during motor imagery. *The neurophysiological foundations of mental and motor imagery* 47-61.

- Stinear CM, Byblow WD (2003) Motor imagery of phasic thumb abduction temporally and spatially modulates corticospinal excitability. *Clinical Neurophysiology* 114:909-914.
- Stinear CM, Byblow WD (2004) Modulation of corticospinal excitability and intracortical inhibition during motor imagery is task-dependent. *Experimental Brain Research* 157:351-358.
- Stinear CM, Byblow WD, Steyvers M, Levin O, Swinnen SP (2006a) Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. *Experimental Brain Research* 168:157-164.
- Stinear CM, Fleming MK, Byblow WD (2006b) Lateralization of unimanual and bimanual motor imagery. *Brain research* 1095:139-147.
- Sutton JR, Reeves JT, Wagner PD, Groves BM, Cymerman A, Malconian MK, Rock PB, Young PM, Walter SD, Houston CS (1988) Operation Everest II: oxygen transport during exercise at extreme simulated altitude. *Journal of Applied Physiology* 64:1309-1321.
- Svensson P, Romaniello A, Arendt-Nielsen L, Sessle BJ (2003) Plasticity in corticomotor control of the human tongue musculature induced by tongue-task training. *Experimental Brain Research* 152:42-51.
- Tanaka H, Matsugi A, Okada Y (2017) The effects of imaginary voluntary muscle contraction and relaxation on cerebellar brain inhibition. *Neuroscience Research*.
- Taniguchi S, Kimura J, Yamada T, Ichikawa H, Hara M, Fujisawa R, Shimizu H, Tani T (2008) Effect of motion imagery to counter rest-induced suppression of F-wave as a measure of anterior horn cell excitability. *Clinical Neurophysiology* 119:1346-1352.

- Tarchanoff G (1890) About galvanic skin response from the excitation of sensorial organs and different psychic activities. *Pflugers Arch Eur J Physiol* 46:46-55.
- Taylor J, Shaw D (2002) The effects of outcome imagery on golf-putting performance. *Journal of sports sciences* 20:607-613.
- Taylor JL (2006) Stimulation at the cervicomedullary junction in human subjects. *Journal of electromyography and Kinesiology* 16:215-223.
- Taylor JL, Butler JE, Gandevia S (2000) Changes in muscle afferents, motoneurons and motor drive during muscle fatigue. *European journal of applied physiology* 83:106-115.
- Taylor JL, Todd G, Gandevia SC (2006) Evidence for a supraspinal contribution to human muscle fatigue. *Clinical and Experimental Pharmacology and Physiology* 33:400-405.
- Terao Y, Ugawa Y (2002) Basic mechanisms of TMS. *Journal of Clinical Neurophysiology* 19:322-343.
- Tokmakidis SP, Léger LA (1992) Comparison of mathematically determined blood lactate and heart rate “threshold” points and relationship with performance. *European journal of applied physiology and occupational physiology* 64:309-317.
- Tomprowski PD, Ellis NR (1986) Effects of exercise on cognitive processes: A review. *Psychological bulletin* 99:338.
- Toni I, Krams M, Turner R, Passingham RE (1998) The time course of changes during motor sequence learning: a whole-brain fMRI study. *Neuroimage* 8:50-61.

- Tucker R (2009) The anticipatory regulation of performance: the physiological basis for pacing strategies and the development of a perception-based model for exercise performance. *British journal of sports medicine* 43:392-400.
- Tucker R, Rauch L, Harley YX, Noakes TD (2004) Impaired exercise performance in the heat is associated with an anticipatory reduction in skeletal muscle recruitment. *Pflügers Archiv* 448:422-430.
- Ueda T, Kurokawa T (1995) Relationships between perceived exertion and physiological variables during swimming. *International journal of sports medicine* 16:385-389.
- Ugawa Y, Uesaka Y, Terao Y, Hanajima R, Kanazawa I (1995) Magnetic stimulation over the cerebellum in humans. *Annals of neurology* 37:703-713.
- Ulmer H-V (1996) Concept of an extracellular regulation of muscular metabolic rate during heavy exercise in humans by psychophysiological feedback. *Cellular and Molecular Life Sciences* 52:416-420.
- Vergeer I, Roberts J (2006) Movement and stretching imagery during flexibility training. *Journal of sports sciences* 24:197-208.
- Vernet-Maury E, Robin O, Dittmar A (1995) The ohmic perturbation duration, an original temporal index to quantify electrodermal responses. *Behavioural brain research* 67:103-107.
- Vorobiev V, Govoni P, Rizzolatti G, Matelli M, Luppino G (1998) Parcellation of human mesial area 6: cytoarchitectonic evidence for three separate areas. *European Journal of Neuroscience* 10:2199-2203.



- Wakefield C, Smith D, Moran AP, Holmes P (2013) Functional equivalence or behavioural matching? A critical reflection on 15 years of research using the PETTLEP model of motor imagery. *International Review of Sport and Exercise Psychology* 6:105-121.
- Wallace LK, Slattery KM, Coutts AJ (2009) The ecological validity and application of the session-RPE method for quantifying training loads in swimming. *The Journal of Strength & Conditioning Research* 23:33-38.
- Wallin BG, Fagius J (1986) The sympathetic nervous system in man—aspects derived from microelectrode recordings. *Trends in neurosciences* 9:63-67.
- Wang Y, Morgan WP (1992) The effect of imagery perspectives on the psychophysiological responses to imagined exercise. *Behavioural brain research* 52:167-174.
- Wehner T, Vogt S, Stadler M (1984) Task-specific EMG-characteristics during mental training. *Psychological research* 46:389-401.
- Weinberg RS, Seabourne TG, Jackson A (1981) Effects of visuo-motor behavior rehearsal, relaxation, and imagery on karate performance. *Journal of sport psychology* 3:228-238.
- White A, Hardy L (1995) Use of different imagery perspectives on the learning and performance of different motor skills. *British Journal of Psychology* 86:169-180.
- Whiting H, Den Brinker B (1982) Image of the act. In: *Theory and research in learning disabilities*, pp 217-235: Springer.
- Wilke K, Keil F, Wittern K, Wepf R, Biel S (2004) Immunolabelling is essential for the differentiation of human axillary apoeccrine glands. *Journal of Investigative Dermatology* 123:A87-A97.

- Williams J, Pearce AJ, Loporto M, Morris T, Holmes PS (2012) The relationship between corticospinal excitability during motor imagery and motor imagery ability. *Behavioural brain research* 226:369-375.
- Williamson J, McColl R, Mathews D, Mitchell J, Raven P, Morgan W (2001) Hypnotic manipulation of effort sense during dynamic exercise: cardiovascular responses and brain activation. *Journal of Applied Physiology* 90:1392-1399.
- Williamson J, McColl R, Mathews D, Mitchell J, Raven P, Morgan W (2002) Brain activation by central command during actual and imagined handgrip under hypnosis. *Journal of Applied Physiology* 92:1317-1324.
- Windhorst U, Boorman G (1995) Overview: potential role of segmental motor circuitry in muscle fatigue. In: *Fatigue*, pp 241-258: Springer.
- Wright CJ, Smith D (2009) The effect of PETTLEP imagery on strength performance. *International Journal of Sport and Exercise Psychology* 7:18-31.
- Wright CJ, Smith DK (2007) The effect of a short-term PETTLEP imagery intervention on a cognitive task. *Journal of Imagery Research in Sport and Physical Activity* 2.
- Wu T, Kansaku K, Hallett M (2004) How self-initiated memorized movements become automatic: a functional MRI study. *Journal of neurophysiology* 91:1690-1698.
- Yágüez L, Nagel D, Hoffman H, Canavan A, Wist E, Hömberg V (1998) A mental route to motor learning: improving trajectorial kinematics through imagery training. *Behavioural brain research* 90:95-106.

- Yahagi S, Kasai T (1998) Facilitation of motor evoked potentials (MEPs) in first dorsal interosseous (FDI) muscle is dependent on different motor images. *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control* 109:409-417.
- Yahagi S, Shimura K, Kasai T (1996) An increase in cortical excitability with no change in spinal excitability during motor imagery. *Perceptual and motor skills* 83:288-290.
- Yang G, Pan F, Gan W-B (2009) Stably maintained dendritic spines are associated with lifelong memories. *Nature* 462:920.
- Yao WX, Ranganathan VK, Allexandre D, Siemionow V, Yue GH (2013) Kinesthetic imagery training of forceful muscle contractions increases brain signal and muscle strength. *Front Hum Neurosci* 7:561.
- Yue G, Cole KJ (1992) Strength increases from the motor program: comparison of training with maximal voluntary and imagined muscle contractions. *Journal of neurophysiology* 67:1114-1123.
- Zilles K (1992) Neuronal plasticity as an adaptive property of the central nervous system. *Annals of Anatomy-Anatomischer Anzeiger* 174:383-391.
- Zvolensky MJ, Vujanovic AA, Bernstein A, Leyro T (2010) Distress tolerance: Theory, measurement, and relations to psychopathology. *Current Directions in Psychological Science* 19:406-410.