



UNIVERSIDADE DE LISBOA
Faculdade de Motricidade Humana

**Brain-muscle coupling and intermuscular coordination in high-speed knee movements
performed to fatigue and their role on hamstring strain injuries**

José Pedro de Almeida Martins Correia

Orientador: Professor Doutor Sandro Remo Martins Neves Ramos Freitas

Co-orientadores: Professor Doutor João Pedro Casaca de Rocha Vaz, Professor Doutor Erik
Witvrouw

Tese especialmente elaborada com vista à obtenção do grau de Doutor em Motricidade Humana, na
Especialidade de Comportamento Motor

Tese por compilação de artigos, realizada ao abrigo da alínea a) do nº2 do artº 31º do Decreto-Lei nº
230/2009



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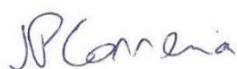
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Faculdade de Motricidade Humana – Universidade de Lisboa, 17/04/2024

Assinatura



Dedicatória

Aos meus pais, porque tudo o que sou e consigo alcançar é graças que me deram e ensinaram em todos os momentos da vida. Continuo a aprender com eles todos os dias as coisas mais importantes que existem. Que seja assim por muito tempo.

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Este trabalho pertencente ao projeto HamStrong foi suportado por fundos nacionais através da FCT – Fundação para a Ciência e a Tecnologia, I.P., no âmbito do projeto HamStrong Ref.^a PTDC/SAU-DES/31497/2017 (<http://doi.org/10.54499/PTDC/SAU-DES/31497/2017>) e através de uma bolsa de doutoramento (SFRH/BD/143927/2019, <https://doi.org/10.54499/SFRH/BD/143927/2019>). O custo de publicação do estudo “Brain and muscle activity during fatiguing maximum-speed knee movement”, publicado na revista *Journal of Applied Physiology*, foi suportado pela Faculdade de Motricidade Humana.



Brain-muscle coupling and intermuscular coordination in high-speed knee movements performed to fatigue and their role on hamstring strain injuries

Abstract

The decrease in finger movement rate with maximum-speed repetitive limb movement (i.e., motor slowing) has shown a consistent response and a strong supraspinal control dependence. Studying a larger segment would have implications not only for establishing a common motor slowing behavior but also for central and peripheral maximal exercise regulation mechanisms. Additionally, high-speed leg movement is also a relevant hamstring injury mechanism in football, and the supraspinal repercussions of these injuries remain unexplored. This project aimed to i) characterize the leg motor slowing, its measurement reliability, and its associated electrophysiology; ii) determine whether a simple motor slowing task can differentiate footballers with and without hamstring injury history; and iii) investigate differences in brain and muscle activity between footballers with and without hamstring injury history. A literature review was first conducted to establish the current knowledge on fast movement control. Next, correct task execution and normative data for the leg motor slowing response and the associated brain and muscle electrophysiology were established in healthy individuals. The same task was then applied in footballers, where those with previous hamstring injury showed a higher movement rate, brain activity suggesting higher task cognitive load and attentional resource use, and lower muscle activity and agonist-antagonist co-contraction. Finally, finger and leg motor slowing were compared in footballers; although both showed a similar trajectory, there was a greater finger motor slowing. The main conclusions are i) leg movement rate can be measured reliably and shows a clear motor slowing pattern associated with brain activity decreases after an initial peak, decreasing agonist muscle activity, and decreasing corticomuscular coherence with fatigue; ii) a simple maximum-speed movement task was able to differentiate footballers with and without hamstring injury history; and iii) footballers with previous hamstring injury show a greater central resource use and lower muscle activity during a maximum-speed task.

Keywords: motor slowing, electroencephalography, electromyography, hamstring strain injury, fatigue

Ligação cerebromuscular e coordenação intermuscular em movimentos de alta velocidade do joelho até à fadiga e o seu papel nas lesões musculares dos isquiotibiais

Resumo

A diminuição da frequência gestual dos dedos com movimentos repetitivos de máxima velocidade (*motor slowing*) tem demonstrado uma resposta consistente e uma forte dependência do controlo supraspinal. O estudo de um segmento maior permitiria estabelecer um comportamento comum de *motor slowing* mas também mecanismos regulatórios centrais e periféricos do exercício. O movimento rápido das pernas é também um mecanismo relevante de lesão dos isquiotibiais no futebol, e as suas repercussões supraespinais permanecem inexploradas. Este projeto teve como objetivo: i) caracterizar o *motor slowing* das pernas, a sua fiabilidade, e a eletrofisiologia associada; ii) determinar se uma tarefa simples de *motor slowing* diferencia futebolistas com e sem historial de lesões nos isquiotibiais; e iii) investigar as diferenças na atividade cerebral e muscular entre jogadores de futebol com e sem historial de lesões nos isquiotibiais. Foi realizada uma revisão da literatura para estabelecer o conhecimento atual sobre o controlo de movimentos rápidos. A execução correta da tarefa, dados normativos de *motor slowing* das pernas e a eletrofisiologia cerebral e muscular associada foram estabelecidos em indivíduos saudáveis. A mesma tarefa foi aplicada em futebolistas, onde aqueles com lesão prévia nos isquiotibiais apresentaram uma frequência gestual mais alta, atividade cerebral demonstrativa de uma maior carga cognitiva e uso de recursos atencionais, e atividade muscular e co-contração agonista-antagonista mais reduzidas. Finalmente, o *motor slowing* dos dedos e das pernas foi comparado em futebolistas; embora ambos tenham mostrado uma trajetória semelhante, houve uma maior perda nos dedos. As principais conclusões são: i) a frequência gestual das pernas pode ser medida de forma fiável e mostra um padrão claro de *motor slowing* associado a diminuições na atividade cerebral após um pico inicial, diminuição da atividade muscular agonista e da coerência corticomuscular com fadiga; ii) a tarefa usada foi capaz de diferenciar futebolistas com e sem historial de lesão nos isquiotibiais; e iii) futebolistas com lesões anteriores nos isquiotibiais mostram um maior uso de recursos centrais e menor atividade muscular durante uma tarefa de máxima velocidade.

Palavras-chave: motor slowing, eletroencefalografia, eletromiografia, lesão dos isquibiais, fadiga

Resumo desenvolvido

A execução de movimentos rápidos, especialmente quando estes são repetidos, apresenta especificidades importantes em termos de controlo motor. Estas especificidades são especialmente importantes a nível central, uma vez que estes movimentos requerem uma elevada sincronização de unidades motoras e um *input* supraespinal significativo. Para além disso, são caracterizados por um padrão de atividade cortical contínua, por oposição a movimentos mais lentos, que apresentam um padrão intermitente. Também a fadiga associada a estes movimentos repetidos tem uma forte base supraespinal, nomeadamente em termos da degradação da qualidade do comando motor central, o que entre outros fatores leva a uma perda de frequência gestual em esforços máximos, denominada *motor slowing*. Este fenómeno tem sido sobretudo observado em movimentos de segmentos menores como os dedos e pés. Contudo, os movimentos rápidos do membro inferior, pela sua maior massa, podem apresentar diferenças importantes tanto ao nível do padrão de atividade cerebral (e consequentemente de *motor slowing*) como de atividade muscular, bem como da ligação centro-periferia.

Os movimentos rápidos do membro inferior têm também uma grande relevância funcional e constituem um mecanismo importante de lesões musculares dos isquiotibiais. Estas lesões, por sua vez, são as lesões musculares mais frequentes no futebol e apresentam por isso um grande impacto desportivo, financeiro e na carreira dos futebolistas, também devido à elevada recorrência. Apesar da relevância dos movimentos rápidos para estas lesões e da importância do controlo supraespinal, existe uma grande falta de conhecimento sobre o impacto das lesões musculares dos isquiotibiais na atividade cerebral e muscular durante movimentos rápidos do membro inferior. Os objetivos deste projeto foram assim i) caracterizar o *motor slowing* das pernas, a sua fiabilidade, e a eletrofisiologia associada; ii) determinar se uma tarefa simples de *motor slowing* diferencia futebolistas com e sem história de lesões nos isquiotibiais; e iii) investigar as diferenças na atividade cerebral e muscular entre jogadores de futebol com e sem história de lesões nos isquiotibiais.

A revisão da literatura efetuada descreveu o conhecimento atual relativamente ao controlo motor de movimentos rápidos em indivíduos saudáveis e do impacto da fadiga nestes mecanismos de controlo motor tanto a nível central como periférico. A partir desta análise da literatura foi também extraída informação relevante para determinar os parâmetros da tarefa a ser usada nos estudos subsequentes de forma a otimizar a exigência supraespinal e promover o aparecimento de *motor slowing*. Esta tarefa consistiu em blocos consecutivos de movimentos repetidos de flexão-extensão do joelho executados a velocidade máxima. As áreas de atividade cerebral analisadas através de eletroencefalografia (EEG) foram também

baseadas nas localizações que nesta revisão mostraram maior modulação de atividade durante a execução de movimentos rápidos.

De forma a assegurar a correta execução da tarefa, nomeadamente em termos da manutenção da amplitude de movimento desejada, foi realizado um estudo piloto (n=12) que confirmou esta execução dentro dos parâmetros estabelecidos. Esta análise da amplitude de movimento foi realizada durante a execução da tarefa através de marcadores refletivos. A importância desta execução devia-se ao facto de não haver feedback visual ou tátil durante a tarefa para assegurar a manutenção da amplitude de movimento.

Seguidamente, foi avaliada a atividade cerebral, muscular, e a frequência gestual ao longo da tarefa de flexão-extensão do joelho desenhada (8 blocos de 10 s com 5 s de descanso em decúbito ventral) em duas sessões (n=19). A frequência gestual foi determinada através da colocação de acelerómetros no tornozelo. A atividade cerebral foi medida em 4 elétrodos (2 centrais e 2 frontais) e a atividade muscular foi recolhida nos flexores (bíceps femoral e semitendinoso) e extensores (vasto lateral, reto femoral, e vasto medial) do joelho. De forma a analisar a ligação funcional entre a atividade cerebral e muscular ao longo da tarefa, foi calculada a coerência corticomuscular (i.e., entre os sinais EEG e de eletromiografia (EMG)). Antes e após da tarefa, foram realizadas contrações voluntárias isométricas máximas de flexão e extensão do joelho de forma a determinar o efeito agudo da tarefa no momento de força máximo e na taxa de produção de força (TPF), medida em quatro períodos consecutivos de 50 ms. Estas medições foram também realizadas no estudo seguinte. Este estudo revelou que esta tarefa teve um impacto significativo na grande maioria dos parâmetros analisados. A frequência gestual diminuiu até ao quarto bloco da tarefa; após este período, verificou-se uma estabilização. Foi registada uma diminuição generalizada da atividade cerebral após um pico inicial e uma diminuição da atividade muscular dos flexores. A coerência corticomuscular também diminuiu ao longo da tarefa, mas de forma mais visível nos extensores do que nos flexores do joelho. Verificou-se ainda uma diminuição no momento de força máximo e na TPF dos flexores até aos 150 ms. A reprodutibilidade da frequência gestual foi boa a excelente ao longo dos 8 blocos, enquanto que a reprodutibilidade dos parâmetros neurofisiológicos foi na maior parte dos casos moderada a boa.

Seguidamente, foi aplicado o mesmo protocolo a uma amostra de futebolistas (n=108) com (n=39) e sem (n=69) historial de lesão dos isquiotibiais nas 2 épocas anteriores. Este estudo revelou que os futebolistas com lesão prévia mostraram ter uma frequência gestual significativamente maior, especialmente nos primeiros 3 blocos. Foram também registadas diferenças na atividade cerebral; os futebolistas com lesão prévia mostraram alterações que

sugerem uma maior carga cognitiva e uso de recursos atencionais durante a realização da tarefa, especialmente na segunda metade. Quanto à atividade muscular, os futebolistas com historial de lesão mostraram uma menor amplitude do reto femoral e bícípíte femoral, bem como uma menor quantidade de co-contracção entre flexores e extensores. Este resultado sugere que uma lesão muscular dos flexores afeta também o padrão de recrutamento da musculatura antagonista. Apesar de se terem registado diminuições significativas da coerência corticomuscular em todos os pares analisados, estas diminuições foram semelhantes entre atletas com e sem historial de lesão. Foi ainda verificado que o bícípíte femoral (mais frequentemente afetado por lesões musculares) mostrou ter uma coerência corticomuscular significativamente mais baixa do que todos os outros pares EEG-EMG analisados. No que toca às alterações no momento de força máximo e TPF pré-pós tarefa, verificou-se um padrão semelhante ao estudo anterior, com uma diminuição significativa de ambos os parâmetros nos flexores do joelho e nenhuma alteração significativa nos extensores.

Tendo a conta as diferenças encontradas na frequência gestual das pernas no estudo anterior, de seguida verificou-se se essas diferenças se verificavam também em futebolistas (n=32) ao realizar a mesma tarefa mas com os dedos. Apesar de se terem registado reduções significativas da frequência gestual em ambas as tarefas, não foram desta vez encontradas diferenças entre atletas com e sem historial de lesão dos isquiotibiais na amostra global. Contudo, verificaram-se diferenças significativas na frequência gestual das pernas entre os atletas testados na pré-época (mais rápidos) e na segunda metade da época (mais lentos). O outro ponto de destaque deste estudo foi o facto de que tanto a frequência gestual dos dedos como a das pernas se ajusta a um modelo logarítmico, mas com um maior declive (i.e., maior perda de frequência gestual) nos dedos.

Ao longo deste projeto, e relativamente aos objetivos propostos, foi assim possível verificar que i) a frequência gestual das pernas pode ser medida de forma fiável e mostra um padrão claro de *motor slowing* associado a diminuições na atividade cerebral após um pico inicial, diminuição da atividade muscular agonista e da coerência corticomuscular com fadiga; ii) a tarefa usada foi capaz de diferenciar futebolistas com e sem historial de lesão nos isquiotibiais, sobretudo quando medida na pré-época; e iii) futebolistas com lesões anteriores nos isquiotibiais mostram um maior uso de recursos centrais e menor atividade muscular durante uma tarefa de máxima velocidade.

Scientific outputs associated with the doctorate

Scientific articles

Correia JP, Vaz JR, Domingos C, Freitas SR. From thinking fast to moving fast: motor control of fast limb movements in healthy individuals. *Rev Neurosci*. 2022;33(8):919-950. Published 2022 Jun 8. doi:10.1515/revneuro-2021-0171

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Abbreviations

ACL, anterior cruciate ligament; AG1, first agonist burst; AG2, second agonist burst; ANT, antagonist burst; AUC, area under the curve; BF, biceps femoris; CCI, co-contraction index; CKC, corticokinematic coherence; CMC, corticomuscular coherence; CNS, central nervous system; CV, coefficient of variation; EEG, electroencephalography; EMG, electromyography; ERD, event-related desynchronization; ERS, event-related synchronization; fMRI, functional magnetic resonance imaging; HSI, hamstring strain injury; ICC, intraclass correlation coefficient; M1, primary motor cortex; MEP, motor evoked potentials; MN, motor neuron; MR, movement rate; MRI, magnetic resonance imaging; MU, motor unit; MVC, maximum voluntary contraction; MVIC, maximum voluntary isometric contraction; OR, odds ratio; PMC, premotor cortex; RF, rectus femoris; RFD, rate of force development; ROM, range of motion; RSA, repeated sprint ability; RTD, rate of torque development; SEM, standard error of the mean; SM1, primary sensorimotor cortex; SMA, supplementary motor area; SP, silent period; ST, semitendinosus; TMS, transcranial magnetic stimulation; VL, vastus lateralis; VM, vastus medialis

Thesis conception and structure

This work was based on an extremely simple and basic observation which is often overlooked (or even forgotten) in the rehabilitation, sports science, and sports medicine fields: just as there is no voluntary movement without effectors, there is also no (meaningful and context-appropriate) voluntary movement without the brain. If we want to get to know the motor system building, then it is not possible to see only what happens in the basement. Indeed, the need for more studies combining central and peripheral neurophysiological measures with behavioral motor outputs (Seidel-Marzi & Ragert, 2020) and the potential of merging neuroscience with biomechanics and physiology to further our understanding of how the central nervous system regulates and adapts motor responses (Enders & Nigg, 2016) have been highlighted.

This project was designed to contribute to two different but associated fields. First, it aimed to clarify the electrophysiology behind maximum-speed repetitive movement and the regulation of fatigue associated with leg repetitive movement. Second, in a more field-based perspective, the aim was to apply this knowledge to a sports injury model, in this case of hamstring injuries in football. Completing this project therefore allowed for a knowledge advancement in both fields while promoting interdisciplinary research, which is recognized as increasingly important in today's research world.

In order to achieve this purpose, the following steps were taken. First, the general introduction outlined the relevance of the physiological and field aspects of the work in light of the current literature (Chapter I). Then, the thesis chapters are organized to reflect the flow of the performed work. In Chapter II, the current literature concerning the physiology of fast limb movement from planning to execution and its modifying factors, as well as the effects of training and fatigue, are reviewed. This helped not only to design and set the parameters for the experimental studies but also to highlight some knowledge gaps that the rest of the project would help address. Starting the experimental studies, we first sought out to determine if the execution of the designed task would comply with the range of motion requirements in the absence of visual or tactile feedback, since this was an important aspect for the subsequent studies (Chapter III). Next, baseline electrophysiological data in healthy individuals the between-day repeatability of the brain, muscle, and performance outcomes were established (Chapter IV). This allowed to set a benchmark for the following studies and to see what effect on central and peripheral features of motor control the task would have. We then moved on to the more applied aspect of the project in chapter V, determining whether the effects of the designed task on brain and muscle activity, as well as task performance, would be able to retrospectively differentiate footballers with and without

hamstring injury history (HSI). To conclude the experimental studies, we finally tested whether finger and leg performance in the same task are associated to help establish whether a common performance regulation mechanism is present, if there are differences in upper and lower limb joint performance in a lower limb-trained sample (footballers), and if both tasks differentiate players with and without HSI history (Chapter VI).

CHAPTER I – GENERAL INTRODUCTION

High-speed movement: physiological bases, relevance, and the concept of motor slowing

The ability to move fast has played an important role in the human experience since prehistoric times. Currently, the importance of maximum movement speed is perhaps more evident in sports, especially in high-performance settings, where small differences can have a large impact on the final outcome. However, there is ample evidence that movement speed has important implications at other completely different levels such as music (Nolet, 2013), preventing a fall (Maffiuletti et al., 2016), cognitive decline (Bramell-Risberg et al., 2010), economics (Shadmehr & Ahmed, 2020), central nervous system integrity (Bartzokis et al., 2010), and even mortality risk (Metter et al., 2005).

Fast movements also have relevant and distinct physiological features across the motor system, from the generation of the motor command to the observed behavior. One of these features is a greater involvement and resource usage of the central motor system. The first aspect of note regarding this involvement is the fact that in maximum speed movement (or with such an intention), most motor units (MUs) are recruited before force development and movement even start (Desmedt & Godaux, 1977; Van Cutsem et al., 1998). This means that these movements have a greater dependence on internal motor programs, since the motor parameters are largely defined before any observable behavior, and there is little room for adjustments based on peripheral feedback (feedforward motor control). Second, it has been reported that the maximum contraction speed is mostly dependent on the motor neuron recruitment speed and maximal MU discharge rate (Del Vecchio et al., 2019; Duchateau & Baudry, 2014), both of which have an important central component. Accordingly, the level of brain activity is usually positively correlated with movement speed in a wide network comprising areas of the frontal and parietal cortices, cerebellum, and midbrain (including the basal ganglia) (Kunieda et al., 2000; Lutz et al., 2004; Sauvage et al., 2013; Shirinbayan et al., 2019; Toma et al., 2002). Third, movements performed above a certain rate threshold show a distinct control mechanism. At lower rates (i.e., up to 1.5-2 Hz), sensory input is integrated for each individual movement (Kawashima et al., 1999; Mayville et al., 1999), and there is individual temporal electroencephalographic (EEG) activity modulation for each movement (Toma et al., 2002). As the movement rate (MR) increases, there is a shift towards pre-attentive and rhythmical motor control, which relies less on peripheral feedback integration (Kunesch et al., 1989; Mayville et al., 1999), and continuous EEG activity is seen (Toma et al., 2002). Thus, fast (repetitive or isolated) movement places a specific challenge to the central nervous system, even in cases of unresisted movement.

Another aspect is related to the mechanisms of rapid force generation. The level of voluntary activation in the first 50-75 ms has been reported to be the main determinant of the rate of force development (RFD) (Maffiuletti et al., 2016). In turn, the level of voluntary activation is directly related to the descending neural drive; accordingly, it has been reported that the neural drive produced in the initial phase of an explosive contraction is predominantly supraspinal (Del Vecchio et al., 2019). This also highlights the importance of central motor control in generating high movement speeds.

Peripherally, fast movements are characterized by a distinct EMG sequence, the triphasic pattern, which is increasingly present as movement speed increases (Brown & Gilleard, 1991). Briefly, this pattern is composed of two agonist bursts interspersed by an antagonist burst. These bursts have the function of accelerating the segment (first agonist burst), deceleration (antagonist burst), and adjusting the final position to the desired target (second agonist burst) (Cheron et al., 2007; Cooke & Brown, 1990). Factors such as segment inertia and the intended range of motion can induce temporal and amplitude modulation of these bursts. This pattern and its influencing factors are described in greater detail in Chapter II.

Finally, at the behavioral level, an important phenomenon associated with (repetitive) fast movement is motor slowing, which is characterized by a decrease in MR 10-30 s after movement onset. This has been shown mostly in finger but also in foot, elbow, and eye movements performed at the maximum MR, which indicates that this phenomenon is independent of the muscle group (Bächinger et al., 2019; Corcos et al., 2002; Rodrigues et al., 2009). Motor slowing has been explained by mechanisms such as the loss of surround inhibition at the motor cortex (Bächinger et al., 2019; Kassavetis et al., 2014), which is characterized by an increased net excitability of adjacent cortical networks and leads to higher coactivation of agonist and antagonist muscles, decreasing movement efficiency. Conversely, other authors have found increased M1 intracortical inhibition in a fatiguing finger tapping task (Arias et al., 2015; Madrid et al., 2018). The specific origin of motor slowing also remains unclear. Intracortical timing inhibition mediated by GABAergic circuits have been implicated by the impairment of the control of the rapid change of movement direction (Madrid et al., 2016, 2018). However, Beck and Hallett highlight that although surround inhibition can be observed at the motor cortex, it may originate and be maintained by motor signals from the basal ganglia, therefore having a subcortical origin (Beck & Hallett, 2011). The specific mechanisms and contribution of cortical and subcortical pathways to motor slowing therefore still warrant research (Beck & Hallett, 2011; White & Hall, 2008).

Despite the indications that motor slowing is a generalized feature of repeated fast unresisted movement, the existing studies have focused on small joints. Since segment

inertia has been shown to play a role on the EMG pattern of fast movements (Marsden et al., 1983; Pfann et al., 1998; Shapiro et al., 2004), and considering that specific EMG changes are also associated with motor slowing, a larger joint such as the knee (associated with the heavier leg segment) may show different features compared to the analyzed smaller joints. Moreover, lower limb motor control also shows specific features relative to the upper limb. Knee unilateral movements show less sensorimotor lateralization on functional magnetic resonance imaging (fMRI) not only than finger and elbow movements but also than other lower limb joints (Kaprili et al., 2006.; Luft et al., 2002); lower limb joints have also shown a greater somatotopic sensorimotor and cerebellar overlap as well as different activation patterns compared to upper limb joints (Kaprili et al., 2007). Additionally, the typical functional patterns of the upper (low load, asymmetrical, and fine motor skills) and lower (high load, symmetrical, and directed for balance and stability) extremities are distinct (Goel & Paloski, 2016). Finally, changes in motoneuron excitability induced by fatigue have been shown to differ between the upper and lower limb, with the lower limb showing a lesser decrease in excitability and a quicker recovery after fatigue, a clearer distinction between the spinal- and cortical-induced silent periods (Temesi et al., 2019; Vernillo et al., 2020), and a recent meta-analysis called for further studies on the effect of lower limb training on corticospinal adaptations (Woodhead et al., 2023). A study of the effect of brain stimulation on motor slowing also highlighted the need for studies which combine central and peripheral measurements with behavioral outcomes and their application in sport settings (Seidel-Marzi & Ragert, 2020).

The burden and mechanism of hamstring injuries in football

Hamstring strain injuries (HSI) are the most frequent injury in sprinting/kicking sports (H. Liu et al., 2012), representing 12-17% of all injuries (Ekstrand et al., 2011, 2016) and 37% of muscle injuries in football (Ekstrand et al., 2016). HSIs also have a high recurrence rate (12-48%) (Freckleton & Pizzari, 2013; H. Liu et al., 2012) and lead to an average absence of 17 days per injury (Ekstrand et al., 2016). In a 25-player squad, 5-6 HSI occur per season (Ekstrand et al., 2011, 2016). The injury risk is 6-9 times greater in matches than in training (Ekstrand et al., 2011, 2016) and is greater at the end of each half, when fatigue levels are increased (Woods, 2004). This highlights the importance of analyzing hamstring function and motor behavior in a fatigued state.

HSIs constitute a significant performance but also financial burden in football. Considering the estimated average absence of 17 days (H. Liu et al., 2012), each HSI can have a cost of around €280 000 for elite teams. However, players of lower competitive levels, whether

lower professional, semi-professional or amateur, can also be seriously affected (Hägglund et al., 2016; Kekelekis et al., 2023), since injuries can affect their physical and mental health (Jansen et al., 2019) and the chances of securing playing contracts to maintain or assist their livelihood.

The risk factors for HSIs have been extensively studied (Ekstrand et al., 2011, 2016; Goldman & Jones, 2011; Lee et al., 2018; McCall et al., 2015; Van Beijsterveldt et al., 2013). However, this has not led to a decrease in injury incidence in elite footballers; in fact, there is a continuous growth trend (Ekstrand, Bengtsson, et al., 2023; Ekstrand et al., 2016; Palmer et al., 2023). Part of this growth may be explained by the increase in match exposure and in the physicality of the game; indeed, the high-speed distance covered in a match (commonly associated with HSIs) has increased in multiple competitions (Hostrup & Bangsbo, 2023). Nevertheless, current injury data shows the issue is far from being solved. The only risk factor consistently found in the literature is previous injury history (Ekstrand et al., 2011; Goldman & Jones, 2011; Van Beijsterveldt et al., 2013). Other parameters such as strength (Van Dyk et al., 2016, 2017, 2018) and flexibility (Maniar et al., 2016; Witvrouw et al., 2003) have shown an inconsistent or nonexistent association with injury risk. Therefore, the need to establish solid risk factors for HSIs and to understand the physiology behind their occurrence remains.

As for the injury mechanisms, sprinting is often pointed as a causative factor in football (Huygaerts et al., 2020). However, a recent video analysis found an almost equal distribution between sprinting- and stretching-related HSIs, highlighting that the main injury mechanism is more specifically related to high-speed eccentric actions (Gronwald et al., 2022). Another study found that over 70% of HSIs in soccer occur at high or very high horizontal speeds (Jokela et al., 2023). It may therefore be more accurate to say that high-speed movement (rather than sprinting) is the main HSI mechanism in football. Accordingly, it has been reported that players perform up to eight times more accelerations (Schuermans et al., 2017), which present a greater mechanical and metabolic challenge than constant-speed sprinting (Haugen et al., 2014), than sprints per match. Nevertheless, straight sprinting definitely has a great sport-specific relevance; in football, it constitutes the most frequent action before goals are scored for both the scoring and assisting player (Faude et al., 2012), despite accounting for only 1-12% of the distance covered (Di Salvo et al., 2010). Accordingly, repeated sprinting is commonly used to assess multiple aspects of hamstring performance and injury risk (Brocherie et al., 2015; Røksund et al., 2017). As an example, a greater drop in speed (Røksund et al., 2017) and horizontal force production (Lord et al., 2019) was seen in players with HSI history after repeated sprinting. However, repeated

sprinting is a whole-body activity with complex performance and metabolic interactions as well as multiple limiting factors, which may introduce some limitations when using this task as a test for the hamstrings.

The relevance of central motor control of fast movements and associated fatigue for HSIs

Having established on one hand laboratory findings about the neurophysiological basis of high/maximum-speed movement, namely in terms of central nervous system (CNS) demands, and on the other the field-based burden of HSIs in football as well as relevant injury mechanisms, the question arises: how are these two seemingly distant worlds related?

As mentioned earlier, fatigue and high-speed actions are important factors in HSI risk; it is therefore worth exploring what is known about these two factors and how they interact in respect to HSIs in football. Fatigue induced by fast repetitive unresisted movements has an important supraspinal component (Madrid et al., 2018), rather than what is seen in isometric fatigue, which is more related to muscle contractile properties and spinal regulation (Arias et al., 2015). It is worth noting, however, that these findings originated from finger tapping studies, and it remains unclear whether the same pattern would be seen for lower limb movement. As mentioned earlier, sprinting (which can be considered a form of repetitive fast movement) has a significant performance relevance in football and may be performed at MRs of up to 4.6 Hz (Miyashiro et al., 2019), falling comfortably above the threshold associated with continuous EEG activity and feedforward motor control described before, thus requiring more supraspinal resources. This greater resource allocation impacts the available attentional resources, which are already in high demand in football, as the player has to focus on the ball, the field of play, other players, and on their own motor plans. Interestingly, a recent editorial and scoping review reported that decreased neurocognitive ability or increased cognitive load are associated with altered lower limb mechanics and a direct increase in non-contact injury risk (Huddleston et al., 2023; Reyes et al., 2022).

Given its ecological validity, as well as its relevance for football, HSI occurrence, and exercise regulation mechanisms, it is no surprise that repeated sprinting has been used by multiple studies to gain a better understanding of mechanisms that not only are associated with performance but also may explain why some individuals are at greater risk of sustaining HSIs (Brocherie et al., 2015; Ishøi et al., 2020; Røksund et al., 2017). The hamstring rate of torque development (RTD) in the first 100 ms is associated with sprinting performance (Ishøi et al., 2019). A higher contraction speed is a predictor of sprint time (Loturco et al., 2019)

and may contribute to a greater MR, which is the most relevant parameter during the sprint acceleration phase (Maćkała et al., 2015), and as stated earlier, accelerations are far more frequent than sprinting in football. A greater drop in speed (Røksund et al., 2017) and horizontal force production (Lord et al., 2019) was seen in players with HSI history after repeated sprinting.

Repeated sprinting leads to fatigue-related performance decrements. In turn, fatigue is one of the most studied factors regarding sprint-related performance and injuries. Studies of repeated sprint ability (RSA) state that performance decrements start from the first to the third sprint and that these changes have an important supraspinal component (Girard et al., 2011; Goodall et al., 2015; Pinniger et al., 2000). Studies of repeated explosive contractions have shown that fatigue has a greater impact on RTD within the first 50 ms of contraction and that this is due to decreased voluntary activation and neural efficacy (Buckthorpe et al., 2014; Morel et al., 2015).

Given the speed demands and short muscle contraction periods associated with sprinting, intermuscular coordination plays a crucial role (Buckthorpe et al., 2019; Girard et al., 2011). Both agonist and antagonist recruitment speed may be relevant for sprinting performance since their adequate coordination allows for faster accelerations and decelerations (Jaric, 2000; Jarić et al., 1995). The ability to change the recruitment pattern within the hamstrings and synergistic muscles seems to be important to maintain sprinting speed (Edouard et al., 2018). Girard et al. also mention that changes in coordination, namely between the vastus lateralis (VL) and biceps femoris (BF), are a source of power reduction during repeated sprinting (Girard et al., 2011). The ability to maintain rectus femoris (RF) and BF (but not VL) activity amplitude has been correlated with better RSA (Brocherie et al., 2015). Fatigued repeated sprinting also leads to increased hamstring EMG activity duration and earlier cessation of RF activity during the swing phase (Pinniger et al., 2000).

Intermuscular coordination has also been studied in other knee flexion tasks and occasionally in association with HSI history. In submaximal isometric knee flexion tasks, a negative correlation between semitendinosus (ST), BF, and semimembranosus (SM) EMG activity imbalance and the time to fatigue has been found in healthy volunteers (Avrillon et al., 2018). In a similar task, previously injured athletes showed a lower contribution of the injured muscle to the knee flexion moment, which was compensated by a greater contribution of non-injured muscles (Avrillon et al., 2020). On the contrary, in previously injured athletes performing an eccentric knee flexion protocol, Schuermans et al. found a more symmetrical post-task hamstring metabolic activity pattern between the BF and ST on fMRI (Schuermans et al., 2014). The same authors showed that a post-task imbalance

between the BF and ST using the same method is another parameter potentially associated with initial HSI risk (Schuermans et al., 2016). These studies performed in healthy volunteers and injured athletes show that the intermuscular recruitment pattern is affected by HSI but there have been contradictory findings. Moreover, both these groups of authors highlight the importance of further studying the association between hamstring intermuscular coordination pattern and injury risk.

A bilateral difference in hamstring intermuscular coordination has been found in athletes with HSI history, even after completing rehabilitation (Avrillon et al., 2020). The importance of central motor control for high-speed actions is also shown by the fact that motor neuron recruitment speed and maximal MU discharge are the best predictors of contraction speed, and that the neural drive produced in the initial phase of an explosive contraction is predominantly supraspinal (Del Vecchio et al., 2019).

Despite this, information about supraspinal changes in athletes with HSI history is scarce; there have, however, been reports of greater intracortical inhibition in previously injured recreational athletes, which the authors suggested explained the persistent strength deficits even after completing rehabilitation (Buhmann et al., 2022a). The same research group also found lower voluntary activation in athletes with HSI history, which was explained by a decrease in afferent input (Buhmann et al., 2022a). Collectively, these studies point out that central changes may be behind the persistent hamstring strength and activation deficits which contribute to recurrence (Cavaleri et al., 2023; Fyfe et al., 2013). Additionally, Cavaleri et al. found evidence of corticomotor reorganization variability in response to experimentally-induced hamstring pain, with responses ranging from cortical facilitation to depression. This variability was suggested to originate from differences in cortical thickness, kinesiophobia, and exercise history (Cavaleri et al., 2023).

Real or simulated football matches provide another (more ecological) window into the effects of task-specific fatigue on the hamstrings. Grazioli et al. found a greater decrease in hamstrings RTD than on maximal voluntary contraction after a football match (Grazioli et al., 2019), while Nagahara et al. state that football-specific fatigue impairs the maximal sprinting speed rather than horizontal force production (Nagahara et al., 2016). Studies of simulated football matches have found a greater loss in eccentric hamstring torque at higher movement speeds (Greig, 2008; Greig & Siegler, 2009) and in hamstring RTD in the first 25, 50, and 70 ms (Marshall et al., 2014).

On the other hand, Wilmes et al., while concluding that post-match fatigue resulted in a decreased ability of the hamstrings to decelerate the leg (due to greater peak knee

extension angle during sprinting), did not find decreases in knee flexion RTD (Wilmes et al., 2021).

Nevertheless, and despite the presented logical role of supraspinal motor control and of the fatigue seen at this level for HSIs, and also considering the displayed potential mechanisms involved, actual evidence of cortical implications of HSIs is still missing. However, a body of knowledge is starting to be established about the neuroplasticity associated with other musculoskeletal injuries.

Evidence of neuroplasticity in other musculoskeletal injuries

In light of this lack of evidence of cortical adaptations (regardless of them being a cause or a consequence), and in order to further justify looking into this topic, it is beneficial to consider the existing evidence of such changes in other musculoskeletal injuries.

The injury with the greatest amount of evidence is probably anterior cruciate ligament (ACL) rupture and reconstruction. Athletes with ACL rupture have shown a pre-injury decreased connectivity between the left primary sensory cortex and the right posterior lobe of the cerebellum (Diekfuss et al., 2019) as well as neuromechanical de-coupling following ACL reconstruction (An et al., 2019). A previous ACL rupture has also been shown to lead to increased and widespread cortical inhibition, as evaluated by a choice reaction time task (Sherman et al., 2023). In addition to these functional changes, there are also reports of structural cortical changes in multiple motor areas, even years after the injury (Flanagan et al., 2021). In terms of EEG activity, individuals with previous ACL rupture have shown greater EEG power in multiple frequency bands during walking, jogging, and landing tasks (Miao et al., 2017). Higher frontal theta and lower parietal alpha power was also detected after ACL reconstruction in a joint angle reproduction task, indicating altered focused attention and sensorimotor processing (Baumeister et al., 2007).

In chronic low back pain, changes in the location and organization of cortical representations of deep and superficial back muscles have been reported and associated with a reduced motor control of these muscles (Brumagne et al., 2019). Finally, chronic tendinopathy has been associated with an increased cortical inhibition and imbalance between excitatory and inhibitory commands of muscle activation around the painful tendon (Rio et al., 2016). These functional and structural changes may also be relevant to HSIs, since inhibition-excitation and sensorimotor processing mechanisms share a common basis.

Unanswered questions

Considering the presented overview of the literature relevant to the topic, this project aimed to provide answers to remaining questions:

- What is known about the motor control of fast limb movements and how it is affected by fatigue and training? (Chapter II and III)
- Does lower limb motor slowing share the same pattern and physiological mechanisms as those of the upper limb? (Chapters IV and VI)
- Can a maximal speed leg movement task provide insight into central mechanisms of fatigue and performance regulation? (Chapters IV and VI)
- Does such a task cause an impact on maximal and fast force production? (Chapter IV and V)? Can these parameters differentiate footballers with and without HSI history? (Chapter V)
- Can the performance in a non-ecological task designed to challenge central motor control be used to differentiate footballers with and without HSI history? (Chapter V)
- Do footballers with previous HSI show altered brain and muscle activity during such a task compared to their uninjured counterparts? (Chapter V)
- Is finger and knee motor slowing associated? If so, can both MRs differentiate footballers with and without HSI? (Chapter VI)
- Does chronic lower limb training (i.e., in footballers) benefit performance in a lower limb maximum MR task? (Chapters V and VI)
- Does chronic lower limb training affect finger and knee MR performance differently? (Chapter VI)

CHAPTER II – FROM THINKING FAST TO MOVING FAST: MOTOR CONTROL OF FAST LIMB MOVEMENTS IN HEALTHY INDIVIDUALS

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Abstract

The ability to produce high movement speeds is a crucial factor in human motor performance, from the skilled athlete to someone avoiding a fall. Despite this relevance, there remains a lack of both an integrative brain-to-behavior analysis of these movements and applied studies linking the known dependence on open-loop, central control mechanisms of these movements to their real-world implications, whether in the sports, performance arts, or occupational setting. In this review, we cover factors associated with the planning and performance of fast limb movements, from the generation of the motor command in the brain to the observed motor output. At each level (supraspinal, peripheral, and motor output), the influencing factors are presented and the changes brought by training and fatigue are discussed. The existing evidence of more applied studies relevant to practical aspects of human performance is also discussed. Inconsistencies in the existing literature both in the definitions and findings are highlighted, along with suggestions for further studies on the topic of fast limb movement control. The current heterogeneity in what is considered a fast movement and in experimental protocols makes it difficult to compare findings in the existing literature. We identified the role of the cerebellum in movement prediction and of surround inhibition in motor slowing, as well as the effects of fatigue and training on central motor control, as possible avenues for further research, especially in performance-driven populations.

Keywords: feedforward control; electroencephalography; electromyography; motor slowing; movement rate; rhythmic movement

INTRODUCTION

The importance of being able to perform movements at high speeds permeates multiple areas. This is perhaps more obvious in the world of sports. For example, in the Tokyo 2020 Olympic Games, the difference between a gold medal and not reaching the podium in the

100 m male event was 100 ms (International Olympic Committee, 2021); indeed, maximal speed sprinting is a prime example of the importance of fast movement rates, with an average stride rate of 4.6 Hz seen in maximal speed sprinting (Miyashiro et al., 2019). This relevance, however, is also seen in other sports; shoulder internal rotation speeds may reach 7700°/s during a baseball pitch (Matsuo et al., 2001), and a karate punch is executed in under 300 ms (Martinez de Quel and Bennett, 2014; Vences Brito et al., 2011). The relevance of movement speed and rate has also been highlighted in studies performed in competitive settings, especially when the available movement time is limited and contraction times may be as short as 50-250 ms (Aagaard et al., 2002; Boccia et al., 2018; Faude et al., 2012; Maffiuletti et al., 2016), and in injury prevention (Maffiuletti et al., 2016; Morel et al., 2015). Moreover, movement speed is also crucial for other performance-driven populations such as musicians; indeed, piano pieces may require 72 bimanual movements per second (Nolet, 2013; Wadman et al., 1979). Even in everyday life, the ability to move and/or produce force rapidly is crucial for allowing quick adaptations to the environment (Takatoku and Fujiwara, 2014; Wagner and Smith, 2008), such as in preventing falls in the elderly or patient populations (Aagaard et al., 2002; Maffiuletti et al., 2016). Movement speed has also been reported to have broader implications such as in brain myelin integrity (Bartzokis et al., 2010), all-cause mortality risk (Metter et al., 2005), cognitive decline in older adults (Bramell-Risberg et al., 2010), and even an economic relevance – walking and everyday transaction speed is higher in larger and higher income cities (Shadmehr and Ahmed, 2020). Thus, both movement and contraction speed have a major performative, functional, cognitive, and socioeconomic relevance. However, to the best of our knowledge, a review of the factors influencing the control and performance of such movements from the generation of the central command to the observed behavior has not been conducted. Therefore, this review aimed to: 1) provide a brain-to-behavior summary of aspects related to fast limb movement planning and execution; 2) determine current inconsistencies in the findings and definitions present in the relevant literature; and 3) highlight the most relevant aspects and areas of missing research on this topic. It should be noted, however, that this review focuses on human studies and on limb movements, which means that studies on animal models and of saccadic, head, and trunk movements are not within the scope of this review unless no other evidence is available.

The review begins by detailing the regional distribution and patterns of brain activity associated with fast limb movements, as well as its influencing factors, including cranial stimulation, limb dominance, and emotions. To complete this supraspinal overview, specific fatigue and training mechanisms are discussed. The focus then progresses to the peripheral mechanisms, where special attention is given to the triphasic electromyographic (EMG)

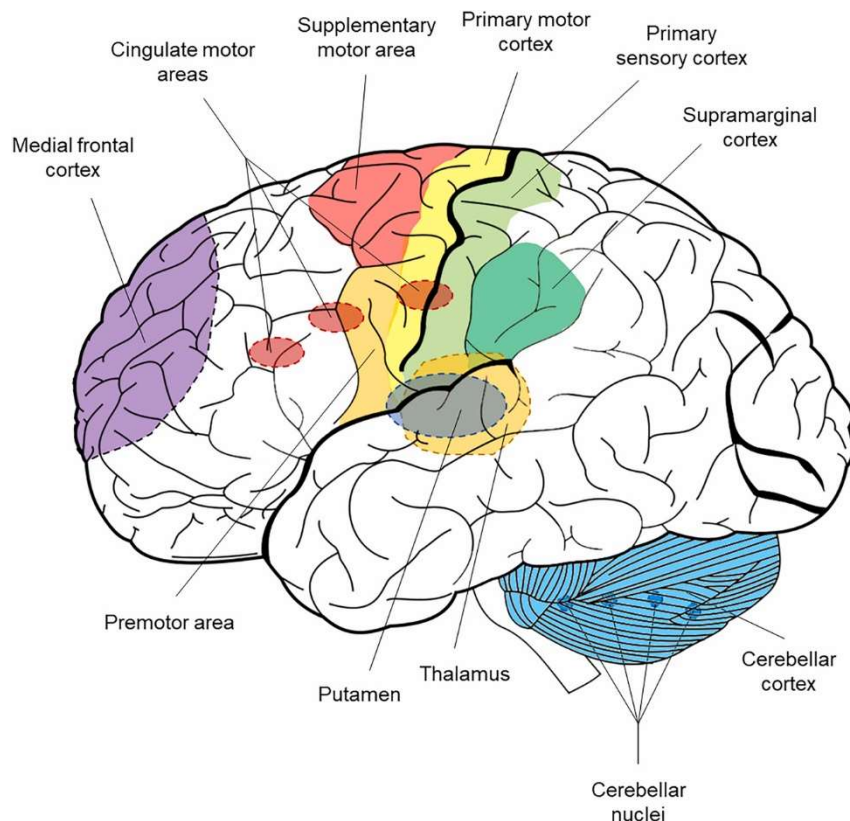
pattern and its modulating factors. The influence of training and fatigue is also analyzed at the peripheral level. Finally, the functional implications of the discussed speed-related motor control features and suggestions for further studies are presented.

CENTRAL FEATURES OF FAST LIMB MOVEMENT CONTROL

Regional distribution of brain activity associated with movement speed

In order to better understand the mechanisms behind the programming and execution of these movements, it is useful to start at the brain regions showing speed-dependent activity, since they constitute the starting point of the descending motor command. Regarding this aspect, most studies have found an increase in brain activity with greater movement rate or speed at different areas such as the primary motor cortex (M1) (Agnew et al., 2004; Ashe and Georgopoulos, 1994; Blinkenberg et al., 1996; Jäncke et al., 1998b; Kawashima et al., 1999; Lutz et al., 2004; Park et al., 2008; Rao et al., 1996; Sadato et al., 1997; Sauvage et al., 2013; Schlaug et al., 1996; Toma et al., 2002), medial frontal area (Toma et al., 2002), premotor cortex (PMC) (Kawashima et al., 1999; Mayville et al., 1999), supplementary motor area (SMA) (Agnew et al., 2004; Jäncke et al., 1998b, 1998a; Mayville et al., 1999; Schlaug et al., 1996), cingulate motor area (Lutz et al., 2004), and cerebellum (Agnew et al., 2004; Lutz et al., 2004; Park et al., 2008; Sadato et al., 1997) and cerebellar nuclei (Lutz et al., 2004). These activity patterns were mostly seen in hand/finger and foot movement rate tasks, since the imaging methods used to assess brain activity do not usually allow large joint movement to be assessed. The topographical distribution of these areas is depicted in Figure 1.

Figure 1. Topographic distribution of areas with speed-mediated activity. A dashed outline indicates areas visible only on a medial section.



Regarding the regions mentioned above, although they have been presented individually, it is essential to realize that they form a network to produce movement, even for primary tasks like single-joint movements or locomotion (Cheng and Gu, 2018; Konoike and Nakamura, 2020). The PMC and SMA are involved in motor planning and sequencing and project to M1, modulating the descending motor command (Herz et al., 2017; Scott, 2004; Tanaka and Kirino, 2017; White and Hall, 2018). In turn, the SMA receives higher-order input from the more rostral cingulate motor areas (Asemi et al., 2015; Loh et al., 2018), as opposed to caudal motor areas, which have greater connections with the motor cortex (Loh et al., 2018). Cingulate motor areas also have descending corticobulbar projections to the brainstem (White and Hall, 2018). Finally, the cerebellum also has multiple connections both at the cortical and basal ganglia levels. Although the exact role of the cerebellum is still a matter of debate, there are bidirectional pathways between the cerebellum and the motor and somatosensory cortices in order to perform a continuous monitoring of movement states (Bastian, 2006; Pisotta and Molinari, 2014; Therrien and Bastian, 2019). The cerebellum also has projections to the thalamus, basal ganglia, and brainstem which are relevant for the

regulation of movement onset/rhythmicity, as well as inhibition of undesired movement (Scott, 2004; White and Hall, 2018).

Increased activity in the contralateral M1 has been seen in terms of hemodynamic magnetic resonance imaging (MRI) response with greater finger movement rates, which can be attributed to the need to generate a stronger command (and activate more motor units at a higher discharge rate) to produce maximum movement speed (Jäncke et al., 1998; Lutz et al., 2004), while the changes seen in the cerebellum and cingulate motor area may be attributable to their role in monitoring movement parameters generated at M1 and to the increased motivation required to execute movements at a higher rate, respectively (Lutz et al., 2004; Park et al., 2008; Therrien and Bastian, 2019). Other factors possibly involved in this increased activity include the greater focus and timing requirements of faster repetitive movements (Jäncke et al., 1998).

Increases in SMA activity were proposed to be related to increased preplanning requirements and the lack of online feedback at higher movement rates in two positron emission tomography finger tapping studies, since this area is known to be associated with task complexity and movement sequencing (Blinkenberg et al., 1996; Kawashima et al., 1999). In addition to the SMA (Jäncke et al., 1998b), other regions in movement preprogramming include the cerebellum (Bastian, 2006; Cheron and Godaux, 1986; MacKinnon and Rothwell, 2000; Therrien and Bastian, 2019), and M1 (MacKinnon and Rothwell, 2000). A further functional division of the SMA between pre-SMA and SMA proper and their separate roles has been highlighted; the pre-SMA and caudal cingulate cortex have increased activity (evaluated by positron emission tomography or functional MRI) at higher movement rates (Deiber et al., 1999; Kawashima et al., 1999) but also at rates lower than the “comfortable” speed (Kawashima et al., 1999). These findings suggest the pre-SMA has a role in the self-generation of parameters such as the movement rate (Deiber et al., 1991; Kawashima et al., 1999), while the SMA proper showed no changes with movement rate, but only with aspects related to movement sequence and cueing (Deiber et al., 1999). A recent review has also highlighted the role of the SMA in controlling internal movement rhythms (Konoike and Nakamura, 2020) through its projections to M1.

Toma et al. (2002) stated that thumb repetitive movements cued by a metronome executed at 3-4 Hz showed continuous electroencephalographic (EEG) activation and coupling at the motor cortices, as opposed to movements performed at up to 1 Hz, where every period of activation was followed by a period of deactivation (Toma et al., 2002). This suggests that the brain does not have time to prepare every individual movement at higher movement rates and that movements are controlled rhythmically (i.e., what is regulated is the inter-

movement interval) rather than individually (each movement controlled independently of the previous and next ones) (Jäncke et al., 1998; Sadato et al., 1997; Toma et al., 2002). It has also been noted that a reversed fast movement pair (e.g., flexion/extension) is centrally preplanned as a single movement (Stancák and Pfurtscheller, 1995; Takatoku and Fujiwara, 2014). Thus, repetitive fast movements join these two properties: they are controlled rhythmically and each reversed movement (e.g., flexion/extension pair) is generated as one entity. This fact becomes especially relevant when thinking of actions characterized by this pattern such as running, and how this control method may influence how we approach motor control research about these movement patterns. The movement tasks involved in most of these studies were finger tapping paradigms, since this task involves less body movement and allows for better data acquisition. Wrist (Deiber et al., 1991; MacKinnon and Rothwell, 2000) and elbow (Takatoku and Fujiwara, 2014) movements were also studied.

In another perspective, an almost continuous reduction in EEG α - (8-12 Hz) and β - (16-20 Hz) band power at the contralateral primary sensorimotor cortex (SM1) and medial frontal area, reflecting greater activation, was also found for faster movements (Toma et al., 2002). Using a similar paradigm, another study found that faster movements were associated with decreased activity at the contralateral SM1; however, this reduction was explained by the fact that a spontaneous transition from syncopated (anti-phase, which is more cognitively demanding) to synchronized (in-phase, less demanding) movement occurred at about 2 Hz, which may have masked the increase in activity caused by the increased movement rate (Mayville et al., 1999). This transition was also associated with a shift in EEG activity from the contralateral SM1 to more frontal areas such as the PMC, SMA, and prefrontal cortex (Mayville et al., 1999). This switch to an in-phase movement pattern with higher rates has been noted by other authors who studied wrist movements when moving a dowel (Van Der Wel et al., 2009) and may arise from the need to preserve processing capacity.

Despite the general pattern of increased brain activity with increased movement rate/speed found in most studies, these increases are not linear within each region or between regions, with some studies failing to find such an association (Marty et al., 2015; Thickbroom et al., 1999). However, the Marty et al. (2015) study analyzed corticokinematic coherence (CKC) during finger flexion and not isolated brain activity per se. Hsu et al. (2018) found increased frontal α -band amplitude modulation frequencies in slow compared to fast finger movement rates, but the slow and fast movement rates used in this study were 0.14 and 1 Hz, respectively (Hsu et al., 2018). This means that the slow rate required a greater cognitive effort to remember the movement interval and that the fast rate was lower than that typically required to elicit a specific control mode (1.5-2 Hz), also falling in the “comfortable” range of

movement rate which has been associated with decreased activity of the pre-SMA and anterior cingulate cortex (Kawashima et al., 1999). The existence of this “comfortable” movement rate has been described by the preferred frequency hypothesis, which states that people tend to move close to the resonance frequency (Van Der Wel et al., 2009), and slower or faster rates would lead to the need for an increased activity pattern. (Kawashima et al., 1999). The fact that greater functional connectivity was found in frontal areas in slow movements supports the greater cognitive demands of slow tasks (Hsu et al., 2018). Similar findings were reported by a previous study from the same research group regarding α - and β -band oscillatory activity (Hsu et al., 2016). Again, the fast movement rate considered by this study (1 Hz) may have originated these findings.

It is interesting to note that imagined movements also show a rate effect on EEG activity. A linear increase in α - and β -band activity was present in both imagined and performed metronome-paced hand clenching movements at rates ranging from 0.5 to 3.5 Hz (Yuan et al., 2010).

Overall, when considering the activity patterns of fast limb movements, two major conclusions arise. First, there is a general trend of increased activation with movement speed across the brain regions involved in preplanning and execution. Second, faster repetitive movements show a separate motor control mechanism in which the motor commands are generated before the start of movement and that have a reduced influence of on-line/peripheral feedback, thus operating in an open-loop fashion. Moreover, the movement rate threshold at which this control strategy is adopted for repetitive movements seems to be situated at 1.5-2 Hz (Jäncke et al., 1998; Mayville et al., 1999; Neilson, 1972; Sadato et al., 1997; Toma et al., 2002). However, some studies consider rates below this threshold as “fast” (Hsu et al., 2016; Hsu et al., 2018), which may be confusing when comparing with other studies using rates above this threshold to classify movements as fast, limiting the possibility of pooling or comparing results.

As stated in the previous paragraphs, there is a threshold separating the adoption of motor control strategies in fast and slow movements. The neural basis of these different strategies can therefore be described by comparing the findings associated with different movement speeds. At finger/hand movement rates below 2 Hz, there is integration of visual and sensory input at the cortical level for each individual movement (Kunesch et al., 1989; Mayville et al., 1999), as well as transient EEG coupling and decoupling between the primary sensory motor and medial frontal cortices (Toma et al., 2002). Conversely, at rates above 2 Hz, M1 activity changes indicate less attentional/conscious control, which is suggestive of a shift to a subcortical predominance in the motor control of high movement rates (Kawashima

et al., 1999; Mayville et al., 1999). Thus, at rates typically above 2 Hz, there is a preattentive and rhythmical control of movement which relies less on peripheral feedback integration (Kunesch et al., 1989; Mayville et al., 1999), as well as no decoupling of EEG motor areas, showing continuous activation and monitoring of movement timing (Toma et al., 2002). Similarly, different cortical and subcortical pathways have been identified in fast and slow adjustments to ongoing movement. In slow adjustments, there are voluntary responses coordinated by a cortical pathway involving the prefrontal and motor cortices. However, in fast adjustments, there is a more automatic response involving projections of subcortical structures such as the superior colliculus, pontine nucleus, and cerebellum to the reticulospinal tract (Potocanac and Duysens, 2017). This mode of control is in line with the putative role of the cerebellum as a movement sensor and in predicting future movement states (Bastian, 2006; Pisotta and Molinari, 2014; Therrien and Bastian, 2019). Nevertheless, it should be stressed that these two modes of control do not suddenly switch between each other; rather, there is likely a continuum that is adjusted according to task demands (Kunesch et al., 1989).

Central activity patterns at the various movement stages

After reviewing the spatial distribution of brain regions with speed-related activity modulation, it is also crucial to understand the temporal distribution of these patterns in respect to movement planning, execution, and recovery. The next sections will describe this distribution in detail.

Movement preprogramming

If fast movements rely mostly on feedforward control and existing internal models, then movement preprogramming is a key aspect for their accurate execution. Indeed, as stated earlier, areas related to movement preprogramming show differentiated activity with movement speed. This central preprogramming of movement parameters has been identified in multiple paradigms of discrete and repeated finger, wrist, elbow, and jumping fast/ballistic movements (Cheron and Godaux, 1986; Jäncke et al., 1998; MacKinnon and Rothwell, 2000; Marsden et al., 1983; Shapiro et al., 2004; van Soest and Bobbert, 1993; Wadman et al., 1979). Evidence for this preprogramming has been provided by findings such as the first agonist burst (AG1) of the triphasic pattern (a sequence of three agonist and antagonist bouts of EMG activity, described later in greater detail) occurring fully before

movement onset (Benecke et al., 1985; Cheron and Godaux, 1986; Del Vecchio et al., 2019; Forgaard et al., 2013; Kudo and Ohtsuki, 1998; Takatoku and Fujiwara, 2010). Additionally, a period after the AG1 burst start ranging from 70 to 100 ms across studies (MacKinnon and Rothwell, 2000; van Soest and Bobbert, 1993; Wadman et al., 1979). has also been proposed to be unaffected by peripheral feedback, given the existence of the electromechanical delay and the latency of even the fastest reflex loop. However, human movements may be performed entirely within this period ranging from the start of the AG1 burst to 100 ms after, which means that some degree of movement parameter encoding must take place before there is time for peripheral feedback to be available. Although an analysis of pathological conditions is not within the scope of this review, studies of elbow and shoulder movements in deafferented patients have also found evidence of pre-coded movement parameters, which lends further support to this idea (Forget and Lamarre, 1987; Palmer et al., 1994; Sanes and Jennings, 1984). Forget and Lamarre, however, noticed that the movement deceleration precision decreased, which suggests that the antagonist burst is influenced by feedback and that the initial movement phase is the most dependent on open-loop mechanisms (Forget and Lamarre, 1987; Gielen et al., 1984).

Nevertheless, as highlighted by Cheron and Godaux, this does not mean that this programming cannot be influenced after its generation (Cheron and Godaux, 1986). Rather, it suggests that the movement preprogramming exerts a more decisive influence in the early phase of fast movements. In a study of fast goal-directed arm movements, inter-stimulus intervals for movement reversal or continuation ≥ 100 ms led to changes in muscle activity pattern (Gielen et al., 1984). Another study of movement inhibition also found that for instructions to stop elbow movements within 100 ms of a go signal, there were no changes in the AG1 burst (Kudo and Ohtsuki, 1998). Both these findings are in line with the previously mentioned period of feedforward motor control dependency.

It has been suggested that the AG1 and antagonist bursts of the triphasic pattern have a different origin. While the AG burst is associated with a descending command from M1, the antagonist burst is hypothesized to originate subcortically in the cerebellum (MacKinnon and Rothwell, 2000). This notion is supported by another study showing that the cerebellum generates a predictive command to be sent to the antagonist muscle by the motor cortex (Vilis and Hore, 1980). This different burst origin and current controversies in the literature will be discussed later in greater detail. Nevertheless, the role of the cerebellum in feedforward motor control has also been highlighted; the cerebellum may participate in feedforward control by providing a command related to the predicted sensorimotor state (forward model) or to the future movement parameters (inverse model) (Bastian, 2006).

Another study also highlighted the role of the cerebellum as a predictive movement sensor, working to improve the accuracy of forward models, namely in their temporal accuracy, which is crucial for fast movements relying on feedforward control (Therrien and Bastian, 2019). Another study argues that both types of control can be carried out by the cerebellum (Wolpert and Kawato, 1998); however, it has been mentioned that the exact parameters predicted by the cerebellum remain unclear (Bastian, 2006).

The main takeaways of movement preprogramming in fast limb movements are therefore that 100 ms from movement onset seems to be the threshold before which planned movement parameters are harder to be affected, with later movement periods being more open to peripheral feedback. Moreover, the role of the cerebellum in predicting movement states should be further explored.

Pre-movement silent periods

Pre-movement silent periods (SPs) are brief intervals of decreased or absent agonist activity shortly before a brisk or ballistic contraction (Arias et al., 2015a; Van Cutsem and Duchateau, 2005). They have been studied under two different perspectives in fast finger repetitive (Arias et al., 2015a; Madrid et al., 2016, 2018) and discrete elbow and ankle (Conrad et al., 1983; Moritani, 1993; Mortimer et al., 1987; Van Cutsem and Duchateau, 2005) movements. In the first case, SPs induced by transcranial (TMS) and cervicomedullary magnetic stimulation have been used to differentiate between spinal and supraspinal fatigue. These studies have consistently shown that the TMS-SP (but not that of cervicomedullary magnetic stimulation) increased after fatiguing fast finger tapping, suggesting the presence of increased M1 inhibition at the corresponding somatotopic area and that repeated fast unresisted movements cause fatigue of intracortical inhibitory but not spinal circuits. As mentioned by the authors of those studies, these findings indicate that cortical and spinal circuits predominate in regulating timing and force, respectively (Arias et al., 2015; Madrid et al., 2018, 2016).

Regarding fast discrete movements, the study of SPs has focused on their pre-movement relevance. In general, it has been found that the existence of a pre-movement SP allows for a non-refractory state to be created and greater synchronization of motor unit recruitment, thus enabling faster force production and contraction speed. This phenomenon has been observed both in upper (Conrad et al., 1983; Moritani, 1993; Mortimer et al., 1987) and lower limb (Van Cutsem and Duchateau, 2005) movements. An associated finding is that the pre-movement SP has been found to increase with movement speed (Conrad et al., 1983;

Moritani, 1993; Mortimer et al., 1987), which highlights its role in allowing for a greater motor unit firing synchronization. The existence of a pre-movement SP in ballistic contractions has been suggested to be due to disfacilitation of motor neurons and supraspinal presynaptic inhibition (Van Cutsem and Duchateau, 2005), since SP latencies are shorter than the time required for postsynaptic spinal interneuronal inhibition (Moritani, 1993). It is also interesting to note that this pre-movement SP is present not only with ballistic movement execution, but also with movement intention (Van Cutsem and Duchateau, 2005), which highlights its central origin and is in line with the changes seen after bouts of repeated fast movements stated above. The main roles of SPs in fast limb movements thus seem to be related to allowing for a greater amount of motor units to be recruited simultaneously and to assist in creating inhibitory patterns to allow for improved execution in repetitive movement.

Event-related changes before, during, and after fast movement execution

Another way of analyzing movement phenomena related to motor control is through studies of changes in EEG oscillatory activity frequency. These changes can be categorized as event-related synchronizations (ERS), characterized by an increase in power in a given frequency band, or desynchronizations (ERD), which correspond to a decrease in band power (Iwane et al., 2019; Pfurtscheller and Lopes da Silva, 1999). Both ERS and ERD thus correspond to time-locked phenomena representing parameters responsible for controlling neural network oscillations (Pfurtscheller and Lopes da Silva, 1999). Given their association with specific events in movement preparation, execution, and recovery, they offer an important window to identifying functionally relevant patterns of brain activity. This functional relevance specific to each change is detailed below.

Studies have focused on ERD/ERS in the β - (Alegre et al., 2002; Gilbertson et al., 2005; Iwane et al., 2019; Ofori et al., 2015; Stancák and Pfurtscheller, 1996a, 1995; Wheaton et al., 2009; Yuan et al., 2010; Zhang et al., 2020), but also in the α - (including mu-rhythm, a spectral peak around 10 Hz associated with motor planning and execution)(Bächinger et al., 2019; Iwane et al., 2019; Ofori et al., 2015; Stancák and Pfurtscheller, 1996b; Yin et al., 2016; Yuan et al., 2010), γ - (30-200 Hz) (Bächinger et al., 2019; Ofori et al., 2015), and θ -band (4-8 Hz)(Ofori et al., 2015) activity. Zhang et al. (2020) found a decrease in β -band EEG power during ballistic finger movements which was accompanied by a greater ERS rebound than in self-paced movements and that this rebound was proportional to movement speed but not to EMG activity. Conversely, there were no differences between ballistic and self-paced finger abduction movements in pre-movement ERD in SM1 (Zhang et al., 2020).

Also using finger movements, an earlier study reported that increased β -band activity and oscillation synchrony at SM1 (signs of ERS) are associated with motor slowing and with difficulties in processing new movements, thus favoring the existing movement state. These authors also state that there may be a period of increased β -band synchrony before movement onset in which the ability to process new movements is impaired (Gilbertson et al., 2005). Also during movement but in a fast repetitive finger flexion-extension task, significant γ - γ and γ - θ coupling was observed within a network composed of the M1, PMC, and SMA. Connectivity differences within this network were also found. While the same band coupling pattern was present from the PMC to both the SMA and M1, feedback from M1 to the other two regions showed different coupling patterns, suggesting the presence of asymmetrical cortical feedback/feedforward connections (Chen et al., 2009; Herz et al., 2012).

The presence and magnitude of β -ERDs have also been studied and compared between fast active and passive wrist and elbow movements (Alegre et al., 2002; Iwane et al., 2019). While passive movement speed showed an association with the contralateral β rebound and ipsilateral mu-ERD, active movements showed a stronger ipsilateral mu- and β -ERD. This increased ipsilateral mu-ERD with increased speed was associated with speed-dependent inhibition. As for the contralateral increase in β rebound, it may be explained by the modulation caused by increased afferent input. Conversely, movement type or speed had no effect on the contralateral mu- and β -ERD (Iwane et al., 2019). In a comparison between ballistic active and passive wrist movements, it was shown that both movement types showed a significant β -ERD recorded at central EEG electrodes at movement onset (more bilateral) and a post-movement β -ERS (more contralateral). The difference between active and passive movements was that the β -ERD started earlier in active movements (1.5 s before movement onset vs. at movement onset) (Alegre et al., 2002). A pre-movement lateral parietal (and less significantly premotor) β -ERD was also seen in another study which required individuals to mentally plan a fast repetitive movement before receiving an order to either execute or suppress it. This ERD slowly increased during the preparation phase and was seen continuously throughout movement duration when the order to move was given, but was only briefly present if an order to suppress movement was given (Wheaton et al., 2009). These findings highlight the role of the parietal cortex in planning and executing but also in suppressing voluntary fast movements.

Stancák and Pfurtscheller analyzed the time course of β -ERDs before, during, and after fast and slow finger movements from EEG electrodes placed over the motor areas bilaterally. A significant contralateral β -ERD was present from 2.0 to 0.5 s before movement regardless of

movement speed, which was suggested to represent a generalized cortical activation to prepare voluntary movement. From 380 ms before to movement onset, β ERD was seen bilaterally (left finger) and contralaterally (right finger). The only speed-related differences found were in the ERD duration and recovery period (Stancák and Pfurtscheller, 1996a). An earlier study by the same authors confirmed that β -rhythm recovered earlier (600-700 ms) after fast movements. This study also found conflicting results compared to the authors' later work in the sense that fast movements led to a significantly higher sensorimotor β -ERD over the left sensorimotor electrodes than slow movements (Stancák and Pfurtscheller, 1995).

Movement-related cortical potentials are another method for detecting time-locked events during different movement phases. In 2-Hz repetitive finger movements, it has been reported that there was a pre-movement movement-related cortical potential peak occurring on average 57 ms before EMG onset originating from M1 and another on average 93 ms after EMG onset originating from the primary sensory cortex (Gerloff et al., 1997). Similarly, motor-related magnetic fields located at the contralateral M1 were found to peak at 37 and 102 ms after EMG onset of finger movements, corresponding to motor and post-movement (with inverse polarity) fields (Gerloff et al., 1998). These three peaks (pre-movement movement-related cortical potential, motor field, and post-movement magnetic fields and movement-related cortical potential) were hypothesized to correspond to stages of precentral motor processing, corticospinal volley generation, and afferent feedback processing (Gerloff et al., 1998; Gerloff et al., 1997). The latter peak is especially relevant since it indicates that afferent feedback is not processed significantly before this period, lending further support to the 100-ms threshold for planned movement parameter irreversibility.

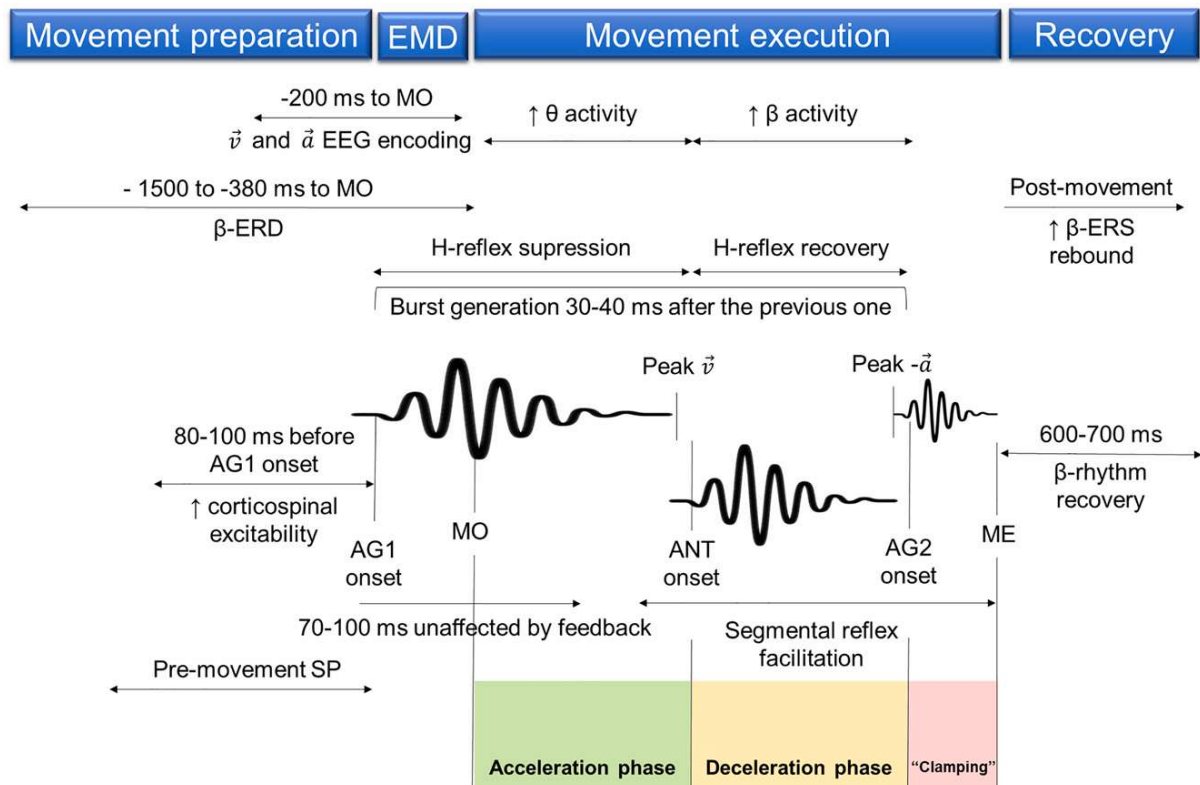
In the α -band, a greater decrease in event-related power synchronization at SM1, but not in the premotor dorsal area or SMA, has been found immediately after a finger tapping motor slowing task compared with a control condition. This power decrease also showed a longer recovery time after the motor slowing task, whereas no changes were seen in β - and γ -band activity (Bächinger et al., 2019). These post-task changes were attributed to the presence of widespread top-down inhibition which recovers gradually after movement is stopped. A study of mu-rhythm changes found no differences in the temporal pattern of sensorimotor ERDs between fast and slow movements. There was, however, a larger premotor ERD associated with movements with increased EMG amplitude (Stancák and Pfurtscheller, 1996b). This phenomenon was attributed to an increased neuronal preactivation at the primary sensory cortex, reflecting the need for increased recruitment.

The most comprehensive analysis of changes in the entire EEG power spectrum during fast movements is possibly the one performed by Ofori et al. (2015), since these authors analyzed changes in a wide range of frequencies during ballistic goal-directed upper limb movements. Increased θ -band activity was found during the acceleration phase in the contralateral motor area, while increased β -band activity in the same region was more evident in the deceleration phase. In the ipsilateral side, a decrease in α - and increase in γ -band activity were seen close to movement termination. These findings highlight the wide range of event-related frequency changes across motor areas during a ballistic movement. The authors suggest that while θ -band activity is associated with the facilitation of sensorimotor processing and thus is more present at the beginning of movement, α -band activity is associated with inhibitory networks, which explains its decreased activity during movement. As for β -band activity, it was hypothesized that the changes seen during movement deceleration were related to its role in motor slowing and in the return to tonic muscle activity (Ofori et al., 2015).

Finally, changes in both EEG α - and β -band activity have also been found in imagined movements, with a linear relationship between (imagined) movement speed and ERD magnitude of central EEG electrodes in a period ranging from 200 ms to 2 s. These changes were most evident in the central electrodes placed over motor areas bilaterally (Yuan et al., 2010).

To summarize these event-related changes, a timeline of the events occurring before, during, and after a typical undisturbed discrete fast limb movement is provided in Figure 2.

Figure 2. Timeline of events in a typical fast discrete limb movement



a, acceleration; AG1, first agonist burst; AG2, second agonist burst; ANT, antagonist burst; EMD, electromechanical delay; ERD, event-related desynchronization; ERS, event-related synchronization. ME, movement end; MO, movement onset; SP, silent period; v , velocity.

Other aspects related to central motor control of fast limb movements

Movement speed, velocity, and acceleration encoding

Thus far, we have outlined which areas mediate the planning and execution of fast movements and described the phenomena associated with each movement stage. However, there are two obvious but crucial issues in the motor control of fast limb movements: how, when, and where are speed, velocity, and acceleration encoded? And how can we find evidence of that encoding? Although different evaluation methods and movement tasks have been used, there is substantial evidence regarding the encoding and regulation of movement speed (non-directional) as well as velocity and acceleration (directional) by the central nervous system (Bradberry et al., 2010; Freund and Büdingen, 1978; Hammer et al., 2016; Iwane et al., 2019; Ofori et al., 2015; Paninski et al., 2004; Shirinbayan et al., 2019;

Turner et al., 2003; Wang et al., 2007; Yang et al., 2015). This evidence has arisen from studies of hand, elbow, and upper limb multijoint movement.

A study found that movement speed and acceleration were encoded in the EEG activity not only during movement execution, but also during planning (i.e., from -200 ms to movement onset) in thumb goal-directed movements at maximum speeds. This encoding was evaluated through event-related changes in α - [region of interest: occipital and parietal-occipital cortices) and β -band (region of interest: frontal and frontal-central lobes)] power. While speed showed similar encoding properties during both phases, peak acceleration showed greater encoding accuracy during movement preparation. Decoding these parameters was therefore more accurate when both phases were considered (Yang et al., 2015). Evidence of speed encoding in brain activity has also been detected even in passive movements in the form of a strong association between contralateral mu- and β -ERD and passive movement speed, which was attributed to the different amounts of afferent input reaching the motor cortex. Ipsilateral mu-ERD was also found to be related to passive movement speed, but this association was attributed to inhibitory processes (Iwane et al., 2019); however, it should be considered that only elbow movement rates up to 2 Hz were used.

Using intracranial EEG, Hammer et al. found a speed encoding peak not only in β -band activity, but also in the high γ band (55-300 Hz) and even reaching frequencies of 600-1000 Hz. These high-frequency power changes were focally located in the PMC. Speed encoding at lower frequencies (<50 Hz) was characterized by a decrease in power, while for higher frequencies (>50 Hz), an increase in power was seen for the fastest speed. These authors also highlight that speed encoding predominated over velocity encoding, indicating that the directional component of speed is less strongly encoded (Hammer et al., 2016). Additionally, it has been found that θ -band power was correlated with both peak acceleration (more strongly) and speed (less strongly), while β -band activity was more prominent during the deceleration phase and was correlated with movement time. These authors also highlight the importance of acceleration encoding in the motor cortex among kinematic parameters (Ofori et al., 2015).

Regarding the spatiotemporal distribution of the contribution to velocity decoding, it has been noted that the PMC and inferior parietal lobule were the greatest sources of information and that this contribution was stronger at 60 ms in the past (Bradberry et al., 2010). A functional MRI study also found a significant correlation between blood oxygen level-dependent activation and wrist movement speed in the contralateral SMA proper and premotor dorsal area. This was also seen in the putamen (bilaterally) and ventroanterior and ventrolateral

thalamic nuclei, highlighting the role of the motor cortico-basal ganglia loop in speed regulation (Shirinbayan et al., 2019). According to an earlier study, in this loop, the SMA and PMC provide input to the putamen, which modulates thalamic activity; the loop is then closed by thalamic projections to SMA and PMC (Alexander and Crutcher, 1990). Further details about the role of this loop, namely in motor slowing, are provided in the supraspinal fatigue section.

Sauvage et al. analyzed areas associated with speed regulation in imagined and executed foot movement sequences using functional MRI and found specific speed-related activation of the supramarginal cortex and cerebellum (anterior vermis, lobules VI-VIII) in both movement types. Conversely, putamen and thalamic activity were only detected during fast movement execution (Sauvage et al., 2013). These authors postulate that the anterior vermis contributes to the speed command in anticipated movements and modulates PMC and supramarginal cortex activity during mental imagery. The increased activity in lobule VIII was explained by the increased necessity of relying on internal models for the execution of fast movements, which, as stated earlier, are less reliant on peripheral input, since this lobule is involved in the central programming of complex movements (Sauvage et al., 2013). Another study also found MRI evidence of the ipsilateral anterior cerebellum's role in speed encoding, but mostly in lobule V, in a wrist flexion/extension task at different speeds. Conversely, the contralateral SMA and putamen activity were not found to be modulated by movement parameters during a wrist flexion task (Stark-Inbar and Dayan, 2017).

Paninski et al. found a diffuse representation of hand velocity encoding within M1 and that individual neurons carry approximately equal small amounts of information. These authors also highlighted that velocity coding is contained in a narrow time window and preceded behavior by about 100 ms (Paninski et al., 2004). In a reaching movement paradigm, Wang et al. also found evidence of simultaneous hand position and velocity encoding and that there was a 122-ms delay between reconstructed and actual velocity (Wang et al., 2007). The delay found in both studies is similar to that previously mentioned where movement parameters are under a greater influence of central preprogramming. It is worth noting, however, that these two studies were performed on non-human primates.

Contrary to most studies, Turner et al. found evidence of reduced SM1 activity in speed encoding. Rather, the strongest effect of speed was noted in the bilateral putamen and ipsilateral cerebellum (Turner et al., 2003). However, the task used in this study was a smooth pursuit tracking task and not a discrete or repetitive movement, which may explain these differences. Nevertheless, studies of region-dependent speed encoding show that a wide range of areas may be involved in this process. This may be due to differences in the

experimental paradigms, individuals' familiarity with the movement being requested, and measurement methods. Still, these differences also constitute evidence of the central nervous system's plasticity in encoding movement speed/velocity and its adaptability to task requirements.

Coherence measures

Coherence measures are used to determine the coupling between two signals in the frequency domain (Bourguignon et al., 2012; Farina et al., 2014). Coherence can thus be analyzed between pairs of signals with the same origin (e.g., EEG-EEG) or with different signal types (e.g., CKC, between brain-derived signals such as EEG or magnetoencephalography and limb kinematics, or corticomuscular coherence, between EEG and EMG). Most studies of coherence measures involving fast movements have focused on CKC during repetitive movements. These studies show a remarkable agreement in the increased CKC at the movement rate and its first harmonic in finger and hand movements (Bourguignon et al., 2011, 2012, 2013; Marty et al., 2015; Piitulainen et al., 2013; Piitulainen et al., 2013). This association has been shown to be maintained in movement rates of 1-3 Hz, showing that it is not exclusive of the fastest movements (Marty et al., 2015). Considering this uniformity, CKC has been highlighted as an indicator of peripheral proprioceptive input to motor-related areas (Bourguignon et al., 2013; Piitulainen et al., 2013). It is worth noting that one of these studies (Bourguignon et al., 2013) found significant CKC (frequency range: 2.5 – 5.5 Hz) in 100% of tested individuals in finger movements at about 3 Hz. This role is further highlighted by the fact that CKC is present even in passive movements with a magnitude similar to that of active movements (Piitulainen et al., 2013).

As for the spatial distribution of coherence sources, existing studies consistently mention the dominant role of the contralateral SM1 (Bourguignon et al., 2011, 2012, 2013; Marty et al., 2015; Piitulainen et al., 2013; Piitulainen et al., 2013). Other regions found to contribute to CKC include the central sulcus and pre-central sulcus (Bourguignon et al., 2013), the ipsilateral SM1, contralateral dorsolateral prefrontal cortex, and contralateral posterior parietal cortex (Bourguignon et al., 2012).

The fact that CKC is strongly correlated with different movement rates and reflects the influence of peripheral input is still compatible with the previously mentioned rhythmic (rather than individual) control seen in faster movement rates. It may be, then, that M1 uses the peripheral input as a measure of inter-movement interval, adjusting the temporal structure of central commands as necessary, and not to compute individual movement parameters.

Although less studied, corticomuscular coherence has also been reported in fast finger and wrist movements (Bourguignon et al., 2013; Conway et al., 2004). A study found that corticomuscular coherence originating from the contralateral M1 was mostly found below 12 Hz in a fast wrist tracking movement paradigm; it was also short-lasting (about 100 ms) and originated early in the movement (Conway et al., 2004). Of note, this period of corticomuscular coherence is similar to that of the predominance of central preprogramming of movement parameters (MacKinnon and Rothwell, 2000; van Soest and Bobbert, 1993; Wadman et al., 1979) and of the delay between velocity encoding and observed behavior (Paninski et al., 2004).

Coherence analyses therefore provide a useful method of determining the functional coupling between central and peripheral areas; however, the tasks used to study this connection have been somewhat limited due to signal quality constraints in more dynamic tasks.

Role of the H-reflex

In comparison with studies evaluating motor evoked potentials (MEPs) and event-related potentials in fast movements, there has been a limited number of studies analyzing the relevant properties of the H-reflex to fast movement control, which may be related to the larger role of spinal circuits in force rather than speed regulation. Nevertheless, in a comparison of H-reflex amplitude in fast wrist movements, MacKinnon and Rothwell found that when a muscle (flexor carpi radialis) was functioning as an agonist (i.e., during wrist flexion), there was a linear relationship between H-reflex amplitude and the preceding EMG agonist burst. However, this relationship was not seen when the same muscle was acting as an antagonist (i.e., during the deceleration phase). The H-reflex therefore followed a pattern of suppression during the AG1 burst and recovery during the antagonist burst. These authors suggested that this points to a subcortical origin of the antagonist burst of the triphasic EMG pattern, with this burst being modulated by peripheral input. It was proposed that cerebellar output may drive the antagonist burst through subcortical pathways (MacKinnon and Rothwell, 2000). Another study proposed that even the AG1 burst may be individual to reflex modification if fast movements are subjected to sufficient perturbation. A random assisting or opposing torque of 8-15 Nm was applied to fast elbow movements, which led to the AG1 onset occurring 25-60 ms earlier with the opposing torque even without cutaneous feedback. Since these changes occurred before 60 ms, they were outside of the

timing of voluntary reactions. These changes were therefore attributed to mechanical and reflex reactions to the perturbation (Adamovich et al., 1997).

Casabona et al. evaluated the Hmax/Mmax ratio of the gastrocnemius and soleus in explosive movement-trained individuals (sprinters and volleyball players) and found that trained individuals had a lower ratio which was driven by a lower Hmax amplitude. These authors state that since the H-reflex is regarded as a measure of small motoneuron (MN) activity, the findings reflect the greater presence of large, fast MNs in the explosive movement-trained population. It is then hypothesized that this difference may not only be purely genetic but also be caused by a training-related change of small, slow MNs into large, fast MNs (Casabona et al., 1990).

FACTORS AFFECTING CENTRAL CONTROL MECHANISMS

After reviewing the mechanisms behind the central control of fast limb movements, it is also important to determine how they can be affected. The next section will therefore cover the existing evidence on extrinsic and intrinsic factors which may influence those mechanisms.

Cranial stimulation

Technological improvements have driven the expansion of cranial stimulation, and its effects on fast movement control and performance are no exception. Different forms of cranial stimulation such as TMS, transcranial direct stimulation, and alternating current stimulation have been used to gain insight on the control mechanisms of fast movements. Jäncke et al. (2004) used repetitive TMS at 1 Hz for 10 min on 3 distinct locations (left M1, cerebellum, and brachial plexus as a control site) in a finger tapping paradigm and found that the right maximum tapping speed decreased only after M1 stimulation, while other locations showed no effect. There was also no effect on the performance of tapping at convenient speeds or on fastest tapping of the left hand. These authors therefore suggested that M1, but not the cerebellum, is directly involved in generating fastest movement speeds and that the effects of stimulation are task- and location-specific; the latter effect has also been found by other studies on this topic (Jäncke et al., 2004; Palmer et al., 1994). However, another study which applied TMS to the cerebellum 50 ms after the cue to perform a ballistic wrist extension task found changes in the EMG pattern associated with the task (discussed later in greater detail) and concluded that the cerebellum is involved in the control of the triphasic pattern, namely in its temporal distribution (Hiraoka et al., 2009). Also in a somewhat opposing view, Wassermann et al. found that TMS at 125% of motor threshold for an average of 204 ms at 1

and 20 Hz led to an increase in maximum finger tapping frequency, but the effect was only significant for the 1-Hz stimulation. This effect, however, was seen regardless of whether stimulation was applied to M1 or 5 cm anterior or posterior. This fact, together with the inhibition of MEPs found in this study, seems contradictory; the authors mention that the increased tapping frequency may have been caused by increased post-stimulus alertness rather than by specific corticospinal modulation (Wassermann et al., 1996).

TMS has also been found to delay fast movement onset in ballistic movement reaction tasks (Day et al., 1989; Meyer and Voss, 2000; Palmer et al., 1994). Meyer and Voss found that when suprathreshold TMS was applied to the ipsilateral M1 at 25-65 ms before finger movement onset, a delay of 40 ms was seen in reaction time. This was explained by the activity of inhibitory interhemispherical networks mediated by the corpus callosum. However, it is interesting to note that the motor command to move was still preserved, although moved later in time (Meyer and Voss, 2000). Irlbacher et al. also found evidence of interhemispheric inhibition in the form of a SP in the EMG pattern with a post-stimulation delay of 30 ms which lasted for a further 30 ms after using TMS on the ipsilateral M1 during a ballistic wrist flexion task (Irlbacher et al., 2006). Similar findings to those of Meyer and Voss were reported by another study where a magnetic stimulus to M1 led to a delay in wrist movement reaction time. This delay averaged 50 ms but was directly proportional both to stimulus intensity, reaching up to 150 ms, and to the time from the auditory cue to the stimulus up to 60 ms (i.e., the longer the interval, the greater the delay) (Day et al., 1989). Also in accordance with Meyer and Voss (Meyer and Voss, 2000), the motor program, as evaluated by the EMG agonist/antagonist pattern, was shifted later in time, but the structure was maintained. The most likely explanation put forth by the authors was that stimulation suppressed the transmission of cortical information, rendering the affected neurons unresponsive (Day et al., 1989). Another study also found evidence of a delay in muscle activity onset in a ballistic shoulder abduction task which was greater when the stimulus was applied just before the burst was expected to occur. Interestingly, these authors found that transcranial stimulation not only delayed the local muscle activity (i.e., ipsilateral deltoid), but also of muscles associated with postural adjustments (i.e., contralateral latissimus dorsi) (Palmer et al., 1994). These findings point to the supraspinal origin of fast movement programs and that these may also include a more global pattern involving postural adjustments (Day et al., 1989; Palmer et al., 1994).

The use of TMS over the contralateral M1 wrist motor hotspot in a ballistic wrist reaction task has been shown to cause a rise in corticospinal excitability as evaluated by changes in the MEP/integrated EMG ratio. In this study, the rise occurred 20-60 ms before the main AG

burst, which is lower than the 80-100 ms period cited by most studies. The authors explained this difference by their trial-by-trial analysis, rather than using the delay from the average of multiple trials (Hortobágyi et al., 2017).

Another aspect related to movement speed which has been found to be modulated by cranial stimulation (in this case, anodal transcranial direct stimulation) is motor slowing (Seidel-Marzi and Ragert, 2020a; Seidel and Ragert, 2019). The authors of these two studies obtained conflicting results. In the earlier study, transcranial direct stimulation applied over the contralateral M1 leg area (at an intensity of 2 mA over 20 min with 30-s up and down ramps at the beginning and end) showed no effect both on reaction time or maximum tapping frequency of the upper and lower extremities (Seidel and Ragert, 2019). In a later study, the same paradigm and transcranial direct stimulation parameters led to decreased motor slowing during a foot (but not hand) maximum rate tapping task. This effect was seen in athletes [both hand- (volleyball players) and foot-dominant (football players)] and non-athletes similarly (Seidel-Marzi and Ragert, 2020a). These findings are in line with previously mentioned studies in the location-specific effects of cranial stimulation (Jäncke et al., 2004; Palmer et al., 1994), but add that the effects on motor slowing do not seem to depend on sporting discipline or history of sports training. The effect of transcranial direct stimulation on motor slowing was hypothesized to be related to increased motor cortex excitability, a prolonged facilitation of corticospinal pathways, and/or improved synergist muscle coupling (Seidel-Marzi and Ragert, 2020a). The first two factors are in line with studies which postulate that the causes of motor slowing of repetitive fast movements are supraspinal and related to the fatigue of the central drive (Bächinger et al., 2019; Rodrigues et al., 2009).

In a somewhat opposing paradigm, Pogosyan et al. found that alternating current stimulation applied at β -range frequencies (20 Hz) was able to slow the maximum reaction speed in a visuomotor joystick manipulation task as evaluated by increased frequency-specific corticomuscular coherence. This decrease was greater with increased initial speeds. These findings point to a causal relationship between increased β -band synchrony and slower movement speeds. This relationship is in line with the proposed role of β -band activity in tonic contractions and its suppression during voluntary movement (Pogosyan et al., 2009).

To summarize, the field of cranial stimulation has been quickly expanding, leading to an increased number of studies. Although there are some more consensual findings, such as in the association between stimulation parameters and movement delays, the location and task specificity of these methods as well as significant differences in experimental paradigms have led to conflicting evidence on the modulation of fast movement control.

Limb dominance and hemispheric specialization

Studies of the effect of lateral dominance on movement speed and rate have focused on brain activity and pathway excitability (Hervé et al., 2005; Jäncke et al., 1998; Park et al., 2008; Stancák and Pfurtscheller, 1996a; Teo et al., 2012b; Yuan et al., 2010) and/or measures of performance (Barut et al., 2013; Brown et al., 2004; Hervé et al., 2005; Nalçaci et al., 2001; Shimoyama, 1990; Teo et al., 2012b; Todor et al., 1982) in finger tapping, wrist, and shoulder movements. Multiple studies have found a greater movement rate or speed in the dominant side (Shimoyama, 1990; Teo et al., 2012a; Todor et al., 1982). However, the complex relationship between hand skill and preference has also been highlighted (Hervé et al., 2005). Non-right handers have shown better tapping scores when the sum of both hands was considered, indicating that they show a greater ability to perform movements at a higher rate with their non-dominant hand compared to right handers. This indicates a left hemisphere specialization for fast movements and movement temporal resolution (Nalçaci et al., 2001). Todor et al. mention that this improved right hand performance may be associated with the superiority of the left hemisphere in terms of temporal movement structuring (Todor et al., 1982). Stancák and Pfurtscheller described inter-hemispherical differences in β -ERD from the motor preparation to the post-movement period in brisk finger movements of left and right fingers. Up to 0.5 seconds before movement, β -ERD was similar regardless of side or movement speed. However, from the start of EMG activity to movement onset ($\approx$ 0.4 to 0 s), β -ERD was seen bilaterally for left-hand movements but only unilaterally for right hand movement. This was suggested to be due to a lower ability of the right M1 to activate or inhibit the homotopic M1 area. During and after brisk movements, there was a predominance of EEG-evaluated β -ERD at anterior electrodes regardless of movement side; however, in the left hemisphere, this was more located at the posterior electrodes (Stancák and Pfurtscheller, 1996a). Another study found that while movement speed encoding was detected in both hemispheres for both left and right hand movements, changes in α - and β -band activity were greater in the contralateral hemisphere and not related to movement speed (Yuan et al., 2010). Park et al. found higher contralateral (left) SM1 and bilateral cerebellar activation at faster (subsecond) movement speeds. However, changes in the contralateral (left) cerebellum were only significant for right hand movements, which was attributed to the increased contribution of the ipsilateral (right) cerebellum at higher speeds (speed-dependent modulation) due to the increased coordination demands (Park et al., 2008). Differences in anatomical inter-hemispheric asymmetries relevant to the performance of fast movements have also been identified between right- and left-handed individuals. In

right-handed individuals, the amount of left central sulcus grey matter was positively associated with right hand speed, while in left-handed individuals, there was a positive relationship between right central sulcus grey matter amount and right hand speed. This finding also points to a greater specialization of fast movements in the left hemisphere of right-handers as evidenced by the amount of grey matter in the SM1, while in left handers this association shows greater variability or is even reversed (Hervé et al., 2005). A greater left side movement variability was also found in an earlier study (Todor et al., 1982). This variability has also been shown to differ between sides; changes in the intertapping interval with time at maximum voluntary rate have shown a biphasic and linear pattern for right and left finger movements, respectively (Barut et al., 2013)

Agnew et al. also found evidence of a left hemisphere specialization in movement rate modulation through a corticostriatal pathway involving the left PMC, thalamus, and putamen with right hand movements, while the opposite was not seen for left hand movements (Agnew et al., 2004). These findings are supported by findings of a greater correlation between the activity of left motor and premotor areas and foot movement rate (Sauvage et al., 2013). The authors of the latter study suggest that there is a specialization of the left corticostriatal pathway in controlling movement rate in comparison with the right side. Therefore, the left hemisphere assists in controlling speed in movement of both sides.

The effect of limb dominance on fast movement control thus seems to show a left hemisphere specialization, as seen by measures of movement speed and variability. Nevertheless, the dominant side still seems to show a relative superiority in movement rate, even considering the complex interplay between sides and asymmetrical central control mechanisms.

Role of emotion

Although frequently overlooked in the training and performance settings, emotion has been shown to play a role in the execution of fast movements. A recent study found that a negative emotional state induced by a set of neutral or negative images led to decreased movement speed in a key-pressing task (Li et al., 2019). This negative state was associated with a larger P1 amplitude and θ oscillation at the occipital and temporal cortices and a lower late contingent negative variation; the influence of negative emotions was therefore more evident in the late movement preparation phase. The slower movement caused by negative emotions was explained by the additional resources required for their processing compared to neutral stimuli (Li et al., 2019). As mentioned earlier, fast movements are associated with

increased brain activity (Blinkenberg et al., 1996; Jäncke et al., 1998) and there are common pathways between emotional and motor processing (Groenewegen and Trimble, 2007; Stoodley and Schmahmann, 2010). One of such relevant regions is the striatum, which is involved in controlling movement rate (Agnew et al., 2004; Sauvage et al., 2013). Negative emotions have also been shown to play a role in M1 plasticity by intracortical GABAergic pathway modulation (Koganemaru et al., 2012), which plays a role in motor slowing (Arias et al., 2015a; Bächinger et al., 2019; Madrid et al., 2018). These circuits' excitability has also been shown to play a role in the control of fast movements. A similar effect was also found on overall reaction times: negative stimuli led to longer overall reaction times (both in the reaction and movement time components) than positive or neutral ones in a key-pressing task with the dominant hand. These findings suggest that a negative emotional state influences both movement preparation and execution. These results were also explained based on the additional resources dedicated to emotional over motor processing (Hälbjerg et al., 2011).

Although the two previous studies analyzed the effect of negative emotions, they did not include anger. Despite being a negative emotion, anger has effects on the arousal/motivation level, which may lead to different results. Indeed, it has been reported that the arousal caused by a startle versus a tone cue was associated with a faster movement time, EMG rise time, and a steeper EMG gradient in a bimanual isometric wrist and finger extension task (Coombes et al., 2007). Given the importance of the centrally-generated drive on these EMG parameters (Del Vecchio et al., 2019), these changes may represent central processes associated with emotional processing. Additionally, anger and happiness were both found to be positively associated with the performance of explosive movements such as a countermovement jump and ball throwing (Rathsclag and Memmert, 2013). However, these authors did not provide brain activity correlates associated with these findings. Nevertheless, an important point raised by that study is the specific effect of each emotion's action tendency (e.g., lashing out for anger) on tasks with similar features such as a countermovement jump or ball throwing (Rathsclag and Memmert, 2013). Regarding this matter, another study found that negative stimuli led to faster reactions, which may be associated with the avoiding tendency induced by the negative images (Coombes et al., 2007). The separate influence of emotional valence (appetitive or defensive) and intensity (arousal level) was analyzed, and it was found that reaction times were faster and force amplitude and MEPs elicited by TMS were greater after exposure to negative images and reacting through ballistic wrist and finger extension. These authors concluded that movement speed and force production were related to the emotional valence, while the level of arousal was associated with corticospinal excitability (Coombes et al., 2009).

Another aspect associated with the role of emotion on movement speed is the concept of movement vigor. This can be thought of as a measure of the value we attribute to a movement target and results of an interaction between the desire to obtain a reward sooner and the higher effort required by higher speeds (Shadmehr and Ahmed, 2020; Summerside et al., 2018). It has been shown that the perception of reward and effort can influence individuals' decision-making regarding movement speed. Interestingly, associations were found between the will to exert effort and neural circuits. The same authors also mention that this willingness is highly individual and may even be seen as a personality trait (Reppert et al., 2018). This particularity is a matter of interest since the affected neural circuits are also involved in motor control, resulting in impairments in peak velocity (Da Silva et al., 2018). In other words, the brain's evaluation of reward, effort, and time directly impacts vigor (Reppert et al., 2018). Recently, it was reported that constant and increasing rewards are associated with less (Shadmehr et al., 2016) and greater (Summerside et al., 2018) vigor, respectively. In terms of limb movement output, increased vigor can be observed through changes in reaction and movement time, showing that it modulates both movement onset and duration. Therefore, movement speed is not only a function of economy of effort, as thought in older models of motor control; instead, the expected reward may override the importance of economy (Summerside et al., 2018). The neural basis of how this perceived reward determines vigor and consequently influences limb movement speed has also been identified and involves a network including the striatum, globus pallidus internus, and the thalamus (Reppert et al., 2018; Shadmehr et al., 2016). Different types of striatal medium spiny neurons activate the direct and indirect basal ganglia pathways. These pathways are described in greater detail in the next section; nevertheless, activation of the direct and indirect pathways are purported to increase and decrease movement vigor, respectively (Shadmehr et al., 2016). In turn, the response of striatal neurons to cortical input (and consequently their output to other structures in the basal ganglia) are modulated by dopamine and serotonin concentrations (Reppert et al., 2018; Shadmehr and Ahmed, 2021).

To summarize, current evidence shows that both the emotional state and our perception/expectation of reward influence movement speed. This may have an underexplored relevance in high-pressure, stressful, or emotional performance settings as well as an impact on the field of neuroeconomics.

Central effects of training and fatigue

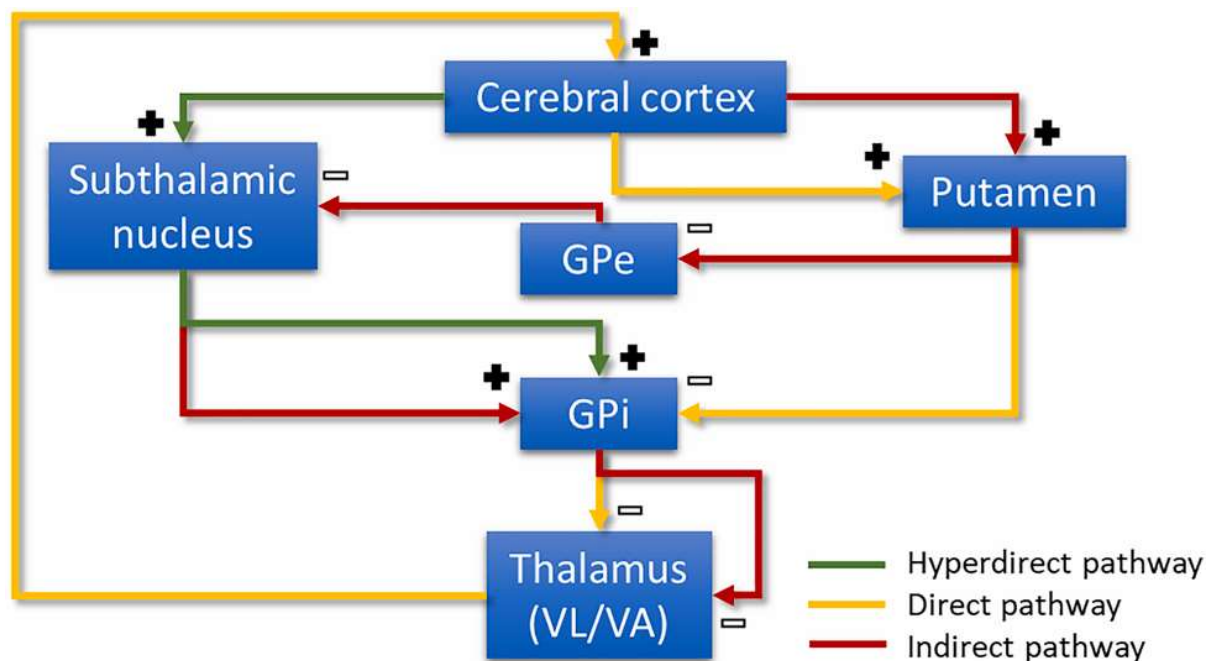
Supraspinal fatigue after repetitive fast movements

Various studies have pointed to a supraspinal origin of fatigue during repetitive movements performed near or at maximum voluntary rate (Arias et al., 2015a; Arias et al., 2012; Bächinger et al., 2019; Madrid et al., 2016; Rodrigues et al., 2009). Madrid et al. found that a decrease in movement rate in a finger tapping task was accompanied by an increased post-task SP during maximum voluntary contraction if induced by transcranial but not cervical stimulation, indicating a supraspinal origin of this fatigue. This study also found similarly increased spinal excitability after 10 and 30 s of finger tapping but different decreases in movement rate, which led the authors to conclude that spinal excitability is not a marker of fatigue in maximum voluntary rate tasks, differently from what is seen in maximal isometric tests (Madrid et al., 2016). Similar findings regarding TMS- and cervicomedullary magnetic stimulation-induced SPs were also found in another study after a short period of finger tapping at maximum voluntary rate. The authors posited that since the TMS-SP originates from inhibitory cortical interneurons which project to the corticospinal tract, the fatigue seen after the finger tapping task had a supraspinal origin (Arias et al., 2015a).

Motor surround inhibition

The concept of center-surround inhibition (SI) was originally proposed for the sensory system, but it has also been demonstrated to be present in the motor system, where it is characterized by a decrease in excitability in motor areas surrounding that corresponding to the intended motor program, thus facilitating selective movement execution (Beck and Hallett, 2011; Sohn and Hallett, 2004). This phenomenon is governed by corticobasal networks which comprise the hyperdirect, direct, and indirect pathways (Figure 3).

Figure 3. Representation of the hyperdirect, direct, and indirect pathways



GPe, globus pallidus externus; GPi, globus pallidus internus; VA, ventroanterior; VL, ventrolateral.

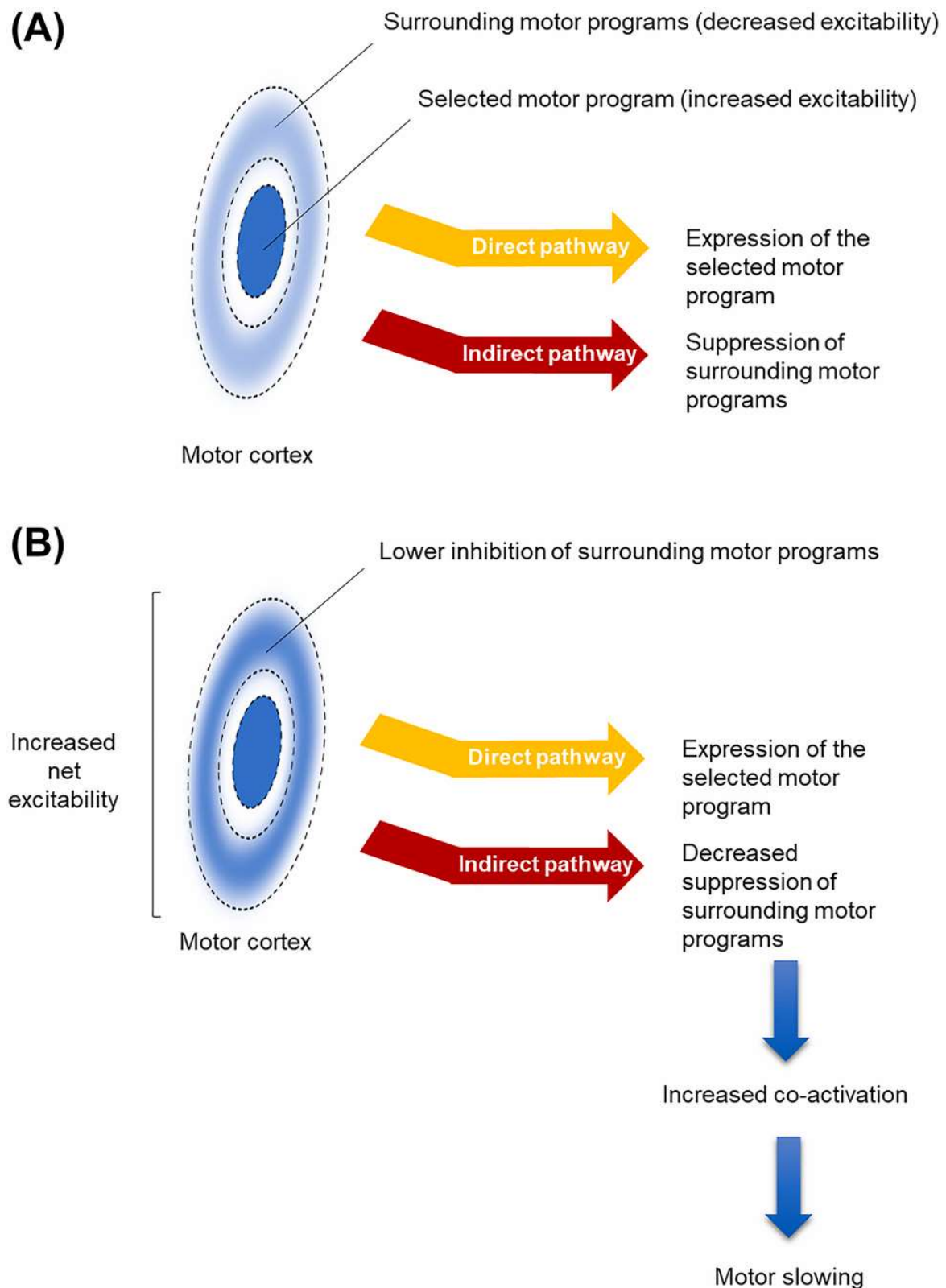
Adapted from White and Hall (2018) and Jahanshahi et al. (2015).

Each of these pathways has a distinct functional significance to the occurrence of SI. When a motor command is produced, the hyperdirect pathway produces a suppression of both the selected and surrounding programs through the inhibition of thalamic areas by the globus pallidus internus. Subsequently, the expression of only the desired motor program is promoted by the disinhibition of the intended motor areas caused by pallidal neurons in the direct pathway. Finally, the indirect pathway reinforces the suppression of competing motor programs by excitatory inputs from the subthalamic nucleus to the globus pallidus internus (Beck and Hallett, 2011; Jahanshahi et al., 2015; Nambu et al., 2002; White and Hall, 2018).

However, the motor slowing caused by repetitive movement is associated with a breakdown of SI at M1 induced by motor fatigability (Figure 4) (Bächinger et al., 2019). While normally SI suppresses competing motor programs through the pathways described above and allows for fluid movement patterns (A), in a fatigued state, the cortical net excitability increases as a result of the decreased inhibition of surrounding motor programs (B), leading to decreased movement efficiency and motor slowing. It is important to stress, though, that even in the situation seen in (A), there is not a complete inhibition of the surrounding motor programs, nor are they completely expressed in (B). Rather, there is just a decrease in their inhibition (Sohn and Hallett, 2004). Despite there being unclear aspects about the generation of motor

SI, current evidence supports its supraspinal origin (Beck and Hallett, 2011; Sohn and Hallett, 2004). Sohn and Hallett found decreased little finger MEPs during voluntary movements of regions with reduced cortical connections such as the leg and mouth, despite the increase in spinal excitability. This led the authors to conclude that SI may be mediated by subcortical and not intracortical networks (Sohn and Hallett, 2004). Nevertheless, it is still present and detected at the motor cortex (Bächinger et al., 2019; Beck and Hallett, 2011). This has been demonstrated as the origin of the motor slowing in fast repetitive movements by Bächinger et al. These authors found an increase in net cortical excitability associated with motor slowing which was caused by a gradual breakdown of SI at M1, leading to a broader activation of neurons encoding movement direction and consequently to a less efficient and precise descending motor command. It is worth noting that this phenomenon was observed in repetitive movements of different body regions, which points to its generalized nature (Bächinger et al., 2019). Despite this feature, the exact mechanisms of motor SI generation, including the relative involvement of cortical and subcortical pathways, remain a matter of debate (Beck and Hallett, 2011; White and Hall, 2018).

Figure 4. Loss of surround inhibition with repetitive fast movement performance



(A) Presence of surround inhibition in a rested state; (B) Breakdown of surround inhibition with fatigue.

Alternative supraspinal fatigue mechanisms

Adding to the debate on the SI generation and its role on motor slowing, alternative fatigue mechanisms have been proposed. Signs of post-exercise potentiation, but not of fatigue of M1 or corticospinal motor neurons, have been found after a fast finger tapping task despite the decrease in movement rate. These authors hypothesized that the fatigue generated may have had a very fast recovery period not detectable by the experimental setup and that peripheral factors such as changes in the contraction-relaxation cycle, a longer relaxation time, or limitations associated with adenosine triphosphate resynthesis times may have played a role (Arias et al., 2012).

Rodrigues et al. (2009) suggested that the performance deterioration seen in finger tapping at maximum voluntary rate is a result of a breakdown of central motor control due to the demands imposed on cortical and subcortical structures by this task. Indeed, these authors suggest that both fatigue of the central command to flex and extend and of the command to switch between movement directions occurs (Rodrigues et al., 2009). Interestingly, another study showed that this breakdown can be attenuated even by short-term training and M1 neuromodulation, thus allowing for the maximum voluntary rate to be maintained for a longer period (Teo et al., 2012b). Finally, Zanette et al. (1995) monitored recovery through changes in MEPs every 5 min after 1 min of thumb abduction-adduction at the maximum voluntary rate and found three distinct stages of MEP amplitude. First, there was a 5-min quick depression phase, which was then followed by a 10-min phase of maximal depression. Finally, a slow recovery phase was observed until the end of the experiment (35 min). There was also a lack of changes in M and F waves, indicating the supraspinal origin of these changes. Further evidence of this origin was found through a 40% reduction in the motor representation area sites evoking a motor response. These authors proposed that a transitory reduction in motor representation was caused by intracortical presynaptic modulation, which would be associated with decreased cortical excitability during repeated thumb abduction (Zanette et al., 1995) and is somewhat contradictory to some of the previously mentioned findings regarding central markers of fatigue induced by fast repetitive movements (Bächinger et al., 2019).

Training effects

In this section, we will cover the effects of both acute (i.e., practicing a specific task over a short period for a specific study) and chronic (i.e., prolonged practice associated with professional routines which involve fast limb movements) training on supraspinal/central measures.

Studies of trained populations who routinely perform fast/explosive movements, such as elite volleyball attackers (Tyč et al., 2005) and badminton players (Pearce et al., 2000), provide a window to the effects of continued training at the supraspinal level. Both these studies used TMS to determine the functional reorganization of the motor cortex. In elite badminton players, there was a lateral shift of the cortical hand motor representation area as well as decreased cortical excitability compared to social players (Pearce et al., 2000). Similar findings were present in volleyball players, where a larger representation of the proximal medial deltoid and a greater overlap of proximal and distal muscles were found compared to runners (Tyč et al., 2005).

Training has also been found to lead to changes in pre-movement inhibitory patterns. After a short practice of a ballistic thumb abduction task, healthy subjects showed improvements in maximum acceleration which were associated with a steeper and closer to movement onset release of cortical inhibition. This was measured through the period of short-interval cortical inhibition induced by paired pulse TMS over the adductor pollicis brevis M1 hotspot. Performance improvements were associated with decreased GABAergic release immediately before movement, showing the role of its modulation on motor performance (Dupont-Hadwen et al., 2019). A similar training task led to an association between increased acceleration and increased MEP facilitation and corticomotor excitability in young but not older individuals (Rogasch et al., 2009). Changes in preparatory activity have also been evaluated using functional MRI. Training a maximum speed sequential finger tapping task induced an increase in preparatory activity within a cortical network comprising the bilateral inferior parietal lobule, anterior intraparietal sulcus, and contralateral M1 (Hamano et al., 2021).

PERIPHERAL FEATURES OF FAST LIMB MOVEMENT CONTROL

In the sections above, the central mechanisms behind the motor control of fast limb movements were reviewed. Following in the brain-to-behavior pathway of this review, the patterns of muscle activity associated with these movements will be discussed, focusing on the triphasic pattern, its modulating factors, and the effect of fatigue on a peripheral level.

The triphasic pattern

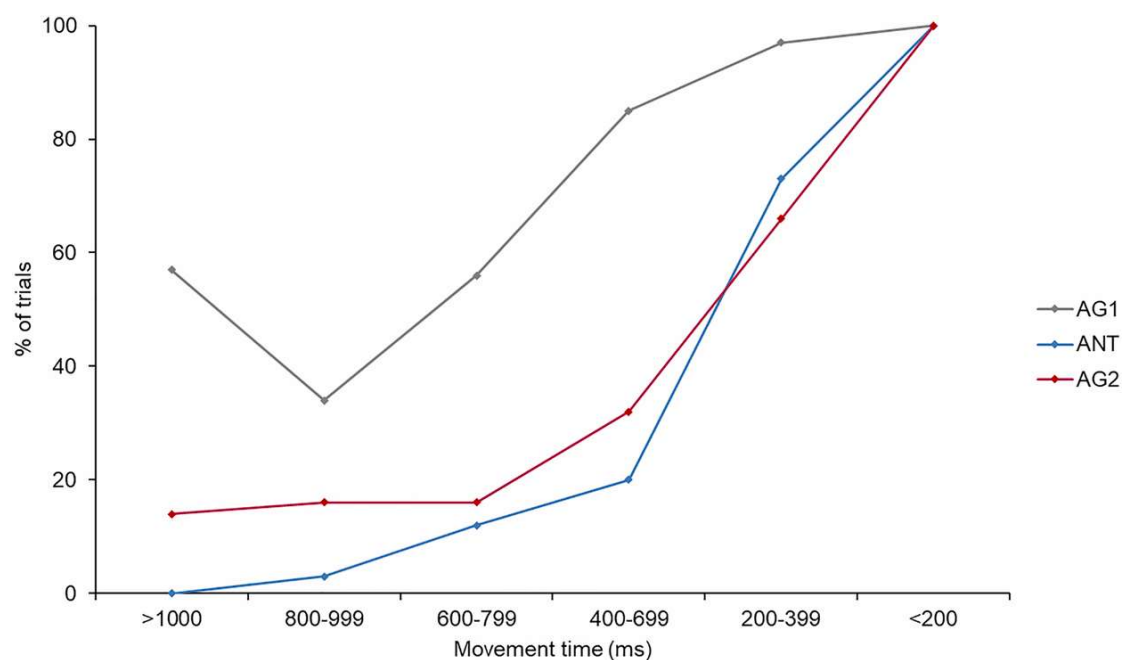
The most widely studied peripheral phenomenon associated with fast movement execution is undoubtedly the triphasic EMG pattern. Generally speaking, this pattern is composed of

three sequential bursts of EMG activity interspersed by periods of EMG silence and is mostly seen in fast movements. First, there is an initial agonist burst to start the desired movement. Then, there is an increase in antagonist muscle(s) activity in order to provide a braking force when approaching the movement target. Finally, another smaller agonist burst is present to fine-tune the final movement position (Brown and Cooke, 1981; Cheron et al., 2007; Mustard and Lee, 1987). This pattern was first identified by Wachholder and Altenburger in 1926 (Wachholder and Altenburger, 1926) and has since been extensively analyzed under different perspectives such as its origin/function (Berardelli et al., 1996; Bullock and Grossberg, 1992; Cooke and Brown, 1990; Day et al., 1989; Del Vecchio et al., 2019; Forget and Lamarre, 1987; Gielen et al., 1984; Hortobágyi et al., 2017; Irlbacher et al., 2006; Kudo and Ohtsuki, 1998; MacKinnon and Rothwell, 2000; Palmer et al., 1994a; Takatoku and Fujiwara, 2014) and timing/coordination (Adamovich et al., 1997; Corcos et al., 2002; Day et al., 1989; Gielen et al., 1984; Hortobágyi et al., 2017; Irlbacher et al., 2006; Jarić et al., 1995; Kudo and Ohtsuki, 1998; MacKinnon and Rothwell, 2000; Takatoku and Fujiwara, 2014; Zehr and Sale, 1994). The influence of factors such as segment inertia (Benecke et al., 1985; Cheron and Godaux, 1986; Latash, 1994; Marsden et al., 1983; Mustard and Lee, 1987; Pfann et al., 1998; Shapiro et al., 2004; Sherwood et al., 1988), movement amplitude/distance (Benecke et al., 1985; Brown and Cooke, 1981; Cheron and Godaux, 1986; Corcos et al., 1988; Freund and Büdingen, 1978; Marsden et al., 1983; Mustard and Lee, 1987; Pfann et al., 1998; Takatoku and Fujiwara, 2010; Yamazaki et al., 1995), movement intent (Benecke et al., 1985; Kudo and Ohtsuki, 1998; Takatoku and Fujiwara, 2010), and fatigue (Bächinger et al., 2019; Corcos et al., 2002; Rodrigues et al., 2009) has also been reported. These studies have included tasks such as finger tapping, elbow flexion/extension, wrist flexion/extension, and ankle dorsiflexion. These factors are discussed in detail below.

As highlighted earlier, this pattern has been known to be present during fast movements even in deafferented individuals (Forget and Lamarre, 1987; Palmer et al., 1994; Sanes and Jennings, 1984). Its universal nature has also been noted through its detection in both isotonic and isometric wrist and elbow actions (Gordon and Ghez, 1984; Sanes and Jennings, 1984) and through its continuous presence throughout the lifespan (Rich, 1990). However, the detection of this pattern has two requirements: a high movement speed and the presence of active deceleration (Forget and Lamarre, 1987). Regarding the speed requirement, it has been shown in an elbow flexion task that slower movements are characterized only by continuous agonist activity (Brown and Gilleard, 1991; Mustard and Lee, 1987) since the muscles' viscoelastic properties provide a sufficient braking stimulus (Jarić et al., 1998), while other studies have proposed movement times at which this pattern

is more likely to be present (Figure 5) (Hallett and Marsden, 1979; Sanes and Jennings, 1984). Active deceleration is also required so that the antagonist burst is generated; in addition to the lack of antagonist activity in slower movements highlighted previously, it has been shown that in upper limb movements that are planned without an intent to stop and are halted mechanically, the antagonist burst is not present or is extremely reduced (Wadman et al., 1979).

Figure 5. Percentage of trials in which each of the EMG bursts are present according to movement time



AG1, first agonist burst; ANT, antagonist burst; AG2, second agonist burst;. Constructed with data from Brown and Gilleard (1991).

Origin and generation

To better understand this pattern, it is relevant to provide its characterization and the function of each of its components. Hannaford and Stark termed the AG1, antagonist, and second agonist burst (AG2) bursts as action, braking, and clamping pulses (Hannaford and Stark, 1985), respectively, providing a functional nomenclature. This nomenclature has since been adopted by other researchers (Cheron et al., 2007; Forgaard et al., 2013). As will be detailed in the following sections, these bursts can be modulated by task, muscle, and joint

constraints. Nevertheless, in fast goal-directed movements, the AG1 burst can be thought of being responsible for the acceleration stimulus, the antagonist burst as the agent of deceleration/braking when approaching a target, and the AG2 as responsible for fine-tuning the final position at the desired target whether single- or multi-joint upper limb movements are performed (Berardelli et al., 1996; Brown and Gilleard, 1991; Cheron et al., 2007; Cooke and Brown, 1990; Hannaford and Stark, 1985; Irlbacher et al., 2006; Roy et al., 1988; Wadman et al., 1979; Wierzbicka et al., 1986; Wierzbicka and Wiegner, 1992). The AG1 burst duration has been proposed to determine movement time (Benecke et al., 1985; Cooke and Brown, 1990; Sherwood, 2008) and the regulation of movement speed has been associated with the early (30 ms) period of AG1 activity (Corcos et al., 1989). However, as mentioned later in the intermuscular coordination section, the antagonist burst may also contribute to decrease movement time (Wierzbicka et al., 1986; Wierzbicka and Wiegner, 1992).

As stated earlier, a reduced movement time is a requirement for the emergence of the triphasic pattern. It has been shown that this pattern develops systematically as movement time is progressively reduced (Figure 5) rather than suddenly switched on at a determined movement time threshold. Notably, all three bursts were always found with movement times <200 ms (Brown and Gilleard, 1991). This is in line with the proposed movement time requirement of 250 ms proposed by Hallett and Marsden (Hallett and Marsden, 1979).

Another aspect relevant for the appearance of the triphasic pattern is acceleration; it was reported that in isometric contractions, peak torque must be reached within 100 ms for all the bursts to appear (Sanes and Jennings, 1984). Another study also found that when an AG1 burst was present, it had an average duration of 189 ms. The antagonist burst duration, however, decreased as a function of movement time (Brown and Gilleard, 1991). It is interesting to note that these authors found two different functions of the AG2 burst depending on movement time. In slower movement times, this burst occurred before the end of movement and therefore contributed to propel the limb to the target position. Conversely, in faster movement times, the AG2 burst occurred when reaching the target, acting to stabilize the limb at the target position (Brown and Gilleard, 1991).

The central origin of the triphasic pattern has been proposed by various earlier studies (Day et al., 1989; Desmedt and Godaux, 1977; Forget and Lamarre, 1987; Hallett and Marsden, 1979; Mustard and Lee, 1987; Sanes and Jennings, 1984; Wadman et al., 1979) using fast wrist and elbow movement tasks. A more recent study found an increase in the MEP:integrated EMG ratio using sub-threshold, low-intensity TMS in a fast wrist extension

task, which also suggests a cortical origin of the pre-burst increased excitability (Hortobágyi et al., 2017).

The triphasic pattern have been reported to be executed serially, since interfering with one burst affected the subsequent ones, and generated within 30-40 ms of the preceding one. This was found due to the induction of SPs at various times during the triphasic pattern using TMS (Irlbacher et al., 2006). The same authors, along with others, argue that in addition to the more consensual involvement of the motor cortex in the AG1 burst (Day et al., 1989; Irlbacher et al., 2006; Liang et al., 2008), the presence of interhemispheric inhibition detected by their paradigm in all phases of the triphasic pattern means that the motor cortex is also involved in the antagonist and AG2 bursts. A study of changes in the triphasic pattern of ballistic wrist flexion movements with practice showed a close relationship between the firing patterns of AG1 and AG2, also pointing to a similar cortical origin (Liang et al., 2008). Conversely, as mentioned earlier, MacKinnon and Rothwell (2000) reported that TMS to the contralateral motor cortex led to increased excitability before AG1 but not before antagonist, suggesting that the antagonist burst has a different (subcortical) origin. However, a later study proposed a reconciliation between these two views by suggesting that tonic cortical activity allows for maintaining the excitability of subcortical pathways that generate the antagonist burst (Irlbacher et al., 2006).

The cerebellum has also been found to (partially) influence the triphasic pattern in a study which used TMS 50 ms before ballistic wrist extension and found a significant decrease in AG1 latency and increased antagonist activity. This was explained by changes in cerebellar excitability, which in turn led to a faster rise in cortical excitability and the smaller AG1 latency. On the contrary, the increased antagonist activity was proposed to be caused by a modification of the motor program rather than changes in cortical excitability in a ballistic wrist extension task (Hiraoka et al., 2009). These two mechanisms of action are in line with the previously described distinct origin of the AG1 and antagonist bursts proposed by MacKinnon and Rothwell (2000). Another study provided further evidence to conciliate the ideas of serial burst execution and independent programming of the AG1 relatively to the antagonist and AG2 bursts. Using an acoustic startle at AG1 onset, the antagonist and AG2 bursts were elicited earlier in short movements, while in longer movements the same stimulus did not lead to changes in the EMG pattern in fast elbow extension. These findings led the authors to conclude that the two later bursts (antagonist and AG2) may be independently programmed and not fully defined before movement onset (Forgaard et al., 2013).

As previously mentioned, the triphasic pattern has also been seen in isometric tasks (Gordon and Ghez, 1984; Sanes and Jennings, 1984) and in deafferented individuals, although with varying changes in timing and amplitude (Forget and Lamarre, 1987; Palmer et al., 1994; Sanes and Jennings, 1984). Both these findings support the notion that somesthetic and muscle spindle input are not essential for the pattern generation but contribute to the fine tuning of fast movements, especially of the later bursts.

Collectively, these studies suggest the possibility that both cortical and subcortical areas participate in burst generation, with mutual influences on changes in excitability. Although most studies hint at the central origin of the pattern, inconsistencies increase from earlier to later bursts, and the exact role of central structures in each burst is still not fully determined. The complex nature of these interactions and remaining inconsistencies mean that this topic still needs to be explored in the future.

The triphasic pattern as a marker of intermuscular coordination during fast movements

Considering the movement times and rates mentioned previously, intermuscular coordination, whether between agonists and antagonists or between synergistic muscles, is of paramount importance for the proper execution of fast movements. Increased agonist and antagonist acceleration ability has been shown to decrease elbow extension movement time by increasing the acceleration time and stopping the moving limb in a shorter time, respectively (Jarić et al., 1995). Another study highlighted the role of the antagonist burst in decreasing movement time, stating that decreased antagonist activity leads to a smaller AG1 burst due to the lack of a braking force (Wierzbicka and Wiegner, 1992). It has also been found that the AG1 burst ends near to peak movement velocity, at which time antagonist activity starts, followed by the onset of AG2 after peak deceleration. The same study found that antagonist amplitude increased with elbow flexion speed, which as mentioned earlier is related to the need for stronger deceleration, but burst duration was kept constant (Forget and Lamarre, 1987).

Temporal modulation is thus a crucial factor in intermuscular coordination. A study of wrist ballistic movements found that performance improvements associated with practice were caused by temporal rather than amplitude modulation. After practice, individuals displayed shorter AG1 and AG2 bursts, indicating increased movement efficiency, and decreased latencies of the antagonist and AG2 bursts. Admitting a central origin of the triphasic pattern, this would mean that the descending motor command improved with practice. Performance

effects were seen through the lower movement time, target error, and variability, but maximum velocity did not change (Liang et al., 2008).

Fast reversed movements (e.g., flexion/extension) offer an important window to study motor programming and agonist/antagonist coordination since the muscle groups switch roles during movement execution. Most studies agree that fast reversed movements are planned as a single movement rather than as two superimposed movements (Gottlieb, 1998; Stancák and Pfurtscheller, 1995; Takatoku and Fujiwara, 2014), although with some inconsistencies. An earlier study noted that in a fast elbow flexion/extension paradigm, compared to a single-direction movement, there was a more sudden offset of the AG1 burst, which was explained by the need to decrease flexion torque in one direction more quickly so that the extensors could accelerate the limb in the opposite direction more easily. The same study found a greater latency (but not amplitude) of the antagonist burst, despite the increase in net extension torque. This delayed antagonist onset was proposed to be related to the more sudden AG1 offset; since there is a more sudden drop in flexor activity, extensor activity starts later so that the net torque is preserved until the target is reached (Gottlieb, 1998). However, later work by Takatoku and Fujiwara (2014) found no changes in antagonist latency between elbow single-movement and reversal tasks, which suggested that the onset timing structure was unchanged. Rather, this study found an extended AG1 duration, increased AG-antagonist coactivation, and increased antagonist amplitude and duration in the reversal task. Thus, AG and antagonist activity showed different patterns between single-direction and reversed movements, which led the authors to conclude that what determines the motor command structure is the final position, even if the initial target is the same (Takatoku and Fujiwara, 2014). Nevertheless, antagonist coactivation has also been found in non-reversed ballistic movements (Zehr and Sale, 1994). The increased antagonist duration and amplitude is in line with the findings of another study of movement reversal which proposed that movement deceleration in one direction and acceleration in the opposite direction are performed continuously (Almeida et al., 2006). This latter study, however, found a more linear relationship between AG/antagonist activity and the corresponding joint torque (Almeida et al., 2006) in reversed shoulder and elbow movements, unlike what was observed in a study of wrist and ankle movements at various speeds (Gottlieb, 1998). Current literature therefore seems to indicate that there are still inconsistencies in the AG-antagonist burst interaction in fast reversed movements.

Modulators of EMG activity during fast limb movement

Body segment inertia

The effect of segment inertia on EMG activity has been studied both by comparing segments with different inertia (e.g., finger, wrist, forearm)(Marsden et al., 1983; Pfann et al., 1998) or by artificially increasing/decreasing the inertial load of a segment (Benecke et al., 1985; Cheron and Godaux, 1986; Latash, 1994; Mustard and Lee, 1987; Shapiro et al., 2004; Sherwood et al., 1988). In segments with larger inertia (e.g., forearm vs. finger), in order to increase movement speed, both amplitude and time modulation of the AG1 burst must occur (Benecke et al., 1985), since the required force is beyond that achievable only by amplitude modulation. As for the antagonist burst, segments with higher load show a longer movement time, which means that there is a longer period between the AG1 and antagonist bursts (Cheron and Godaux, 1986). This notion was supported by another study which found increased amplitude and duration of the antagonist burst in fast elbow flexion movements compared to those of the thumb (Marsden et al., 1983). These studies show that in heavier segments, there is both the need for increased agonist activity to overcome the added inertia and increased antagonist activity to provide a sufficient braking force. This is supported by earlier findings of a greater area (amplitude x duration) of both AG1 and antagonist bursts with loaded fast elbow movements (Lestienne, 1979). Conversely, the viscoelastic properties of low-inertia segments such as the fingers provide a greater contribution to movement deceleration, thus decreasing the need for antagonist activity (Cheron and Godaux, 1986; Marsden et al., 1983; Mustard and Lee, 1987). Benecke et al. (1985) added that the movement time invariance seen in finger movements does not occur in segments such as the forearm. The increased inertial load of the latter segment means that an increase in movement amplitude is associated with increased movement time due to neural and biomechanical constraints (Benecke et al., 1985). Interestingly, by decreasing the elbow moment of inertia, the elbow flexion EMG pattern approximated that of the wrist, which constitutes further evidence of the effect of inertia on motor control mechanisms (Pfann et al., 1998).

As for the effects of changing inertia within the same segment, it has been found that an unpredicted 40% decrease in maximum speed elbow flexion inertia led to no changes in antagonist latency but to increased antagonist amplitude compared to a predicted decrease, which was also associated led to a lower antagonist latency (Latash, 1994). These findings suggest that in fast movements, when changes in inertia are unexpected, the initial motor program is less affected. Conversely, when the individual knows that there will be a lower inertia (and thus a faster movement time), the antagonist burst has to occur earlier and does

not need to have a large magnitude since a lower braking force is required. These changes were suggested by the authors to reflect both changes in the central command and in reflex feedback activity (Latash, 1994).

In opposition to studies of decreased inertial load, the addition of expected loads up to 1500 g in fast elbow flexion movements led to an increased duration of both the AG1 and antagonist bursts, but only in large (80°) amplitude movements (Benecke et al., 1985). This burst modulation is similar to what was mentioned above between body segments with different inertia and also points to a preprogramming of EMG bursts when the inertial load is known (Cheron and Godaux, 1986; Latash, 1994). Mustard and Lee (1987) also found an increase in the size of the AG1 burst without changes in the structure of the EMG pattern when a load was added to fast elbow flexion movements, but there were no such changes on the antagonist burst amplitude, which in fact even decreased with the added load. This was explained by the lower need to provide a braking force since this was done by the load. These authors add that this modification of the antagonist burst was done by peripheral input when the added load was detected, and that the EMG pattern, although generated from learned motor programs, may be modified at the spinal level to adjust the antagonist burst (Mustard and Lee, 1987). The difference in the antagonist burst amplitude with additional load between studies may be related to the position of the movement relative to the action of gravity. Somewhat conflicting results were also found in another study of fast reversed (i.e., flexion-extension) elbow movements, which reported that with increased inertial loads, EMG amplitude (and joint torque) increased but there were no changes in the duration of the EMG bursts (Sherwood et al., 1988). This was probably due to the fact that the individuals were required to maintain the movement time across loading conditions, which led to the lack of prolongation of the EMG bursts, as opposed to studies where movement time was extended with added load and which therefore allowed for longer EMG bursts. The authors suggest that these changes represent a strategy of altering the motor program using a single parameter (acceleration) but maintaining a fixed temporal structure in order to promote motor processing economy (Sherwood et al., 1988). A similar temporal structure was also found in another study of loaded elbow movements (Lestienne, 1979). Finally, the timing of EMG responses to fast elbow flexion movements with light or heavy loads in which a further load was randomly added was studied (Shapiro et al., 2004). These authors found that EMG responses occurred 170-250 ms after the AG1 burst onset and that the onset of these responses was correlated with the expected peak velocity time; the average latency from this time to the response was about 40 ms. This response magnitude increased from light to heavy loads. The response pattern and latency led the authors to suggest that in fast point-to-point movements, the movement control relies on feedforward mechanisms from the AG1

burst to the expected time of peak velocity and that during the second half of the movement, segmental reflexes are facilitated. The response to an unexpected load would therefore be a product of the error between predicted (central motor program) and actual (proprioceptive input) velocity and facilitated segmental reflexes (Shapiro et al., 2004).

To summarize, existing evidence suggests that increased segment inertia may increase both EMG burst duration and amplitude, with lighter segments relying more on passive tissue properties for deceleration. However, task predictability may modify this relationship.

Movement amplitude and distance

As is seen in studies on the effect of segment inertia, the effect of movement amplitude on the EMG pattern of fast movements has been mostly studied on the upper limb (elbow, wrist, and fingers). Common findings among multiple studies include the positive association between maximum speed and movement amplitude/distance (Benecke et al., 1985; Corcos et al., 1988; Freund and Büdingen, 1978; Mustard and Lee, 1987; Takatoku and Fujiwara, 2010; Wadman et al., 1979) and the increased AG1 (Benecke et al., 1985; Cheron and Godaux, 1986; Corcos et al., 1988; Mustard and Lee, 1987; Pfann et al., 1998; Takatoku and Fujiwara, 2010; Wadman et al., 1979), antagonist (Brown and Cooke, 1981; Takatoku and Fujiwara, 2010), and AG2 (Mustard and Lee, 1987; Takatoku and Fujiwara, 2010) burst duration. The increased number of studies showing evidence of AG1 distance modulation indicate that this is the most stable burst, as mentioned earlier. It has also been pointed out that this burst is predominately responsible for determining movement distance (Wierzbicka et al., 1986) and that the AG1 and antagonist burst onset are controlled differently (Takatoku and Fujiwara, 2010). These findings point to the predominance of modulation of burst duration in the performance of fast movements of increasing amplitude. Indeed, Pfann et al. (1998) suggest that there is a movement amplitude cut-off from which the modulation of the AG1 switches from amplitude to duration. Although this amplitude is variable among individuals, the relative value among joints is more stable. These authors found that it is lower for dorsiflexion movements, intermediate for elbow movements, and higher for wrist movements. These differences are proposed to be due not to a different control strategy but to each joint's biomechanical constraints (Pfann et al., 1998). Further evidence of a similar control strategy among different joints was found in another study which reported that the slope of the association between EMG burst slope and movement amplitude was similar for all tested muscles during fast elbow and hand movement. The same study found a similar duration of the EMG onset-peak contraction speed interval for all movement amplitudes. It

was therefore suggested that the contraction speed is centrally adjusted so that all synergists have a similar contraction time and act synchronously regardless of amplitude (Freund and Büdingen, 1978).

Another common finding is the increased AG1-antagonist interval with increased amplitude (Brown and Cooke, 1981; Cheron and Godaux, 1986; Corcos et al., 1988; Marsden et al., 1983; Mustard and Lee, 1987) in upper limb fast/ballistic movement tasks. This is a logical finding since when performing movements at maximum speed, movement time increases with amplitude. However, there are also conflicting findings, especially for the antagonist burst, which has been noted to have a wider inter-individual variation (Corcos et al., 1988). This is also an expected finding given its greater task dependence and the fact that it is more subjected to feedback modulation (Forget and Lamarre, 1987; Gielen et al., 1984). The antagonist (and AG2) burst modulation have been mentioned as being associated with greater movement speeds at higher (80°) versus lower (40°) fast elbow extension movements. The same study concluded that movement speed and timing are adjusted by agonist/antagonist coactivation (Takatoku and Fujiwara, 2010). Antagonist activity was also suggested to be responsible for decreasing movement time for a given amplitude by allowing for a greater braking activity in less time near the end of the movement; there was an asymptotic relationship between peak displacement and antagonist burst magnitude (Wierzbicka et al., 1986). Conversely, other studies have found decreased or no difference in antagonist activity and/or duration with increasing amplitude/distance (Benecke et al., 1985; Brown and Cooke, 1981; Cheron and Godaux, 1986; Marsden et al., 1983; Mustard and Lee, 1987; Wadman et al., 1979).

Findings regarding the AG2 burst and its changes with movement amplitude are even more variable and not as frequently reported. The onset of AG2 has been found to be related to that of AG1 (but not antagonist) and to contribute for adjusting the final joint position (Takatoku and Fujiwara, 2010). In addition to its duration modulation mentioned above, the AG1-AG2 interval has been shown to increase with movement amplitude, which is in line with and may be explained by the same mechanism as the AG1-antagonist interval (Mustard and Lee, 1987).

Taken together, studies of the effect of movement amplitude on the EMG pattern show a greater agreement in the findings related to AG1, which is then progressively lost in the antagonist and AG2 bursts. Although there are signs of similar central control strategies for different joints and muscles, later bursts are individual to increased peripheral modulation and are thus more task- and individual-dependent.

Task/movement intent

Although to a lesser extent than inertial load and movement amplitude/distance, the task and movement intent dependency of the triphasic pattern has also been explored mostly through upper limb single-joint fast movement tasks (Benecke et al., 1985; Kudo and Ohtsuki, 1998; Takatoku and Fujiwara, 2010; Wadman et al., 1979). and has important implications for the mechanisms behind the programming and execution of the triphasic pattern. Wadman et al. (1979) found that during the first 100 ms of a fast wrist movement, the EMG pattern seems to be unaffected by the task distance (7.5 to 30 cm). However, when movements across these distances were randomly blocked, antagonist activity decreased with increased distance compared to undisturbed movements (Wadman et al., 1979).

It has been proposed that the triphasic EMG pattern is present not only in self-terminated movements, as has mostly been studied, but also in brief (but not sustained) isometric contractions (albeit with timing changes). Sanes and Jennings (1984) concluded that this is evidence that the triphasic pattern is characteristic of any motor action which requires a fast reversal of joint torque direction. This would also explain the reduced or absent antagonist activity in movements that are not planned to be stopped (Sanes and Jennings, 1984), as mentioned previously. The same study mentions that the brain adjusts the motor program of muscle recruitment according to different task types (isotonic, isometric, or torque-pulse tasks) (Sanes and Jennings, 1984).

Movement cueing also plays a role in the motor control of fast movements. It has been shown that peak velocity decreases after 20 s of maximum-velocity non-cued movements, while the same was not seen for internally cued movements. These differences led those authors to conclude that the ability to maintain peak velocity during ballistic movements is more dependent on sensorimotor integration than on cognitive processing (Mogensen and Jakobsen, 2001).

Effects of training and fatigue seen at the peripheral level

As is the case in all motor processes, EMG parameters undergo training-related adaptations and fatigue-related impairments. In this regard, martial arts movements have also been the focus of studies analyzing training effects on muscle activity patterns during fast limb movement (Dinn and Behm, 2007; Olsen and Hopkins, 2003; Rodrigues Ferreira and Brito, 2010; Zehr et al., 1997). In a study comparing the performance of a karate punch between

athletes and non-athletes, the latter showed a lower movement speed. This decreased speed was underpinned by a shorter shoulder flexion duration, thus providing less acceleration. The higher speed shown by athletes was also accompanied by a shorter arm flexor electromechanical delay. Conversely, the arm flexor antagonists were activated later (i.e., closer to the AG1 burst end), thus allowing for more acceleration time (Rodrigues Ferreira and Brito, 2010). In contrast with these findings, an earlier study did not find differences in movement time or peak velocity between karate athletes and untrained individuals. There were also no differences in agonist/antagonist recruitment patterns. Rather, karate athletes showed an increased rate of torque development and peak acceleration (Zehr et al., 1997). Also in karate athletes, increased acceleration but also shorter AG1 rise times compared to non-athletes were found (Mortimer and Webster, 1983). These different findings may have been caused by the fact that the latter studies used a simple elbow extension task, while Ferreira and Brito (2010) used a more sport-specific movement, which would have a greater potential to be affected by motor learning and intermuscular coordination (Zehr et al., 1997). Another study which used punching training to determine the effects of dynamic versus isometric training reported increased agonist (triceps) activity in the dynamic training group not accompanied by increases in force. This was explained by an increase in motor unit firing synchrony and frequency. The same study also found decreased movement time after dynamic compared to isometric punch training (Dinn and Behm, 2007). which is compatible with the explanation provided by the authors related to motor unit adaptations. On this topic, Zehr and Sale (1994) have published an interesting review in which they mention neuromuscular adaptations specific to ballistic training such as a shorter twitch and contraction time, increased contraction speed, increased integrated EMG activity, and increased motor unit synchronization and excitability. One interesting hypothesis raised in that review is that changes in muscle fiber composition may be driven by MN plasticity (Zehr and Sale, 1994). On this topic, and in a somewhat opposing perspective to the H-reflex findings of Casabona et al. (1990) presented earlier, a later study reported that the distribution of motor unit potential velocities in the biceps brachii was significantly different between sprinters and endurance athletes during an elbow flexion/extension (an untrained task for both athletes), suggesting the mostly inherited nature of this distribution (Klaver-Król et al., 2010). This nature vs. nurture debate on the effects of training on MN size could therefore constitute an interesting research avenue.

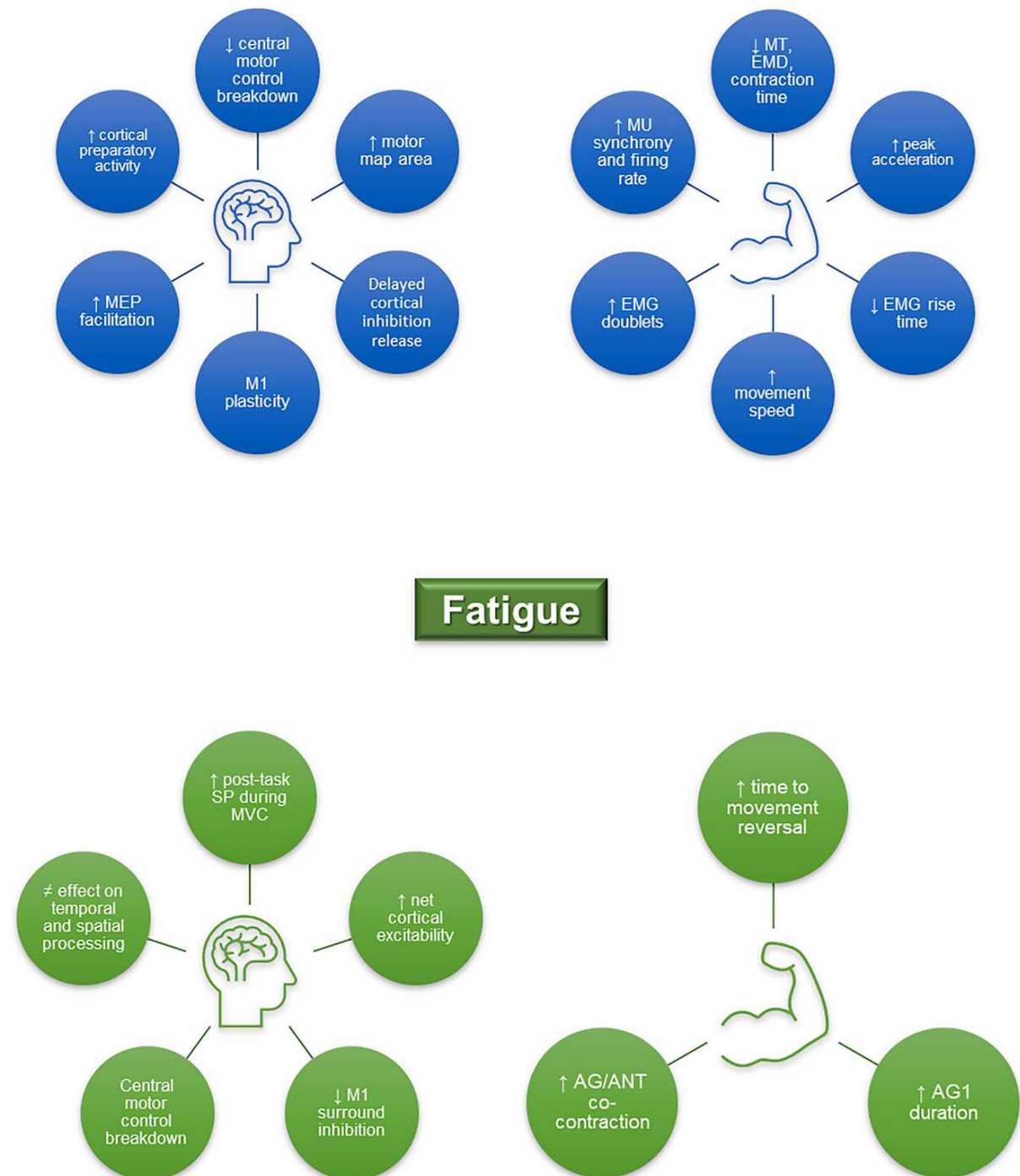
Neuromuscular adaptations were also studied after a dynamic dorsiflexion training program, which led to an earlier onset of EMG activity, increased motor unit firing rate, and increased presence of doublets in the EMG bursts (Van Cutsem et al., 1998), thus providing a physiological basis for the changes in contraction speed and movement time mentioned

above. The same study, in addition to an earlier one of a ballistic ankle dorsiflexion task noted that despite other training-induced changes, the motor unit recruitment order principle was maintained (Desmedt and Godaux, 1977; Van Cutsem et al., 1998). The specific effects of ballistic/fast dynamic training were also highlighted in a more recent report, who found that this type of training led to a decrease in maximum kicking force but increased movement speed. These authors also found that individuals with higher skill (i.e., martial artists) showed greater adaptations than control individuals (Olsen and Hopkins, 2003). Despite these consistent findings of increasingly optimized fast movement performance in athletes, a study has found that the baseline differences in reaction and movement times seen in athletes compared to non-athletes can be attenuated in as little as four days of training (Yandell and Spirduso, 1981). Finally, studies of the pre-movement SP have also found a training effect, with individuals more experienced in performing fast/ballistic movements requiring a smaller SP for motor unit synchronization (Conrad et al., 1983; Van Cutsem and Duchateau, 2005).

As for the effects of fatigue, a study of elbow flexion/extension reversal movements executed before and after an isometric fatigue protocol found a gradual decrease in maximum movement velocity with increased fatigue which, at higher fatigue levels, was accompanied by increased time to reversal and target undershooting, reduced burst amplitude, increased biceps burst duration, and a delay in the peak triceps burst amplitude. However, the relative temporal structure of the EMG pattern was maintained. This suggests that fatigue affects the spatial and temporal movement processing differently (Tschoepe et al., 1994). Another study also found an increase in AG1 duration at high fatigue levels (75% reduction in wrist flexion maximum voluntary contraction). This increase was explained as a strategy to compensate for the reduced MN firing rate that is associated with fatigue in order to maintain movement parameters (Berardelli et al., 1984). These two studies show that high levels of fatigue are needed to induce changes in the EMG pattern. However, Rodrigues et al. (2009) found that a 20-s bout of finger movements at the maximum voluntary rate led to a change in the EMG agonist/antagonist pattern from alternating peaks to a less effective co-contraction pattern. These changes were not accompanied by decreases in maximum voluntary force or single-trial movement speed, which led the authors to conclude that they were due to a breakdown of central control and not peripheral fatigue (Rodrigues et al., 2009). These findings were confirmed by Bächinger et al. (2019), who stated that increased agonist/antagonist coactivation was found as fatigue was induced by a repeated tapping test and that this increased coactivation was the only EMG-related parameter associated with the decrease in

movement speed. A summary of the effects of training and fatigue at the central and peripheral levels can be seen in Figure 6.

Figure 6. Central (left) and peripheral (right) effects of training and fatigue on the execution of fast limb movements



AG, agonist; AG1, first agonist burst; ANT, antagonist; EMD, electromechanical delay; EMG, electromyography; MT, movement time; MU, motor unit; M1, primary motor cortex; MVC, maximum voluntary contraction; SP, silent period.

Other muscle-related factors associated with fast movement performance

Van Soest and Bobbert have proposed that the existence of the force-length relationship makes muscles act as a zero-lag peripheral feedback system which reduces the effects of perturbations (to an extent) during explosive, open-loop movements such as vertical jumping. This allows the motor system to introduce a control element in movements which would otherwise not be within reach of neural modulation (van Soest and Bobbert, 1993). Another study investigated the role of muscle thixotropy on the execution of ballistic wrist movements. It was found that performing either oscillatory or a fast antagonist prestretch a few seconds before a ballistic wrist flexion movement increased movement speed. Although the authors mention that neural factors such as post-activation potentiation may play a role, it was argued that changes in the muscles' passive behavior, such as the elimination of short-range stiffness, were the major factor behind these results (Axelson, 2005). These findings are in line of those of Castellote et al. (2004), who report that performing rapid oscillations before a ballistic wrist movement leads to a shorter movement time and a faster movement onset through a decreased electromechanical delay. These authors propose that this lower delay is caused by changes in viscoelastic element tension, leading to a lower resistance to be overcome at movement onset. Pre-movement rapid oscillations may also prevent the formation of more stable actin-myosin bridges, which is also favorable for movement initiation (Castellote et al., 2004).

Muscle properties have also been shown to play a different role in the maximum movement and contraction speed. While the maximum contraction speed is limited by neural factors (MN firing rates) (Del Vecchio et al., 2019; Freund and Büdingen, 1978), the maximum movement speed/rate is limited by the muscle's mechanical properties (Neilson, 1972); indeed, muscle viscosity has been shown to play a role in movement velocity by affecting the symmetry ratio, since it increases the time needed for agonist contraction and decreases that of the antagonist braking (Jaric et al., 1998).

Functional implications of movement speed and motor slowing

In addition to reviewing central and peripheral mechanisms specific to fast limb movements, it is crucial to see the functional implications of these movements and their real-world impact. Indeed, the need for a greater interaction between the fields of neuroscience and performance medicine has been championed by a previous overview of brain-muscle interactions and highlighted in recent studies on the application of neurodiagnostics in sports

(Cheron et al., 2016; Enders and Nigg, 2016; Perrey and Besson, 2018; Seidel-Marzi and Ragert, 2020b)

Studies of repetitive movements performed at the maximum voluntary rate have consistently shown decreases in movement rate/speed ranging from 7 to 35% in bouts of 10-30 s (Arias et al., 2015; Bächinger et al., 2019; Heuer et al., 2002; Heuer and Schulna, 2002; Madrid et al., 2018, 2016; Mogensen and Jakobsen, 2001; Rodrigues et al., 2009; Seidel-Marzi and Ragert, 2020a). It is worth noting, however, that only three of these studies involved tasks other than finger tapping (Bächinger et al., 2019; Mogensen and Jakobsen, 2001; Seidel-Marzi and Ragert, 2020a). Interestingly, in two-finger tapping, it has been noted that the decrease in movement rate was highly dependent on the chosen finger pair, pointing to the relevance of both anatomical and neural interactions between segments in the performance of fast repetitive finger tapping movements (Aoki et al., 2003).

Findings relative to the effect of a fast repetitive movement task on maximum voluntary contraction have not been unanimous. While most studies have found that there was no loss in maximum voluntary contraction after such tasks (Bächinger et al., 2019; Madrid et al., 2018; Rodrigues et al., 2009; Teo et al., 2012a), other studies have provided opposing findings of a decrease of approximately 10% after a finger tapping task (Arias et al., 2015a; Madrid et al., 2016).

Any strategies to counter the appearance of motor slowing and promote movement speed development could therefore have a positive impact in a wide range of activities. Skilled pianists have been found to show movement patterns at higher tempi which are more dependent on sensorimotor integration than on stylistic/expressive goals. These faster patterns were also noted to contradict typical music teaching recommendations (Bella and Palmer, 2011). Also in expert pianists, the maximum single finger (but not wrist and elbow) tapping voluntary movement rate (but not years of practice) was found to be a predictor of keystroke rate, which may constitute a performance advantage (Furuya et al., 2015).

In another perspective, voluntary activation in the first 50-75 ms has been found to be the main determinant of rate of torque development (Maffiuletti et al., 2016), which is a crucial parameter in multiple sporting activities (Aagaard et al., 2002; Ishøi et al., 2019). Sprinting is a particularly studied activity in this sense; higher contraction speed is a predictor of sprint time (Loturco et al., 2019) and may contribute to a greater movement rate, which is the most relevant parameter during the sprint acceleration phase (Maćkała et al., 2015).

Where do we go now?

This review has shown multiple aspects relevant to the control of fast limb movements that remain to be clarified. One of them is the lack of consensus on what constitutes a “fast” movement. While the definition of a ballistic action is more consensual, different authors use different thresholds of movement time/rate in studies involving fast (but not ballistic) motions. This may lead to contradictory findings in the motor control mechanisms and findings associated with these movements. A more standardized (and objective) definition of what constitutes a fast movement should therefore be established in order to better compare findings between studies. A possible option would be to consider the presence of EMG triphasic pattern as the criterion for discrete movements and the presence of signs of rhythmic (rather than discrete) movement control for repetitive movements. However, not all studies may be able to measure such parameters; an easier method of distinguishing movements according to their speed therefore still needs to be established.

Other prevailing inconsistencies and unclear aspects in the literature were also noted. These include the exact role of the cerebellum in predicting movement parameters, the motor planning of fast reversed movements (i.e., as a single or two movements), the mechanisms of motor SI generation and its role in motor slowing, and the relative contributions of genetics and training in the distribution of fast MNs. How fatigue affects the central and peripheral markers of motor control and performance has also been the source of some inconsistencies in the literature.

In addition to these effects of fatigue, this review discussed the central and peripheral modulators of fast movement control. Knowledge of these factors is important not only for researchers when designing experimental paradigms but also for movement-related professionals to bear in mind in their practice.

Another aspect brought to light in the present work is the relative lack of more field-based studies in specific (non-pathological) populations. Given the preponderance of supraspinal structures for motor control in the analyzed movements, the number of identified findings and mechanisms associated with fast limb movement performance and execution, and the described broad relevance of these movement types, it would perhaps be expected that there would be more applied studies analyzing the impact of the aspects discussed in this review. Based on this knowledge, future studies should focus on procedures to improve them on variables such as injury risk, indices of function, performance measures (whether in sport, artistic, or occupational settings), and other measures pertaining to cognitive and social benefits for the general population. Such studies could provide useful knowledge in

fields such as sports, performance arts, and occupational medicine, but also broader benefits at a more societal level considering the association of these movements with longevity, cognition, and socioeconomic factors.

CONCLUSIONS

This review outlined aspects relevant to the planning and execution of fast movements from the brain to the muscle and movement parameters that may influence these control mechanisms. There were some inconsistencies found in the literature which may be explained by the complexity of these mechanisms and the task dependency effect on movement planning and execution. Most notably, future studies should strive to standardize a definition of what constitutes a fast movement.

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Conflicts of interest

The authors have no conflicts of interest to declare.

Data sharing statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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CHAPTER III – RANGE OF MOTION REMAINS CONSTANT AS MOVEMENT RATE DECREASES DURING A REPETITIVE HIGH-SPEED KNEE FLEXION-EXTENSION TASK

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Abstract

Maintaining the range of motion in repetitive movement tasks is a crucial point since it directly influences the movement rate. Ensuring the movement amplitude can be reliably maintained when motor function is assessed by measuring the maximum movement rate is therefore a key consideration. However, the performed range of motion during such tasks is often not reported. This study aimed to determine whether individuals are able to maintain an intended range of motion during a knee flexion/extension maximum movement rate task in the absence of tactile and visual feedback. Twelve healthy male individuals performed knee flexion/extension at maximum speed for eight 10-s blocks in a 45° arc between 45 and 90°. The range of motion was monitored using a marker system and the movement rate was measured. The performed range of motion was not significantly different from the 45° arc during the task despite a 13.47% decrease in movement rate from the start to the end of the task. Nevertheless, there was only anecdotal evidence of no difference from 45° in most blocks, and on the second and seventh blocks, there was anecdotal evidence of differences in the Bayesian one-sample test. There was also no significant shift in the maximum flexion/extension angles throughout the task. Male healthy individuals were thus able to perform a consistent average predefined knee range of motion in a maximum movement rate task even with decreases in movement rate. This was achieved without constraint-inducing devices during the task and using only basic equipment and verbal feedback.

Introduction

Tasks involving the execution of repeated movements performed at the maximum voluntary rate have been extensively used to gain insight on the mechanisms of central motor control of fast and/or rhythmic movements (Bächinger et al., 2019; Madrid et al., 2018; Rodrigues et al., 2009). Such paradigms are also used to study motor slowing, i.e., the loss in movement rate/speed with fatigue induced by repetitive movements (Bächinger et al., 2019; Seidel-Marzi & Ragert, 2020) and the processes involved in cognitive and movement disorders (Bramell-Risberg et al., 2010; Teo et al., 2014).

However, an important aspect which is often overlooked in these studies is ensuring that the desired range of motion (ROM) is achieved and remains unaltered throughout the task when visual/tactile feedback is not available or feasible. This factor is crucial since the range of motion of fast movements alters the agonist/antagonist muscle recruitment pattern (Pfann et al., 1998; Takatoku & Fujiwara, 2010). It is also worth noting that the effect of movement amplitude on muscle activity varies across joints, likely due to differences in biomechanical constraints (Pfann et al., 1998). Previous studies of fast movements have used strategies such as physical barriers (Stark-Inbar & Dayan, 2017), wearable goniometers (Madrid et al., 2018) or visual inspection (Blinkenberg et al., 1996) as means to monitor amplitude.

However, barriers and attached devices may influence free movement performance, especially at maximum speeds, and visual inspection carries a degree of subjectiveness. Thus, it remains necessary to determine whether the correct ROM is performed when movement is executed without performance-influencing constraints. Moreover, wearable devices may not be available in all settings; ensuring the intended ROM is maintained without such equipment would allow for movement rate experiments to be carried out with greater rigor in a wider range of settings.

Even in cases where some objective measure is taken, there is still a lack of reporting of the range of motion performed during the task when it is not firmly set by mechanical constraints. Rodrigues et al. do provide information about the performed range of motion in a maximum movement rate task and found that it was maintained (Rodrigues et al., 2009), but in a finger tapping task. Since body segment inertia also affects the central and peripheral motor control mechanisms (Marsden et al., 1983; Pfann et al., 1998; Rodrigues et al., 2009), it remains necessary to verify if the range of motion is maintained in tasks involving maximum movement rate in heavier segments such as the leg, where greater muscle work is required to move and stop the segment.

If the range of motion changes during a task where movement rate is being measured, this

may induce bias in the measured rate, as it is easy to understand that a smaller range of motion allows for a greater movement rate. However, as already mentioned, most previous studies have not reported how both these parameters change during such tasks when mechanical constraints are not present. Moreover, one of the factors contributing to the widespread findings of motor slowing in maximum movement rate tasks in the absence of fatigue may be the decrease in the range of motion. This is another aspect that underlies the importance of reporting the range of motion in such tasks.

The aim of this study was therefore to determine whether individuals are able to maintain compliance with an intended range of motion during a knee flexion/extension maximum movement rate task in the absence of tactile and visual feedback and in the presence of motor fatigue when a standard familiarization procedure is carried out and verbal feedback is given. We hypothesized that individuals would maintain the intended range of motion throughout the task.

Methods

Sample

Male individuals between 18 and 39 years were recruited by word of mouth from the student population of the institution. Exclusion criteria were 1) history of lower limb surgery; 2) history of central nervous system injury or disease; 3) current injury or disease preventing the execution of the experimental protocol. All individuals signed an informed consent form prior to participating in the study, which was approved by the local institutional review board (8/2021). A total of 12 male right-side dominant individuals (20.67 ± 3.55 years old, 1.76 ± 7.87 m, 71.0 ± 9.32 kg) participated in the study. We previously found in a study using the same task that a sample size of 13 subjects would be enough to obtain a 99% power for detecting a significant decrease in movement rate over the eight blocks with a variance explained by the effect of 0.631 and a within-group variance of 3.784, corresponding to an effect size of $\eta^2 = 0.14$ (unpublished data under processing). However, since this power was achieved after recruiting 12 individuals, we did not increase the sample size further. Males were recruited since they have been shown to produce faster movement rates (Hubel et al., 2013) and greater acceleration and deceleration forces (Ives et al., 1993) than females. Since movement rates are more likely to decrease when the initial movement rate is higher in repetitive movement tasks, we considered that studying only males would more likely lead to a significant reduction in movement rate, thus allowing us to better display any differences between movement rate and ROM. Moreover, a recent study has shown no sex differences

in knee joint position sense (Azevedo et al., 2021).

Knee joint kinematic assessment

An optical tracking camera system (V120 Trio, OptiTrack, Corvallis, OR) was used with a sampling rate of 120 Hz to capture the knee range of motion during a bilateral fast knee flexion/extension task. The capture system was placed parallel to the plane of motion, at about 1 m from the right knee. Three reflective markers were fixed on the right greater trochanter, lateral knee joint line, and lateral malleolus, so the knee sagittal angle could be determined. The marker coordinates were recorded using Motive 2.3.0 (NaturalPoint Inc., Corvallis, OR). Since this is a self-contained system with three fixed cameras in a bar, it is pre-calibrated; nevertheless, measurement accuracy was confirmed using a known angle. Only the right limb was assessed; this was because 1) we did not expect the ROM to be different between sides due to the need to coordinate both legs to maintain a rhythmic pattern; 2) previous studies knee joint position sense have also measured only one limb (Relph & Herrington, 2016; Ribeiro & Oliveira, 2010); and 3) no interlimb differences were found when measuring both limbs in joint position error tasks (Cug et al., 2016; Nagai et al., 2019).

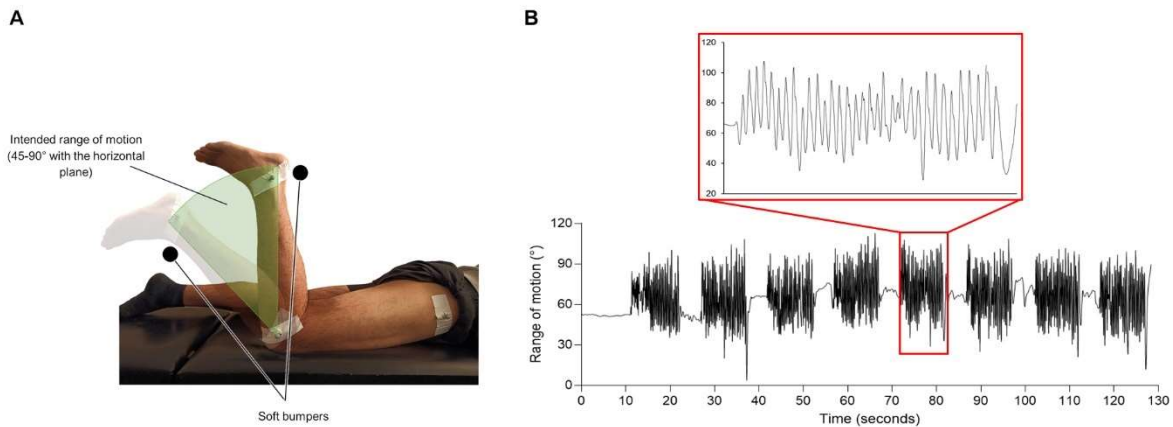
Protocol

Upon arrival, individuals completed a basic anthropometric screening and completed a 5-min warm-up on a stationary bicycle (Ergomedic 828E, Monark, Vansbro, Sweden) at ~70 rpm. Following the warm-up, individuals were familiarized with the maximum knee flexion/extension movement rate task in a prone position (Figure 7). They were asked to perform alternating repeated flexion/extension movements with both legs as fast as they could in a 45° arc between 45 and 90° of knee flexion aligned with the horizontal plane (i.e., 90° corresponded to a vertical alignment between the knee and ankle markers). Before the experimental task, soft bumpers were used so that the individuals could understand and practice the required knee range of motion for the task. These bumpers were not used during the experimental task to avoid any potential constraints to movement performance. Individuals were given the necessary time to familiarize with the correct range of movement and to demonstrate being able to perform the required range at full speed for a few seconds.

Verbal feedback was given during the task when needed.

The task consisted of eight 10-s blocks of fast alternating knee flexion/extension movements performed, with a 5-s rest between blocks. The 10-s duration was chosen since this period has been found to show the greatest decrease in movement rate (Bächinger et al., 2019). Verbal encouragement was provided during the task in order to ensure a maximum effort.

Figure 7. Schematic representation of the familiarization procedure (A) and sample output of the knee angle throughout the task (B)



Data processing

The knee angle was calculated using the markers' X and Y axes coordinates, corresponding to the sagittal plane, through dedicated Matlab (The Mathworks Inc., Natick, MA) code, which was also used to detect each movement cycle and the corresponding maximum and minimum knee flexion values. The knee range of motion (i.e. arc) was obtained by calculating the difference between the maximum knee flexion and extension angle for each movement. A representative example can be seen in figure 7B. As there may be greater variability in the ROM in the first cycles of each block, the first four knee flexion/extension cycles were discarded from the ROM analysis. The knee movement rate of each block was determined by counting the number of flexion/extension cycles in each block divided by the duration of the block (10 s) to provide the movement rate in Hz; no movement cycles were excluded from this count. The average range of motion of each block was calculated using the values of each knee flexion/extension cycle, while the range of motion coefficient of variation (CV) was calculated by dividing the standard deviation by the mean range of all movement cycles in each block and used as a measure of between-subject variability. CVs were classified as very good ($\leq 10\%$), good ($10\% < CV \leq 25\%$), moderate ($25\% < CV \leq 35\%$), or poor ($> 35\%$). The slope of the angles during the task was used as a measure of change

in the maximum and minimum angles between which the individuals performed the flexion/extension movements and was calculated from the linear trendline of all angles during the task excluding the 5-s rest periods (i.e, one slope per individual comprising the eight 10-s movement blocks); a visual representation can be seen in figure 7B. Finally, the standard error of the mean (SEM) ROM was calculated by dividing the standard deviation by the square root of the sample size as a measure of the deviation from the intended 45° in the same unit to provide a better understanding of the practical meaning of the achieved variation.

Statistical analysis

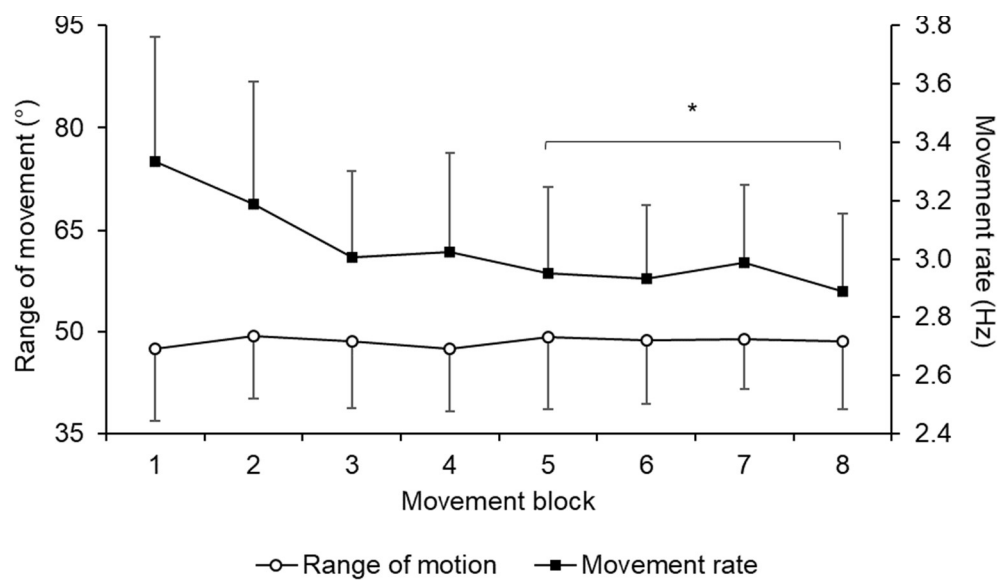
SPSS version 25 (IBM Corp., Armonk, NY) was used for all analyses. The normality of data distribution was checked using the Shapiro-Wilk test for each variable. Continuous data are presented as mean and 95% confidence interval. The average knee range of motion, the SEM, and its coefficient of variation were determined for each individual and each block. Changes in the average range of motion and movement rate across blocks were evaluated using a one-way repeated measures ANOVA, with Greenhouse-Geisser correction in case data sphericity was not present. Post-hoc testing with Bonferroni correction was performed in case significant differences were found. To determine if the range of motion was significantly different from the intended 45° in each block, we used a Bayesian one-sample test. This test was chosen to allow for establishing the weight of the evidence in favor or against the null hypothesis, as measured by the Bayes factor, and thus avoid the dichotomous nature of the one-sample t-test. The same test was used to determine if the slope of the angles was significantly different from zero during the whole task as a measure of the shift in minimum/maximum knee flexion angles. Finally, to check the association between movement rate and range of motion, the Pearson correlation coefficient was calculated between the values for the same block. P-values <0.05 were considered statistically significant. Partial eta squared values (η_p^2) and Cohen's d are presented as a measure of effect sizes for the ANOVA and t-tests, respectively. Effect size values were interpreted according to (Cohen, 2013) and Bayes factorss were interpreted according to (Jeffreys, 1961). Statistical power is presented whenever significant differences were found as presented by the statistical software output.

Results

Movement rate

The movement rate significantly decreased across the eight blocks (Figure 8) from 3.34 ± 0.42 Hz in the first block to 2.89 ± 0.27 Hz in the last block (-13.47% ; $p < 0.001$; $\eta^2 = 0.456$; power: $>99\%$). Post-hoc testing revealed significant differences between the first and the fifth to eighth blocks ($p = 0.005$ to 0.029 , Table 1). The individual changes in movement rate can also be seen in Supplementary Figure 1.

Figure 8. Changes in movement range and rate throughout the task



* significantly different from the first block ($p < 0.05$)

Table 1. Movement rate and range of motion findings for each movement block

	Movement block							
	1	2	3	4	5	6	7	8
Movement rate (Hz)	3.3 ±0.42	3.2 ±0.42	3.0 ±0.31	3.0 ±0.37	2.9 ±0.30	2.9 ±0.24	3.0 ±0.26	2.9 ±0.27
Average ROM (°)	47.4 ±10.58	49.3 ±9.20	48.6 ±9.84	47.5 ±9.21	49.1 ±10.51	48.7 ±9.34	48.8 ±7.34	48.6 ±10.04
Movement rate/ROM correlation	-0.292 p=0.36	-0.310 p=0.33	0.248 p=0.44	0.239 p=0.45	0.096 p=0.77	-0.250 p=0.43	-0.327 p=0.33	-0.173 p=0.61
One-sample ROM t-test	p=0.45 d=0.22	p=0.13 d=0.47	p=0.23 d=0.36	p=0.36 d=0.28	p=0.20 d=0.39	p=0.20 d=0.39	p=0.10 d=0.52	p=0.24 d=0.36
ROM CV (%)	21.69 [15.85; 27.53]	18.08 [13.02; 23.15]	19.59 [14.19; 24.99]	18.50 [13.50; 23.49]	20.63 [14.88; 26.38]	18.51 [13.40; 23.62]	14.29 [10.33; 18.25]	19.96 [14.45; 25.47]
ROM SEM (°)	3.05	2.66	2.84	2.66	3.03	2.70	2.12	2.90

ROM, range of motion; CV, coefficient of variation; SEM, standard error of the mean. The one-sample bayesian test is relative to the mean difference to 45° in each block. The CV represents the variation of all movement cycles in each block relative to the mean. The SEM represents the error relative to the “true” mean.

Range of motion

The range of motion did not change significantly during the task ($p=0.865$, $\eta^2=0.022$; Figure 8). On average, individuals performed movements in a range from 47.58° (95% CI [40.70; 54.14]) to 49.47° (95% CI [43.47; 55.15]) across blocks, with CVs ranging from 14.29 to 21.69% (all classified as “good”). As for the deviation from 45° in each block, the Bayesian one-sample test p-values showed that the average movement arc was not significantly different from the intended 45° in any block ($p=0.074$ to 0.404 ; $d=0.56$ to 0.25). The largest effect size ($d=0.56$) was seen in the seventh block. BFs were in the 1-3 range, indicating anecdotal evidence of no differences, in all but the second and seventh blocks. In these two

blocks, the BFs were 0.90 and 0.60, respectively, indicating anecdotal evidence of differences from 45°. The slope of the knee angles during the whole task was also not significantly different from zero, with moderate evidence in favor of no differences (slope: 0.00058 ± 0.00060 ; $p=0.743$; $BF=3.42$; $d=0.09$), and there were no significant correlations between movement rate and range of motion for each block ($r=-0.327$ to 0.248 ; $p=0.326$ to 0.766). The differences from the intended 45° ranged from 2.59° (95% CI [-3.97; 9.14]) to 4.48° (95% CI [-1.21; 10.16]). Finally, the SEM ranged from 2.02 to 2.98°, with the smallest and largest values being recorded in the seventh and first blocks, respectively. Detailed results are shown in Table 1 and the individual changes in ROM can be seen in Supplementary Figure 2.

Discussion

In this study, we aimed to determine whether compliance with an intended range of motion during a knee maximum movement rate task is achieved and maintained using standard familiarization and verbal feedback in the absence of visual and tactile cues. Our findings showed that there was no significant change in the average range of motion during the task despite the drop in movement rate and, most importantly, that the deviations found do not have a practical or clinical relevance. These findings are discussed below in greater detail.

As hypothesized, the average range of movement was close to the intended value and stable throughout the task. However, despite the lack of a significant difference to the intended 45°, the effect size of this difference was moderate for the seventh block; moreover, this effect size tended to increase during the task, showing that individuals may deviate more meaningfully from the intended range later in the task when fatigue is more likely to be present. Additionally, it should be noted that the BFs indicate only anecdotal evidence of no differences, and there was anecdotal evidence of differences in two blocks despite the absence of a significant p-value. While this greater evidence of differences may be explained by some fatigue in the seventh block, in the second it may have been due to a difficulty in adapting quickly to the task needs after the initial block, considering that this task is not usually performed by most people.

Maintaining the minimum and maximum angles throughout the task may be relevant since performing knee movements at a range closer to full flexion and extension forces muscles to act at different points of the force-length curve, thus influencing the demands of the task for the agonist and antagonist muscle groups. Moreover, it has previously been noted that joint position sense may be altered by fatigue (Proske, 2019); in the knee, fatigue has been

known to lead to a perception of increased flexion (Proske, 2019). Changes in joint position sense were previously found to be similarly present whether the knee flexors or extensors were fatigued (Ribeiro et al., 2011) and to be present after both a 10 and 50% decrease in hamstrings peak torque was induced (Gear, 2011). However, our findings suggest that the individuals did not undergo major changes in their joint position sense or that verbal feedback was sufficient to prevent this, as the slope of the angle trendline during the task was not significantly different from zero. This indicates that there was no shift to a more flexed or extended position in which the 45° range of motion was performed. Additionally, the SEM and CV of the range of motion were relatively stable throughout the entire task with the exception of a slight decrease in the seventh block SEM. Nevertheless, the ROM 95% CIs and the average differences showed that individuals tended to go over the performed range of motion rather than falling short. This may be due to the high-speed nature of the task; there is less time to process kinesthetic feedback, which may lead to delays in the command to activate the antagonist. Moreover, it has been shown that repetitive movements performed at over 2 Hz are controlled rhythmically rather than individually (Toma et al., 2002), which may further delay the adjustments to the correct ROM.

It is also worth noting that movement range (shorter vs. longer ranges) alters the EMG activity pattern of movements performed at maximum speed; longer ranges of motion have been noted to lead to increases in EMG burst amplitude and in the inter-burst interval (Mustard & Lee, 1987; Takatoku & Fujiwara, 2010). Even without visual or tactile feedback, individuals were able to comply with a set range of motion in high-speed knee flexion/extension cycles. This shows that using simple equipment and procedures, it was possible to instruct subjects towards maintaining a ROM within an acceptable limit during a high-speed movement task. This can be attested by the average differences of 2.59 - 4.48° relative to the intended 45° and the SEMs, which ranged from 2.12 to 3.05°. Both these parameters showed values lower than the minimum detectable change in knee sagittal motion reported in previous studies of both clinical populations (Geiger et al., 2019; Guzik et al., 2020) and of healthy participants performing higher speed movements such as running (Bramah et al., 2021). This suggests that the difference from the intended range found in our study does not have a clinical or practical relevance. Finally, The CVs were classified as “good” in all blocks, which indicates that between-subject variability was not a major issue.

Conversely, movement rate decreased, showing that the differences in movement rate were not associated with the performed range of motion. These findings suggest that the changes in movement rate were not due to modifications in the performed range of motion. This is further supported by the lack of a significant correlation between these two parameters. As

previously mentioned, studying changes in movement rate is relevant in multiple fields. In such experimental paradigms, being able to maintain the same movement range is a crucial aspect when performing maximum movement rate tasks that induce motor slowing, as changes in movement rate may be influenced by the range performed rather than by performance limitations. Although most previous studies of maximum movement rate have been performed in the fingers, this difference in muscle work is especially true for segments with larger inertia such as the leg (Marsden et al., 1983; Pfann et al., 1998), where changes in movement range affect the amount of muscle work required more drastically. However, since the decrease in movement rate found here is in line with previous studies of maximum movement rate performed using finger tapping tests (Madrid et al., 2018; Rodrigues et al., 2009), this suggests that the loss in movement rate in these tasks does not depend on segment inertia.

Thus, the present results lend some support to the idea that individuals may be able to maintain a desired range of movement even during a high-speed task and in the absence of visual or tactile feedback. Our study may therefore help researchers use similar tasks more confidently even when it is not possible to objectively measure the range of motion, as in settings without the necessary equipment, or if such equipment would influence the movement performance. Additionally, our findings may encourage future studies to report the performed range of motion in maximum movement rate tasks.

We understand that our work has some limitations. Only a small number of young male healthy individuals were recruited, so the results may not necessarily apply to other demographics or to patients with movement disorders. However, it is not expected that the regulation of the range of motion would be substantially different in other non-pathologic populations. Additionally, the sample was sufficient to achieve a very high statistical power (>99%) for detecting the significant decrease in movement rate during the task. Finally, only the right limb was measured; however, as explained earlier, it is not expectable that the results for the left limb would be markedly different. Future studies should therefore expand our preliminary findings to other healthy and pathological populations.

Conclusion

Male healthy individuals are able to perform a consistent average predefined knee range of motion in a maximum movement rate task even with decreases in movement rate after a

short familiarization period and verbal feedback during the task.

Acknowledgements

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CHAPTER IV – BRAIN AND MUSCLE ACTIVITY DURING FATIGUING MAXIMUM-SPEED KNEE MOVEMENT

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Abstract

While the underlying mechanisms behind upper limb (e.g., finger) motor slowing during movements performed at the maximum voluntary rate have been explored, the same cannot be said for the lower limb. This is especially relevant considering the lower limb's larger joints and different functional patterns. Despite the similar motor control base, previously found differences in movement patterns and segment inertia may lead to distinct central and peripheral manifestations of fatigue in larger joint movement. Therefore, we aimed to explore these manifestations in a fatiguing knee maximum movement rate task by measuring brain and muscle activity, as well as brain-muscle coupling using corticomuscular coherence, during this task. A significant decrease in knee movement rate up to half the task duration was observed. After an early peak, brain activity showed a generalized decrease during the first half of the task, followed by a plateau, while knee flexor muscle activity showed a continuous decline. A similar decline was also seen in corticomuscular coherence, but for both flexor and extensor muscles. The electrophysiological manifestations associated with knee motor slowing therefore showed some common and some distinct aspects compared to smaller joint tasks. Both central and peripheral manifestations of fatigue were observed; the changes seen in both EEG and EMG variables suggest that multiple mechanisms were involved in exercise regulation and fatigue development.

Keywords: movement rate, electroencephalography, electromyography, motor control, fatigue

Introduction

Repetitive unloaded movement at maximum voluntary rate has been shown to lead to decreases in movement rate; this phenomenon has been referred to as motor slowing (Bächinger et al., 2019; Madrid et al., 2018; Rodrigues et al., 2009). This performance loss is proposed to have a predominantly central origin (Arias et al., 2015; Bächinger et al., 2019; Rodrigues et al., 2009). The involved mechanisms may include fatigue of intracortical inhibitory circuits, leading to less fluid (and thus slower) movement patterns (Arias et al., 2015; Bächinger et al., 2019; Madrid et al., 2018). It has also been proposed that fatigue of the central motor command to switch between movement directions drives this decrease, manifested as a loss of a clear agonist/antagonist electromyographic (EMG) activity pattern (Rodrigues et al., 2009). On a different perspective, Zanette et al. (Zanette et al., 1995) found a significant decrease in the size of the motor representation area and decreased cortical excitability mediated by intracortical presynaptic modulation after a thumb adduction 1-min maximum voluntary rate task. Thus, uncertainties remain regarding the mechanisms of motor slowing in healthy individuals.

To the best of our knowledge, the patterns of brain and muscle activity associated with knee motor slowing have not been previously explored. While it is true that various motor control mechanisms have been shown to be similar across body regions (Freund & Büdingen, 1978; Grosse et al., 2002; Pfann et al., 1998), there are also factors that differentiate upper and lower limb motor control both at central and peripheral levels. Knee unilateral movements show less sensorimotor lateralization than finger and elbow movements on functional magnetic resonance imaging (fMRI) as well as differences to other lower limb joints (Kaprili et al., 2006; Luft et al., 2002); lower limb joints have also shown a greater somatotopic sensorimotor and cerebellar overlap as well as different activation patterns compared to upper limb joints (Kaprili et al., 2007). As for peripheral differences, segment inertia has been shown to affect EMG activity patterns in fast/ballistic movements (Benecke et al., 1985; Chéron & Godaux, 1986; Pfann et al., 1998). The increased inertia of the leg compared to the fingers or wrist may lead to different EMG activity patterns. Additionally, the typical functional patterns of the upper (low load, asymmetrical, and fine motor skills) and lower (high load, symmetrical, and directed for balance and stability) extremities are distinct (Goel & Paloski, 2016). Finally, changes in motoneuron excitability induced by fatigue have been shown to differ between the upper and lower limb (Temesi et al., 2019; Vernillo et al., 2020). Therefore, the physiology behind knee motor slowing may show important differences to the existing upper limb findings.

Additionally, this study can contribute to the debate on maximal exercise regulation mechanisms, considering the controversy on the degree of central and peripheral contributions, and respond to the need to determine the degree of cortical involvement in rhythmic movements.

In a previous preliminary study, we found significant knee motor slowing using the same task as in this study (Correia et al., 2022). In order to further substantiate those findings and to shed light on the associated physiological mechanisms, the main objective of this study is to determine what measures of brain and muscle activity are associated with the loss of knee movement rate with repetitive movement. As a secondary objective, considering the highly dynamic nature of the used task and the natural motor control variability, we aimed to evaluate the between-session group behavior and the test-retest reliability of these parameters.

Methods

Sampling and study criteria

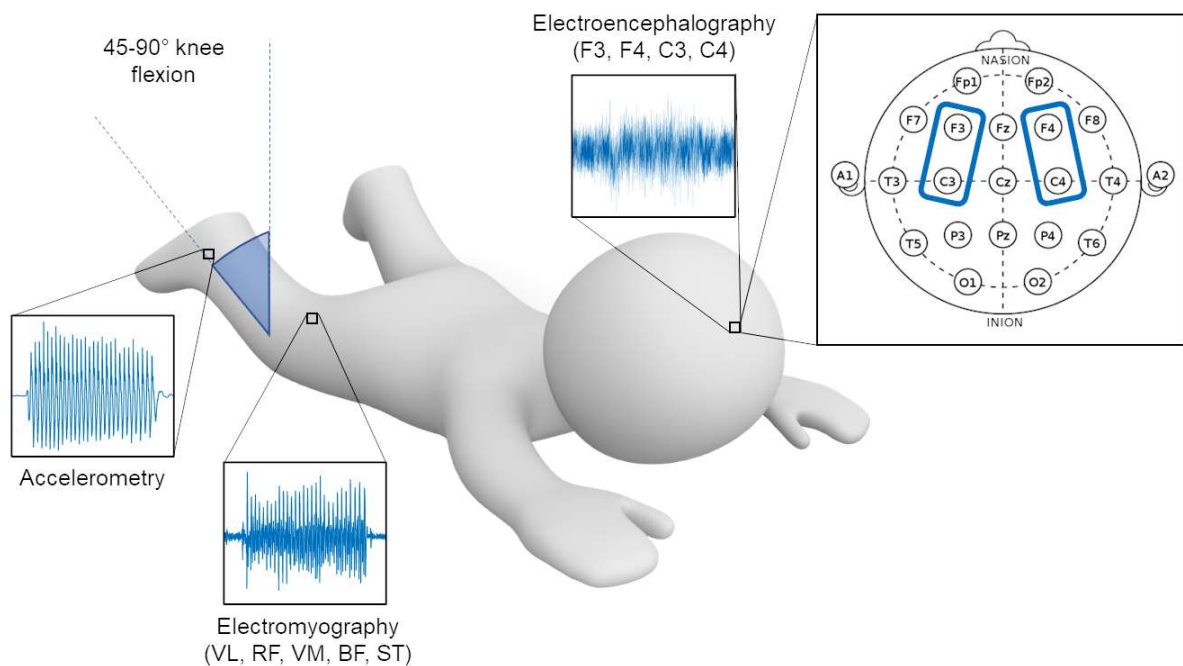
A convenience sample was recruited from the local institution. Males between 18 to 39 years were included. Exclusion criteria were 1) a history of knee, hip, or central nervous system surgery; 2) a history of hip or knee structural musculoskeletal injury; 3) any contraindication to ventral decubitus; 4) any condition which prevented participants from performing the requested movement; 5) regular (>2 times/week) training of any sporting discipline. Males were chosen for this study since they show greater movement rates and performance decrement in maximal intermittent tasks such as repeated sprinting (Hubel et al., 2013; Laurent et al., 2010), making significant changes more likely to happen and consequently detect the associated mechanisms. The age limit was placed since that is the threshold after which the maximum motor speed starts to decrease (Bartzokis et al., 2010).

The study was approved by the local institutional review board (approval number: 8/2021) and all participants provided written informed consent. Sample size calculation was performed using G*Power 3.1.9.4 (Heinrich-Heine-Universität Düsseldorf, Düsseldorf, Germany). Considering changes in movement rate during the task, a sample size of 20 individuals was required to achieve a power of 0.95 with a partial eta squared effect size (η^2)=0.15 over eight repeated measurements.

Experimental protocol

Participants undertook two experimental sessions separated by at least a week. Upon arrival, anthropometric data (age, height, body mass) were collected. Participants then completed a 5-min warm-up on a stationary bicycle at a comfortable rate (≈ 70 rpm) without added resistance. Subsequently, participants were placed in the prone position in a table and asked to perform unloaded bilateral alternating knee flexion/extension movements at their maximum voluntary rate over eight blocks of 10 s with 5 s of rest between blocks (Figure 9). Movements were performed in the 45-90° range; before starting, participants were familiarized with this range of motion as long as needed through the use of soft bumpers. Afterwards, these bumpers were removed, and participants performed 2-3 s of knee flexion/extension movements at the maximum voluntary rate to confirm they had correctly familiarized themselves with the desired range of motion. The accuracy of the range of motion using this familiarization was confirmed previously (Correia et al., 2022).

Figure 9. Depiction of the experimental setup along with raw data from each analysis



VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus.

We chose a short movement arc to increase the direction change challenge, since it has been reported that increased cortical activity is needed for the change between flexor and extensor movement (Wieser et al., 2010). The prone position was chosen since we aimed to design a task in which the anti-gravity work was performed by the knee flexors and to remove visual feedback, as it has been shown to affect the control of high-speed movements (Goel & Paloski, 2016). Participants were instructed to maintain their movement rate as high as possible throughout the entire task through verbal encouragement and were instructed to make any corrections to the range of motion if needed. Brain activity, muscle activity, and movement rate were monitored during this task using electroencephalography, electromyography, and accelerometry, respectively.

Dynamometry

Before and after the study task, knee flexion and extension MVIC were measured at 45° of knee flexion in the prone position using an isokinetic dynamometer (Biodex System 3, Biodex, Shirley, NY) in a counterbalanced order across participants. Individuals were stabilized using waist (for both flexion and extension) and knee (for extension) straps and asked to develop their maximum force as fast as possible from a resting condition; two measurements were performed separated by one minute and the highest value was used for the analysis. Torque data were collected using the acqknowledge software (v3.9.1, BIOPAC Systems, Goleta, CA) at a sampling frequency of 1000 Hz. Post-task measurements were started within 30 s of task completion and the right side was evaluated in all participants.

Electroencephalography

A 24-channel EEG device (Vertex SC823, Meditron Eletromedicina Ltda, São Paulo, Brazil) was used according to the international 10–20 system with online referencing to two electrodes placed at the mastoid processes; the sampling frequency was 250 Hz and electrode configuration was as shown in Figure 9. Before starting data collection, a circuit impedance ≤ 10 k Ω was ensured in all electrodes, and an analog band-pass filter (0.1–70 Hz) was applied by the amplifier.

Electromyography and accelerometry

Five wireless electrodes (Trigno, Delsys, Natick, MA) were placed on the right vastus lateralis (VL), rectus femoris (RF), vastus medialis (VM), biceps femoris (BF), and semitendinosus (ST) according to SENIAM recommendations (Hermens et al., 2000) and secured with adhesive tape. Prior to electrode placement, the skin was shaved and cleaned with alcohol to decrease skin impedance. EMG data were collected at a sampling frequency of 1926 Hz. The EMG system applied a bandpass filter of 10-850 Hz. Two additional electrodes were placed on the lateral malleoli to collect accelerometry data at a sampling frequency of 148 Hz.

As in previous studies of bilateral lower limb movement rate, we did not differentiate individuals according to dominance (Yoshida et al., 2017a, 2017b). EMG data were assessed on the right limb. This approach was used since the main focus was on the central motor control aspects of fast movements; the left hemisphere (which is primarily responsible for right limb movement) has been shown to have a degree of specialization in controlling fast repetitive movement (Yoshida et al., 2017a, 2017b), and there is a different association with dominance in the structure of the left and right hemispheres (Hervé et al., 2005). This also led to the right side being evaluated in the dynamometer in order to be able to compare torque/rate of torque development (RTD) and EMG data.

Data processing

Data were processed using Matlab scripts (MathWorks Inc., Natick, MA). To analyze the EEG and EMG signals, we discarded the first and last seconds of each movement block of EEG and EMG signals to achieve better signal stability, resulting in 8-s periods for each block. For the movement rate calculation, the entire 10-s period was used since it is not affected by signal stability. Movement rate was determined using the number of accelerometer peaks during each block; the presented values correspond to the movement rate of each limb. To calculate the duration of each movement cycle, the number of accelerometry samples between each two consecutive peaks were divided by the sampling rate. We then determined the 25th and 75th percentiles of cycle duration for each block as a measure of the change in cycle duration that would account for the different number of cycles across participants and blocks.

Torque data were filtered using a fourth-order low-pass Butterworth filter with a 10-Hz cutoff. Knee flexion and extension torque data were used to calculate the RTD. The torque onset was determined manually using a 1 N window as this has been reported to produce reliable

onsets and to preserve the early RTD period more effectively (Maffiuletti et al., 2016). We used two periods of early (0-50 and 50-100 ms) and two periods of late (100-150 and 150-200 ms) RTD. The flexion/extension MVIC ratio was calculated by dividing the two values corresponding to the attempt with the highest value within each session. MVIC and RTD values were normalized to body weight.

EEG data were high-pass filtered at 1 Hz, notch filtered at 50 Hz to remove line noise, and low-pass filtered at 50 Hz using fourth-order, zero-lag Butterworth filters. Independent component analysis was performed using EEGLAB (Delorme & Makeig, 2004) to remove muscle, eye, line noise, mechanical, and other artifacts from the filtered EEG signal using visual inspection to determine the components to be removed. Artifacts were identified based on their waveform and biological plausibility. If these artifacts could not be removed in an isolated manner using independent component analysis, artifact subspace reconstruction was used to minimize signal loss. The EEG power was calculated for the theta (4-7.9 Hz), alpha (8-14.9 Hz), beta (15-30.9 Hz), and gamma (31-50 Hz) bands for each 8-s period of the task. We chose to analyze the EEG data up to 50 Hz since there is a negligible amount of signal content above this frequency in healthy individuals (Mima et al., 2000). We calculated two EEG power measures: each band's relative power as a percentage of the total signal power and the normalized power referenced to the first block. These parameters were calculated to account for the inter-individual variability and allow for more accurate comparisons. All EEG measures were calculated for four electrodes placed over areas associated with cortical motor planning and execution and which have been shown to have movement rate-associated activity: F3, F4, C3, and C4 (Figure 9).

EMG data were high-pass filtered at 20 Hz, notch filtered at 50 Hz to remove line noise, and low-pass filtered at 450 Hz using fourth-order, zero-lag Butterworth filters. The signal was then full-wave rectified and the root mean square (RMS) of the amplitude was calculated using 250 ms windows with a 125 ms overlap. The three 250-ms windows with the highest values were selected from each block, averaged, and normalized to the value from the first block. This normalization of EMG amplitude to that of a similar action being investigated has been recommended for high-velocity muscle actions (Ball & Scurr, 2013). Two EMG co-contraction indices were calculated as a measure of agonist-antagonist coordination; one between the VL and BF (CCI_{lat}) and another between the VM and ST (CCI_{med}). Both indices were calculated as the percentage of overlap between the RMS areas of the corresponding muscles for each block (Lo et al., 2017).

Corticomuscular coherence (CMC)

To analyze the time-frequency functional coupling of EEG and EMG signals, wavelet coherence was calculated as described by Yoshida et al. (Yoshida et al., 2017b) using a publicly available MATLAB package (Wavelet Toolbox). Morlet wavelet coherence has previously been used in rhythmic tasks as it is a good choice in terms of time and frequency resolution in the analysis of nonstationary signals (J. Liu et al., 2019; Yoshida et al., 2017b). For the coherence analysis, EMG signals were high-pass filtered at 3 Hz (instead of 20 Hz) and downsampled to 250 Hz to match the EEG sampling rate. Wavelet coherence was determined in the 1-50 Hz range; the threshold for coherence significance (CT) was calculated using the following equation (Yoshida et al., 2017b):

$$CT = 1 - \left[\frac{1}{N} \left(1 - \frac{\alpha}{100} \right) \right]^{\frac{1}{L-1}}$$

where N is the number of frequency bins and α is the confidence level (95% in our study). Considering the cyclic nature of our task, we defined L as the number of cycles completed by each participant, as done in a previous study using a task of this type (Yoshida et al., 2017b). CMC was calculated between the signals of the C3 electrode and each muscle's EMG signal. Two coherence outcomes were used; first, the total area of coherence above the CT was calculated across the 1-50 Hz spectrum for each block. Second, time-frequency maps of the observed coherence were constructed to provide a qualitative CMC analysis.

Statistical analysis

Data normality was tested using the Shapiro-Wilk test. A two-way repeated measures ANOVA (2 sessions $\times$ 8 blocks) was used to test changes in movement rate, EEG power, EMG RMS, and significant CMC across the eight blocks and between the two sessions. To test for changes in cycle duration, a two-way repeated measures ANOVA (2 percentiles $\times$ 8 blocks) was used. Post-hoc testing with Bonferroni adjustment for multiple comparisons was made to determine significant differences between individual blocks (a total of 28 comparisons). Partial eta squared (η_p^2) values were used as a measure of effect size and classified as small (0.01-0.06), medium (0.06-0.14), and large (>0.14) (Cohen, 2013). The pre-post task and between-session differences in MVIC and RTD variables were tested using a two-way repeated measures ANOVA [2 measurements (pre, post) $\times$ 2 sessions]. The test-retest intraclass correlation coefficients (ICC) were calculated using a two-way

mixed model and an absolute agreement definition (Koo & Li, 2016). In cases where the assumptions for the use of parametric ICCs were violated (i.e., normality and homogeneity of variances (Bobak et al., 2018)), a nonparametric concordance coefficient was calculated using the “nopaco” R package version 1.0.5 (Kuiper & Hogenboezem, 2017). Considering the number of variables in the electrophysiological analyses (EEG, EMG, and CMC), and in order to decrease the number of analyses, we determined the test-retest reliability of the percentage of change (block 1-block 8) and of the linear slope of the change over the eight blocks. These coefficients were classified as poor (<0.5), moderate ($0.5-0.75$), good ($0.76-0.9$), and excellent (>0.9) (Koo & Li, 2016). In addition to the ICCs, the test-retest standard error of measurement was also calculated as an index of reliability and calculated from the mean error term of the corresponding ANOVA, as it has the advantage of being independent from the ICC (Weir, 2005). Correlations between MVC and RTD were calculated using Pearson’s or Spearman’s correlation coefficient, depending on data normality. Statistical analyses were performed using SPSS version 25 (IBM Corp., Armonk, NY) and R Studio version 1.2.5042 (Posit Software, Boston, MA). P-values <0.05 were considered significant.

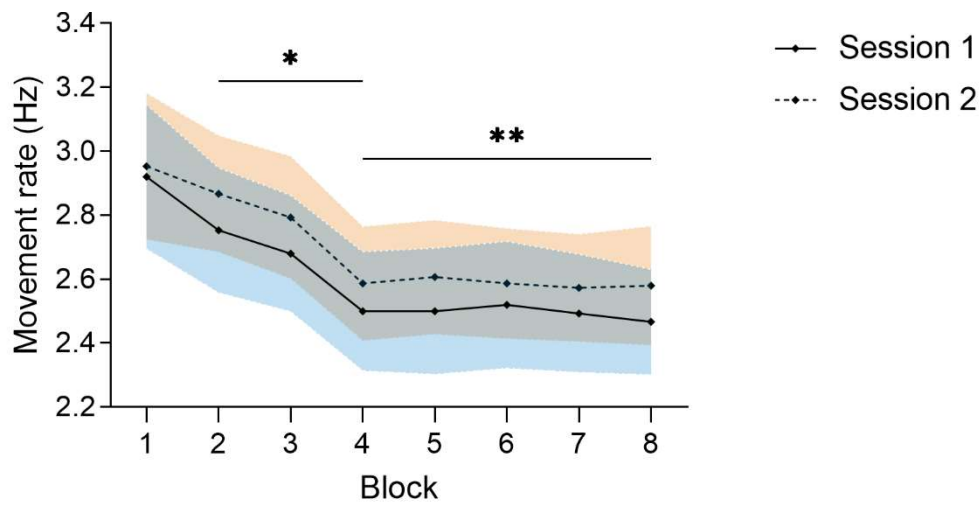
Results

Nineteen participants (age: 25.9 ± 6.4 years; height: 1.77 ± 0.08 m; weight: 74.7 ± 11.2 kg) were included in the study. The average gap between sessions was 9.1 ± 3.4 days. We did not enroll the initially planned 20 participants since the intended power was already exceeded with this sample size.

Movement rate and cycle duration

There was a significant effect of the block factor, showing a decrease in movement rate ($p < 0.001$, $\eta_p^2 = 0.786$, power > 0.99) but no significant differences between sessions ($p = 0.079$, Figure 2). In both sessions, 93-96% of the decrease in movement rate occurred in the first four blocks. Post-hoc testing revealed significant differences between the first and second to fourth blocks and between the first three and last five blocks (Figure 10). There was no significant block $\times$ session interaction ($p = 0.788$). The ICCs for the movement rate ranged from 0.74 to 0.92 (good to excellent) across movement blocks (Table 2).

Figure 10. Decreases in movement rate during the task



The shaded areas represent the 95% confidence interval for the first (blue) and second (orange) sessions. *significantly different from the first block ($p < 0.05$). **significantly different from the first three blocks ($p < 0.05$).

Table 2. Movement rate test-retest outcomes

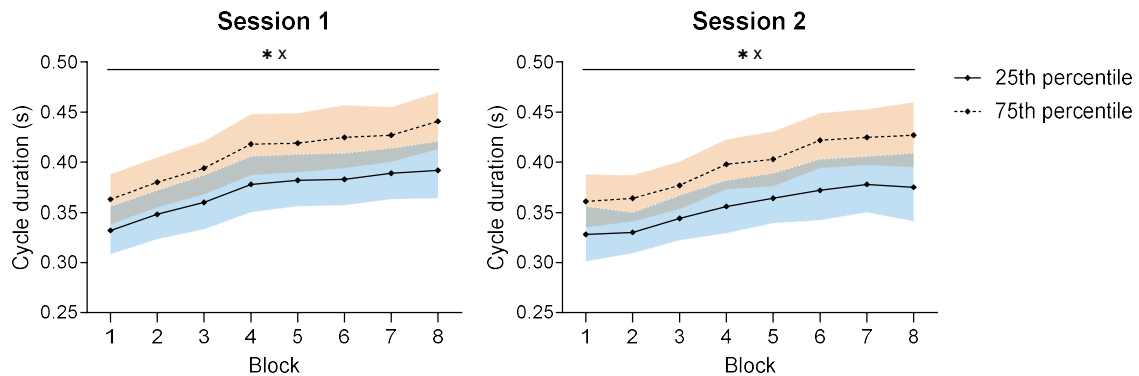
Test-retest outcomes		
Block	ICC (95% CI)	SEM (Hz)
1	0.852 (0.559 - 0.95)	0.20
2	0.805 (0.385 - 0.934)	0.16
3	0.891 (0.675 - 0.963)	0.15
4	0.740 (0.291 - 0.908)	0.23
5	0.888 (0.670 - 0.962)	0.14
6	0.915 (0.760 - 0.970)	0.14
7	0.912 (0.754 - 0.969)	0.13
8	0.858 (0.607 - 0.950)	0.16

ICC, intraclass correlation coefficient; CI, confidence interval; SEM, standard error of measurement

As for cycle duration, there was a significant effect of both the block (session 1: $p < 0.001$, $\eta_p^2 = 0.59$, power > 0.99 ; session 2: $p < 0.001$, $\eta_p^2 = 0.69$; power > 0.99) and percentile (session 1: $p < 0.001$, $\eta_p^2 = 0.93$, power > 0.99 ; session 2: $p < 0.001$, $\eta_p^2 = 0.94$; power > 0.99) factors, as well

as significant block $\times$ percentile interactions in both sessions (session 1: $p=0.01$, $\eta_p^2=0.17$, power=0.85; session 2: $p=0.026$, $\eta_p^2=0.17$, power=0.77). Most of the increase in cycle duration was seen in the first four blocks, with the second half of the task showing more modest increases (Figure 11).

Figure 11. Changes in the 25th and 75th percentiles of movement cycle duration during the task

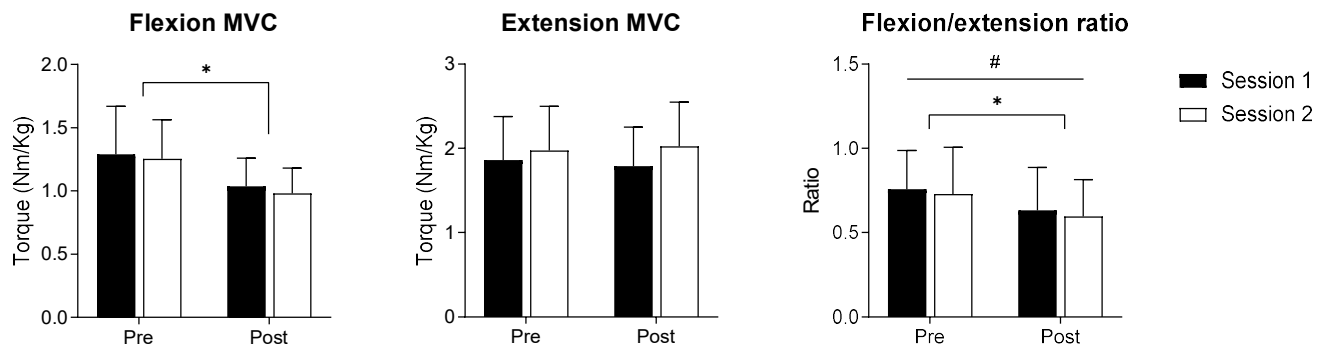


The shaded areas represent the 95% confidence interval for the first (blue) and second (orange) sessions.

Maximum voluntary contraction and rate of torque development

There was a significant post-task decrease in the knee flexion MVIC ($p<0.001$, $\eta_p^2=0.60$; power >0.99) and in the flexion/extension ratio ($p=0.001$, $\eta_p^2=0.49$; power=0.96), while no significant post-task changes were seen in extension ($p=0.962$; $\eta_p^2<0.001$; power=0.05). The pre-post task percentage of change in flexion MVIC, extension MVIC, and flexion/extension ratio were -21.1 (-13.1 to -29.0)%, -1.4 (-12.5 to 9.8)%, and -14.0 (-2.8 to -25.3)% for session 1 and -12.7 (-3.1 to -22.3)%, 3.2 (-9.2 to 15.6)%, and -21.1 (-12.6 to -29.6)% for session 2. As for the differences between sessions, there was a significant session effect for the flexion/extension ratio ($p=0.005$, $\eta_p^2=0.40$; power=0.861) but not for the isolated flexion ($p=0.12$; $\eta_p^2=0.15$; power=0.34) or extension ($p=0.06$; $\eta_p^2=0.21$; power=0.48) measurements (Figure 12). There were also no significant measurement $\times$ session interactions ($p=0.18$ to 0.83). The pre-task ICCs for the best MVIC attempt were 0.88, 0.83, and 0.95 for knee flexion, extension, and the flexion/extension ratio, respectively. The post-task flexion, extension, and flexion/extension ratio ICCs were 0.80, 0.70, and 0.99, respectively (moderate to excellent, Table 3).

Figure 12. Pre-post changes in peak torque and rate of torque development



*significant pre-post differences ($p < 0.05$); #significant between-session differences ($p < 0.05$)

Table 3. Flexion and extension peak torque and flexion/extension ratio ICCs and SEMs

Variable	Measurement	Test-retest outcomes	
		ICC (95% CI)	SEM
Flexion	Pre	0.88 (0.69 – 0.96)	0.158 Nm/kg
	Post	0.80 (0.45 – 0.93)	0.118 Nm/kg
Extension	Pre	0.83 (0.54 – 0.94)	0.282 Nm/kg
	Post	0.70 (0.19 – 0.89)	0.324 Nm/kg
Flexion/extension ratio	Pre	0.95 (0.87 – 0.98)	0.078
	Post	0.99 (0.96 – 0.99)	0.044

ICC, intraclass correlation coefficient; CI, confidence interval; SEM, standard error of measurement.

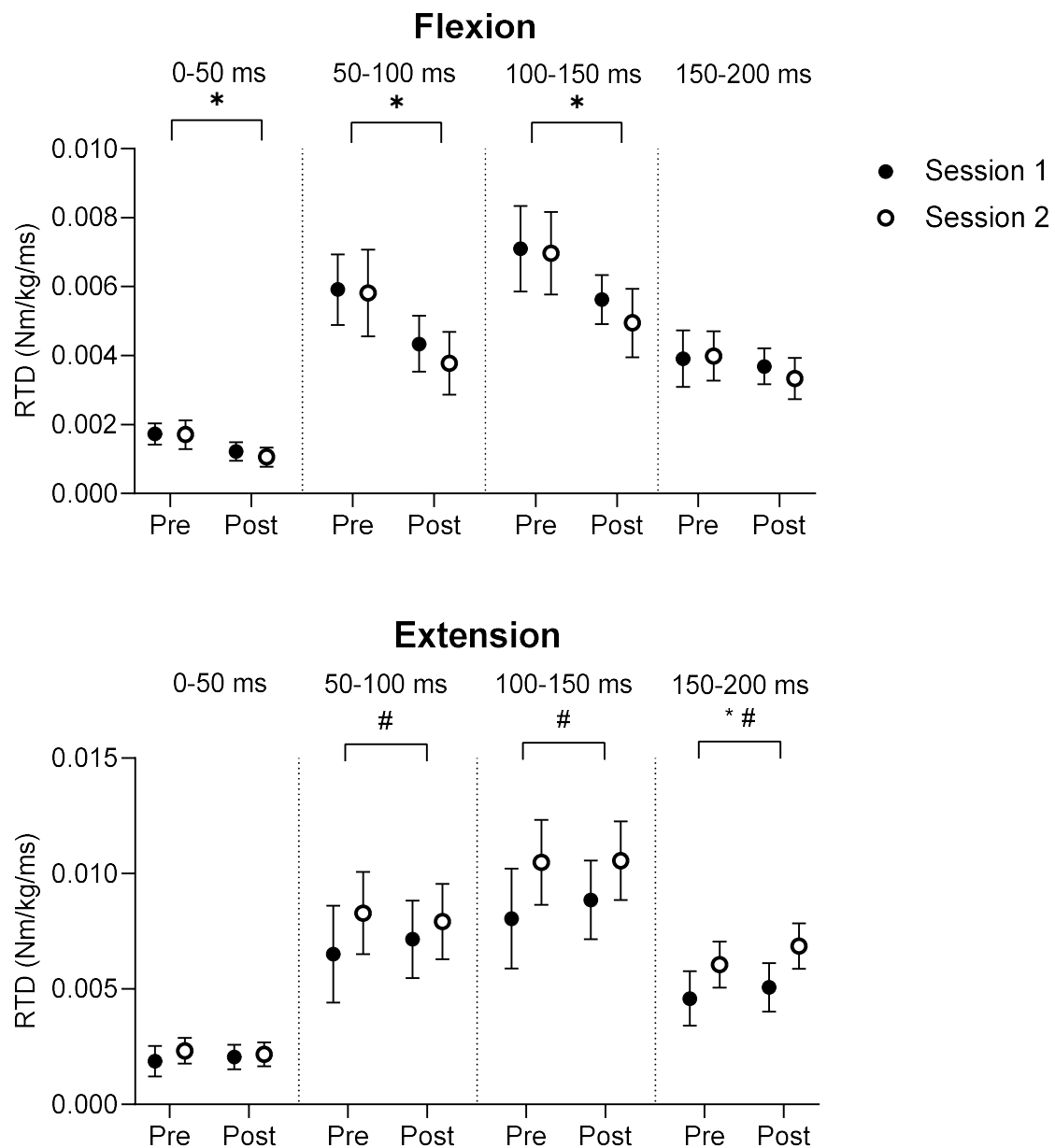
Regarding the RTD variables, the only significant pre-post task changes in extension RTD were seen in the 150-200 ms period ($p = 0.030$; $\eta_p^2 = 0.26$; power = 0.61). Conversely, there were significant post-task decreases in flexion RTD during the 0-50 ($p = 0.002$; $\eta_p^2 = 0.47$; power = 0.94), 50-100 ($p = 0.002$; $\eta_p^2 = 0.45$; power = 0.92), and 100-150 ms ($p = 0.005$; $\eta_p^2 = 0.40$; power = 0.86) periods. There were also significant pre-post decreases in the flexion/extension ratio in the 0-50 ($p < 0.001$; $\eta_p^2 = 0.65$; power = 0.98), 50-100 ($p < 0.001$; $\eta_p^2 = 0.66$; power = 0.99), and 100-150 ms ($p = 0.002$; $\eta_p^2 = 0.61$; power = 0.97) periods (Figure 13).

Between-session differences were not present in flexion RTD ($p = 0.263$ to 0.742).

Conversely, there were higher extension RTD values in the second session in the 50-100 ms ($p = 0.048$; $\eta_p^2 = 0.22$; power = 0.52), 100-150 ms ($p = 0.007$; $\eta_p^2 = 0.38$; power = 0.83), and 150-200 ms ($p < 0.001$; $\eta_p^2 = 0.53$; power = 0.98) periods (Figure 13). There was a significantly

higher flexion/extension RTD ratio in the first session in the 100-150 ($p=0.031$; $\eta_p^2=0.36$; power=0.62) and 150-200 ms ($p=0.004$; $\eta_p^2=0.55$; power=0.92). As was the case for the torque variables, there were no significant measurement $\times$ session interactions ($p=0.31$ to 0.59) (Figure 13).

Figure 13. Pre-post task changes in rate of torque development in both sessions



*significant pre-post differences ($p<0.05$); #significant between-session differences ($p<0.05$)

The pre-task flexion RTD ICC values ranged from 0.5 to 0.57 (moderate to good), while the post-task values ranged from 0.41 to 0.78 (poor to good). As for extension RTD, the pre-task ICC values ranged from 0.45 to 0.87 (poor to good), while the post-task values ranged from 0.1 to 0.82 (poor to good, Table 4).

Table 4. Rate of torque development test-retest outcomes

Pre-task								
	0-50 ms		50-100 ms		100-150 ms		150-200 ms	
	ICC (95% CI)	SEM	ICC (95% CI)	SEM	ICC (95% CI)	SEM	ICC (95% CI)	SEM
Flexion	0.79 (0.40 – 0.92)	0.00043	0.81 (0.47 – 0.93)	0.0013	0.75 (0.29 – 0.91)	0.0015	0.26 (- 1.22 – 0.74)	0.0014
Extension	0.84 (0.52 – 0.94)	0.00058	0.81 (0.39 – 0.93)	0.0019	0.73 (0.13 – 0.91)	0.0022	0.55 (- 0.98 – 0.83)	0.0016
Flexion/ extension ratio	0.15 (- 1.35 – 0.72)	0.42	0.31 (- 0.81 – 0.77)	0.32	0.48 (- 0.40 – 0.82)	0.21	0.45 (- 0.51 – 0.81)	0.28
Post-task								
	0-50 ms		50-100 ms		100-150 ms		150-200 ms	
	ICC (95% CI)	SEM	ICC (95% CI)	SEM	ICC (95% CI)	SEM	ICC (95% CI)	SEM
Flexion	0.83 (0.54 – 0.94)	0.00028	0.78 (0.42 – 0.92)	0.00097	0.63 (0.05 – 0.86)	0.0012	0.51 (- 0.30 – 0.82)	0.00088
Extension	0.53 (- 0.35 – 0.83)	0.00082	0.56 (- 0.21 – 0.84)	0.0025	0.59 (- 0.02 – 0.85)	0.0024	0.62 (- 0.17 – 0.88)	0.0012
Flexion/ extension ratio	0.74 (0.60 – 1)*	0.32	0.25 (- 1.32 – 0.75)	0.25	0.38 (- 0.67 – 0.78)	0.18	0.22 (- 0.58 – 0.69)	0.30

ICC, intraclass correlation coefficient; CI, confidence interval; SEM, standard error of measurement.

*nonparametric concordance coefficient

Regarding the correlations between MIVC and RTD, there was a similar pattern in both sessions, with a greater number of significant correlations in extension than in flexion; significant flexion and flexion/extension ratio correlations were seen mostly in the 150-200 ms period (Table 5).

Table 5. Correlations between MVIC and RTD pre- and post-task in both sessions

Session 1		RTD							
		0-50 ms		50-100 ms		100-150 ms		150-200 ms	
MVIC	Flexion	Pre -0.241 p=0.32	Post 0.043 p=0.86	Pre -0.229 p=0.35	Post 0.112 p=0.65	Pre -0.177 p=0.47	Post 0.317 p=0.19	Pre -0.037 p=0.88	Post 0.588 p=0.008
	Extension	0.568 p=0.011	0.247 p=0.30	0.561 p=0.012	0.324 p=0.18	0.537 p=0.018	0.521 p=0.022	0.267 p=0.27	0.748 p<0.001
	Flexion/ex tension ratio	0.319 p=0.23	-0.119 p=0.65	0.445 p=0.08	0.067 p=0.80	0.434 p=0.09	0.444 p=0.08	0.255 p=0.34	0.870 p<0.001
Session 2		RTD							
		0-50 ms		50-100 ms		100-150 ms		150-200 ms	
MVIC	Flexion	Pre 0.172 p=0.51	Post 0.057 p=0.83	Pre 0.245 p=0.34	Post 0.061 p=0.82	Pre 0.430 p=0.09	Post 0.087 p=0.74	Pre 0.682 p=0.002	Post 0.173 p=0.51
	Extension	0.464 p=0.06	0.64 p=0.006	0.488 p=0.047	0.665 p=0.004	0.568 p=0.02	0.741 p<0.001	0.6 p=0.01	0.720 p<0.001
	Flexion/ex tension ratio	0.299 p=0.24	0.413 p=0.13	0.366 p=0.15	0.107 p=0.70	0.497 p=0.04	0.073 p=0.79	0.636 p=0.006	-0.032 p=0.91

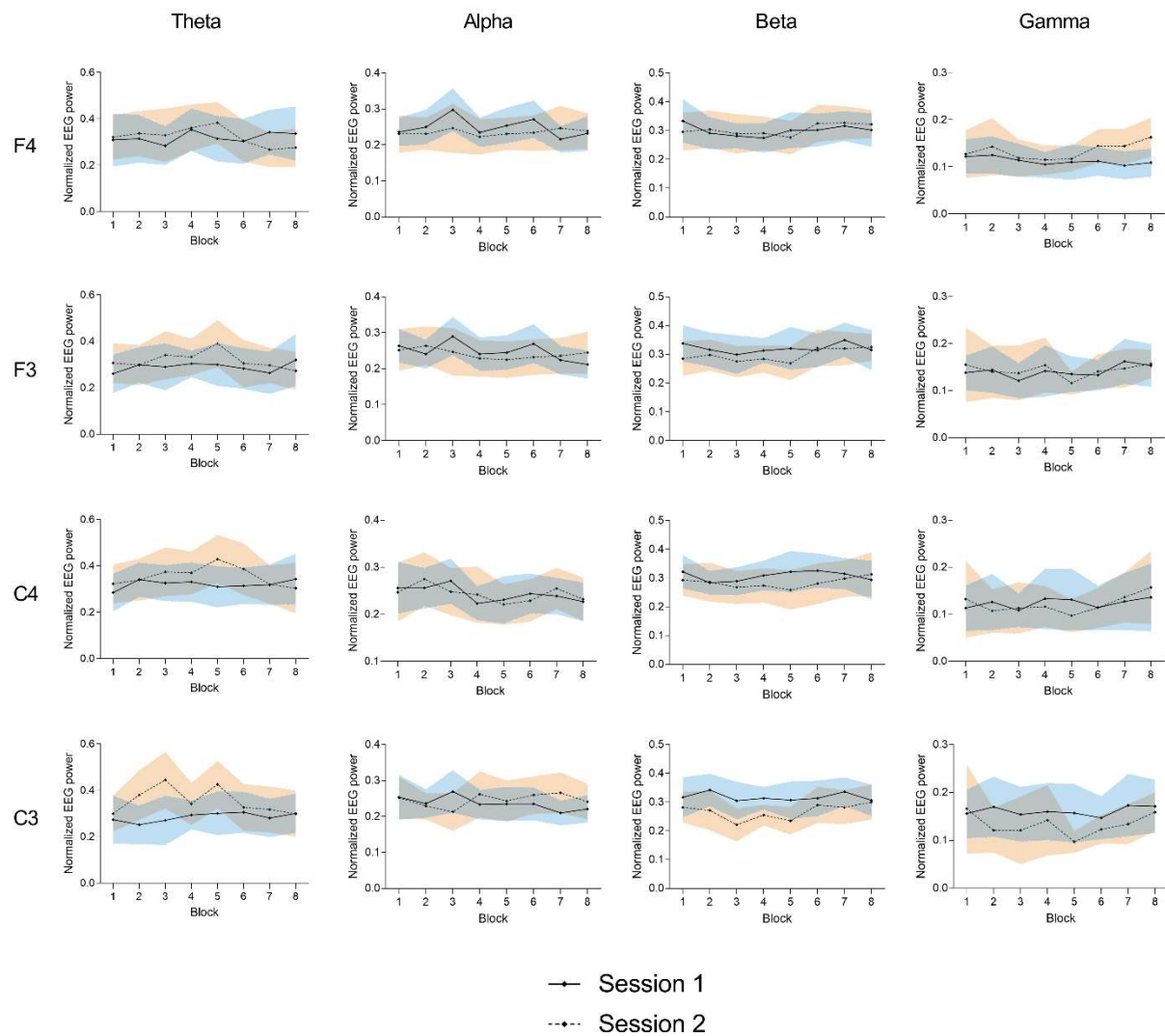
Values in bold denote significant correlations. MVIC, maximum voluntary isometric contraction; RTD, rate of torque development

Electroencephalography

In the relative band power analysis, there was no significant effect of the block factor in any electrode (F4: p=0.340 to 0.573; F3: p=0.144 to 0.450; C4: p=0.242 to 0.660; C3: p=0.297 to 0.925), as well as no differences between sessions (F4: p=0.235 to 0.953; F3: p=0.382 to 0.919; C4: p=0.370 to 0.979; C3: p=0.078 to 0.563, Figure 14). The relative EEG power

nonparametric concordance coefficients ranged from 0.64 to 0.88 (moderate to good) for the percentage of change from the first to the last block and from 0.62 to 0.80 (moderate to good) for the slope of the changes over the eight blocks (Table 6).

Figure 14. Changes in relative theta, alpha, beta, and gamma EEG power during the task



The shaded areas represent the 95% confidence interval for the first (blue) and second (orange) sessions.

Table 6. Relative EEG power test-retest outcomes

		Test-retest outcomes		
EEG channel	Frequency band	Parameter	ICC (95% CI)	SEM
F4	θ	Pre-post	0.768 (0.626 - 1)	144.4%
		Slope	0.658 (0.547 - 1)	0.037
	α	Pre-post	0.708 (0.597 - 1)	48.2%
		Slope	0.667 (0.573 - 1)	0.011
	β	Pre-post	0.623 (0.532 - 1)	43.4%
		Slope	0.756 (0.642 - 1)	0.016
	γ	Pre-post	0.689 (0.568 - 1)	82.2%
		Slope	0.652 (0.562 - 1)	0.0078
F3	θ	Pre-post	0.795 (0.674 - 1)	81.1%
		Slope	0.824 (0.716 - 1)	0.019
	α	Pre-post	0.616 (0.515 - 1)	52.1%
		Slope	0.684 (0.579 - 1)	0.010
	β	Pre-post	0.669 (0.562 - 1)	46.0%
		Slope	0.740 (0.641 - 1)	0.0098
	γ	Pre-post	0.722 (0.604 - 1)	88.3%
		Slope	0.694 (0.591 - 1)	0.0097
C4	θ	Pre-post	0.746 (0.631 - 1)	65.9%
		Slope	0.732 (0.616 - 1)	0.025
	α	Pre-post	0.666 (0.554 - 1)	29.7%
		Slope	0.656 (0.582 - 1)	0.0087
	β	Pre-post	0.680 (0.569 - 1)	44.9%
		Slope	0.738 (0.615 - 1)	0.013
	γ	Pre-post	0.683 (0.574 - 1)	127.7%

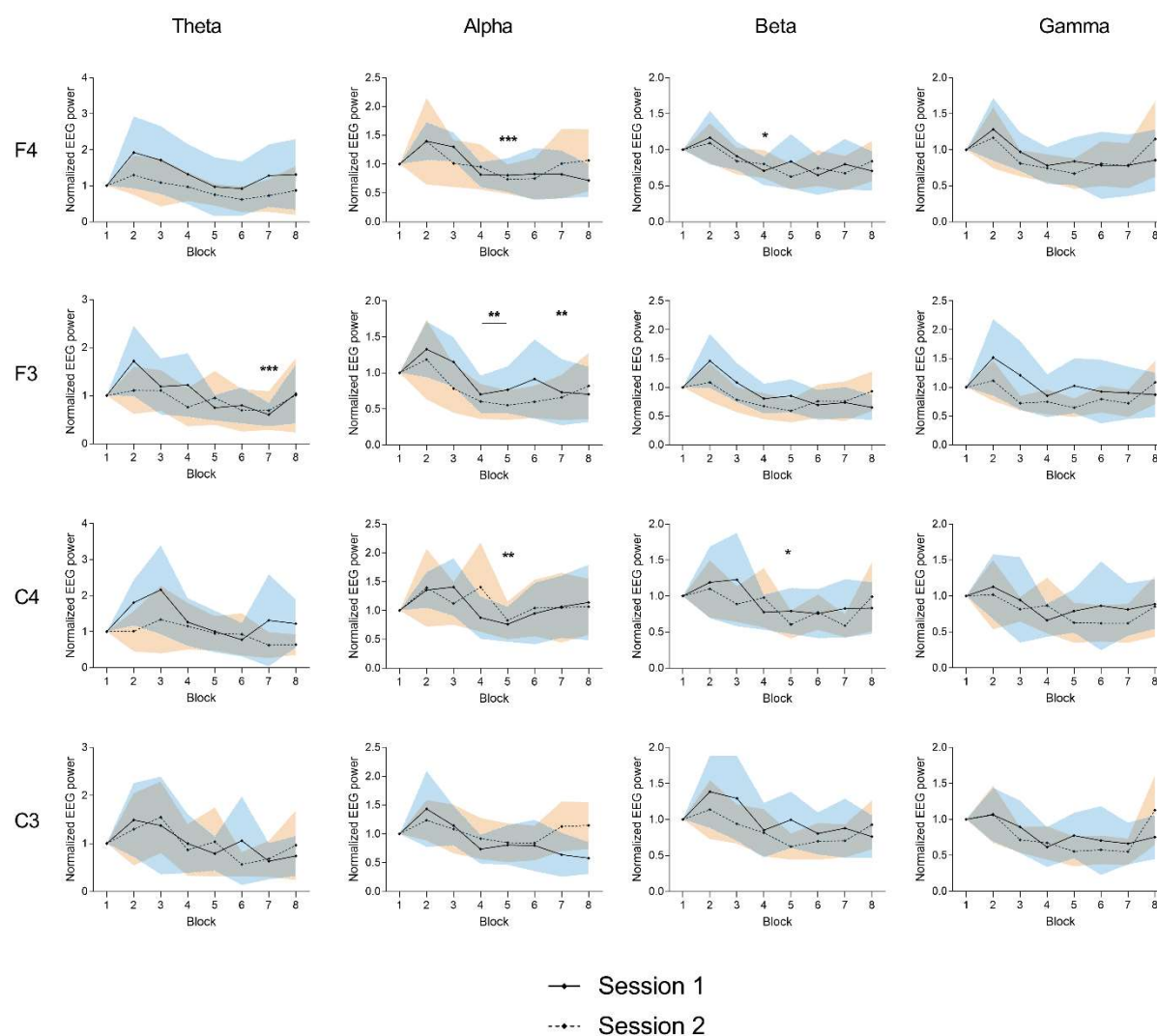
C3	θ	Slope	0.675 (0.573 - 1)	0.015
		Pre-post	0.762 (0.783 - 1)	73.5%
	α	Slope	0.698 (0.576 - 1)	0.029
		Pre-post	0.720 (0.601 - 1)	39.6%
	β	Slope	0.653 (0.571 - 1)	0.010
		Pre-post	0.744 (0.623 - 1)	81.7%
	γ	Slope	0.762 (0.642 - 1)	0.014
		Pre-post	0.723 (0.598 - 1)	155.1%
		Slope	0.678 (0.555 - 1)	0.0093

ICC, intraclass correlation coefficient; CI, confidence interval; SEM, standard error of measurement.

In the normalized EEG power analysis, a significant effect of the block factor was seen in all frequency bands at the F4 (theta: $p=0.02$, $\eta_p^2=0.223$, power=0.78; alpha: $p=0.011$, $\eta_p^2=0.228$, power=0.82; beta: $p=0.002$, $\eta_p^2=0.286$, power=0.93; gamma: $p=0.013$, $\eta_p^2=0.223$, power=0.81) and F3 electrodes (theta: $p=0.02$, $\eta_p^2=0.247$, power=0.77; alpha: $p<0.001$, $\eta_p^2=0.311$, power=0.96; beta: $p=0.005$, $\eta_p^2=0.270$, power=0.88; gamma: $p=0.015$, $\eta_p^2=0.206$, power=0.80) was observed. In the central electrodes, a significant effect of the block factor was only seen in the C3 electrode for the alpha ($p=0.010$, $\eta_p^2=0.203$, power=0.86) and beta ($p=0.001$, $\eta_p^2=0.238$, power=0.96) bands. The results of post-hoc testing regarding significant differences between individual blocks can be seen in Figure 15. In general, these differences tended to show lower EEG power in the later blocks compared to the peak EEG power at the second or third block.

There were no significant differences in normalized EEG power between sessions in any electrode (F4: $p=0.215$ to 0.878 ; F3: $p=0.363$ to 0.553 ; C4: $p=0.197$ to 0.858 ; C3: $p=0.287$ to 0.289). The normalized EEG power nonparametric concordance coefficients ranged from 0.64 to 0.88 (moderate to good) for the percentage of change from the first to the last block and from 0.62 to 0.80 (moderate to good) for the slope of the changes over the eight blocks (Table 7).

Figure 15. Changes in normalized EEG power during the task



The shaded areas represent the 95% confidence interval for the first (blue) and second (orange) sessions. Asterisks indicate significant differences ($p < 0.05$) from the block indicated by the number of symbols.

Table 7. Relative EEG power test-retest outcomes

EEG channel	Frequency band	Parameter	Test-retest outcomes	
			ICC (95% CI)	SEM
F4	θ	Pre-post	0.642 (0.523 - 1)	60.3%
		Slope	0.712 (0.608 - 1)	0.126
	α	Pre-post	0.724 (0.596 - 1)	49.8%

F3	β	Slope	0.738 (0.628 - 1)	0.083
		Pre-post	0.688 (0.594 - 1)	41.5%
	γ	Slope	0.752 (0.626 - 1)	0.054
		Pre-post	0.759 (0.648 - 1)	50.7%
	θ	Slope	0.677 (0.568 - 1)	0.110
		Pre-post	0.629 (0.515 - 1)	86.1%
	α	Slope	0.718 (0.603 - 1)	0.134
		Pre-post	0.723 (0.593 - 1)	52.1%
	β	Slope	0.706 (0.592 - 1)	0.078
		Pre-post	0.761 (0.658 - 1)	25.1%
	γ	Slope	0.797 (0.686 - 1)	0.054
		Pre-post	0.803 (0.671 - 1)	34.3%
C4	θ	Slope	0.631 (0.529 - 1)	0.122
		Pre-post	0.729 (0.604 - 1)	49.5%
	α	Slope	0.655 (0.559 - 1)	0.138
		Pre-post	0.747 (0.621 - 1)	46.9%
	β	Slope	0.710 (0.595 - 1)	0.104
		Pre-post	0.722 (0.605 - 1)	73.7%
	γ	Slope	0.735 (0.606 - 1)	0.071
		Pre-post	0.773 (0.634 - 1)	58.7%
	θ	Slope	0.760 (0.634 - 1)	0.110
		Pre-post	0.878 (0.783 - 1)	49.8%
C3	α	Slope	0.771 (0.655 - 1)	0.010
		Pre-post	0.682 (0.553 - 1)	47.7%
	β	Slope	0.619 (0.507 - 1)	0.078
		Pre-post	0.678 (0.565 - 1)	37.7%
	γ	Slope	0.701 (0.583 - 1)	0.078
		Pre-post	0.740 (0.618 - 1)	47.0%
	θ	Slope	0.692 (0.567 - 1)	0.078
		Pre-post		
	α	Slope		
		Pre-post		
	β	Slope		
		Pre-post		
	γ	Slope		
		Pre-post		

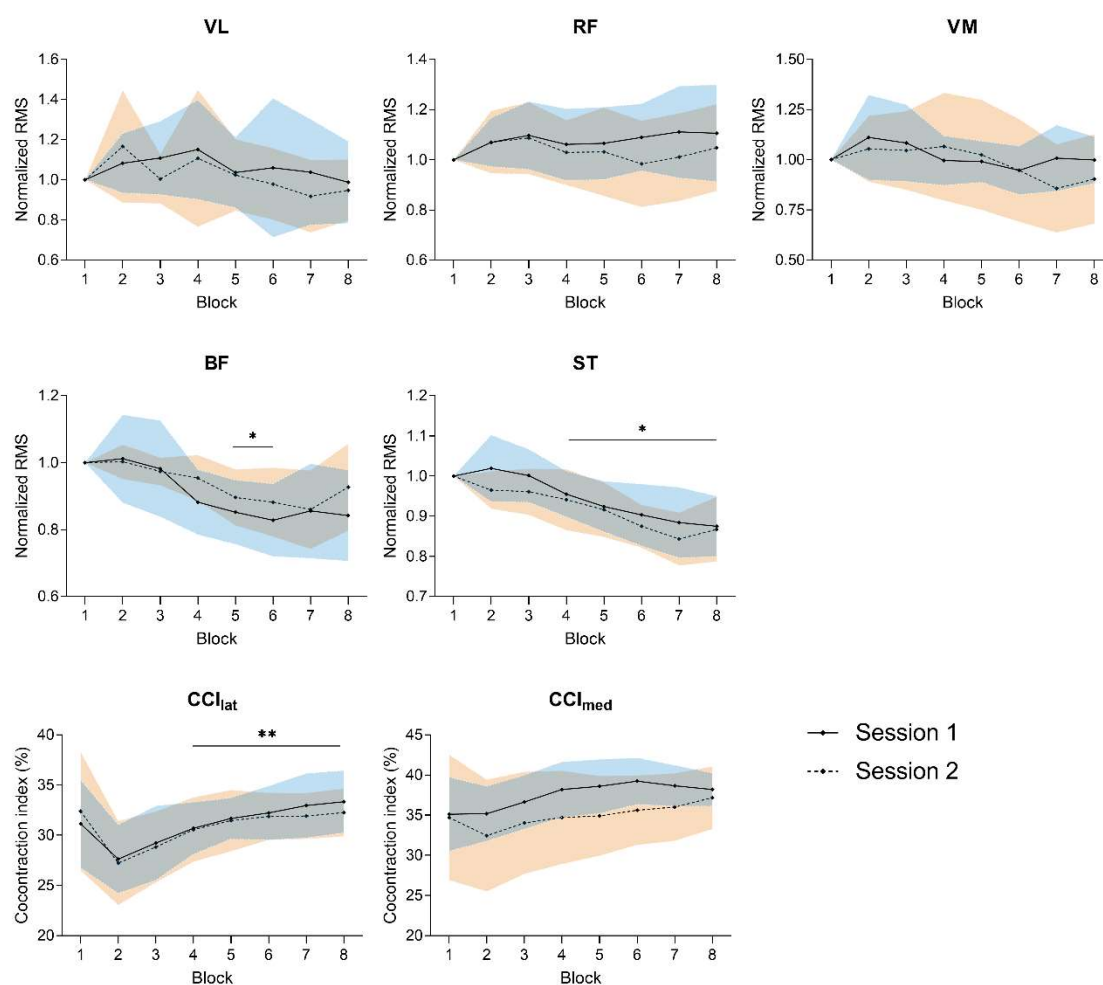
ICC, intraclass correlation coefficient; CI, confidence interval; SEM, standard error of measurement.

Electromyography

The change in RMS across blocks also showed a similar pattern in both sessions. In the knee flexors, there was a significant effect of the block factor, with a decrease in BF ($p=0.003$, $\eta_p^2=0.30$, power=0.91) and ST ($p<0.001$, $\eta_p^2=0.43$, power >0.99) amplitude. Post-hoc testing revealed significant differences between the first and fifth and sixth blocks for the BF and between the first and fifth to eighth blocks for the ST. Conversely, there was no significant effect of the block factor in the normalized RMS of the knee extensors ($p=0.144$ to 0.584). There were also no significant block $\times$ session interactions for the flexor ($p=0.392$ to 0.757) and extensor ($p=0.298$ to 0.766) muscles (Figure 16).

As for the cocontraction indices, CCI_{lat} showed a significant effect of the block factor ($p=0.001$, $\eta_p^2=0.375$, power=0.97). Post-hoc testing revealed that there was a significant increase from the second to the fourth to eighth blocks. On the contrary, despite the positive slope, CCI_{med} showed no significant changes during the task ($p=0.092$). There were also no significant block $\times$ session interactions ($p=0.550$ to 0.799) (Figure 16). The EMG and CCI nonparametric concordance coefficients ranged from 0.65 to 0.79 for the percentage of change from the first to the last block and from 0.62 to 0.80 (both moderate to good) for the slope of the changes over the eight blocks (Table 8). There were no significant between-session differences in any of the EMG variables ($p=0.29$ to 0.894).

Figure 16. Changes in normalized EMG activity and co-contraction indices during the task



The shaded areas represent the 95% confidence interval for the first (blue) and second (orange) sessions. Asterisks indicate significant differences ($p < 0.05$) from the block indicated by the number of symbols. RMS, root mean square; VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus; CCI_{lat}, lateral co-contraction index; CCI_{med}, medial co-contraction index.

Table 8. EMG variables test-retest outcomes

Test-retest outcomes			
Muscle	Parameter	ICC (95% CI)	SEM
VL	Pre-post	0.722 (0.583 - 1)	29.5%
	Slope	0.623 (0.531 - 1)	0.083
RF	Pre-post	0.784 (0.686 - 1)	26.2%

	Slope	0.787 (0.675 - 1)	0.034
VM	Pre-post	0.767 (0.664 - 1)	25.5%
	Slope	0.728 (0.614 - 1)	0.044
BF	Pre-post	0.790 (0.680 - 1)	15.1%
	Slope	0.792 (0.685 - 1)	0.025
ST	Pre-post	0.727 (0.623 - 1)	11.4%
	Slope	0.656 (0.573 - 1)	0.020
CCI_{lat}	Pre-post	0.653 (0.551 - 1)	31.5%
	Slope	0.728 (0.583 - 1)	0.799
CCI_{med}	Pre-post	0.693 (0.576 - 1)	34.1%
	Slope	0.715 (0.596 - 1)	1.056

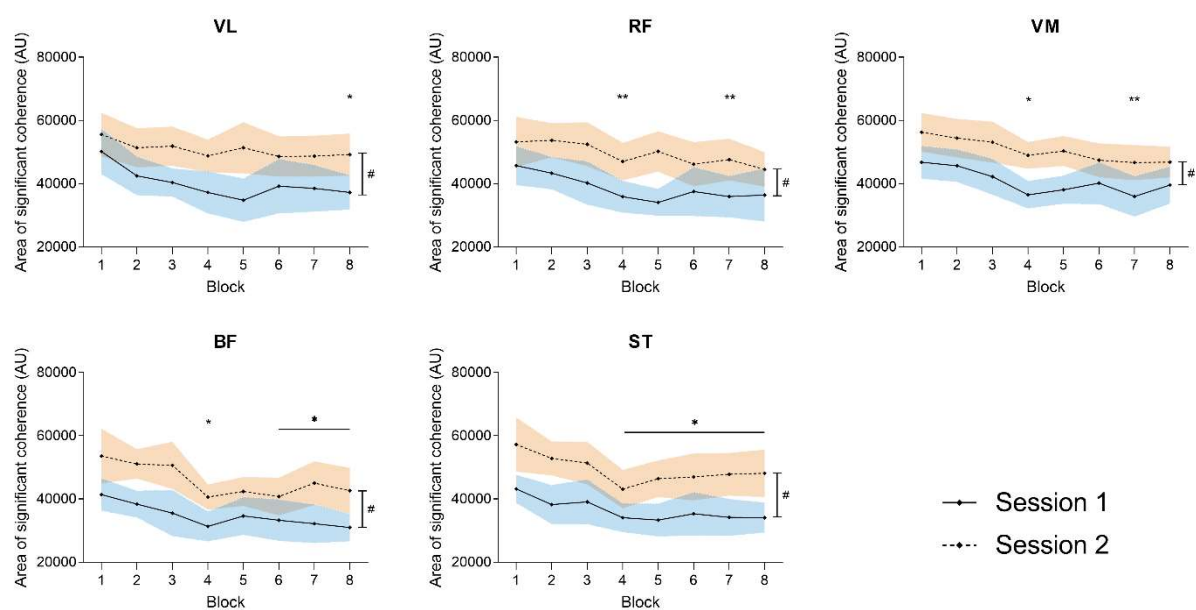
ICC, intraclass correlation coefficient; CI, confidence interval; SEM, standard error of measurement; VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus; CCI_{lat}, lateral co-contraction index; CCI_{med}, medial co-contraction index.

Corticomuscular coherence

There was a significant effect of the block factor for the area of significant CMC, with a decrease in all muscles (VL: $p=0.002$, $\eta_p^2=0.324$, power=0.94; RF: $p=0.003$, $\eta_p^2=0.268$, power=0.93; VM: $p<0.001$, $\eta_p^2=0.302$, power=0.98; BF: $p<0.001$, $\eta_p^2=0.392$, power=0.99; ST: $p<0.001$, $\eta_p^2=0.374$, power=0.98). The results of post-hoc testing can be seen in figure 17; these differences tended to show lower CMC in the second half of the task. There was also a significant effect of the session factor for all muscles, with higher values in session 2 (VL: $p=0.001$, $\eta_p^2=0.624$, power=0.97; RF: $p<0.001$, $\eta_p^2=0.715$, power >0.99; VM: $p<0.001$, $\eta_p^2=0.674$, power=0.99; BF: $p<0.001$, $\eta_p^2=0.392$, power=0.99; ST: $p<0.001$, $\eta_p^2=0.374$, power=0.98). There were no significant block $\times$ session interactions for any EEG-EMG pair ($p=0.285$ to 0.813). Regarding the test-retest analysis, the significant coherence area nonparametric concordance coefficients ranged from 0.683 to 0.790 for the pre-post differences and from 0.667 to 0.814 (both moderate to good) for the slope of the change during the task (Table 9).

The first block images in the time-frequency CMC maps (Figure 18) show two zones with the highest absolute values, located around 3 and 6-8 Hz. While the 3-Hz CMC generally manifested from 4-6 s, the 6-8 Hz CMC was frequently present throughout the entire 8-s period. In line with the significant coherence analysis, a generalized decrease in absolute CMC can be observed from the first to the last block, especially in the frequency zones mentioned above.

Figure 17. Decreases in the area of significant coherence during the task



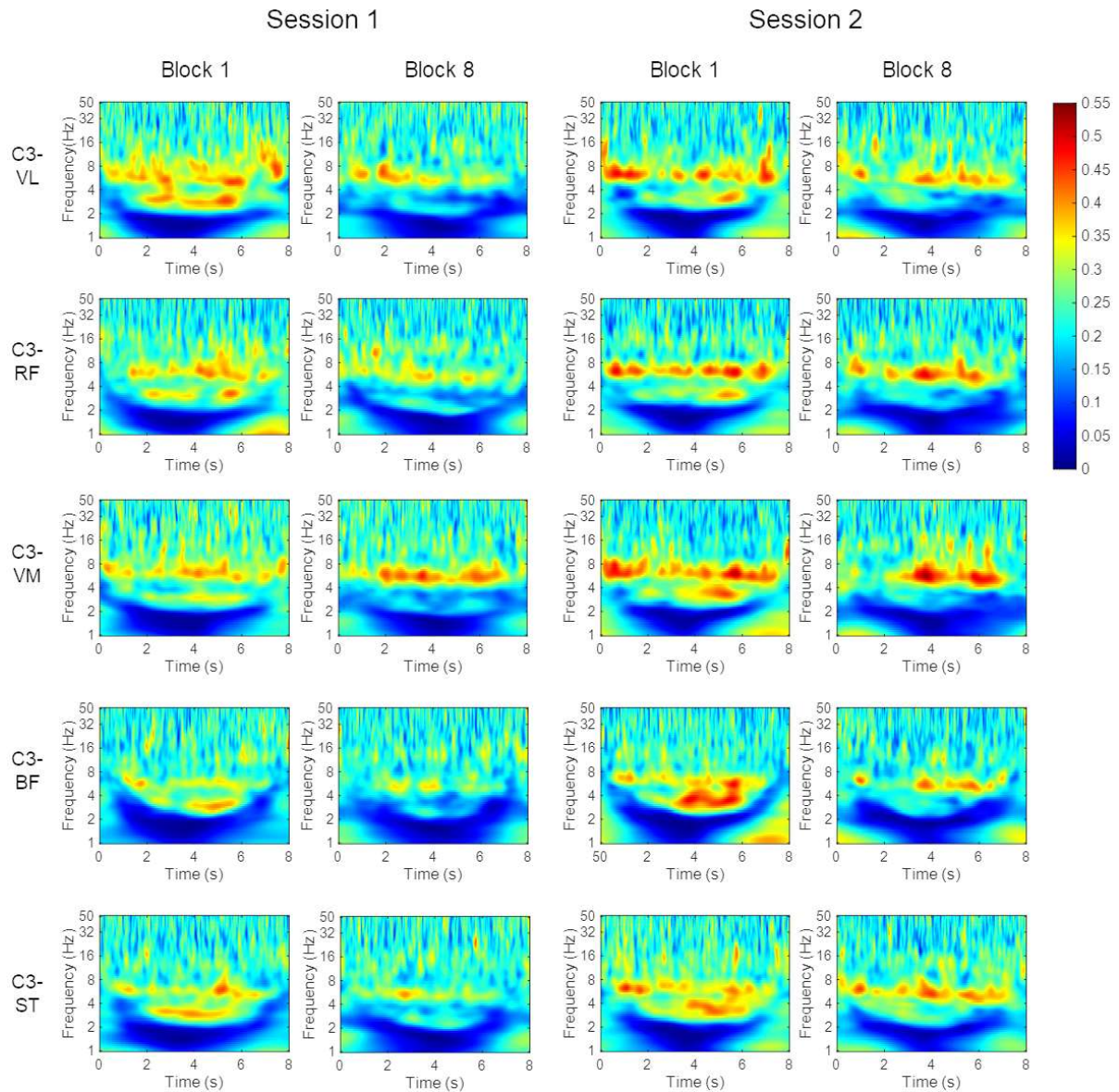
The shaded areas represent the 95% confidence interval for the first (blue) and second (orange) sessions. Asterisks indicate significant differences ($p < 0.05$) from the block indicated by the number of symbols. #significant between-session differences ($p < 0.05$). VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus.

Table 9. Corticomuscular coherence test-retest outcomes

Test-retest Outcomes			
Coherence pair	Parameter	ICC (95% CI)	SEM
C3-VL	Pre-post	0.702 (0.577 - 1)	18.4%
	Slope	0.667 (0.551 - 1)	1365
C3-RF	Pre-post	0.728 (0.621 - 1)	23.4%
	Slope	0.775 (0.659 - 1)	1120
C3-VM	Pre-post	0.790 (0.683 - 1)	16.1%
	Slope	0.814 (0.714 - 1)	966
C3-BF	Pre-post	0.726 (0.626 - 1)	17.6%
	Slope	0.743 (0.633 - 1)	1140
C3-ST	Pre-post	0.771 (0.657 - 1)	12.6%
	Slope	0.781 (0.657 - 1)	787

ICC, intraclass correlation coefficient; CI, confidence interval; SEM, standard error of measurement. VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus.

Figure 18. Time-frequency maps of corticomuscular coherence in the first and last blocks between the C3 EEG electrode and each muscle



VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus.

Discussion

Knee movement rate significantly decreased until half of task duration followed by a plateau until the end. In association with this decrease, we found both central and peripheral electrophysiological changes. There were significant decreases in normalized EEG power, especially at the frontal electrodes, while the CMC analysis showed a decrease in brain-muscle functional coupling during the task. EMG testing revealed a decrease in knee flexor normalized RMS and increased VL/BF co-contraction after the second block. The torque and

RTD variables followed the same trend of EMG amplitude, with significant decreases in post-task knee flexion MVIC and RTD.

The degree of knee motor slowing was similar to what we previously observed in a preliminary study (Correia et al., 2022). The loss of movement rate (-15.8% and -12.9% in the two sessions) is comparable, albeit slightly lower, than what has been observed in finger tapping tasks of 10-30 s in total (18-27%) (Arias et al., 2015; Madrid et al., 2018; Rodrigues et al., 2009) and closer to similar periods of foot tapping (~15%) (Bächinger et al., 2019; Seidel-Marzi & Ragert, 2020), despite the difference in task parameters. Considering the longer duration of our task (8 blocks of 10 s vs. a single 10-30 s period in the cited studies), a greater loss could be expected. However, unlike we hypothesized, the movement rate decreased only until the fourth block (i.e., 55 s). Nevertheless, the good to excellent movement rate ICCs and the standard errors of measurement indicate that these measures' between-session stability. Comparatively, finger motor slowing has been found to plateau only after about 120 s of continuous tapping, corresponding to a 40% decrease in movement rate (Madinabeitia-Mancebo et al., 2020). Knee motor slowing thus seems to show some similar and some different properties relatively to smaller joints. On one hand, the plateau in knee movement rate was reached at a lower percentage of decrease (13-16% and 25-40% for the knee and fingers, respectively). On the other hand, the trajectory of decrease shows similarities, with a steep decrease in the first stages of the task and a gradual smoothing until a plateau at around 50% of task duration (for comparison, please see (Bächinger et al., 2019; Madinabeitia-Mancebo et al., 2020)). The larger segment inertia may play a role in these differences. While small joint all-out repetitive movement does not present a significant metabolic and homeostatic challenge, our task has greater muscle work and energy demands due to the larger mass being moved, which may have led to a plateau at a lower percentage of performance loss in order to ensure homeostatic regulation. Interestingly, the ATP-PCr system's contribution during maximal exercise starts plateauing at about 50 seconds (Gastin, 2001), which corresponds approximately to the point where the movement rate stabilized in our task. Therefore, energy availability and homeostatic regulation may have played a role in movement rate stabilization after the fourth block. As expected, this stabilization in movement rate in the second half of the task was reflected in the changes in cycle duration, where a similar task was seen.

Changes in MVIC after finger movement rate tasks have been conflicting, with some authors finding significant decreases (Arias et al., 2015; Madinabeitia-Mancebo et al., 2021) and others finding no differences (Madrid et al., 2018; Rodrigues et al., 2009). Our findings align with the first group, since there were significant post-task decreases in flexor but not

extensor MVIC. We believe this was mostly due to the fact that the flexors functioned against gravity and therefore performed more muscle work than the extensors. However, there may also be other factors contributing to this finding. For example, it has been reported that the BF force generation depends more on MU synchronization than the RF due to a greater proportion of type I fibers, requiring a larger or more synchronized motor command to generate maximum force (Higashihara et al., 2022). In this sense, both the increased antigravity work and the post-task central inability to generate a synchronized command to MUs may have played a role.

As for the RTD findings, the ability to produce flexion torque in the first 150 ms was significantly impaired. Central fatigue has been reported to play a role in the decrease of MU firing rates during the early contraction periods (Morel et al., 2015). Accordingly, other central factors are known to influence contraction speed and early RTD, namely the supraspinal drive (latency of MU activation, motor neuron recruitment speed) and presynaptic inhibition (Del Vecchio et al., 2019; Dideriksen et al., 2020; Morel et al., 2015). Both these factors allow for a greater number of MUs to be recruited in a shorter amount of time, thus increasing RTD. Our RTD findings, therefore, suggest the impairment of these supraspinal factors in the post-task flexion torque generation ability. Nevertheless, there was a comparable loss in flexion MVIC and RTD (across all periods) within each session, which suggests that the mechanisms of force production were affected at multiple levels.

There was a significantly higher extension RTD in the second session, which indicates that there may have been a learning effect, especially considering that the participating individuals were not familiar with explosive tasks. Maximum RTD, especially up to 200 ms (Cossich & Maffiuletti, 2020), and MVIC have distinct physiological determinants. The former is more dependent on central aspects, such as MU synchronization and recruitment rate, while the latter is more dependent on muscle factors such as the cross-sectional area (Maffiuletti et al., 2016). Our correlation findings support these different determinants of MVIC and RTD in flexion but not as much in extension, as most periods of extension RTD showed a significant correlation with extension MVIC. The fact that our participants were not trained in explosive or high-resistance tasks may explain why there was a significant between-session increase in extension RTD but not on MVIC. On another perspective, the higher content of fast fibers of the knee extensors compared to the knee flexors may be why there was no corresponding between-session increase in flexion RTD. Finally, since there were significant reductions in both flexor MVIC and RTD, the task used in this study seems to have had an impact at multiple levels of the force generation pathway.

EEG findings partly support the previously mentioned role of homeostatic regulation. After an initial increase, there was a decrease in EEG power which started even before the movement rate stabilized. Post-hoc testing showed that individual inter-block decreases were seen most commonly between an initial peak at the second or third block (i.e., with low fatigue but when movement rate was decreasing) and lower values within the second half of the task (i.e., with greater fatigue but stable movement rate). It has been reported that brain activity increases with fatigue or task demands (Bailey et al., 2008; Enders et al., 2016; J. Z. Liu et al., 2002, 2003); this increased central drive aims to compensate for the decreased peripheral ability to produce force. Our opposing findings may be due to inhibitory activity of group III/IV sensory afferents, whose involvement in both central and peripheral fatigue development has previously been reported (Amann et al., 2015; Sidhu et al., 2018). These afferent signals modulate motoneuron output, leading to decreased muscle activation (Amann et al., 2015). Although speculative, this explanation is supported by our EEG and flexor EMG findings. Supraspinal performance modulation even before task failure or a performance plateau has also been seen in other tasks (J. Z. Liu et al., 2002; Rupp & Perrey, 2008).

There was a similar EEG trajectory during the task across frequency bands and electrodes, characterized by an initial increase (up to block 2-3) followed by a decrease (until block 4-6), more notably at frontal than at central electrodes. Frontal electrodes cover areas such as the prefrontal and the anterior cingulate cortices, which play a role in movement planning and regulation (Herz et al., 2017; Scott, 2004), while central electrodes cover the supplementary motor area and the motor cortex, which are involved in the temporal coding of movement parameters and in producing the descending motor command (Bourguignon et al., 2012; Loh et al., 2017). EEG data thus show that movement planning may have been more affected by our task than the production of the motor command. Additionally, the significant effect of the block factor in all frequency bands at frontal electrodes contributes to the growing evidence that the cortex plays a significant role in rhythmic movement control (Bourguignon et al., 2012; Enders et al., 2016; Jain et al., 2013), in this case, performed at maximum speed.

There were no significant changes in knee extensor EMG. Conversely, both the BF and ST normalized RMS significantly decreased continuously throughout the task despite the movement rate stabilization after the fourth block. These differences between flexors and extensors were probably due to the anti-gravity position of knee flexion in our task. Other studies of maximal lower limb intermittent effort have also found a continuous decrease in EMG amplitude throughout the task (Billaut & Smith, 2010; Brocherie et al., 2015; Mendez-Villanueva et al., 2008, 2012). The decrease in knee flexor EMG amplitude may be caused

by selective fatigue of fast-twitch fibers, since these have been shown to be preferentially recruited during rapid contractions (Hodson-Tole & Wakeling, 2008; Wakeling et al., 2006). It makes sense that the number of motor units sufficiently fast to cope with the movement rate demands decreased continuously during the task, thus explaining the generally continuous decrease in normalized RMS in our study. Considering the changes in EEG power, impaired central recruitment could also be the cause of the flexor EMG amplitude decrease. However, if this was the case, there should not be a continuous decline in EMG amplitude, and it is also not in line with the plateau in movement rate.

Previous studies have found an increase in muscle half relaxation time (Madinabeitia-Mancebo et al., 2021; Madrid et al., 2018), a loss of a clear agonist-antagonist EMG pattern after fatiguing finger tapping tasks (Rodrigues et al., 2009), and a decrease in the agonist-antagonist activation delay in a cycling repeated sprinting task (Billaut et al., 2005). In our study, the fact that CCI_{lat} increased gradually from the second block despite the decrease in BF RMS further suggests a greater temporal agonist-antagonist overlap with increasing fatigue, as previously reported (Rodrigues et al., 2009). This increased overlap may be due to the earlier fatigability of fast-twitch fibers, which would lead to prolonged muscle activation in order to maintain movement rate (Hodson-Tole & Wakeling, 2008; Wakeling et al., 2006). It is logical that this greater EMG overlap/co-contraction and lower availability of fast muscle fibers would lead to a decrease in movement rate; however, in that case, both CCIs should not have continued to increase during the second half of the task. Thus, it seems the continuously worsening EMG overlap with fatigue did not impair movement rate after a certain point. It is also noteworthy that the CCIs continued to increase despite the lack of changes in EEG power, indicating that this was not due to the strength of the central drive. It may therefore be more related to the quality of the motor command than to its intensity, which may be corroborated by the CMC findings discussed below.

There was a decrease in the area of significant CMC in all muscles, reflecting a generalized loss of brain-muscle coupling, which in turn was associated with the decreased movement rate. It is interesting to note that despite the lack of significant changes in knee extensor normalized EMG amplitude, there was still a loss of knee extensor CMC, suggesting that decoupling may occur even in the absence of significant EMG amplitude changes. This may be a sign of a centrally driven generalized loss of coupling between brain and muscle activity during the task, perhaps due to the breakdown of central motor control mechanisms related to the change in movement direction caused by unsustainable task demands suggested by Rodrigues et al. (Rodrigues et al., 2009).

There were two frequency zones of higher CMC in the first block (around 3 and 6-8 Hz). These two zones may represent the movement rate (fundamental frequency, F0) and its first harmonic (F1) frequency. Previous studies of both hand and feet rhythmic movements also found stronger coherence at these two frequencies (Bourguignon et al., 2012; Raethjen et al., 2008). Our task caused a greater decrease in F0 than in F1. It is worth noting that these two frequencies are generated by different cortical regions; while F0 is associated with sensorimotor movement kinematics encoding, F1 has been found to be more prominent in the prefrontal cortex, which is responsible for movement planning, timing, and self-initiation (Abe & Hanakawa, 2009; Bourguignon et al., 2012). We found greater decreases in the F0 range, suggesting an impairment in movement kinematics encoding, which is consistent with the breakdown of the motor command mentioned as a cause of motor slowing mentioned previously (Rodrigues et al., 2009). Thus, isolated EEG changes suggest that movement planning areas are more affected by the task, but CMC losses seem to be more related to the motor command.

Whether maximal exercise performance is regulated to limit the development of catastrophic fatigue remains controversial (Hureau et al., 2014; Thomas et al., 2018). Here, a plateau of performance was reached at about 50% of task duration. Early performance decreases followed by a plateau until task completion have been seen in distinct maximal effort upper and lower limb joint tasks (Brocherie et al., 2015; Hureau et al., 2014; J. Z. Liu et al., 2002; Madinabeitia-Mancebo et al., 2020; Mendez-Villanueva et al., 2008, 2012), suggesting the presence of some common regulation mechanism. Nevertheless, the percentage of decrease in performance at which this plateau is reached is task-dependent (Bächinger et al., 2019; Hureau et al., 2014; Madinabeitia-Mancebo et al., 2020). Our findings suggest that performance was regulated in the absence of catastrophic failure but not exclusively due to peripheral feedback; rather, it seems that multiple systems may have influenced the central motor command and limit further decreases in exercise performance. The level of task performance decrease before this plateau is reached may therefore be both task- and system- (i.e., locomotor, cardiometabolic) specific. Naturally, this requires further confirmation.

Limitations

Despite our attempts to monitor processes from the brain to the motor output, some limitations remain. We did not obtain EMG data from both limbs or from other muscles which

may have played a role in our task (e.g., gastrocnemius). However, since our participants were healthy and the task was bilaterally symmetrical, we did not anticipate significant between-limb differences. We also did not measure fatigue perception, which limits our discussion of task demands. Moreover, the highly dynamic nature of our task means that despite our best efforts to clean the EEG signal, some degree of noise can still be expected, considering the difficult balance between signal cleaning and loss of physiological information. Our findings may also not be generalizable to female participants or other age groups. Finally, although all individuals had at least a week between sessions, the length of this interval was not uniform.

Conclusions

The designed task was able to induce significant knee motor slowing, but this decrease in movement rate stopped halfway through the task. Electrophysiological data suggest that both central and peripheral processes were involved in this slowing. Most notably, we found a decrease in EEG power after an initial peak, followed by a subsequent stabilization, while there was a continuous decrease in flexor EMG activity and increase in co-contraction. CMC decreased during the task, suggesting an impairment of EEG-EMG functional coupling with fatigue. However, no single analysis showed an isolated direct relation with task performance, suggesting that the interaction of changes at various levels was involved in performance regulation.

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CHAPTER V – DOES THE TORTOISE OR THE HARE HAVE A HIGHER RISK OF HAMSTRING STRAIN? MOVEMENT RATE AND BRAIN-MUSCLE COUPLING IN FOOTBALL PLAYERS WITH AND WITHOUT HAMSTRING INJURY HISTORY

Abstract

High-speed actions constitute an important mechanism of hamstring strain injuries (HSIs) in football. These actions have a strong supraspinal base, and changes in brain activity have been noted in other musculoskeletal injuries; however, there is a lack of information about changes in brain-muscle coupling in footballers with HSI history. Therefore, this study aimed to determine if movement speed and brain-muscle activity differ between players with and without HSI history during a high-speed knee movement task. A total of 108 footballers (39 with HSI history) were included and performed a maximum-speed knee flexion-extension task over eight 10-s blocks. During this task, brain and muscle activity of knee flexors and extensors were recorded using electroencephalography (EEG) and electromyography (EMG), respectively, and the movement rate was measured. Players with HSI history showed a higher movement rate in the first half of the task, which was accompanied by higher theta and decreasing alpha EEG activity, lower rectus femoris and biceps femoris activity, and less flexor-extensor co-contraction. Conversely, there were no differences in corticomuscular coherence between groups. The used task was able to differentiate players with and without HSI history; additionally, the former showed EEG activity patterns associated with increased task load and use of attentional resources for sensorimotor integration. EMG findings indicated players with HSI history were able to perform better despite showing overall reduced activity, especially in the rectus femoris and biceps femoris. These findings suggest the need to address both central and peripheral changes in HSI rehabilitation.

Introduction

Despite abundant research on hamstring strain injuries (HSIs) on football players, a high prevalence and recurrence rate remain (Ekstrand et al., 2016, 2023). Multiple potential risk factors have been proposed; however, previous injury remains as the strongest risk factor (Engebretsen et al., 2010; van Beijsterveldt et al., 2013). In turn, there is a greater agreement on the relevance of sprinting as an important HSI mechanism (Huygaerts et al.,

2020); it was also reported that over 70% of HSIs in football occur at high or very high horizontal speeds (Jokela et al., 2022). Sprinting also has a great sport-specific relevance; it constitutes the most frequent action before goals are scored for both the scoring and assisting player (Faude et al., 2012), despite accounting for only 1-12% of the distance covered (Di Salvo et al., 2010). Accordingly, repeated sprinting is commonly used to assess multiple aspects of hamstring performance and injury risk (Brocherie et al., 2015; Røksund et al., 2017), and a greater drop in sprint speed (Røksund et al., 2017) and horizontal force production (Lord et al., 2019) has been seen in players with HSI history. Another important feature of maximal speed sprinting is the importance of intermuscular and interlimb coordination (Takehata et al., 2021; Whitacre et al., 2024). Indeed, a bilateral difference in hamstring intermuscular coordination has been found in athletes with HSI history, even after completing rehabilitation (Avrillon et al., 2020), and fatigue induced by fast repetitive movements has an important supraspinal component (Madrid et al., 2018). The importance of central motor control for high-speed actions is also shown by the fact that motor neuron recruitment speed and maximal motor unit discharge are the best predictors of contraction speed, and that the neural drive produced in the initial phase of an explosive contraction is predominantly supraspinal (Del Vecchio et al., 2019).

As such, it is important to assess both isolated brain and muscle activity in the context of HSIs but also their coupling during high-speed actions. This can be done using methods such as corticomuscular coherence (CMC), which analyzes the functional brain-muscle coupling (Yang et al., 2010) and has been shown to reflect the synchronization of activity at both ends of the corticospinal pathway (Sherman et al., 2023). However, repeated sprinting is a whole-body activity with complex performance and metabolic interactions as well as multiple limiting factors, and it remains challenging to measure brain activity during sprinting. Therefore, to more specifically assess supraspinal changes in athletes with HSI history, a task that mimics the knee intermuscular and interlimb coordination demands of maximal sprinting but with more specific knee agonist-antagonist coordination requirements and a lower metabolic cost would be preferable to determine HSI risk and associated brain and muscle activity. Determining these neurophysiological changes would be important to ascertain whether neurocognitive rehabilitation should be a part of HSI treatment regimens.

Despite their potential relevance, information about supraspinal changes in athletes with HSI history is scarce; there have, however, been reports of greater intracortical inhibition and lower voluntary activation in athletes with HSI history (Buhmann et al., 2020, 2022a). Furthermore, hamstring inhibition has been reported to persist even after completing rehabilitation and to play a role in injury recurrence (Fyfe et al., 2013; Higashihara et al.,

2019; Opar et al., 2012), which also highlights the relevance of looking upstream of the neuromuscular junction in players with HSI history. In other injuries, individuals with anterior cruciate ligament (ACL) tears have shown early post-injury decreased cortical excitability (Zarzycki et al., 2018), increased sensorimotor cortex activity during movement (An et al., 2019; Grooms et al., 2017), and decreased leg representation area volume (Flanagan et al., 2021). Decreased post-ACL injury quadriceps CMC (Sherman et al., 2023) and cross-recurrence (Riehm et al., 2024) have also been reported, showing that musculoskeletal injuries affect the brain-muscle coupling.

Thus, this study aimed to 1) determine whether a maximum knee movement rate task is able to differentiate football players with and without HSI history; and 2) to assess differences in brain and muscle activity and brain-muscle coupling during this task between football players with and without HSI history. We hypothesized that players with HSI history would have a lower movement rate due to previous reports of HSI-associated impaired leg swing movement discrimination (Cameron et al., 2003) and altered hamstrings intermuscular coordination (Schuermans et al., 2016). We also hypothesized that they would show patterns of reduced brain and muscle activity (due to post-injury inhibition) and decreased corticomuscular coherence (as seen in ACL injuries).

Materials and methods

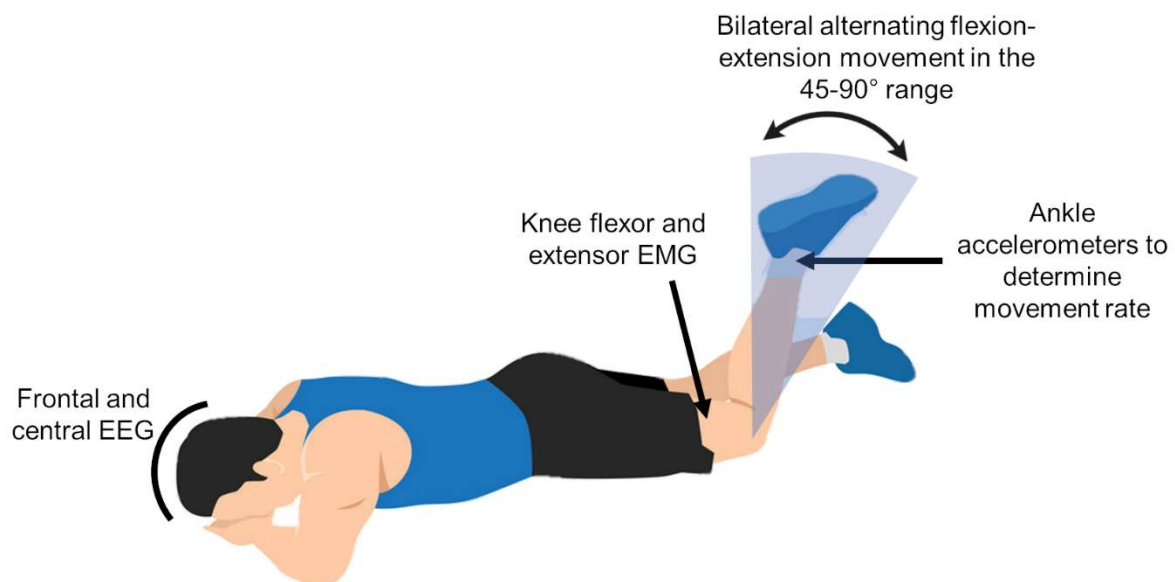
Study design and sample

This was a retrospective study; players were recruited from a total of nine participating clubs from the Portuguese second to fourth tiers, totalling 223 professional and semi-professional players. Despite this difference in professional status, off-field activities have been shown to not influence HSI risk in non-professional players (Brauers et al., 2022). Inclusion criteria were 1) having played football for at least five years; 2) at least three training sessions plus a match per week; 3) no active injury limiting performance. Exclusion criteria were 1) playing as a goalkeeper (due to differences in activity patterns and HSI risk from outfield players (Green et al., 2020)); 2) history of knee, thigh, hip, or central nervous system structural injury or surgery; 3) practicing other sport or structured physical activity ≥ 2 times/week in the last 2 years; 4) any condition preventing the player from completing the study protocol. This study was approved by the institutional review board of Faculdade de Motricidade Humana (approval number: 15/2021); all players signed an informed consent form after all aspects of the study were explained.

Experimental protocol

Prior to the main task, players completed a 5-min warm-up on a stationary bicycle at a comfortable pace (~70 rpm) without added resistance. They were then placed in the prone position on a table and performed a task consisting of eight 10-s blocks of maximum-speed bilateral alternating knee flexion-extension movements between 45 and 90° interspersed by 5-s rest periods (Figure 19). A familiarization period with the required range of motion was included, with soft bumpers serving as a range of motion reference during this period and removed during task performance. Players had as long as they wanted to confirm familiarization. We previously showed that this method led to nonsignificant deviations from the 45-90° knee range of motion (Correia, Vaz, Witvrouw, et al., 2022). Players were instructed to always move as fast as they could, to keep their head as still as possible, and to not clench their eyes or teeth; standard encouragement was given throughout the task. During every rest period, players were asked to report their rating of perceived exertion (RPE) in a 0-10 modified Borg scale.

Figure 19. Depiction of the experimental task and data collection



Data collection

Demographics and injury data

Demographic and football-related data were obtained from players, including height, weight, playing position, HSI history in the previous two seasons, time loss due to HSIs, mechanism and context of injury (training or match), and other injury history. HSI was defined as any sudden onset of posterior thigh musculotendinous pain in the hamstring region which led to training or match time loss. A retrospective period of two seasons has previously been used in studies of football-related HSIs (Røksund et al., 2017; Schuermans et al., 2014). Additionally, the accuracy of hamstring injury self-reporting has been previously confirmed (Gabbe et al., 2003).

Dynamometry

Before and after the main task, players completed a maximum voluntary isometric contraction (MVIC) evaluation using an isokinetic dynamometer (System 3, Biodex Medical Systems, Inc, Shirley, NY). The right side was evaluated in all players, and they were instructed to perform the contraction “as fast and as hard as possible”. Both the knee extension and flexion MVIC were measured in the prone position at 45° of knee flexion. In addition to the waist strap, players had a strap placed just proximal to the knee during all MVICs. Two valid repetitions of each MVIC were performed separated by a one minute interval. The post-task evaluation was started within 30 seconds of finishing the main task and the flexion-extension order was counterbalanced across players. Torque data were collected at a sampling frequency of 1000 Hz.

Electroencephalography (EEG)

EEG data were collected using a 24-channel device (Vertex SC823, Meditron Eletromedicina Ltda, São Paulo, Brazil). The Cz electrode was aligned with the midpoints of the inion and nasion in the sagittal plane and the two preauricular points in the coronal plane, with the remaining electrodes placed according to the international 10–20 system. The signal was online-referenced to two mastoid electrodes and collected at a sampling frequency of 250 Hz. A circuit impedance ≤ 10 k Ω was ensured in all electrodes prior to starting data collection and a 0.1–70 Hz analog band-pass filter was applied by the amplifier.

Electromyography (EMG) and accelerometry

Surface EMG data were collected at a sampling frequency of 1926 Hz in the 10-850 Hz frequency range using a wireless system (Trigno, Delsys, Natick, MA). Electrodes were placed on the right vastus lateralis (VL), rectus femoris (RF), vastus medialis (VM), semitendinosus (ST), and biceps femoris long head (BF) of the right lower limb according to SENIAM recommendations for electrode placement (Hermens et al., 2000) and secured with adhesive tape. Skin preparation included shaving and cleaning with alcohol. Accelerometry data were collected using electrodes placed on the lateral malleoli at a sampling frequency of 148 Hz. A trigger was used to start EEG and EMG/accelerometry data collection simultaneously. The right limb was assessed in all players regardless of their dominance, as the main focus of this study was central motor control; the left hemisphere, primarily responsible for right limb movement, has been shown to specialize in controlling fast repetitive movement (Agnew et al., 2004; Nalçaci et al., 2001). Previous studies of lower limb movement rate have also not categorized participants according to dominance (Yoshida et al., 2017a, 2017b). Considering this functional asymmetry, the different association with dominance of the left and right hemispheres (Hervé et al., 2005), the potentially opposing effects of injury side and dominance, and the fact that all players were symptom-free at the time of testing, we chose to place the EMG electrodes on the right side for all players. Moreover, a systematic review found evidence of no differences in muscle activity between injured and uninjured limbs in individuals with HSI history during maximal speed running (Presland et al., 2021).

Data processing

Data were processed using dedicated Matlab (MathWorks Inc., Natick, MA) scripts; the data processing has been previously described in detail (Correia et al., 2023). Briefly, for EEG and EMG signals, the first and last seconds of each movement block were discarded to increase signal stability; for the movement rate calculation, the entire 10-s period was used. Movement rate was determined by determining the number of accelerometer signal peaks during each block and divided by 10 to present a value in Hz; the presented values correspond to the movement rate of each limb.

Knee flexion and extension torque data were used to calculate the early (0-50 ms and 50-100 ms) and late (100-150 ms and 150-200 ms) RTD. The flexion/extension ratio was also calculated for MVIC values by dividing the two values. Both the MVIC and RTD values were

normalized to body weight to allow for a more accurate comparison. Further details about dynamometry data processing can be seen in Correia et al. 2023.

The EEG power was calculated for the theta (4-7 Hz), alpha (8-14 Hz), beta (15-30 Hz), and gamma (31-50 Hz) bands. We calculated two measures of EEG power for each block: the relative power of each band as a percentage of the total power, and the band power normalized to the first block. EEG measures were calculated for the F3, F4, C3, and C4 electrodes, which correspond to areas associated with motor planning and execution and which show movement rate-mediated activity (Correia, Vaz, Domingos, et al., 2022). Independent component analysis (ICA) was performed using EEGLAB (Delorme & Makeig, 2004) to remove muscle, eye, line noise, mechanical, and other artifacts from the filtered EEG signal using visual inspection to determine the components to be removed. Artifacts were identified based on their waveform and biological plausibility. If these artifacts could not be removed in an isolated manner using ICA, artifact subspace reconstruction was used to minimize signal loss.

The EMG root mean square (RMS) was calculated as a measure of muscle activity and the values were normalized to those of the first block. Two EMG co-contraction indices (CCIs) were calculated as a measure of agonist-antagonist coordination using the percentage of overlap between the activity of the corresponding muscles (Lo et al., 2017); one between the VL and BF (CCI_{lat}) and another between the VM and ST (CCI_{med}).

Corticomuscular coherence (CMC) was calculated as a measure of EEG-EMG functional coupling between the C3 electrode and each muscle's EMG signal. The threshold for coherence significance (CT) was calculated using the following equation (Yoshida et al., 2017c):

$$CT = 1 - \left[\frac{1}{N} \left(1 - \frac{\alpha}{100} \right) \right]^{\frac{1}{L-1}}$$

where N is the number of frequency bins and α is the confidence level (95% in our study). Considering the cyclic nature of our task, we defined L as the number of cycles completed by each player in each block (Yoshida et al., 2017c). This allowed us to have a CT adjusted to each participant and movement block. Two coherence outcomes were used: the total area of coherence above the CT (significant coherence) and time-frequency CMC maps as a qualitative analysis.

Statistical analysis

SPSS version 25 (IBM Corp., Armonk, NY) was used for all analyses. Continuous data are presented as mean and 95% confidence interval (CI) and categorical data are presented as frequencies and percentages. A two-way mixed ANOVA [2 (HSI, no HSI) x 8 blocks] was performed with movement block (within-subject) and HSI history (between-subject) factors for the movement rate, EEG, EMG, and significant CMC, with post-hoc Bonferroni adjustment for multiple comparisons and Greenhouse-Geisser correction if sphericity was not present. Torque and RTD values were compared between injured and non-injured players using a two-way mixed ANOVA [2 (HSI, no HSI) x 2 measurements (pre, post)]. These values were also compared between left- and right-sided injuries using a two-way mixed ANOVA [2 sides (left, right) x 2 measurements (pre, post)] in the injured players subgroup and between left- and right-dominant players using a two-way mixed ANOVA [2 sides (left, right) x 2 measurements (pre, post)] in the whole sample. For the comparison of significant coherence between muscles, a two-way repeated measures ANOVA (5 muscles x 8 blocks) was used. Effect sizes were calculated using partial eta squared (η^2) values and classified as small (0.01-0.06), medium (0.06-0.14), or large (>0.14) (Cohen, 2013).

In order to assess the discriminatory ability of movement rate to differentiate players with and without HSI history, the area under the receiver operating characteristic curve (AUC) was calculated. The cutoff values were chosen according to the point in the curve with the greatest Youden's index. The sensitivity, specificity, and odds ratio of HSI were calculated for the index created based on the AUC analysis. P-values <0.05 were considered statistically significant.

Results

Demographics and injury features

From the original population of 223 players in the nine participating teams, a total of 129 (57.8%) participated in the study, of which 108 (48.4%) were included in the analysis (24.3 $\pm$ 4.2 years old, 1.78 $\pm$ 0.07 m, 73.9 $\pm$ 7.6 kg, 15.5 $\pm$ 4.4 years of football practice, Figure 20). There were 76 right- (70.4%) and 32 left- (29.6%) lower limb dominant players. A total of 39 (36.1%) players had HSI history in the previous two seasons, with an average time loss of 31.6 $\pm$ 25.4 days. The distribution of players and percentage of those with HSI history per playing position can be seen in Table 10. Since there were no significant differences in EMG-related variables between left- and right-side dominant players ($p=0.072$ to 0.875) or

between left- and right-side injuries ($p=0.253$ to 0.678), we proceeded with the analysis of the entire sample as a whole for these variables.

Figure 20. Study flowchart

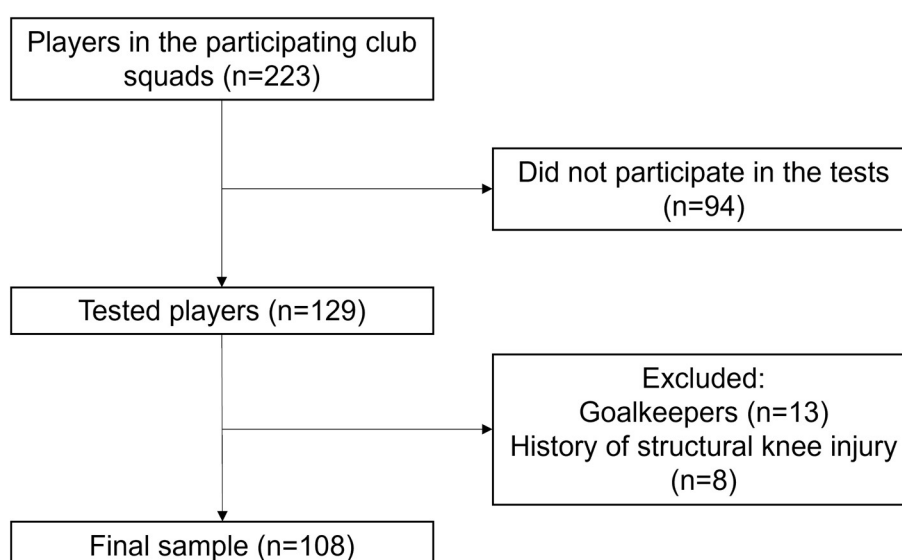


Table 10. Number of players with hamstring injury per playing position

Position	n (%)	HSI history, n (%)
Lateral defenders	20 (18.5%)	11 (55%)
Central defenders	26 (24.1%)	8 (30.7%)
Defensive midfielders	8 (7.4%)	2 (25%)
Central midfielders	15 (13.9%)	3 (20%)
Attacking midfielders	11 (10.2%)	4 (36.3%)
Wingers	17 (15.7%)	6 (35.3%)
Forwards	11 (10.1%)	5 (45.4%)

HSI, hamstring strain injury

Movement rate and perceived exertion

In movement rate testing, there was a significant block $\times$ HSI interaction ($p=0.005$, $\eta_p^2=0.046$, power=0.85) and a significant effect of the block factor ($p < 0.001$, $\eta_p^2=0.568$, power>0.99) caused by a decrease in movement rate. There was also a significant effect of

HSI history ($p=0.031$, $\eta_p^2=0.044$, power=0.58), with players with previous injury showing a higher movement rate (Figure 21A, Table 11).

Table 11. Movement rate and rating of perceived exertion findings

		Block							
Variable		1	2	3	4	5	6	7	8
MR	HSI	3.26	2.96	2.79	2.66	2.52	2.57	2.56	2.59
	No HSI	2.95	2.69	2.64	2.50	2.42	2.49	2.45	2.48
RPE	HSI	4.39	5.88	7.15	7.88	8.52	9.09	9.42	9.67
	No HSI	4.29	5.40	6.48	7.46	8.05	8.63	8.95	9.31

MR, movement rate; HSI, hamstring strain injury; RPE, rating of perceived exertion.

Since the largest differences between players with and without HSI were seen in the first three blocks, we used the number of cycles (cutoff value: 94.5 cycles; AUC=0.650; $p=0.008$) and the movement rate slope (cutoff value: -0.075 Hz/block; AUC=0.626; $p=0.025$) during this period to create a movement rate index which showed a specificity of 82.6% and sensitivity of 41% for differentiating players with and without HSI in the previous two seasons. Players with a positive test (i.e., >94.5 movement cycles and slope <-0.075 Hz/block in the first three blocks) had an odds ratio (OR) of 3.3 [95% confidence interval (CI): 1.36 - 8.06] of having HSI history in the past two seasons (Table 12).

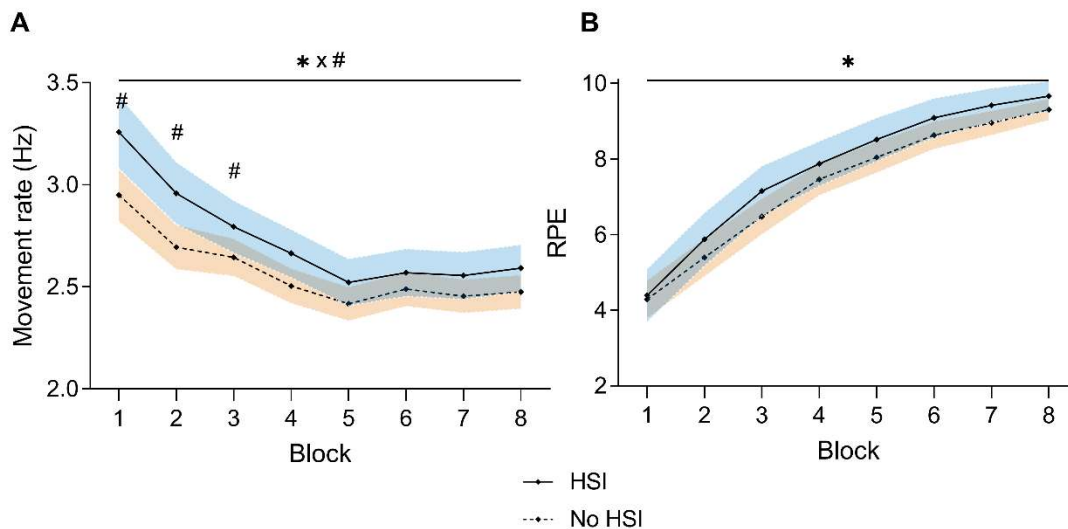
Table 12. Movement rate index and hamstring injury history crosstable

		Movement rate index	
		Positive	Negative
HSI history	Yes	16	23
	No	12	57

HSI, hamstring strain injury

As for the RPE (Figure 21B, Table 11), there was a significant main effect for the block factor ($p < 0.001$, $\eta_p^2=0.79$, power>0.99); the increase in RPE was significant between all blocks (all $p < 0.001$). Conversely, the between-group differences ($p=0.175$) and the block $\times$ HSI interaction ($p=0.503$) were not significant.

Figure 21. Changes in movement rate and rating of perceived exertion in footballers with and without hamstring injury history

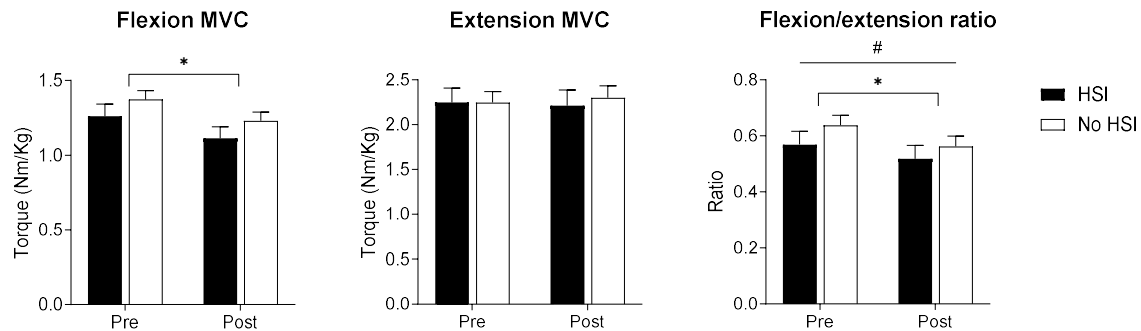


The shaded areas represent the 95% confidence interval for footballers with (blue) and without (orange) hamstring injury history. *significant effect of the block factor ($p > 0.05$); *significant block $\times$ injury interaction ($p > 0.05$); #significant differences between footballers with and without hamstring injury history ($p > 0.05$). RPE, rating of perceived exertion; HSI, hamstring strain injury.

Dynamometry

There were no significant pre-post ($p = 0.673$; $\eta_p^2 = 0.002$; power > 0.07) or between-subject ($p < 0.001$; $\eta_p^2 = 0.565$; power > 0.99) differences in knee extension MVIC. As for knee flexion, there was a significant post-task decrease (-10.9% , $p < 0.001$; $\eta_p^2 = 0.461$; power > 0.99) and a significant difference between players with and without HSI history (HSI: -11.8% ; ; no HSI: -10.4% $p = 0.017$; $\eta_p^2 = 0.055$; power = 0.67). The same pattern was found for the flexion/extension ratio: significant pre-post task differences (-10.9% ; $p < 0.001$; $\eta_p^2 = 0.234$; power > 0.99) and between players with and without HSI history (HSI: -9.3% ; ; no HSI: -11.6% ; $p = 0.044$; $\eta_p^2 = 0.040$; power = 0.52) (Figure 22).

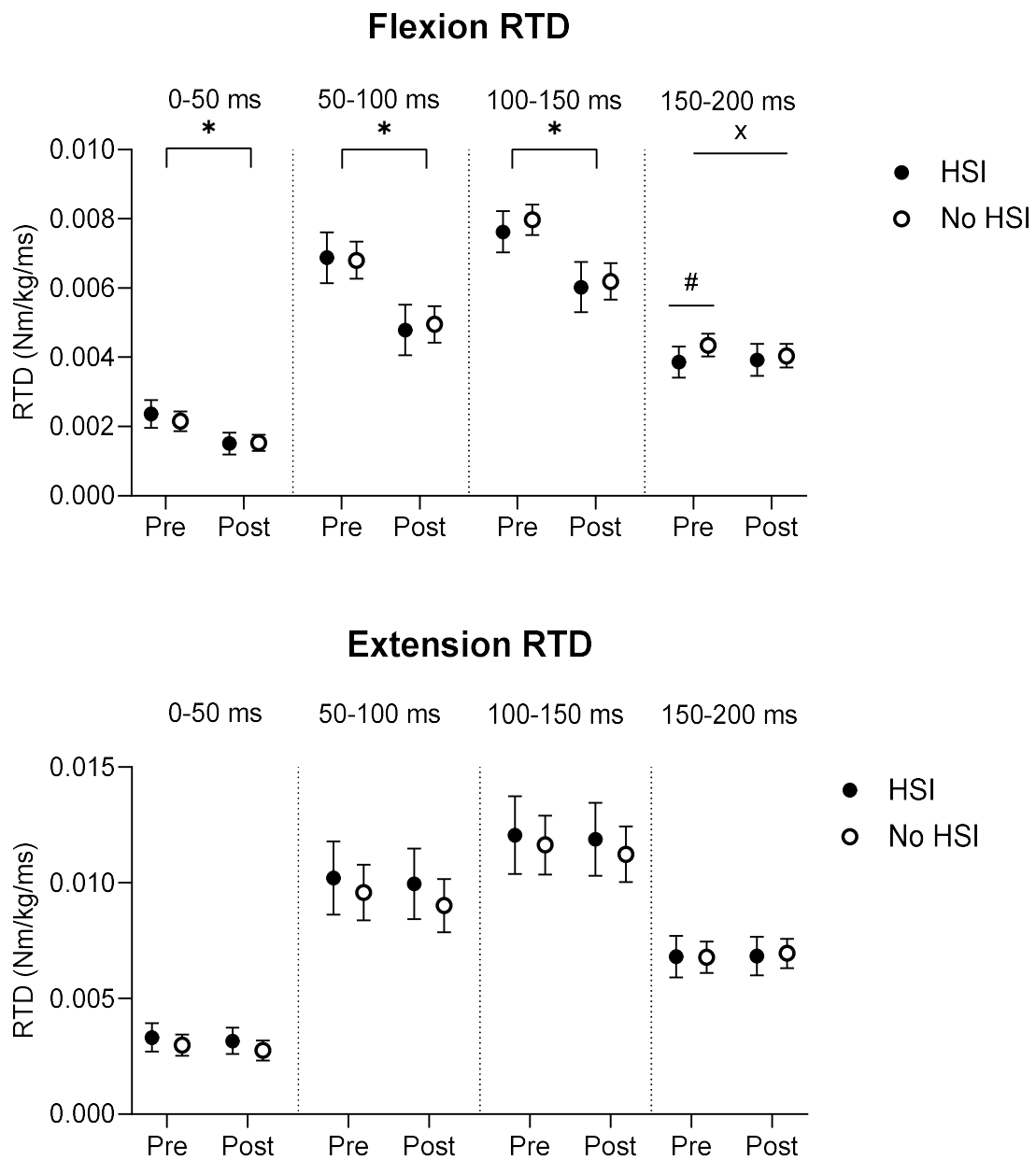
Figure 22. Pre-post task changes in maximum voluntary contraction in footballers with and without hamstring injury history



*significant pre-post difference ($p > 0.05$); #significant difference between footballers with and without hamstring injury history ($p > 0.05$). MVC, maximum voluntary contraction; HSI, hamstring strain injury.

Regarding the RTD results, there were no significant pre-post ($p = 0.20$ to 0.87) or between-groups ($p = 0.22$ to 0.93) differences in extension; there were also no significant measurement $\times$ HSI history interactions ($p = 0.18$ to 0.79). For flexion RTD, there were significant pre-post differences in all time periods except 150-200 ms (0-50 ms: $p < 0.001$; $\eta_p^2 = 0.37$; power > 0.99 ; 50-100 ms: $p < 0.001$; $\eta_p^2 = 0.43$; power > 0.99 ; 150-150 ms: $p < 0.001$; $\eta_p^2 = 0.43$; power > 0.99). Conversely, there were no significant differences between players with and without HSI history in any period ($p = 0.22$ to 0.91) or any significant measurement $\times$ HSI history interactions ($p = 0.18$ to 0.66). There were significant decreases in the flexion/extension RTD ratio in the 0-50 ($p = 0.002$; $\eta_p^2 = 0.10$; power $= 0.87$), 50-100 ($p < 0.001$; $\eta_p^2 = 0.13$; power $= 0.94$), and 100-150 ms ($p < 0.001$; $\eta_p^2 = 0.13$; power $= 0.94$) periods. On the contrary, there were no differences in the RTD flexion/extension ratio between players with and without previous HSI ($p = 0.16$ to 0.32); nevertheless, the post-hoc analysis showed that players with previous HSI had a significantly lower pre-task ratio at 150-200 ms ($p = 0.04$). There was also a significant measurement $\times$ HSI history interaction at this period ($p = 0.04$) (Figure 23).

Figure 23. Pre-post task changes in the rate of torque development in footballers with and without hamstring injury history



*significant pre-post difference ($p < 0.05$); #significant difference between footballers with and without hamstring injury history ($p < 0.05$); *significant pre-post $\times$ injury interaction. RTD, rate of torque development; HSI, hamstring strain injury.

MVIC comparisons between left- and right-side dominant players and between those injured in the right and left side revealed no significant main effect of side either in flexion ($p=0.47$ to 0.85) or extension ($p=0.56$ to 0.95) MVIC or in the flexion/extension ratio ($p=0.68$ to 0.90). There was, however, a significant measurement $\times$ dominant side interaction for flexion MVIC ($p=0.045$; $\eta^2 = 0.039$; power= 0.52). Within-subject differences followed the same pattern of the main analysis.

There were no significant differences between left- and right-side dominant players in flexion or extension RTD at any time period. When comparing players injured in the right and left sides, there was no main effect of the injured side in the flexion or extension RTD at any time point. Post-hoc comparisons revealed only a significant post-task difference in 0-50 ms flexion RTD ($p=0.02$), with players injured on the right side showing significantly lower RTD. Within-subject differences followed the same pattern of the main analysis.

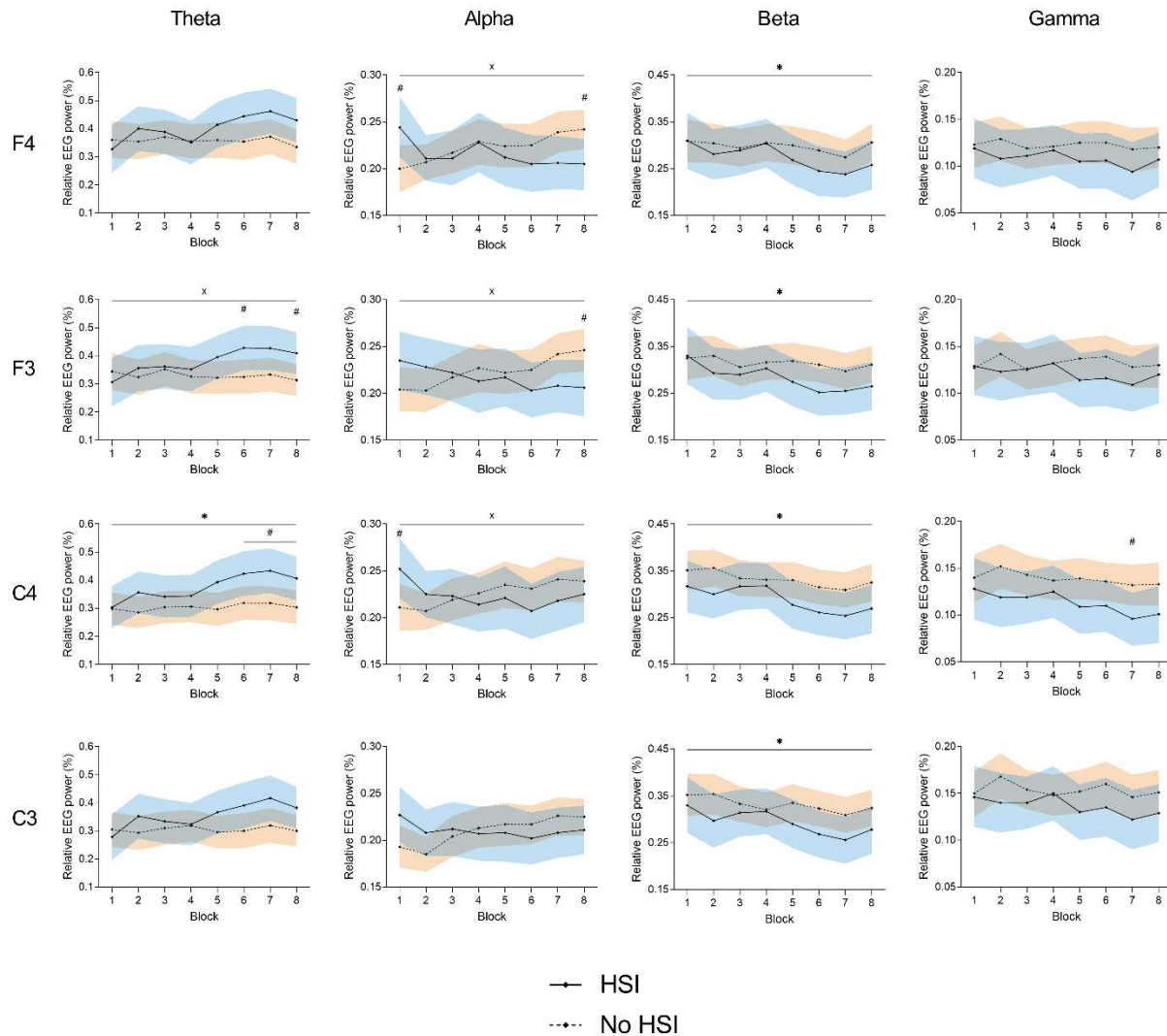
Electroencephalography

Relative band power

There were significant block $\times$ HSI history interactions at F4-alpha ($p=0.007$), F3-theta ($p=0.031$), F3-alpha ($p=0.007$), and C4-alpha ($p=0.039$).

We found a significant movement block effect for F4-beta ($p=0.013$), F3-beta ($p=0.017$), C4-theta ($p=0.008$), C4-beta ($p < 0.001$), and C3-beta ($p=0.008$). No significant main effects of HSI history were found; nevertheless, post-hoc testing revealed significant differences between players with and without HSI history at F4-alpha [first ($p=0.034$) and last ($p=0.018$) blocks], F3-theta (sixth and eight blocks, both $p=0.045$), F3-alpha (last block, $p=0.041$), C4-theta (sixth to eight block, $p=0.024$ to 0.043), C4-alpha (first block, $p=0.049$), and C4-gamma (seventh block, $p=0.046$) (Figure 24 and Supplementary Table 1).

Figure 24. Changes in relative band power in footballers with and without hamstring injury history



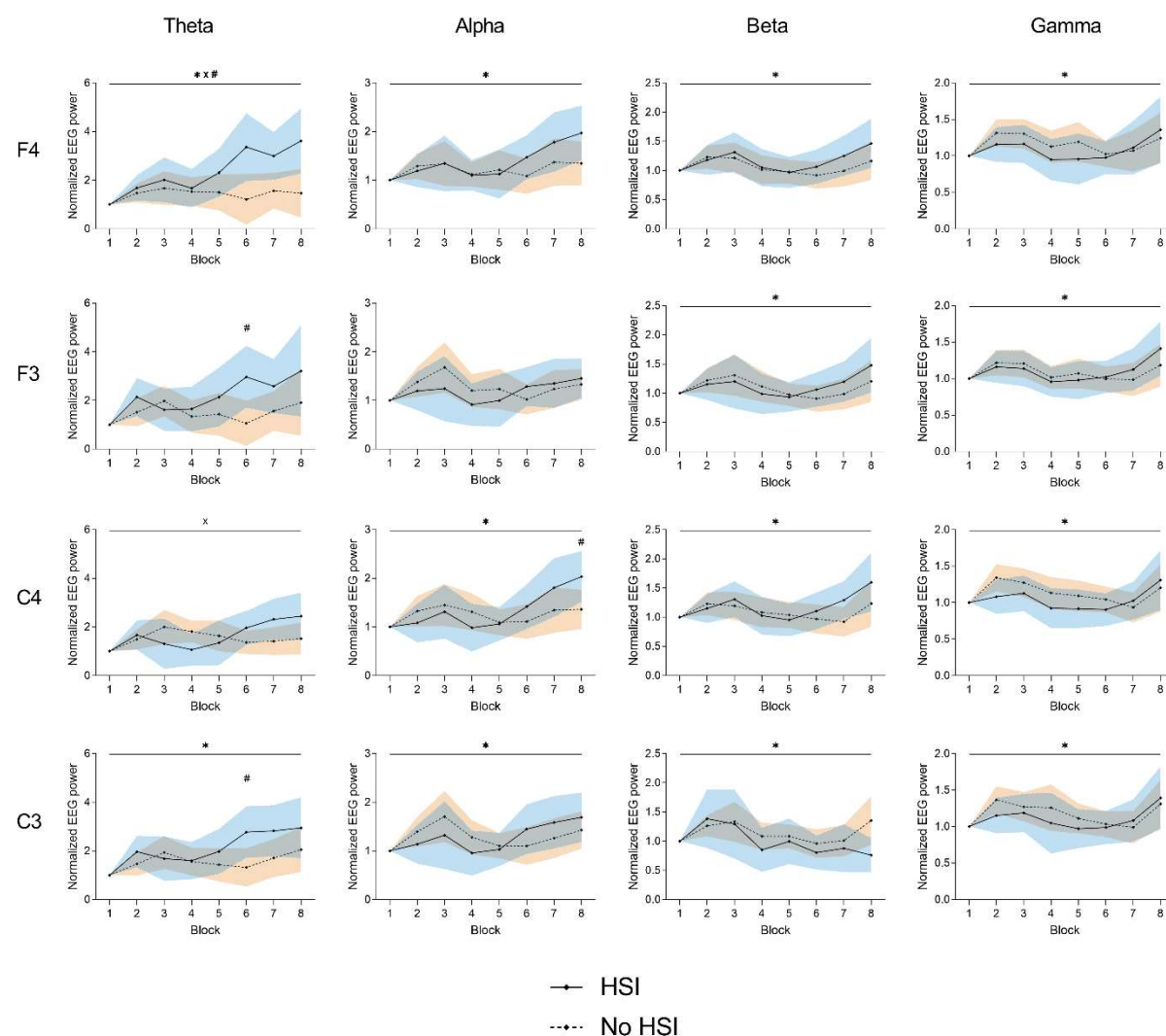
The shaded areas represent the 95% confidence interval for footballers with (blue) and without (orange) hamstring injury history. *significant effect of the block factor ($p > 0.05$); *significant block $\times$ injury interaction ($p > 0.05$); #significant differences between footballers with and without hamstring injury history ($p > 0.05$). RPE, rating of perceived exertion; HSI, hamstring strain injury.

Normalized band power

Significant movement block $\times$ HSI history interactions were found at F4-theta ($p = 0.013$) and C4-theta ($p = 0.042$). A significant movement block effect was seen at all electrodes: F4 (all frequency bands, $p = 0.004$ - 0.049); F3 (beta and gamma, $p = 0.005$ - 0.020); C4 (alpha, beta, and gamma, $p = 0.004$ - 0.012); and C3 (all frequency bands, $p = 0.004$ - 0.022). There was a

significant effect of HSI history at F4-theta ($p=0.021$). Post-hoc testing also revealed differences between players with and without HSI history at F3-theta (sixth block, $p=0.019$), C4-alpha (eighth block, $p=0.047$), and C3-theta (sixth block, $p=0.033$) (Figure 25 and Supplementary Table 2).

Figure 25. Changes in normalized EEG power in footballers with and without hamstring injury history

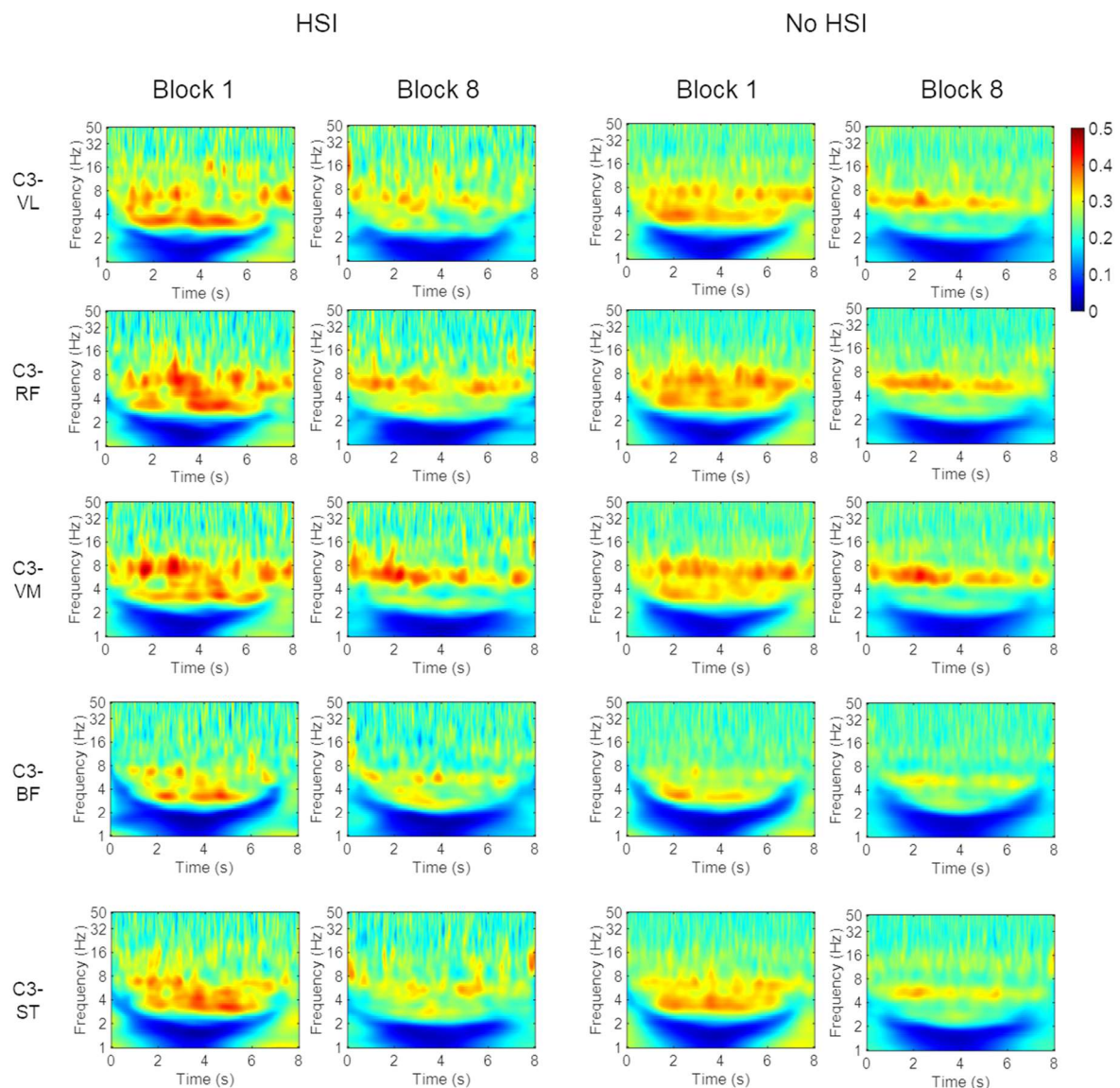


The shaded areas represent the 95% confidence interval for footballers with (blue) and without (orange) hamstring injury history. *significant effect of the block factor ($p>0.05$); *significant block $\times$ injury interaction ($p>0.05$); #significant differences between footballers with and without hamstring injury history ($p>0.05$).

Corticomuscular coherence

The time-frequency maps show a loss in coherence from the first to the last block in all muscles and in both groups. The knee extensors show greater coherence than the flexors, and the two frequency zones with the strongest coherence are around 3-4 and 8-10 Hz. There was a greater loss of coherence in the 3-4 Hz range from the first to the last block (Figure 26).

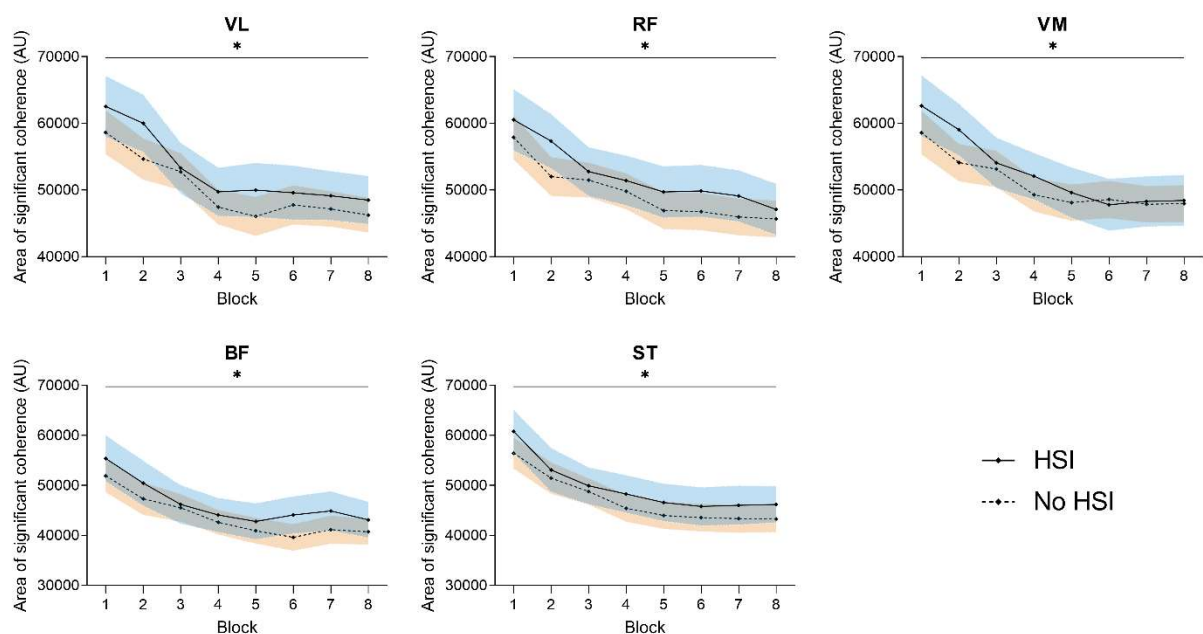
Figure 26. Changes in corticomuscular coherence from the first to the last block in footballers with and without hamstring injury history



HSI, hamstring strain injury; VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus.

In the significant coherence area analysis (Figure 27, Supplementary Table 3), there were no significant block $\times$ HSI interactions ($p=0.252$ to 0.902) or any pairs with a significant effect of HSI history ($p=0.153$ to 0.328). Conversely, all EEG-EMG pairs showed a significant effect of the block factor caused by a decrease in coherence (C3-VL: $p < 0.001$, $\eta_p^2 = 0.284$, power > 0.99 ; C3-RF: $p < 0.001$, $\eta_p^2 = 0.232$, power > 0.99 ; C3-VM: $p < 0.001$; $\eta_p^2 = 0.249$; power > 0.99 , C3-BF: $p < 0.001$, $\eta_p^2 = 0.229$; power > 0.99 ; C3-ST: $p < 0.001$, $\eta_p^2 = 0.285$; power > 0.99). The C3-BF pair showed a significantly lower CMC area than any other muscle (all $p < 0.001$, $\eta_p^2 = 0.494$ to 0.656 , all power > 0.99 , Supplementary Figure 3).

Figure 27. Changes in the area of significant coherence in footballers with and without hamstring injury history



The shaded areas represent the 95% confidence interval for footballers with (blue) and without (orange) hamstring injury history. *significant effect of the block factor ($p < 0.05$). AU, arbitrary units; VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus. HSI, hamstring strain injury.

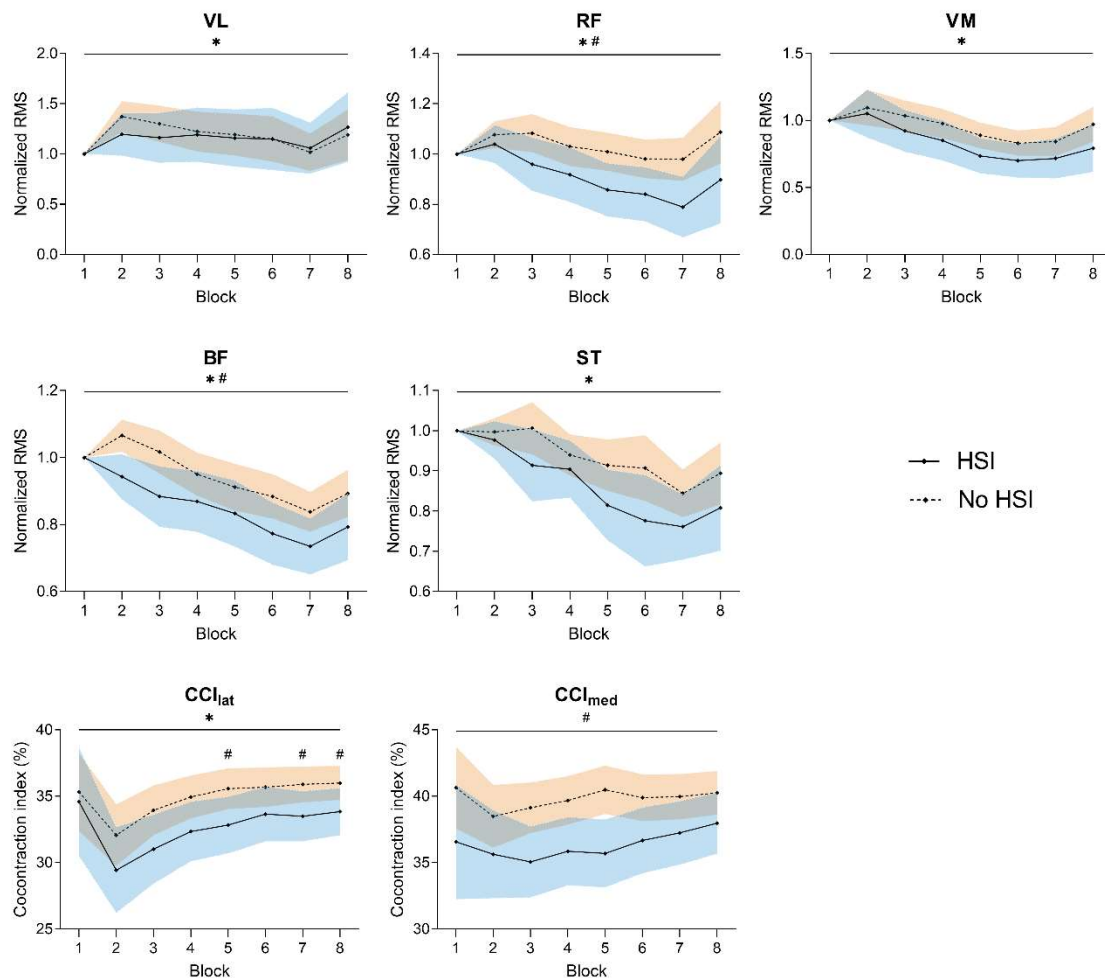
Electromyography

Significant decreases were seen in the normalized RMS of all tested muscles during the task ($p = 0.009$ to < 0.001 ; $\eta_p^2 = 0.037$ to 0.177 ; power = 0.86 to > 0.99). Significant differences between subjects with and without HSI history were seen for the RF ($p = 0.036$; $\eta_p^2 = 0.047$;

power = 0.56) and BF ($p = 0.043$; $\eta_p^2 = 0.045$; power = 0.53), with previously injured players showing lower normalized activity.

As for the co-contraction indices, there was a main effect of the block factor for CCI_{lat} ($p < 0.001$; $\eta_p^2 = 0.095$; power = 0.99), caused by an increase from the second block onwards, but not for CCI_{med} . Conversely, there was a significant effect of HSI history for CCI_{med} ($p = 0.023$; $\eta_p^2 = 0.051$; power = 0.63), with lower values for previously injured players, but not for CCI_{lat} . Nevertheless, post-hoc testing revealed that players with HSI history had a significantly lower CCI_{lat} in the fifth, seventh, and eighth blocks. EMG findings can be seen in Figure 28 and Supplementary Table 4.

Figure 28. Changes in EMG variables during the task in footballers with and without hamstring injury history



The shaded areas represent the 95% confidence interval for footballers with (blue) and without (orange) hamstring injury history. *significant effect of the block factor ($p < 0.05$); #significant block ×

injury interaction ($p < 0.05$); #significant effect of the injury factor or differences between footballers with and without hamstring injury history in individual blocks ($p < 0.05$). RMS, root mean square; VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus; CCI_{lat}, lateral co-contraction index; CCI_{med}, medial co-contraction index.

Discussion

We found significant differences in movement rate between players with and without HSI history, with previously injured players showing a greater movement rate, especially in the first half of the task. In association with the higher movement rate, players with HSI history showed increased EEG theta activity in the second half of the task and decreasing alpha activity, lower RF and BF EMG activity, and a lesser degree of co-contraction.

The findings contradict our original hypothesis of lower movement rate and greater flexor-extensor co-contraction in players with HSI history; nevertheless, this association between movement speed and HSI history is not unprecedented. Previously injured players have shown a higher maximal theoretical sprinting velocity (Ishøi et al., 2020); additionally, footballers classified as having a “fast” muscle fiber typology (as evaluated by the muscle tissue carnosine content) showed a significantly greater prospective risk of HSI (Lievens et al., 2022).

It may be the case, then, that in the same way that the “jumper’s paradox” has been described for patellar tendinopathy, a “football sprinter’s paradox” may exist for HSIs. In this case, players who show greater ability to develop higher contraction speeds and movement rates are shifted to roles where this attribute is more relevant, increasing their sprint distance, exposure to high-speed actions, and consequently the HSI risk. In support of this idea, in our study, the three positions with greater prevalence of HSI history were lateral defenders (55%), forwards (45.4%), and wingers (36.3%), which perform a significantly greater sprinting distance in elite football matches than other positions (Di Salvo et al., 2010). Moreover, in athletes from cyclic movement sports, movement rate increases with the muscle carnosine content, suggestive of a greater fast-twitch fiber percentage (Bex et al., 2017). Additionally, ATPase and FXD1 expression (as a proxy of muscle composition) have also been positively associated with high-speed running/sprinting distance in football match play (Mohr et al., 2016). These findings help understand our results both in terms of movement rate and EMG activity. The increased performance of players with HSI history may be caused by a greater percentage of fast-twitch fibers, which would lead to their selective fatigue during the task and a consequent greater drop in EMG amplitude, since

these fibers are more fatigable and have been shown to be recruited preferentially during high-speed contractions (Wakeling et al., 2006).

The greatest difference in task performance between players with and without HSI history was seen in the first three blocks, while from the fifth block onwards both groups of players showed a stable movement rate, leading to the significant block x HSI history interaction. The index we designed combining the number of cycles and the loss in movement rate during the first three blocks showed high specificity but low sensitivity in differentiating players with and without HSI history. Nevertheless, players with a positive index were over three times more likely to have HSI history. This is especially relevant considering this index was derived from accelerometry values, which are more easily obtained in a field setting than EMG or EEG parameters. We were also able to confirm that this task induced a significant RPE, with players achieving an average value close to maximum effort at the end of the task. RPE increased relatively steadily throughout the entire task, while performance plateaued after the fifth block.

Compared to a previous study with the same task in nonathletic subjects (Correia et al. 2023), we found a slightly delayed performance stabilization in this sample of football players (fifth versus fourth block), as well as lower BF coherence compared to other muscles, which was not as evident previously. There were also significant changes in relative EEG power during the task, which were not found in non-athletes. Conversely, the movement rate trajectory was remarkably similar to that of non-athletes, while normalized EMG amplitude and co-contraction trajectories were relatively similar. This suggests that the athletic level influences the associated neurophysiology more than the motor output in this task.

The task had no effect on knee extension MVIC or RTD. Conversely, there was a significant post-task decrease in knee flexion MVIC and significant decreases in RTD up to 150 ms, indicating that the task affected mostly early torque production. The differences between knee flexion and extension were expected since the knee flexors work against gravity in this task; this also indicates that the task managed to adequately target the hamstrings while sparing the quadriceps in terms of maximum torque production and development. It is worth noting that early (0-100 ms) knee flexion RTD has been significantly associated with short-distance (0-15 m) acceleration ability in football players (Ishøi et al., 2019). This is especially relevant considering that the majority of sprints performed by football players are within 20 m (Andrzejewski et al., 2013). The association between hamstring RTD and HSI has been conflicting, with studies finding a lower RTD in previously injured hamstrings (Buhmann et al., 2022b) or no association between RTD and HSI risk (van Dyk et al., 2018). Our results

are in line with the latter findings. It could be interesting to determine if the simple task used in this study can be used as training to improve early hamstrings RTD.

It was also interesting to note that players with previous HSI tended to show more significant correlations between flexion RTD and MVIC. Since there were no differences in RTD between players with and without HSI history, the reasons for this greater correlation seem to be unclear.

A previous study found an association between early knee extensor RTD and self-reported knee function measures in professional footballers (Cossich et al., 2023); however, we did not find differences in either extensor or flexor RTD between players with and without HSI history. Still, considering the findings of Cossich et al.'s study, it could be work exploring if flexor RTD is also associated with self-evaluated function, especially in players with previous HSI.

Players with HSI history showed an increase in frontal EEG theta activity, which is associated with sensorimotor integration and attention allocation (Baumeister et al., 2012; Cruikshank et al., 2012), during the second half of the task. It is known that fatigue decreases the knee joint position sense ability (Proske, 2019), which may be driven by changes in muscle spindle activity (Ribeiro et al., 2007). In this way, the increase in frontal theta activity in players with HSI history could be driven by additional attentional resources required due to muscle spindle activity being impaired by the combined effects of previous injury and fatigue (since this was seen in the second half of the task), affecting afferent input. Increased theta activity has also been noted in ACL-reconstructed individuals during a force-matching task, which was attributed to a greater neurocognitive involvement (Baumeister et al., 2011). Moreover, it has been extensively reported that ACL injuries lead to knee proprioception deficits and supraspinal changes (Busch et al., 2021; Grooms et al., 2017). Our similar findings of increased frontal theta activity therefore suggest that muscle injuries may also be associated with sensorimotor processing changes, but we cannot conclude if these changes are a cause or a consequence.

Additionally, this increase in theta activity was accompanied by decreased BF and RF activity compared to players without HSI history, despite the fact that the latter showed a worse task performance. Thus, while EMG data suggest a greater efficiency of muscle activity in previously injured players, EEG theta findings tell an opposing story, since previously injured players showed greater activity during the second half of the task but similar performance. Lower EMG activity coupled with higher theta and lower alpha EEG activity, as seen in the HSI group, has also been associated with a predominant external

attentional focus, which indicates a greater cortical inhibitory control and sensorimotor processing ability (Parr et al., 2023; Sherman et al., 2021). Attentional strategies and sensorimotor processing requirements may therefore contribute to the electrophysiological findings associated with improved task performance in the HSI group.

We also found significant HSI $\times$ movement block interactions in relative frontal and central alpha EEG power. This was caused by the decrease in alpha activity in players with HSI history coupled with the increase seen in noninjured players. Alpha power has been associated with both motor planning and execution (Baumeister et al., 2013) and found to decrease in fatigued states (Baumeister et al., 2012, 2013). However, movement rate did not show an association with these opposing patterns of alpha activity. It is therefore unlikely that differences in fatigue or performance levels led to these differences. Since alpha activity suppression has been associated with increased task load/difficulty (Klimesch, 1999; Raufi & Longo, 2022), the combined findings of higher theta and lower alpha activity in HSI players suggest that the task required additional attentional resources for sensorimotor integration (increasing theta activity) and thus imposed a greater cognitive load in these players (decreasing alpha activity). This opposing but associated behavior of theta and alpha activity as a sign of increased workload has previously been reported (Chikhi et al., 2022; Raufi & Longo, 2022).

The C3-BF pair showed significantly lower coherence than any other muscle. This finding is interesting considering that the BF is more commonly affected by HSIs in football (Askling et al., 2013; Ekstrand et al., 2023). However, this lower coherence was seen both in players with and without HSI history. This may be worth exploring further. Contrary to what has been seen post-ACL injury (Riehm et al., 2024; Sherman et al., 2023), athletes with previous HSI did not show lower CMC. This may have been due either to HSIs causing less disruption in brain-muscle communication relatively to ACL injuries or to task differences, as dynamic tasks (such as in our study) have been shown to abolish 15-30 Hz CMC (Kilner et al., 2000), leading to the lack of differences. Fast movement tasks have also shown greater CMC at <12 Hz (Conway et al., 2004), which was confirmed by our findings of stronger coherence at 3-10 Hz in this and in a previous study with the same task (Correia et al., 2023). Since CMC is reported to decrease with fatigue (Yang et al., 2010), which was present in our study, it could also be that it had a greater influence than injury status in the changes in CMC during the task, thus preventing the detection of between-group differences.

EMG studies in athletes with previous HSI have shown lower BF activity (Areia et al., 2019; Higashihara et al., 2019; Opar et al., 2013), which is commonly attributed to persistent inhibition even after rehabilitation (Buhmann et al., 2022a; Fyfe et al., 2013). We add that a hamstring antagonist, the RF, also showed significantly lower activity. This highlights the relevance of agonist-antagonist coupling in motor control, especially in a fast cyclic task such as the one used here, since the antagonists have to adjust to the activity patterns of the agonist in these movements. Indeed, a significant decrease in the RMS of bi-articular antagonists (such as the RF in our case) has been noted in high-intensity cyclical efforts as an adjustment to the fatigue of the power producers (Hautier et al., 2000) (the knee flexors in our task); the RF/BF coordination during sprinting has also been shown to impact the maximum step frequency (Takehata et al., 2021). The degree of agonist-antagonist co-contraction plays a significant role in the maximum movement rate (Rodrigues et al., 2009); RF/BF co-contraction contributes to maintaining posture during the early ground contact phase (Pinniger et al., 2000). It therefore makes sense that players with HSI history showed decreased knee co-contraction in association with their higher movement rate. Conversely, increased knee stiffness (due to greater quadriceps-hamstrings co-contraction) has been reported to have a protective effect against potentially hazardous loads (Teixeira da Fonseca et al., 2004), which may explain why players without HSI history had greater co-contraction.

We believe our study may have an impact in terms of the usefulness of a simple high-speed movement task to differentiate players with and without previous HSI, as well as adding to the existing evidence for the relevance of high-speed actions in HSI risk. Second, we show that differences in brain and muscle activity are present in players with HSI in association with fatigue induced by high-speed movement. It is worth noting that these changes were present regardless of the injured limb or the time since the injury. If both the discriminating nature of the test and the different brain and muscle activity patterns are confirmed by prospective studies, this task may serve as means of both evaluation and training throughout the season to detect and address players at risk, as well as to monitor rehabilitation/readiness, which would have a significant potential application in screening and recovery protocols. Our EEG findings also alert to the importance of monitoring attentional/neurocognitive resources in players with previous HSI as part of rehabilitation, prevention, and recurrence management programs, as suggested for other injuries (Huddleston et al., 2023; Reyes et al., 2022).

Limitations

Our study presents some limitations. First, the retrospective design means that we cannot infer causality from our findings; injuries were also self-reported, which may be influenced by recall bias. Second, our task does not replicate the demands associated with football performance; thus, the outcomes do not represent player behavior during more ecological tasks. Third, the results should not be generalized to female players and to different competitive levels. Fourth, the dynamic nature of our task means that some signal noise and artifacts can still be expected despite the best signal processing efforts. Fifth, we did not consider the influence of leg length/weight differences between players; however, since there were no differences in height or weight, this is unlikely to have affected the results. Finally, since we only collected EMG data from one limb, it is unclear what interlimb differences may have been present.

Conclusion

The simple movement rate task used in this study was able to differentiate football players with and without HSI history and therefore has a potential for field application. Surprisingly, players with a "hare" profile (rather than the "tortoises") showed a higher HSI risk. In association with the movement rate differences, footballers with HSI history showed higher theta EEG power in the second half of the task, an opposing alpha EEG power pattern, lower EMG flexor and RF activity, and a lower degree of co-contraction. However, no differences in brain-muscle coupling were found between groups. Our findings highlight the presence of central and peripheral motor control changes in footballers with HSI history.

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Conflict of interest

None.

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CHAPTER VI – DIFFERENCES BETWEEN UPPER AND LOWER LIMB MOVEMENT RATE AND MOTOR SLOWING IN A LOWER LIMB-TRAINED SAMPLE

Abstract

The study of maximum movement rate (MR) has been crucial for the understanding of the underlying physiology of motor slowing and to detect changes associated with performance and disease. Existing studies show a common motor slowing pattern across body regions; however, there is a lack of studies simultaneously investigating upper and lower limb MR, especially of differently-sized segments such as the legs and fingers. Additionally, we have previously detected differences in leg MR in footballers with hamstring injury history. Thus, we compared leg and finger MR in footballers with hamstring strain injury (HSI) history and in matched controls. We aimed to determine whether i) leg and finger MR show a similar behavior in a fatiguing task, ii) differ between footballers with and without hamstring injuries, and iii) are correlated in a sample of lower-limb trained athletes. Sixteen footballers with HSI history and 16 matched pairs without HSI history performed maximum leg and finger tasks consisting of eight 10-s blocks with 5 s of rest between blocks; the MR was calculated for each block. Both leg and finger MR decreased significantly during the task ($p < 0.001$), and adjusted well to logarithmic models ($r^2 = 0.92-0.97$); however, there was a greater slowing in the fingers than in the legs task (-20.9% vs. -12.9%, $p = 0.049$). Neither task was able to differentiate players with and without HSI history. Our findings suggest that the degree of motor slowing when similar task parameters are used may not be as constant across body regions as previously thought, suggesting joint/segment size alters repetitive movement control performed at maximum speed.

Introduction

Limb movement rate (MR) has been the focus of research as a window to motor control physiology behind repetitive movement not only in healthy individuals (Bächinger et al., 2019; Correia et al., 2024), but also in fields ranging from neurodegenerative disease (Tanigawa et al., 2017) to sports (Seidel-Marzi & Ragert, 2020), and performing arts (Aoki et al., 2005). In sports, MR has been shown to be associated not only with the sporting discipline demands (sprint-, intermediate-, or endurance-type) but also with the muscle typology, with athletes from sprinting disciplines showing a faster muscle typology (Bex et al., 2017).

MR has been found to decrease with maximal repetitive movement in multiple body regions (fingers, foot, leg, and even the eyes), which is termed motor slowing (Bächinger et al., 2019; Rodrigues et al., 2009). Tasks involving all these different body regions tend to show a similar motor slowing pattern (i.e., the trajectory of changes over time) characterized by a marked initial decrease followed by a plateau or a smaller decrease (Arias et al., 2015; Madinabeitia-Mancebo et al., 2020; Seidel-Marzi & Ragert, 2020), which suggests that a common motor control mechanism regulates maximal repetitive movement. Interestingly, studies have shown that this slowing occurs without a corresponding decrease in maximal muscle force (Arias et al., 2015; Rodrigues et al., 2009), suggesting that other factors such as intersegment and intermuscular coordination and activation timing may play a role in the MR decrease.

In athletic populations, finger and foot (evaluated in a skipping task) MR have previously been compared in national- and regional-level footballers, albeit with different task parameters. Nevertheless, a strong correlation between these two rates was found (Chaabouni et al., 2022). Additionally, two previous studies (Seidel-Marzi & Ragert, 2020; Seidel & Ragert, 2019) found no effects of sporting discipline (football vs. handball) in finger and foot MR, which decreased similarly over time. However, these studies did not test the correlation between MRs in each athletic discipline. Still, they suggest that while athletes show a better performance than non-athletes, chronic training of a sport directed to a body region does not influence the MR of a non-trained region. On the contrary, pianists have shown improved finger tapping performance compared to non-musicians, especially in the ring and little fingers (Aoki et al., 2005). It may be the case that finger and foot tapping do not reflect, for example, the exact motor patterns trained by the handballers and footballers in the previously cited studies, explaining the lack of differences.

Despite the existence of studies analyzing upper and lower limb MR, these usually do not employ the same parameters (i.e., intensity, work/rest duration) for upper and lower limb tasks and/or analyze smaller body segments such as the fingers and the foot. Direct comparisons of the MR and motor slowing of body segments of different sizes using similar task parameters are therefore lacking. This is relevant since segment inertia is known to influence limb motor control during fast movements; while smaller segments rely more on passive tissue properties for deceleration, larger/heavier segments such as the leg show greater electromyographic burst amplitude and duration (Correia, Vaz, Domingos, et al., 2022). Performing this comparison would contribute to further establishing the presence of a common performance basis for repetitive movements across body regions even in trained

samples or to suggest that small and large body segments have distinct motor slowing patterns.

In another perspective, we have recently found differences in leg MR between footballers with and without hamstring strain injury (HSI) injury, with previously injured players showing higher MR performance (Correia et al., 2024, under review). We also highlighted the need for confirmation studies considering the unexpected nature of these findings. Moreover, assuming there are common central control mechanisms in repetitive limb movements across body regions, then differences in the MR of other body regions not associated with football performance could also be present in these players. If a finger movement task is also able to provide this difference, its field application would be even easier to implement than a leg movement task due to its lack of impact on training load; it would also show that general coordination mechanisms are impaired in players with HSI history.

This study therefore aimed to determine whether leg and finger MR 1) show a similar behavior (performance decrease and trajectory) in a fatiguing task performed by a lower-limb trained population; 2) are correlated in a sample of lower-limb trained athletes; and 3) differ between footballers with and without previous hamstring injury. We hypothesized that despite the lower limb training of footballers, both leg and finger MR would show a similar pattern of performance decrease when using the same task parameters and that these two MRs would be correlated. We also hypothesized that, as we previously determined, footballers with previous HSI would show a greater leg MR.

Materials and methods

Sampling

We used a matched pairs design in this study. For every player with HSI history, a control player without HSI history and as similar as possible in terms of age, weight, and playing position was selected. When it was not possible to have a player of the same position as a match, a position with similar role was selected (e.g., wing or attacking player). This matching was done blindly to the MR findings. For a medium effect size F of 0.25 and power of 0.80, the sample size required to detect differences in MR among the 8 blocks using two groups was 16. Therefore, we included a total of 16 pairs in this study (32 players; 15 from the first league, 11 from the second league, and 3 from the third league). Inclusion criteria were 1) at least three training sessions plus a match per week; 2) no active injury limiting performance. Exclusion criteria were 1) playing as a goalkeeper (due to differences in

activity patterns and HSI risk from outfield players (Green et al., 2020)); 2) history of knee, thigh, hip, or CNS structural injury or surgery; 3) practicing other sport or structured physical activity twice per week or more; 4) any condition preventing the player from completing the study protocol. This study was approved by the institutional review board of Faculdade de Motricidade Humana (approval number: 11/2022). Data collection took place during the pre-season (21 players, 65.6%) and during an international football break in March (11 players, 34.4%).

Experimental protocol

Upon arrival, players were explained the details of the study and provided written informed consent. A questionnaire concerning anthropometric, football-related (playing position, number of playing years), and HSI injury (HSI history in the previous two seasons, date of injury, time loss) data was administered.

The experimental protocol consisted of leg and finger maximum MR tasks, both performed over eight 10-s blocks with a 5-s rest between blocks. For the finger MR task, players were instructed to tap a phone screen (P Smart, Huawei, Shenzhen, China) as fast as they could with their two index fingers in a standardized hand position and keeping their index fingers straight, using the CNS Tap App (smudge.io, Secret Harbor, Australia), which records the number of taps in each 10-s period. To further validate the comparison between leg and finger MR (ensuring that the performed range of motion was similar in the leg and finger tasks), we performed a pilot experiment in 12 participants not involved in the main analysis where we determined the range of motion performed during the finger task as the difference between the standardized starting position and the point where the index finger touched the smartphone.

To assess the test-retest reliability of the used finger MR app, we enrolled participants not involved in the main study to perform the task on two separate occasions and calculated the two-way mixed effects, absolute agreement intraclass correlation coefficient (ICC) of the MR for each block.

For the leg MR task, players were placed in the prone position and asked to perform knee flexion and extension in a 45-90° arc as fast as they could (Correia, Vaz, Witvrouw, et al., 2022). A familiarization period was included for both tasks with sufficient duration to confirm correct task execution. The order of the tests was randomized and a 5-min rest was allowed between tasks.

Data collection and processing

During the finger task, the number of taps in each block was recorded; the presented values correspond to the total number of taps. The number of taps was divided by 10 to provide a value in Hz. For the leg MR task, accelerometers (PLUX Wireless Biosignals, Lisboa, Portugal) were placed in the lateral malleoli to determine the number of movement cycles, defined by the peaks in the accelerometer data. For an easier comparison of the decreases in leg and finger MR within this study and with other studies, the presented MR values were divided by 2 to reflect the MR of each limb. Both absolute and normalized values (to the first block) are presented. Additionally, the rating of perceived exertion (RPE) was collected using a modified 0-10 Borg scale for both tasks during each 5-s interval between blocks. We determined the adjustment of the MR curves to negative logarithmic trendlines and recorded the individual $\ln$ term of the equation and the r^2 parameter as measures of the slope and goodness of fit, respectively. The percentages of change in MR during the task were calculated as $(\text{block 8 MR} - \text{block 1 MR}) / \text{block 1 MR}$.

Statistical analysis

Changes in leg and finger absolute and normalized MR over the eight blocks were analyzed using a 2 (limb, legs/fingers) $\times$ 8 (block) two-way mixed ANOVA in the whole sample. To further investigate the association between leg and finger MR, we performed a correlation analysis using Pearson's correlation coefficient between the two MRs in each block. Moreover, considering the pattern of performance decrease, the leg and finger MR individual and group mean curves were adjusted to a negative logarithmic trendline and the slope (the $\ln$ term of the trendline) and the goodness of fit (evaluated by the r^2 statistic) of the leg and finger curves was compared between limbs using a repeated measures t-test. We also determined the r^2 statistic for the group average curves. Finally, we compared the percentage of absolute and normalized leg and finger MR loss using a repeated measures t-test.

Differences in leg and finger MR between players with and without HSI history were assessed using a 2 (HSI history, yes/no) $\times$ 8 (block) two-way mixed ANOVA for each of the limbs (leg and finger). As we noticed an unexpected variation between data collection time points (pre-season and in-season), and despite the small sample size, we decided to perform an exploratory analysis of the pre-season and in-season subgroups in terms of leg

and finger MR differences in players with HSI history using separate leg and finger 2 (measurement point, pre-season/in-season) $\times$ 8 (block) two-way repeated measures ANOVAs.

ICCs were classified as poor (<0.5), moderate ($0.5-0.75$), good ($0.76-0.9$), and excellent (>0.9) (Koo & Li, 2016). Correlations were classified as poor ($r \leq 0.3$), moderate ($0.3 < r \leq 0.5$), and strong ($r > 0.5$). Post-hoc tests between individual blocks were also conducted using a Bonferroni correction. Statistical significance was set at $p < 0.05$. Statistical testing was performed using SPSS 28.0 (IBM Corp., Armonk, NY). Curve fitting was performed using MATLAB R2022b (Mathworks, Natick, MA).

Results

Sample characteristics and validity/reliability measures

The validity of comparing leg and finger MR was attested by the measured range of motion in the finger task measured in the pilot experiment, which was $45.8 \pm 11.1^\circ$. The finger MR ICCs ranged from 0.63 to 0.94 (moderate to excellent, Table 13). The final sample was composed of 32 players (age: 24.6 ± 4.5 years; height: 1.80 ± 0.05 m; weight: 76.3 ± 6.2 kg), 16 with HSI history and 16 control matches without HSI history.

Table 13. Intraclass correlation coefficients of finger movement rate across the eight blocks

	Block							
	1	2	3	4	5	6	7	8
ICC	0.83	0.94	0.78	0.80	0.82	0.90	0.77	0.63
p-value	0.006	0.071	0.043	0.183	0.094	0.175	0.255	0.067

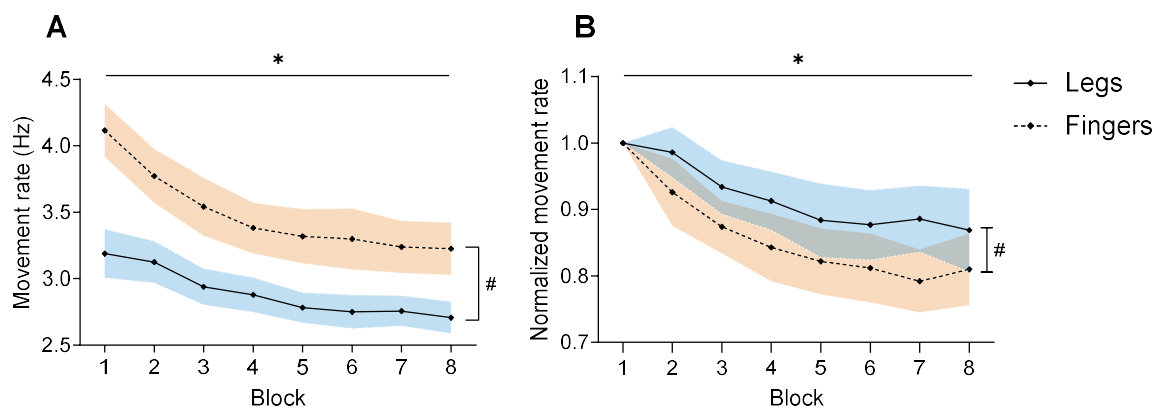
ICC, intraclass correlation coefficient

Between-limb differences in movement rate and rate of perceived exertion and association between leg and finger movement rate

No significant limb $\times$ interactions were found. Significant decreases in both leg (absolute: -12.5%, $p < 0.001$, $\eta_p^2 = 0.39$, power > 0.99 ; normalized: -12.5%, $p < 0.001$, $\eta_p^2 = 0.36$,

power > 0.99) and finger (absolute: -19.5%, $p < 0.001$, $\eta_p^2 = 0.49$, power > 0.99; normalized: -19.6%, $p < 0.001$, $\eta_p^2 = 0.52$, power > 0.99) MR were observed over the eight blocks. As for the comparison of leg and finger MR, we found that there was a significant effect of the limb factor (absolute: $p < 0.001$, $\eta_p^2 = 0.45$, power > 0.99; normalized: $p < 0.001$, $\eta_p^2 = 0.27$, power = 0.96), with higher MRs for the fingers (Figure 29A,B). However, there were no significant correlations between finger and MR in any block (Table 14). The absolute MR curve fitting analysis showed significant differences between the slopes of the leg and finger curves (leg: -0.47; finger: -0.88; $d = -0.51$, $p = 0.017$). However, the goodness of fit was similar for both curves (leg: $r^2 = 0.58$; finger: $r^2 = 0.58$; $p = 0.96$). In the normalized MR curves, however, there were no differences in the slopes (leg: -0.054; finger: -0.08; $p = 0.16$) or in the goodness of fit (leg: $r^2 = 0.52$; finger: $r^2 = 0.47$; $p = 0.43$). The whole-sample average values showed an excellent goodness of fit of negative logarithmic curves for both leg (absolute: $r^2 = 0.93$; normalized: $r^2 = 0.97$) and finger (absolute: $r^2 = 0.96$; normalized: $r^2 = 0.94$). Finally, the comparison of the percentage decrease in MR showed a significantly greater decrease in finger MR (-20.9 vs. 12.9%, $d = 0.40$, $p = 0.049$).

Figure 29. Changes in the whole-sample absolute (A) and normalized (B) leg and finger movement rate over the eight blocks.



The shaded areas represent the 95% confidence interval for the legs (blue) and fingers (orange) movement rate. *significant effect of the block factor; #significant effect of the limb factor.

Table 14. Correlation between absolute leg and finger movement rate values for each block

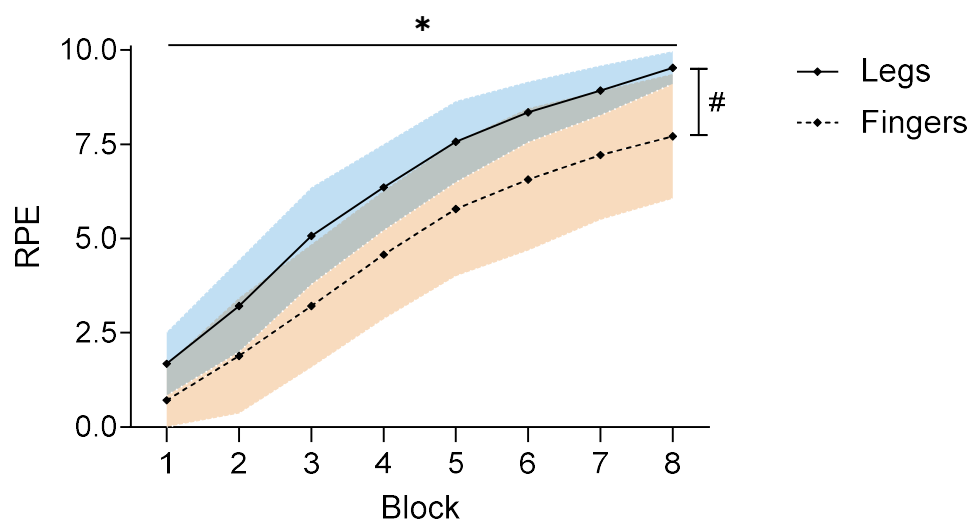
Block		1	2	3	4	5	6	7	8
Whole sample	Correlation	-0.02	-0.232	0.20	0.21	0.31	0.12	0.27	0.26

	p-value	0.91	0.24	0.31	0.89	0.12	0.54	0.18	0.19
HSI history	Correlation	-0.20	-0.42	0.03	0.32	0.29	0.04	0.17	0.31
	p-value	0.52	0.15	0.92	0.28	0.34	0.90	0.57	0.30
No HSI history	Correlation	0.06	-0.07	0.34	-0.01	0.33	0.27	0.47	0.19
	p-value	0.83	0.81	0.24	0.98	0.25	0.36	0.09	0.52

HSI, hamstring strain injury

Regarding RPE, there was no significant limb $\times$ block interaction ($p=0.551$). However, there was a significant effect of both the block ($p < 0.001$, $\eta_p^2 = 0.91$, power > 0.99) and limb ($p=0.019$, $\eta_p^2 = 0.35$, power = 0.69) factors. The RPE increased significantly in both tasks, but the leg task induced a significantly greater RPE. Accordingly, post-hoc testing showed significant differences between all blocks for the leg task, while for the fingers, there were no differences among the first three and between the last two blocks (Figure 30).

Figure 30. Rating of perceived exertion during the leg and finger tasks

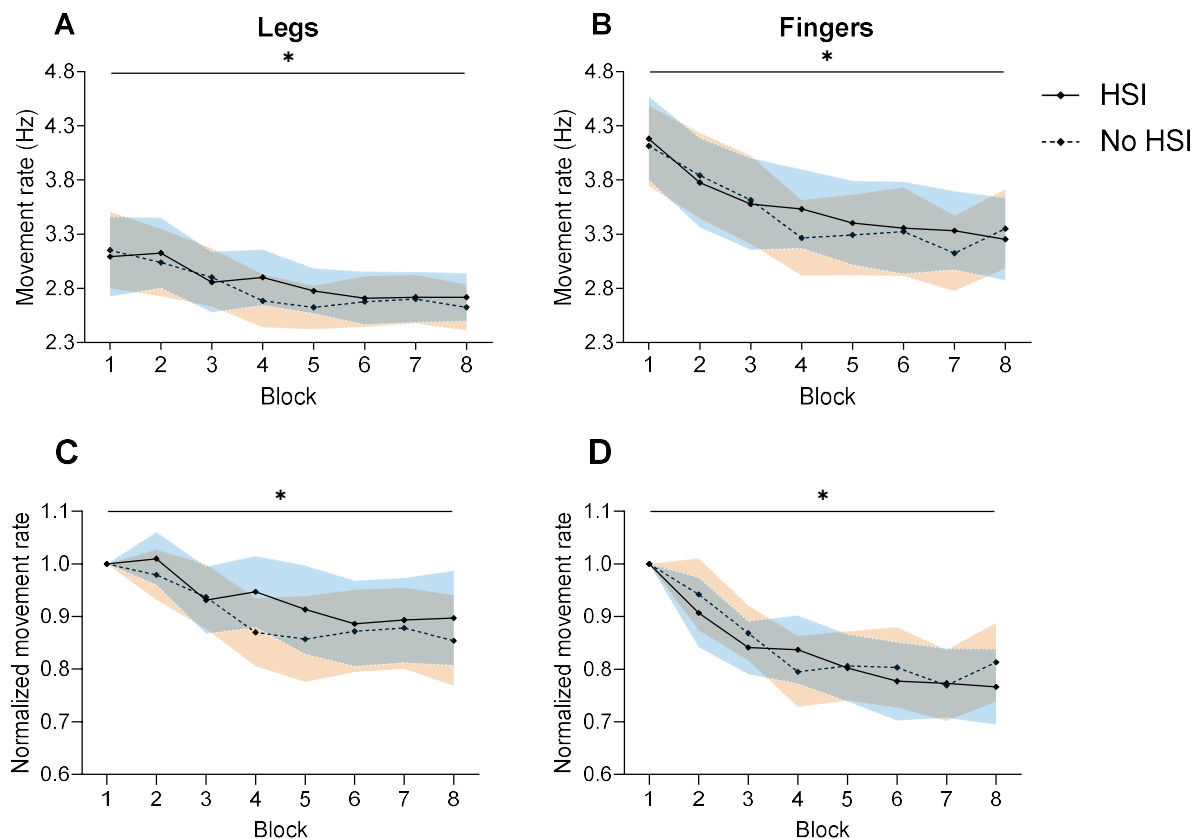


The shaded areas represent the 95% confidence interval for the legs (blue) and fingers (orange) movement rate. *significant effect of the block factor ($p < 0.05$); #significant effect of the limb factor ($p < 0.05$). RPE, rating of perceived exertion.

Effect of hamstring injury history on leg and finger movement rate

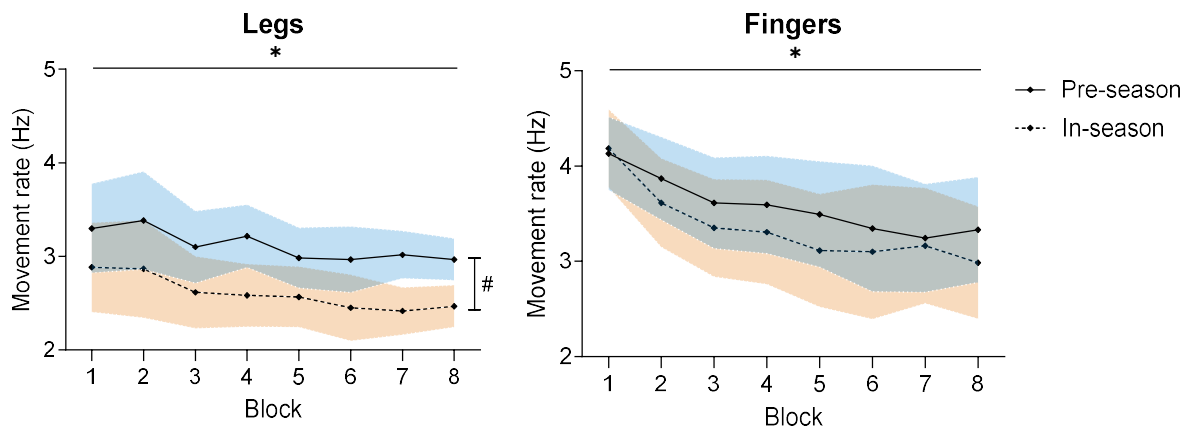
In the comparison of footballers with and without HSI history, there were no significant injury $\times$ block interactions either in the leg or finger tests. The same was seen for differences between players with and without HSI history in both leg (absolute: $p=0.91$; normalized: $p=0.47$) and finger (absolute: $p=0.90$; normalized: $p=0.72$) MR (Figure 31A-D). However, when comparing the pre-season and in-season HSI subgroups, we noted a significant effect of the measurement period for the absolute leg MR ($p=0.029$, $\eta_p^2 = 0.40$, power = 0.64), with players measured in the pre-season showing a higher MR. Conversely, there were no significant differences in the normalized leg MR ($p=0.57$) or in finger MR (absolute: $p=0.48$; normalized: $p=0.30$) (Figure 32).

Figure 31. Changes in absolute (A,B) and normalized (C,D) leg and finger movement rate in footballers with and without hamstring injury history



The shaded areas represent the 95% confidence interval for the movement rate of footballers with (blue) and without (orange) hamstring injury history. *significant effect of the block factor ($p<0.05$); HSI, hamstring strain injury.

Figure 32. Changes in leg and finger movement rate in players evaluated at two different periods (pre-season and in-season)



The shaded areas represent the 95% confidence interval of the movement rate for players measured during the pre-season (blue) and in season (orange). *significant effect of the block factor ($p < 0.05$); #significant effect of the measurement time factor ($p < 0.05$).

Discussion

This study sought to address issues related to different knowledge areas. On a more physiological / motor control perspective, there was a significant reduction in both leg and finger MR over the course of a fatiguing task, with a significant difference between limbs. The absolute MR curves also showed a significantly different slope, with a steeper decrease in finger MR accompanied by a significantly greater decrease in finger MR, the difference was not significant. Conversely, there was a similar goodness of fit for leg and finger MR. No correlations between leg and finger MR were observed. As for the application of MR testing in sports, neither task was able to differentiate footballers with and without HSI history. Nevertheless, the difference found between pre-season and in-season leg MR in footballers with HSI warrants further investigation.

Both legs and fingers showed a reduction in MR until a plateau was reached, which occurred at about halfway through both tasks. However, this stabilization was achieved after different percentages of MR loss for the legs and fingers. In terms of exercise regulation, this may indicate that a lower percentage of MR loss is required until performance stabilization is achieved in larger body segments. A previous finger tapping study found even greater finger MR losses (~40%) before a plateau was reached (Madinabeitia-Mancebo et al., 2020), albeit in a longer task (three minutes of continuous maximal tapping). Our findings of finger MR

loss are more in line with shorter (20-30 s) continuous tasks (Arias et al., 2015; Rodrigues et al., 2009), which means our task parameters (8 x 10 s) may have been insufficient to detect a true plateau, which may be due to the intermittent nature of our task. Nevertheless, there was still a significantly greater performance loss than in leg MR.

It is known that leg and finger muscles involved in the used tasks have slightly different percentages of type II (fast-twitch) fibers, which are especially relevant for maximum-speed movement. While finger muscles (interossei, finger flexors/extensors) have type II fiber percentages ranging from 42% to 56% (Johnson et al., 1973), the percentages for knee flexors and extensors range from 53% to 68% (Evangelidis et al., 2017; Fournier et al., 2022; Horwath et al., 2021). These percentages would suggest an earlier and greater fatigue for the legs; however, we noted a steeper slope and greater performance decrement for the fingers. Thus, it seems that muscle composition is not the factor behind the observed differences in MR loss. The functional differences in movement patterns between the upper (low load, asymmetrical, and fine motor skills) and lower (high load, symmetrical, and directed for balance and stability) limbs (Goel & Paloski, 2016) mean that the movement pattern used is more familiar to the lower limbs. Factors such as intermuscular and interlimb coordination, as well as homeostatic regulation (as detailed below), therefore seem to be more decisive.

Although studies correlating upper and lower limb MR are scarce, two studies have produced contrasting results. Fearing et al. found no correlation between finger and foot tapping performance (Fearing et al., 2001), while another study analyzing the same body segments in athletes found the opposite (Chaabouni et al., 2022). Thus, regarding the issue of the body region specificity, our findings suggest a lack of association between upper and lower limb MR performance, both in the lack of correlation and in the different fatigue behavior. Our study therefore suggests that the magnitude of motor slowing is different depending on segment mass, with a lower performance decrement required to reach a plateau on larger segments. Whether this is due to changes in central movement programming or homeostatic exercise regulation remains to be determined; nevertheless, our findings may mean that the motor slowing behavior is not as universal as previously thought. It would be worth determining the physiological mechanisms behind the differences in the performance decrement between the legs and fingers. In any case, the greater RPE seen in the leg task suggests that more strict exercise regulation mechanisms may have been activated due to the greater mass being moved, leading to the lower performance loss before a MR plateau was reached.

This sample of football players showed a greater finger than leg MR performance decrement. Considering the similar ROM found in both the leg and finger tasks in pilot testing, we assume ROM-related factors were not the source of the differences found in this study. Previous studies in healthy individuals have shown a similar motor slowing behavior between the upper (fingers) and lower (foot) limbs (Bächinger et al., 2019), which could suggest that differences in our study were due to the effect of football training on leg physical conditioning, leading to a lower decrease in MR. Moreover, a previous study found no difference in the degree of hand and foot motor slowing between upper- (handballers) and lower- (footballers) limb trained participants (Seidel-Marzi & Ragert, 2020). However, since footballers in this study showed a similar overall performance to that of non-athletes during the same leg MR task (Correia et al., 2024; Correia, Vaz, Witvrouw, et al., 2022), it is more likely that the dissociation between leg and finger MR highlighted by the different slope and percentage of decrease, as well as by the lack of correlation, is due to different maximal performance determinants between these two segments.

There were no differences in finger or leg MR between footballers with and without HSI history. This is contrary to our previous findings in a larger sample of football players, in which players with HSI history had higher MR (Correia et al., under review). This has two possible causes. First, both the fact that part of the sample was tested at a different time point in the season (March vs. July) or differences in the competitive level (higher division clubs in this study) may have caused these discrepancies in the findings. Second, the value of leg MR in differentiating players with and without HSI may not be as significant as seen in our initial study (Correia et al., under review). However, there was a significant difference in MR between time points in players with HSI history, and our previous findings of players with HSI history displaying a greater MR was also observed in players measured during the pre-season, suggesting that differences in the measurement time (off-season vs. in-season) may have had a greater impact. Although these were two different cohorts, thus preventing a direct comparison, there is existing evidence to support this possibility. Risk factors for HSIs have been noted to change throughout the season (Sim et al., 2023); moreover, sprint and change of direction speed have been noted to decrease during the football off-season regardless of previous HSI (Vicens-Bordas et al., 2020); the same parameters have also been found to fluctuate during a footballing season (Bishop et al., 2022; Fessi et al., 2016). Nevertheless, the possible differences in leg MR throughout the season and their role on HSI risk should be confirmed in future studies. Considering that these differences were not seen in finger MR, it could serve as a control variable for performing comparisons between multiple time points.

Limitations

Naturally, this study has some limitations. Since we only evaluated the motor behavior, we do not know which central and peripheral mechanisms led to the differences between leg and finger findings. This could be addressed by measuring central and peripheral electrophysiological variables during the task and performing a pre-post task comparison in terms of variables such as maximum voluntary contraction, rate of force development, and voluntary activation. Since we only evaluated young athletic males, we are also unsure if these findings are generalizable to other populations. Nevertheless, in terms of the athletic level, we have previously found a similar performance in the leg test in non-athletic individuals (Correia et al., 2024; Correia, Vaz, Witvrouw, et al., 2022). Finally, since we recruited lower limb-trained athletes, it is unclear whether a different motor slowing pattern would be present in upper limb-trained athletes such as handball players or in more specific finger-trained populations such as musicians.

Conclusions

Leg and finger MR show similar dynamics when the same task duration is used but differ in terms of performance decrement in a lower limb-trained sample of footballers. Our findings contrast with the prevailing literature on the association between upper and lower limb MR, suggesting joint/segment size alters repetitive movement control performed at maximum speed. Neither test was able to differentiate footballers with and without HSI history.

Declarations of interest: none

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CHAPTER VII – GENERAL DISCUSSION

This project aimed to answer research questions in a theoretical/fundamental to practical/applied sequence. First, the existing evidence on the motor control of fast limb movements was reviewed, which revealed a paucity of research on lower limb motor slowing, associated brain activity, and its applications in sports. Second, the pattern of lower limb motor slowing and the associated central and peripheral physiological manifestations were analyzed. This study revealed that the trajectory of lower limb motor slowing is largely similar to that of smaller joints, but the percentage of MR loss required to achieve a plateau is lower. It was also found that, unlike what is generally reported for finger tapping tasks, repetitive leg movement leads to decreases in both RTD and MVIC, indicating that both central and peripheral force generating pathways were affected. Accordingly, there were also changes in both brain and flexor muscle activity. Third, the designed task was able to differentiate footballers with and without HSI history; an index was created using parameters from the first three blocks which showed high specificity but low sensitivity. Nevertheless, this simple test, which can be easily applied in a variety of settings, seems to have some clinical value. It was also found that players with and without HSI history have some distinct responses to the leg MR task in association with their performance differences. Footballers with previous HSI history showed a greater drop in muscle activity and less co-contraction despite their better performance. These players also showed brain activity patterns associated with greater task load and attentional resource allocation, indicating that they had to dedicate more cortical resources to task performance than their uninjured counterparts. Finally, both common and differing aspects of finger and leg motor slowing were highlighted; while both segments showed a significant decrease in MR [reinforcing the idea of a common fatigue profile across all joints (Madinabeitia-Mancebo et al., 2021)], the percentage of MR loss was higher for the fingers before a plateau was reached (suggesting that different exercise regulation mechanisms may be limiting performance).

Lower limb motor slowing patterns

The comparison of MR between healthy participants and footballers showed three major highlights: 1) the percentage of loss is greater in footballers (22.6 and 18% in players with and without HSI history vs. 14.4% in the average of the two sessions in healthy participants); 2) the absolute performance level was very similar between healthy participants and non-injured footballers; 3) there was a greater association between the first block performance and percentage of MR loss during the task in footballers than in healthy participants ($r^2=0.2$ vs. $0.1-0.17$). Regarding this last point, this was an inverse correlation, meaning that players

who performed better in the first block wound up having a greater percentage of MR loss. This may be explained by two factors. First, players with a greater fast-twitch fiber content may be able to achieve a higher MR, and since these fibers fatigue faster (White & Hall, 2008), a more pronounced performance decrement would then follow. Second, a higher MR may represent a more serious homeostatic disturbance, meaning that performance must decrease more substantially in order to achieve a sustainable effort. Nevertheless, both factors are speculative, since we did not perform direct measurements related to them; it is also possible that there is an interaction of factors behind this correlation. This interaction and the possible mechanisms of exercise regulation are discussed later.

The similar MR found between healthy participants and footballers without HSI history indicates that for this task, training history does not seem to be advantageous, which is contrary to what has been consistently seen in tasks such as sprinting, where athletes perform better than non-athletes (Clark, 2009; Malinauskas et al., 2014; Wang et al., 2021). This lack of benefit of athletic training also suggests that performance in this task is more determined by factors other than chronic sports training. The distribution of motor unit (Klaver-Król et al., 2010) and muscle fiber types (Billeter & Hoppeler, 2003; Vincent et al., 2007) has been found to have a strong genetic component. Accordingly, this has reflected on an even higher heritability of factors such as RTD (Lykoudi et al., 2015), movement and EMG velocity (Missitzi et al., 2008), and most importantly in this case, of neuromuscular coordination in fast movements (Missitzi et al., 2004). Thus, it may be the case that the skills and physiological basis associated with improved task performance are more predetermined. Nevertheless, since this remains conjectural due to the lack of direct evidence, the need for studies to determine how much practicing this task will improve performance and affect injury risk remains.

One relevant aspect was the consistency of the average MR trajectory across all studies, with a decrease until block 4 (in healthy participants, Chapter IV) or block 5 (in footballers, Chapters V and VI), followed by a plateau until the end of the task. This shows that not only this measurement seems to be stable across training levels and at different short-term time points (as shown by the high ICCs), but that any exercise regulation mechanisms that may have limited the performance of this task are not substantially different between healthy participants and footballers but rather have a more fundamental physiological nature. It is also interesting to note that this pattern is present in different maximal intermittent movement tasks ranging from finger tapping to repeated sprinting (Bächinger et al., 2019; Hureau et al., 2014, 2016; Madinabeitia-Mancebo et al., 2020; Madrid et al., 2018). Thus, even though there are probably different factors limiting, for example, the task used in this project and

finger or foot tapping, in tasks with known duration, performance decreases until a sustainable plateau is reached, tracing a similar curve. This similarity is supported by the analysis of the curve coefficients in Chapter VI, where a similar goodness of fit was found for both finger and leg MR but the fingers showed a greater negative slope, suggesting a greater performance decrement before reaching the plateau. This would suggest that, for a similar duration, differences between body segments are seen mostly in terms of the percentage of performance before a plateau is reached, and constitute a concept of “critical MR” for each segment akin to what has been described for critical power. This regulation of motor output designed to avoid passing a critical fatigue threshold has been proposed in studies of maximal running and cycling repeated sprinting (Hureau et al., 2014, 2016). However, other authors have questioned the existence of such a threshold (Burnley, 2018; Thomas et al., 2018), stating that performance regulation is merely the result of task-specific parameters, which in turn dictate the amount of oxygen that can be delivered to muscles and determine the demands on other systems, thereby adjusting performance and modulating fatigue according to the interaction of those systems.

The greater MR shown by footballers with previous HSI history in the first half of the task was contrary to the initial hypothesis and therefore surprising. The initial hypothesis that players with previous HSI would be slower was based on previous studies showing that athletes with previous HSI have impaired leg swing movement discrimination (Cameron et al., 2003), greater loss of horizontal force after repeated sprinting (Lord et al., 2019), and changes in hamstrings intermuscular coordination, namely in the BF/ST and BF/SM recruitment pattern of injured limbs, with the injured muscle (BF) showing lower activity (Avrillon et al., 2020; Schuermans et al., 2016). Nevertheless, there have been studies showing faster sprinting or movement speed in athletes with HSI history (Ishøi et al., 2020; Røksund et al., 2017), which the present findings tend to support. In any case, the presence of differences in such a quick and inexpensive test and the resulting MR index shows some promise in terms of field applications, which are discussed later.

Electrophysiological changes and the mechanisms behind decreased performance

The observed patterns of brain activity in response to the fatigue induced by the task may be relevant under two different perspectives. First, there are shared brain regions and pathways between motor and cognitive processes (Leisman et al., 2016). Second, it is known that mental/cognitive fatigue increases the perception of effort, limiting performance even in the

absence of physical limitations (Marcora et al., 2009). As mentioned in Chapter IV, multiple studies have reported an increase in brain activity with fatigue or increased exercise intensity, which is explained by the greater central drive needed to compensate for a lower peripheral force generation ability (Bailey et al., 2008; Brümmer et al., 2011; Enders et al., 2016; Schneider et al., 2013). In the studies which included EEG measurements (Chapters IV and V), there was generally an early increase in normalized power, which was then followed by a decrease and subsequent stabilization (in healthy participants) or another small increase in the last two blocks (in footballers). This difference in the final stages of the task may be related to the greater footballers' ability to have an end spurt [a phenomenon commonly seen in athletes towards the end of a race/task (Noakes, 2012)] in brain activity, which was however not accompanied by an increase in MR, possibly because there were no unfatigued MUs that could perform quick changes in direction once again. Nevertheless, this difference in the final stages may indicate that footballers, through continued practice, are able to increase their drive near task completion, which constitutes a valuable skill, for example, during the final stages of a match. Additionally, both healthy participants and footballers showed a similar pattern across EEG electrodes, which suggests both frontal and central brain regions were working in conjunction to perform executive control motor planning, execution, and sensorimotor integration (Brümmer et al., 2011; Enders et al., 2016; J. Z. Liu et al., 2002). Increased theta activity (and the associated decrease in alpha power in footballers with previous HSI) may also indicate a greater loss of inhibition or higher cortical excitability. However, this possible decrease in inhibition did not lead to repetitive movement performance limitations, as previously suggested (Bächinger et al., 2019).

Despite the proposed specialization of the left hemisphere in the control of fast repetitive movement (Nalçacı et al., 2001; Todor et al., 1982), there were no major visible differences in brain activity between hemispheres during the task. This is likely to have been caused by a combination of factors. First, the task was maximal, which means that all available resources were used and makes it harder to detect differences. Second, the task was symmetrical and with limb interdependence (i.e., one limb could not be independently faster than the other). Both these issues may have led to the similar interhemispheric activity pattern at frontal and central electrodes. Accordingly, a lack of interhemispheric differences in symmetrical repetitive tasks was previously reported (Bailey et al., 2008). The same was generally true for differences between frontal and central electrodes; nevertheless, differences between footballers with and without HSI history were more evident in frontal electrodes. The maximum and high-speed nature of the task may have contributed to this similarity as well, as there was a greater need for activity synchronization.

Greater EEG activity is usually seen with increasing exercise intensity and with the onset of fatigue (Bailey et al., 2008; Brümmer et al., 2011; Enders et al., 2016; J. Z. Liu et al., 2002). This is explained by the increased central drive required both when intensity increases and the muscle force generation capacity decreases, respectively. Considering the increasing RPE throughout the task, a continuous increase in EEG power could be expected. However, the general EEG pattern observed here was composed of an early increase followed by a more pronounced decrease until the second half of the task, especially in non-athletes and in footballers without previous HSI. Thus, it may have been the case that EEG power first increased as a response to early fatigue and then decreased in order to adjust to both impaired muscle contraction dynamics (i.e., increased contraction and relaxation time) and to excessive metabolic disturbance, thus not requiring such a strong central drive since performance intensity could not be maintained anyway or as an adjustment to the EMG lower amplitude and greater burst duration, which would not require such intense brain activity. As for a more band-specific look, the most notable findings were seen when comparing footballers with and without HSI history (Chapter V). Unaffected players showed a normalized frontal theta activity plateau during the second half of the task, while those with HSI history showed a significant increase. Greater frontal theta activity has been associated with additional dedication of attentional, perceptive, and error monitoring resources to a task (Doppelmayr et al., 2008; Visser et al., 2022), although not in fatiguing conditions. As discussed in Chapter V, this increase in theta activity in footballers with HSI history can be interpreted by the greater need to dedicate conscious attention to maintain the leg within the range of motion required by the task. In this sense, as is seen post-other injuries (Baumeister et al., 2011; Busch et al., 2021; Lavender et al., 1999), proprioceptive input from muscle afferents would be decreased, requiring more conscious resources to be aware of the leg position, especially in the presence of fatigue. Accordingly, increased frontal theta power has been linked to top-down (as opposed to bottom-up) adjustments of motor responses (Kaiser & Schütz-Bosbach, 2021), further supporting the idea that footballers had to dedicate more cortical resources and depended less on peripheral feedback. There were also relevant differences in the alpha band, especially in the relative EEG power analysis (a measure of how much signal content originates from each band). The importance of alpha-range EEG in both sensorimotor integration and motor planning and execution is well established (Athanasίου et al., 2018; Klimesch et al., 2007; Ofori et al., 2015), and its activity has been found to be modulated by factors such as fatigue (Enders et al., 2016; Suviseshamuthu et al., 2022) and task complexity (Zabielska-Mendyk et al., 2018). Throughout the task, footballers with previous HSI showed an alpha-to-theta shift in their EEG pattern (as observable by the relative decrease in alpha content and both relative and

normalized increase in theta activity). As previously reported (Chikhi et al., 2022; Raufi & Longo, 2022), this shift is suggestive of increased cognitive load (possibly because of the greater reliance on central control and the corresponding conscious attention required to control limb position). It is interesting to note that there is some overlap with the central adaptations seen in footballers with HSI and what has been seen in other musculoskeletal injuries (Baumeister et al., 2007, 2013; Grooms et al., 2017; Needle et al., 2017), namely with the greater use of attentional resources and lower reliance on peripheral feedback. This points to the hypothesis of a similar response of supraspinal motor control to different soft tissue injuries. Naturally, this hypothesis still requires further development and confirmation. However, it is important to consider that task complexity, sensory integration, and fatigue may have opposing influences in the EEG power. These influences may explain the contradicting findings seen in footballers without HSI and non-athletic participants, which despite showing either no changes or an increase in normalized/relative alpha power, which is suggestive of greater inhibition (Suviseshamuthu et al., 2022), also showed a greater flexor-extensor co-contraction.

Although this was more evident in footballers, knee flexor muscles generally showed less CMC than the extensors in both athletic and non-athletic participants. However, the significantly lower BF CMC compared to all other muscles was seen throughout the entire task in footballers and only (and to a lesser degree) in the first and last blocks in healthy participants. The reasons for this isolated lower BF CMC are not clear. If this had only been seen in footballers with previous HSI, it would be logical to attribute this lower brain-muscle coupling to the injury, but this was not the case. This difference also cannot be explained by fatigue, since the pattern was similar throughout the entire task in footballers. The existing literature also does not provide a direct explanation. In a study of lower limb cortical representation using TMS, the hamstrings showed a $\approx 11\%$ longer latency and $\approx 10\%$ lower map volume (a measure of overall excitability of the cortical representation) when compared to the quadriceps. (Davies, 2020) Although a longer latency and decreased excitability could influence the degree of CMC, since both time and the frequency content are present in its calculation, that study did not find differences between medial (ST/SM) and lateral (BF) hamstrings. Another study analyzed differences in the properties of the corticospinal pathway between the RF and BF using TMS stimulus-response curves. The greater response magnitude of the RF was explained by the lower type I fiber content and by a greater difficulty in synchronizing BF MUs, meaning that the BF requires a larger motor command to produce the same force (Higashihara et al., 2022). This more difficult synchronization and greater descending motor requirements could also be a factor in the magnitude of CMC; however, that study did not measure the ST, and this explanation also

does not clarify why the lower BF CMC was seen during the entire task only in footballers. Nevertheless, considering that the ST has a similar composition to the BF (Garrett et al., 1984), these differences in MU synchronization ability may also apply to the ST. Indeed, the electromechanical delay of the knee flexors has been found to be almost twice as long as that of the extensors (44 vs. 27 ms) in isometric explosive contractions (Hannah et al., 2014), which supports the idea of a generalized pattern for all flexor muscles.

There was a significantly higher CMC in all C3-muscle pairs in the second than in the first session of the study in Chapter IV, which was accompanied by a (non-significantly) higher MR throughout the entire task except for the first block. This association of better performance and increased brain-muscle coupling suggests the presence of a small learning effect between sessions. Thus, despite the simplicity and familiarity of the knee flexion-extension cycle, the challenge of maximum speed and quick change of direction introduced an unfamiliar component, suggesting that healthy individuals are not used to being exposed to maximum movement speed. It remains uncertain whether there are any functional benefits to this exposure and to movement speed training, but as stated in Chapter II, increasing movement speed throughout the lifespan has been associated with positive health and functional outcomes. There is some evidence of an association between CMC and motor learning/performance. Hori et al. found an increase in CMC in the second and third trials of a virtual joystick navigation task in association with improved performance, as did Perez et al. after a force control visual task involving leg muscles. Both groups of authors explained these findings through a greater sensorimotor integration of visuospatial information into motor commands (Hori et al., 2013; Perez et al., 2006). In our task, there was no visual feedback, so the information on which to base the motor command would have to come from either the proprioceptive system or from internal motor programs. Nevertheless, the CMC findings from Chapter IV support this association between CMC and motor performance. Conversely, in Chapter V, it was found that despite their better performance, footballers with previous HSI injury did not show improved CMC compared to those without HSI history. This suggests that CMC is more responsive to repetition and learning in response to task novelty than purely with performance when a novel task is performed by differently trained populations.

Flexor EMG activity significantly decreased both in healthy individuals and in footballers. However, significant changes in extensor EMG activity were only seen in footballers. The footballers sample as a whole showed a slightly greater increase in VL and decrease in VM activity than the healthy participants. However, the greatest difference was seen in the RF, with the HSI history group showing a marked decrease in activity compared to both the HSI

history group and what was seen in healthy individuals. Footballers with previous HSI also showed significantly lower BF activity than those without HSI, regardless of the injured limb. A lack of contralateral limb differences in knee flexor activity in previously strained limbs during maximal running was also found in a recent systematic review (Presland et al., 2021). It may be the case that, in symmetrical all-out tasks, where both limbs perform the same movement and there is no possibility of distributing activity between synergists, the non-injured limb activity is adjusted to allow for the cyclical movement to be performed. In such movements, it is known that both agonist and antagonist activity influence fast limb movement duration; while agonists contribute to accelerate the segment, antagonist activity promotes a faster deceleration, thus allowing for a quicker change in direction (Jarić et al., 1995; Liang et al., 2008; Wierzbicka et al., 1986). The fact that footballers with HSI history had a greater drop in RF activity despite the lower co-contraction may mean that they were able to engage both the knee flexors and extensors in short, strong, well-timed bursts at the start of the task, which allowed them to have a higher MR in this period. The decreased ability to maintain these bursts throughout the task would then have led to the decrease in normalized activity and in a similar MR to the players without HSI history in the second half of the task. It is also worth noting that the RF is the only extensor that crosses the hip joint, which means that its activation may also have contributed to a greater segment stability, which is also beneficial for efficient movement. Another possible mechanism behind the decrease in EMG activity seen in the knee flexors (the prime movers in this task) both in healthy participants and in footballers is related to adjustments in burst duration. Accordingly, decreases in EMG activity in response to intermittent maximal cycling have been explained as an appropriate adjustment of MU firing rate to the increased twitch duration caused by fatigue (Billaut & Smith, 2010). In this perspective, it is interesting to note that the subgroup with the best task performance (footballers with previous HSI) showed not only the greatest decrease in BF activity but also the greatest decrease in RF activity. A similar pattern of decreased bi-articular antagonist (the RF in this task) EMG activity as an adaptation to fatigue of the prime movers (such as the BF) has previously been reported (Hautier et al., 2000). The inter-limb coordination between these two muscles has also been noted to correlate with step frequency, but not with running speed or step length, during maximal speed running in track and field athletes (Kakehata et al., 2021). This indicates not only that movement/step rate and overall speed are influenced by different factors but also highlights that the RF and BF, the muscles which showed differences between footballers with and without HSI history, have an important collective role in terms of coordination during fast movements. Additionally, the importance of intermuscular coordination (such as between agonists and antagonists) has been mentioned as a key factor in fast cyclical movement performance,

namely through muscle activation/deactivation dynamics (Neptune & Kautz, 2001; Van Soest & Casius, 2000). In fact, fatigue has been known to decrease the delay between agonist and antagonist activity during maximal intermittent cyclical movements (Billaut et al., 2005), thus promoting a greater overlap in EMG activity. This also supports the increasing co-contraction found in Chapters IV and V. Further supporting evidence for this increased co-contraction can be found in the study of Pinniger et al., which found increased duration of hamstring activity and changes in RF burst timing in fatigued compared to non-fatigued sprinting; these changes provided a basis for the decreased stride rate with fatigue (Pinniger et al., 2000), which may constitute a similar mechanism behind the decreased MR seen across chapters in the present work. A continuous decrease in normalized EMG activity despite a plateau in performance (measured either by speed, power, or work) has been observed in other types of intermittent maximal efforts such as running and cycling sprinting (Billaut & Smith, 2010; Hureau et al., 2016; Mendez-Villanueva et al., 2008). This decreased activity may be caused by the selective fatigue of fast-twitch fibers, thus decreasing EMG amplitude, by impaired muscle contractility (in association with factors such as metabolite accumulation, changes in excitation-contraction coupling and conduction deficits), by adjustments in burst amplitude and duration associated with the decreased contraction speed, or by an interaction of all these factors.

It is clear from the performed studies that motor slowing occurred. As stated in Chapter II, the physiological determinants of upper limb and small joint motor slowing seem to be supraspinal. However, a definite explanation has yet to be provided. One of the hypotheses is the one related to surround inhibition. According to this mechanism, a net increase in cortical excitability occurs with repetitive movement, leading to decreased suppression of unwanted motor programs and increased muscle co-activation (Bächinger et al., 2019). We did register an increase in co-contraction during the task both in healthy individuals and in footballers (with and without HSI history), but the expected associated decrease in alpha band activity in central electrodes, which is associated with the loss of top-down inhibition (Klimesch et al., 2007), was not as clear, being more obvious in footballers with HSI history. Changes in normalized alpha activity were more pronounced in frontal electrodes and had a more wave-like pattern throughout the task, generally with an early increase and then a drop until about halfway of the task, with another increase in the second half of the task seen only in footballers. Nevertheless, there was a clear and continuous decrease in relative alpha activity in footballers with HSI history, suggesting a greater loss of inhibition, and it is worth noting that most of the pathways associated with surround inhibition are located at a subcortical level (Jahanshahi et al., 2015; White & Hall, 2008), making its detection through EEG difficult. Other possible cause of motor slowing proposed in Chapter IV was related to

muscle activity (through increases in the contraction-relaxation cycle duration) and limited time for ATP resynthesis (Arias et al., 2012). Our increased co-contraction throughout the task despite the decrease in flexor activity suggests a prolonged activation of both agonists and antagonists, leading to a greater temporal overlap which would be in line with this hypothesis. The fact that the task performance plateaus at around the time where the ATP-PCr system decreases its contribution also provides indirect evidence that energy availability may have played a role. Finally, the proposition of Rodrigues et al. (Rodrigues et al., 2009) that a breakdown of the central motor command to quickly change movement direction occurs is also substantiated by some of our findings. Like those authors, we also noticed an increased overlap of flexor and extensor EMG activity with fatigue. Additionally, the decrease in CMC seen in Chapters IV and V provides an indirect suggestion of a loss of brain-muscle coupling and thus degradation of the motor command to support this hypothesis.

When analyzing all the footballers tested in the studies presented in Chapters V and VI, a significant positive correlation was found between the MR of the first block and the total MR loss during the task ($r=0.441$, $p<0.001$). Despite the task differences, this association between initial performance and its decrement has been seen in studies of repeated sprinting (Mendez-Villanueva et al., 2008; Yanagiya et al., 2003) and has been suggested to be due to the individual anaerobic contribution (Girard et al., 2011). Accordingly, individuals with a lower reliance in anaerobic metabolism have shown greater fatigue resistance during such tasks (Gaitanos et al., 1993; Mendez-Villanueva et al., 2007). The timing of the MR plateau seen in this project lends some support to this idea, as it falls around the period of the plateau of the ATP-PCr system contribution to maximal effort.

Maximal exercise regulation and the role of fatigue

Both healthy participants and footballers showed changes in the electrophysiological variables measured centrally and at the periphery which can logically be attributable to fatigue, as confirmed by the almost-maximal RPE seen at the end of the leg task.

Traditionally, central and peripheral fatigue have been studied, mentioned, and presented as separate entities, with experimental approaches and measurements aiming to specifically target each component (Davis, 1995; Encarnación-Martínez et al., 2022; Kent-Braun, 1999; Schillings et al., 2003). This distinction has, however, been challenged by authors which state that this distinction is artificial, has prevented the evolution of the understanding of fatigue, and does not reflect the multiple factors and adjustments underpinning the concept of fatigue during exercise (Enoka & Duchateau, 2016; St Clair Gibson et al., 2018). Attempts have been made to provide an integrated model of exercise regulation, encompassing input

from all systems into a unified regulatory framework of fatigue. One such model is the central governor model, which postulates that a brain center integrates input from multiple levels (e.g., cardiopulmonary, musculoskeletal, psychological, endocrine), but also from previous exercise attempts, to regulate motor output through a negative feedback loop. This regulation is therefore based in the relative weighting of all involved factors and is aimed at maintaining homeostasis and failure of any system during exercise (Noakes, 2005, 2011; St Clair Gibson et al., 2018).

Some valid concerns have, however, been raised regarding this model. If this regulatory mechanism regulates exercise output based on the integration of input from all involved systems, then events such as acute musculoskeletal injuries or even exercise-associated cardiac arrest should not occur. Moreover, if it encompasses all possible factors involved in exercise regulation into a governing center, then it is unlikely that the existence of this center can be falsified, which is an essential attribute of any scientifically valid theory (Inzlicht & Marcora, 2016; Marcora, 2008; Shephard, 2009). An alternative model based on the motivational intensity theory proposes that the decision to terminate exercise is taken by the conscious brain, which regulates motor output after considering sensory subconscious input and motivational aspects, rather than using a subconscious governor who collects afferent input and then relays it to the conscious brain (Marcora, 2008). Finally, the concept of “sensory tolerance limit” was created by Hureau et al. and, like the central governor model, is based on the notion that exercise is regulated through a negative feedback loop, but the collection of all feedback and feedforward signals is processed within the central nervous system to regulate exercise intensity and ensure it stays within tolerable levels. This concept also includes the idea that this tolerance limit is variable both between individuals and within tasks (Hureau et al., 2018). Since its original publication, though, it has not been studied and further developed, thus remaining a hypothetical construct.

Throughout the presented studies, signs of changes at both central and peripheral levels were described, and it is clear that a performance decrement was present during the leg and finger tasks. However, this decrement was only seen until the fourth or fifth block, after which no significant changes were noted, despite the instructions to always maintain a maximal effort and the encouragement provided. In association with this decrement, a decrease in muscle activity was seen in the knee flexors (healthy participants) and in flexors and extensors (footballers) in a continuous manner. EEG activity and CMC also showed changes which may be interpreted as signs of fatigue and increasing task load. Thus, the task induced significant effects from the CNS to the observable behavior. However, this did not mean that there was a complete failure of the motor system, as participants performed an

MVIC usually within 20-30s of finishing the task, and the decreases in maximum force generation were only 20-22% in healthy participants and 10-12% in footballers. Moreover, electrophysiological variables continued to change even after MR stabilized. In fact, the only parameter that seemed to reach a critical level was RPE, which suggests that maximal performance was limited (or paced) to avoid excessive discomfort/perturbation caused by the sensation of fatigue and to ensure that the maximum exertion level was only achieved at the end of the task. As pointed out by the proponents of the central governor model, fatigue can be seen as an “emotion” of the motor system, where this sensation serves as a warning sign to decrease performance (Noakes, 2012). RPE (as a subjective measure of fatigue) may therefore arise from the afferent input of all systems involved, depending on exercise mode, intensity, and duration. In support of this notion, several factors such as muscle contractility, arterial O₂ saturation, and voluntary activation have been found to affect all-out performance (Billaut & Smith, 2010; Goodall et al., 2015); moreover, it has been highlighted that despite abundant research, a single sensory cue has yet to be consistently found to be the main determinant of RPE (Venhorst et al., 2018). This interaction of multiple systems involved in exercise performance and regulation is also made evident when comparing the observed finger and leg MR findings. Despite the similar trajectory (greater decrease during the first half of the task followed by a stabilization), the magnitude of motor slowing (as evaluated by the percentage of decrease in movement rate) was greater for the fingers. As this was accompanied by a lower RPE for the fingers, it may be the case that in the presence of lower effort, a greater decrease in MR is “allowed” before reaching a plateau. In this way, the factors limiting maximal exercise performance in repetitive movement may differ between body segments. In this example, despite the presence of common demands between the two tasks, cardiometabolic/energetic factors could be the main determinant of leg MR, considering the higher RPE achieved, while for the fingers aspects related to muscle contractility and the central motor command could be more decisive.

Indeed, if RPE had been the main factor in determining performance, the final (small) increase in leg MR from the seventh to the eighth block occasionally seen in the participants would not be possible. This increase in performance near task completion has been described as the “end spurt” (Foster et al., 2023; Noakes, 2012). Apart from the occasional muscle discomfort in footballers which prompted task interruption for safety reasons, it can be said that whatever exercise regulation mechanism(s) was(were) acting, catastrophic failure of all systems involved in task performance was successfully prevented despite a near-maximum RPE. It is, however, difficult to attribute a greater responsibility in performance regulation to any particular parameter. While evidence to particularly support either the existence of the central governor, sensory tolerance limit, or the motivational

intensity theory may not be evident from the collective findings of this project, they suggest that multiple factors do interact to regulate performance in a brief, maximal task, with no individual factor taking precedence over another. Where this interaction occurs and which systems and structures are involved in integrating information remains to be clarified.

This way, when looking at the combined changes in parameters measured centrally and at the periphery, it is difficult to attribute a more important role in performance regulation or in the development of the sensation of fatigue to an isolated cause. This lack of a single factor behind the sensation of fatigue has also been highlighted in previous physiological reviews on this topic (St Clair Gibson et al., 2003; Venhorst et al., 2018). Accordingly, it has been reported that the decrease in sprint speed (in which MR plays a relevant role) seen during repeated sprinting is likely not caused by a singular mechanism but rather from a complex interaction of neural and muscular factors (Girard et al., 2015).

Motivational aspects and the value attributed to a good performance by each athlete were not determined. The role of emotions and the impact of value attributed to movement goals in movement speed were described as part of Chapter II. In there, it was highlighted that current evidence shows that positive emotions and a greater attribution of value increase movement speed. Although there was no obvious reward as motivation to perform well, the individual competitive nature of each participant (whether athletes or not) and the meaning/value they attributed to performing well may therefore have influenced their performance.

Pre-post task changes in maximal and rapid force production

Since MVIC and RTD have different physiological determinants and show a distinct dependence on muscle and neural factors (Maffiuletti et al., 2016), both parameters were measured before and after the experimental task in chapters IV and V. This was also decided considering the separate impacts on each of these parameters of previous studies of finger tapping tasks performed at the maximum MR (Arias et al., 2015; Madinabeitia-Mancebo et al., 2021; Madrid et al., 2016). Moreover, RTD was particularly of interest, since it is crucial for the performance of movement with reduced contraction times (Morel et al., 2015); particularly, early RTD (0-100 ms) is an essential determinant of the acceleration ability of football players (Ishøi et al., 2019). This period has also been noted to be more sensitive in identifying neuromuscular fatigue (D'Emanuele et al., 2021), as it is more associated with MU behavior (e.g., recruitment speed and maximal discharge rate) (Del Vecchio et al., 2019; D'Emanuele et al., 2021) while late RTD is typically more related and

shares a common physiological basis with MVIC and is more determined by muscle-associated factors such as the cross-sectional area and architecture (Andersen et al., 2010; Andersen & Aagaard, 2006; Folland et al., 2014). As such, a greater correlation is usually found between late RTD and MVIC. However, this was not fully evident in this project's findings. In general, there was a greater correlation between knee extension RTD and MVIC across all time periods, which was not seen in flexion RTD and in the flexion/extension RTD ratio either in healthy individuals or footballers. Nevertheless, in line with what is usually reported (Andersen & Aagaard, 2006; Cossich & Maffiuletti, 2020), flexion and flexion/extension ratio RTD were only correlated with MVIC in later periods (>100 ms), and correlations tended to be larger in later periods.

Decreases in flexion RTD were greater in the 0-50 ms period in both healthy participants and footballers. These decreases were marginally smaller in the 50-100 and 100-150 ms periods, while there were no significant changes in the 150-200 ms period. This shows that the used task had a greater effect on early RTD, which was expected considering the maximum speed and short contraction time requirements of the task. As stated above, early RTD is more dependent on MU recruitment speed and discharge rate. This specific effect on early RTD is another factor showing the ability of this task to target central motor control pathways. In line with the findings from Chapters IV and V, central fatigue has been reported to lead to greater decreases in explosive than in maximal strength (Buckthorpe et al., 2014). Findings from these chapters also reinforce the idea that early RTD is more sensitive to neuromuscular fatigue than both late RTD and MVC (D'Emanuele et al., 2021).

Measuring the effect of the used task in RTD was also considered important in light of how important high-speed actions are in the pathogenesis of HSIs (Gronwald et al., 2022; Jokela et al., 2023). However, despite this relevance, there were no significant differences between players with and without HSI history in any RTD variable, which is in line with previous literature stating that RTD is not associated with HSI risk (Van Dyk et al., 2018). Nevertheless, a recent study by Buhmann et al. found a lower eccentric knee flexion and isometric hip extension RTD in recreational athletes with previous HSI (Buhmann et al., 2022b). The same study also noted that the differences found in isometric hip extension RTD were seen both in the injured and the contralateral limb in comparison with control limbs, which was explained by a decreased descending input to hamstring motoneurons (Buhmann et al., 2022b). In Chapter V, no main effect of the injured side was seen. Thus, both in that chapter's and Buhmann et al.'s study, there were no differences in isometric RTD between the injured and contralateral limb (Buhmann et al., 2022b), suggesting that the mode of

contraction (eccentric vs. isometric) elicits different recruitment demands between injured and non-injured limbs.

It was interesting to note that while healthy participants showed a greater decrease in flexion MVIC than footballers (20-22% vs. 10-12%), the opposite was seen for MR, with footballers showing a greater decrease, although with a difference less pronounced than for MVIC (18-23% vs. 13-16%). This suggests that the task had a greater effect on muscle-related aspects and on maximal force production in healthy participants. As for flexion RTD, the losses in early RTD were comparable between athletes and non-athletes (both around 27-38%, whereas in late RTD, healthy participants tended to show a greater loss (20-31% vs. 20-22% in the 100-150 ms period and 3-19% vs. +6-2% in the 150-200 ms period).

The task used in this project, despite its lack of ecological value, managed to induce greater acute decreases in footballers' early knee flexion RTD than a simulated match (27-36% vs. 16%) (Grazioli et al., 2019). There was also an opposing response in extension RTD between healthy participants and footballers; while the former showed post-task increases in extension RTD (especially in session 1, about 10%), footballers had a small, nonsignificant decrease. This finding suggests that compared to healthy participants' session 1, footballers were more able to use extensor activity to decelerate the leg quicker, thus allowing for a faster change in movement direction. The greater MR of footballers compared to healthy participants' session 1 corroborates this idea. Additionally, the increase in extensor RTD was only seen in the 150-200 ms period in session 2, while the other values were comparable to those of footballers. Accordingly, the MR in session 2 was also more similar to that of the footballers' whole sample. Collectively, these comparisons support the prevailing notion that both agonist (in this case, flexor) and antagonist (extensor) activity both contribute to movement speed (Brown & Gilleard, 1991; Jarić et al., 1995). In fact, since the losses in flexion RTD did not show a substantial difference between athletes and non-athletes, it would seem that the ability to decelerate the leg faster (as measured by losses in extensor RTD) was a more determinant factor in differentiating athletes and non-athletes. The fact that healthy individuals approximated the extensor RTD pattern of footballers (which would be expected to show greater expertise in lower limb movement) in just one session constitutes, along with the previously discussed between-session changes in CMC, a sign of motor learning. Although it can be argued that a single session does not constitute a sufficient training stimulus, differences in movement time (which is associated with early RTD) between athletes and non-athletes have been found to be attenuated in only four days of training (Yandell & Spirduso, 1981).

Contribution to movement neurophysiology and repetitive movement control knowledge

The vast majority of knowledge about the physiological basis of repetitive movement and its associated fatigue has been based on finger tapping studies (Arias et al., 2015; Madrid et al., 2018; Rodrigues et al., 2009). The fact that some studies found similar motor slowing properties in other joints/regions (Bächinger et al., 2019; Tanigawa et al., 2017) has led to the assumption that there are common central principles governing motor slowing and the control of repetitive movement. This project has added relevant information to this topic, as repetitive leg movement and its associated motor slowing had not been explored. The findings point to the fact that the trajectory of the decrease in MR is indeed similar between body regions, suggesting that regardless of the segment involved, maximal MR performance is regulated similarly in terms of the motor slowing pattern (in line with the existing literature) (Bächinger et al., 2019; Hureau et al., 2016; Madinabeitia-Mancebo et al., 2020). However, there were some aspects which show important differences between the leg and other segments. For example, there were significant post-task decreases in knee flexor MVIC, which are not necessarily present in finger tasks (Madrid et al., 2018; Rodrigues et al., 2009), which suggests an impact on maximal force production mechanisms normally attributed more to muscle-related factors. Nevertheless, and despite the existence of a common motor control basis, further relevant structural and functional differences between the fingers and legs also exist at the central level. While the upper limbs (especially the hand/fingers) tend to be used for fine motor skills, lower limbs are more involved in high-load, gross motor tasks (Goel & Paloski, 2016). These functional differences are further shown by an opposing motor evoked potential response to induced hand and knee pain. While hand pain leads to local decreased corticomotor excitability (to protect the segment and avoid pain-inducing activities) and increased knee corticomotor excitability (to move the body away from the source of pain), induced knee pain still increases local corticomotor excitability without any effect on the hand (Rice et al., 2021). Moreover, in healthy individuals, the lower limb has a greater cortical and cerebellar motor representation overlap (Kapreli et al., 2007) and a less lateralized brain activation pattern (Kapreli et al., n.d.), highlighting this lesser ability to produce finer and more coordinated movements compared to the fingers. This greater coordinative ability, in addition to the smaller segment size, allowed for the greater overall finger MR compared to the legs. This occurred despite the known beneficial effects of chronic sports training on the motor and sensory representation of sports-specific body segments (Giacosa et al., 2019; Hänggi et al., 2015; Meier et al., 2016) (i.e., the leg and foot in footballers). Thus, the greater lower limb conditioning of footballers does not seem to be sufficient to overcome the inherent motor coordinative

advantages of fingers; this conditioning was also not associated with a marked increase in leg MR compared to untrained individuals.

Another important difference found in Chapter VI was that the percentage of decrease before a performance plateau is reached was significantly different between fingers and legs. Accordingly, it has been reported that exercise with a small muscle mass leads to greater fatigue at task failure than exercise with larger muscle masses (Burnley, 2018). It has been argued, however, that this greater fatigability with smaller muscles is associated not with muscle-related factors but with limitations related to the cardiovascular and respiratory systems, as when larger masses are involved, mass-specific muscle blood flow is restricted, limiting the muscle mass that can be supported aerobically (Thomas et al., 2018). The present findings therefore support not only this difference in fatigability but also show that it is unlikely that maximal exercise performance is regulated by a common threshold of peripheral fatigability. This implies that some of the knowledge on repetitive movement control and motor slowing may not be applicable when larger segments are involved, and further studies could provide more information about these differences and ultimately about how motor slowing is regulated.

Collectively, the presented findings suggest there are common principles regulating maximum-speed repetitive movement performance across body regions, but that these are adjusted in a task- and region-dependent manner. Together with the fact that no single variable measured across the studies seemed to individually predict performance, this points to the notion that multiple influences (e.g., task parameters, involved body regions, environmental conditions, energy availability, cortical structure and organization) are monitored in each exercise bout, with performance being limited by the weakest link in the chain, regardless of whether it is the musculoskeletal, cardiovascular, or nervous system.

Applying the findings to HSI management and prevention

Despite the non-ecological nature of the designed task, a degree of performance differentiation was visible between footballers with and without HSI history, on which the created index was based. This means that this test and index can be used as a preliminary way of quickly determining HSI risk. Considering the high specificity, the index is particularly useful to assess more accurately which players have a lower likelihood of HSIs. The low material resource demands and reduced impact in terms of persistent fatigue of this test are also advantages, as it allows for the application in a wide variety of settings and without influencing training load.

We found that players with previous HSI were able to achieve higher MRs in the first half of the task, and the risk was about three times higher for players with a positive index (Chapter V). It is obvious to assume that they got injured because of being able to generate higher MRs (and therefore contraction speeds) and not the other way around. Additionally, considering the described relevance of maximal running to football performance, no one wants to train players to slow them down. Therefore, these faster players should engage in training to develop speed endurance to ensure they are able to generate high contraction speeds for longer and in a safe manner. Indeed, additional speed endurance training has been shown to improve intermittent exercise performance (Mohr & Krstrup, 2016; Nyberg et al., 2016), while improving energetic economy even with decreased training volume (Iaia et al., 2009). As players in different positions have different speed demands (Di Salvo et al., 2010), this training should be adapted to these particularities. Existing evidence of adaptations to fast/ballistic training is also encouraging, as it has been shown to increase the MU discharge rate (Van Cutsem et al., 1998), MU synchronization (Conrad et al., 1983; Van Cutsem & Duchateau, 2005), and increased EMG activity (Zehr & Sale, 1994), accompanied by decreases in contraction and movement time (Dinn & Behm, 2007; Zehr & Sale, 1994).

Moreover, since players with HSI history also showed signs of increased cognitive load, especially in the second half of the task, it could be advisable to include cognitive training tasks as part of rehabilitation and prevention measures. Such cognitive training programs have been shown to have positive effects (Hardy et al., 2015; Herold et al., 2018; Millner et al., 2012) on parameters such as cognitive reserve (Hardy et al., 2015), which may be crucial to delay fatigue. Greater effects can be expected when using tasks with adaptive difficulty (Flegal et al., 2019) and when performing simultaneous cognitive and motor tasks (Herold et al., 2018). Response inhibition tasks (e.g. go/no-go, stop signal) have been shown to modulate frontal theta activity (Huster et al., 2013), where significant differences were seen between players with and without HSI history. These tasks and those with interference control (e.g., Stroop task, flanker task, A-X continuous performance task) are known to target areas such as the anterior cingulate and dorsolateral prefrontal cortices (Millner et al., 2012), which not only have important implications for motor control in terms of executive control, top-down attentional control, and response choice and inhibition but are also connected with the motor cortex (Fonken et al., 2016; Narayanan & Laubach, 2006; Wenderoth et al., 2005). Training these neurocognitive skills is especially important considering that open-skill team sports such as football carry high attentional demands associated with both the motor and perceptive domains. Thus, incorporating these two aspects (speed development/endurance and neurocognitive training) in HSI rehabilitation and prevention could be a way to address

the differences found between players with and without HSI history and potentially decrease injury incidence and recurrence.

The task used in this project took into consideration both the fact that hamstring injuries in football are often associated with high-speed eccentric actions (Gronwald et al., 2022) and that the large inertial load present during the swing phase of running increases susceptibility to injury (Chumanov et al., 2011). Additionally, Whiteley et al. reported that 7 of the 15 analyzed professional footballers (from different football codes) showed a decrease in match high-speed running distance after HSI (Whiteley et al., 2021), suggesting that exposure to maximum movement speed is not sufficiently explored during rehabilitation after an index injury. Accordingly, intermuscular coordination and activation differences are known to persist even after concluding rehabilitation (Avrillon et al., 2020; Higashihara et al., 2019), which considering the importance of intermuscular coordination for movement speed, also suggests these coordinative abilities are not being sufficiently explored. Exposure to sprinting has been recommended as a preventive tool (Edouard et al., 2019), and exposure to greater percentages of maximum speed (95% vs. 85%) has been found to decrease lower limb soft tissue injury rates in Gaelic footballers (Malone et al., 2017). Despite this evidence, sprinting/high speed movement exposure and/or progression is largely absent from the findings of systematic reviews on the prevention of HSIs (McCall et al., 2015; Petersen, 2005; Vatovec et al., 2020) and from expert recommendations on the management of HSIs in athletes (Martin et al., 2022). Factors associated with movement speed and intermuscular coordination are also absent from prevailing RTP criteria after HSIs either through medical team surveys (Dunlop et al., 2020) and expert consensus (Zambaldi et al., 2017), which may help explain the post-HSI deficits seen in high-speed running distance mentioned above. A recent survey of 62 Brazilian physiotherapists working in elite football clubs reported that only 46.8% of responders included running assessments in the functional evaluation of athletes with HSI, and only 58.1% and 43.5% included sprinting and intense activity (such as accelerations) performance, respectively, as criteria for return to team training (Valente et al., 2023). Another survey, in this case of medical staff of clubs involved in either the UEFA Champions League or Europa League, has also highlighted the lack of exposure to high-speed actions during training as a key risk factor for hamstring injuries (Ekstrand, Ueblicher, et al., 2023). Nevertheless, a recent editorial has included sprinting (i.e., maximum speed and acceleration) as a key part of HSI risk management (Edouard et al., 2023), and the same research group put forth a screening protocol which includes the mechanical output from maximum sprint acceleration (Lahti et al., 2022). Still, frequent maximum speed practice and monitoring is often not performed due to the view that it is a causative factor for HSIs, leading to avoidance not only for fear of injury but also for staff protection (Edouard et

al., 2019). This was in fact an issue faced during the recruitment of football teams for this project, with frequent claims by the medical or coaching staff that participation would significantly increase the risk of injury for their athletes. Additionally, only one of the participating clubs' staff mentioned including dedicated speed development exercises akin to the designed task in their rehabilitation program. In a personal perspective, it does not make much sense to "protect" athletes from such exposure in training, as the match demands will not be so forgiving, nor are they optional. The task used in this project may help overcome that fear, since while it allows for maximum acceleration and deceleration training (in addition to the coordination challenge), it has a much lower impact on training load than, for example, repeated sprinting. Additionally, its unloaded nature may also help medical teams perceive it as less risky. It may then serve as a stepping stone to improve speed and coordination abilities and reassure the clinical staff that players are able to cope with maximal speed activity as a regular part of their training schedule. Findings from this project also contribute to encourage looking at speed development during the rehabilitation process and more specifically at MR, since as it has been discussed, it seems to involve specific factors not necessarily covered by running speed training (Kakehata et al., 2021).

Limitations

Despite the author's best efforts and intentions, the project and the associated studies still present several limitations. Although one of the main aspects of this work was the analysis of brain activity, only a limited number of cortical areas associated with motor planning and execution were analyzed. Whole-brain and connectivity analyses would have provided a more comprehensive picture of the cortical response to task demands. Moreover, each channel was considered in isolation, which means that any changes in how they relate to each other were missed. In the EMG analysis, only one limb was tested. Although this was done so that a wider set of flexors and extensors could be monitored, that meant any interlimb differences could not be captured by our setup. This decision was also made considering the task symmetry and single degree of freedom, which made interlimb differences less likely to be of a significant magnitude. Considering the very dynamic nature of the used task, electrophysiological signals were bound to be affected by noise, which is not always removable even with the most advanced filtering methods. It is also difficult to achieve a balance between noise removal and the loss of physiologically relevant data. Additionally, additional factors which are known to influence maximal performance, such as oxygenation and motivation, were not measured. As for the participating sample, due to the clubs' scheduling constraints, it was not possible to ensure that the players had an adequate

resting period prior to participating in the experiments, which may have been a source of bias. The lack of prospective data also means that any causal relationship between the differences found in players with HSI history cannot be made.

Moving further

The nature of academic work means that there are always questions left to be answered, and many others raised during the process. This is especially true the more exploratory the chosen topic is. As such, the present project creates significant room for further avenues to be explored.

First, in order to confirm the differentiating ability of the MR parameters created, two important steps are missing: 1) determining whether it can be modified by a specific training program; 2) determining if such changes have a greater benefit for the population at risk (i.e., those with a previous HSI injury). A prospective analysis would also be a significant addition to the present work.

Second, as only an individual analysis of EEG channels was performed, further research should focus on their connectivity, as this would provide additional information about the interaction between brain areas. This would also allow for a comparison to what has been found in other musculoskeletal injuries.

Third, since both brain and muscle activity were significantly affected by task-related fatigue, it would be interesting to determine what is the separate impact of cognitive and muscle fatigue on task performance.

Finally, to validate the differences found between players with and without HSI history, the effect of speed development/endurance training and of incorporating neurocognitive tasks on injury incidence and recurrence should be determined.

Conclusion

This project addressed questions related to the features of lower limb motor slowing and its associated electrophysiology. The implications of these findings both for exercise physiology and in HSI risk were described. Recommendations for further studies were made in order to further our understanding of the global pattern of brain activity associated with lower limb motor slowing, within-season fluctuations in task performance, and in the prospective HSI risk.

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Appendixes and supplementary content

Appendix 1. Authorizations of all co-authors for the compilation of articles

DECLARAÇÃO

Para os devidos efeitos, confirmo que autorizo a compilação dos artigos de que sou coautor incluídos nesta tese.

24 de Março de 2024

A handwritten signature in black ink, appearing to read 'Pedro Luís', is written over a horizontal line.

Pedro Luís

DECLARAÇÃO

Para os devidos efeitos, confirmo que autorizo a compilação dos artigos de que sou coautor incluídos nesta tese.

24 de Março de 2024

Christophe Domingos

Christophe Domingos

DECLARAÇÃO

Para os devidos efeitos, confirmo que autorizo a compilação dos artigos de que sou coautor incluídos nesta tese.

24 de Março de 2024

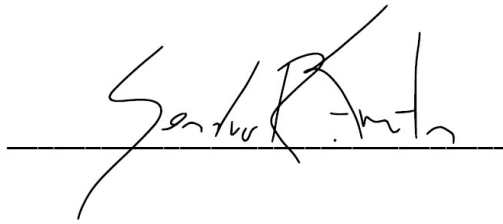
A handwritten signature in black ink, appearing to read 'João R. Vaz', is written over a horizontal line.

João R. Vaz

DECLARAÇÃO

Para os devidos efeitos, **Sandro Remo Martins Neves Ramos Freitas**, confirma que autoriza a compilação dos artigos de que sou coautor incluídos na tese de doutoramento de José Pedro Correia.

Lisboa, 24 de Março de 2024

A handwritten signature in black ink, written over a horizontal line. The signature is stylized and appears to read 'Sandro R. M. N. R. F.'.

Sandro Remo Martins Neves Ramos Freitas

DECLARATION

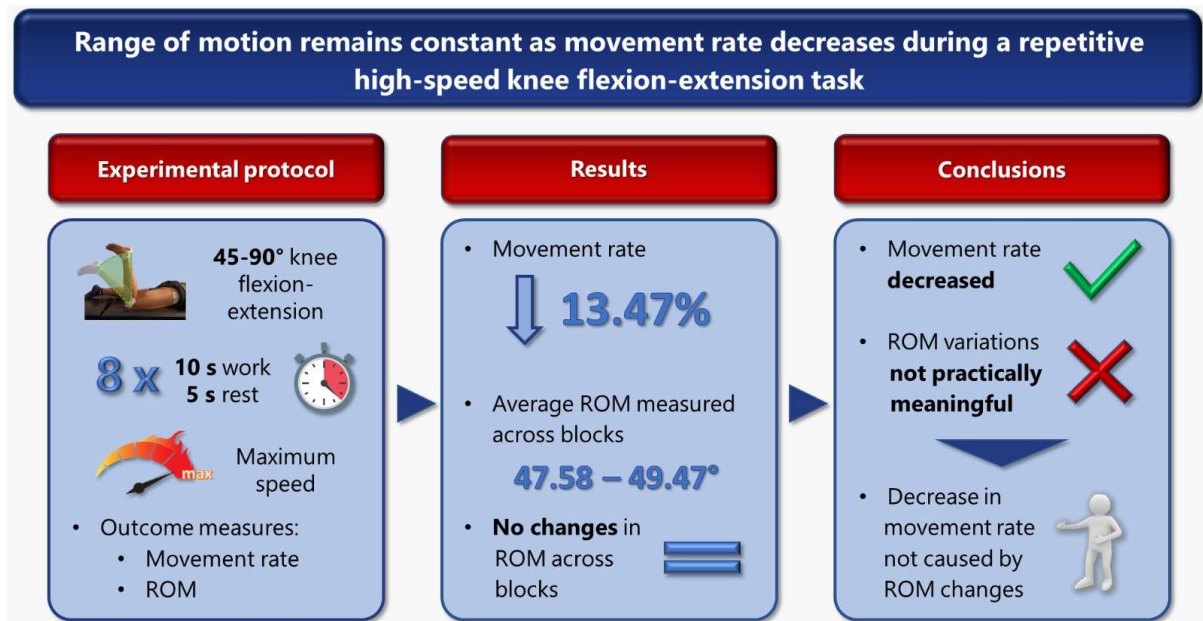
For all due purposes, I confirm my authorization for compiling the articles present in this thesis in which I am listed as a co-author.

24th March 2024

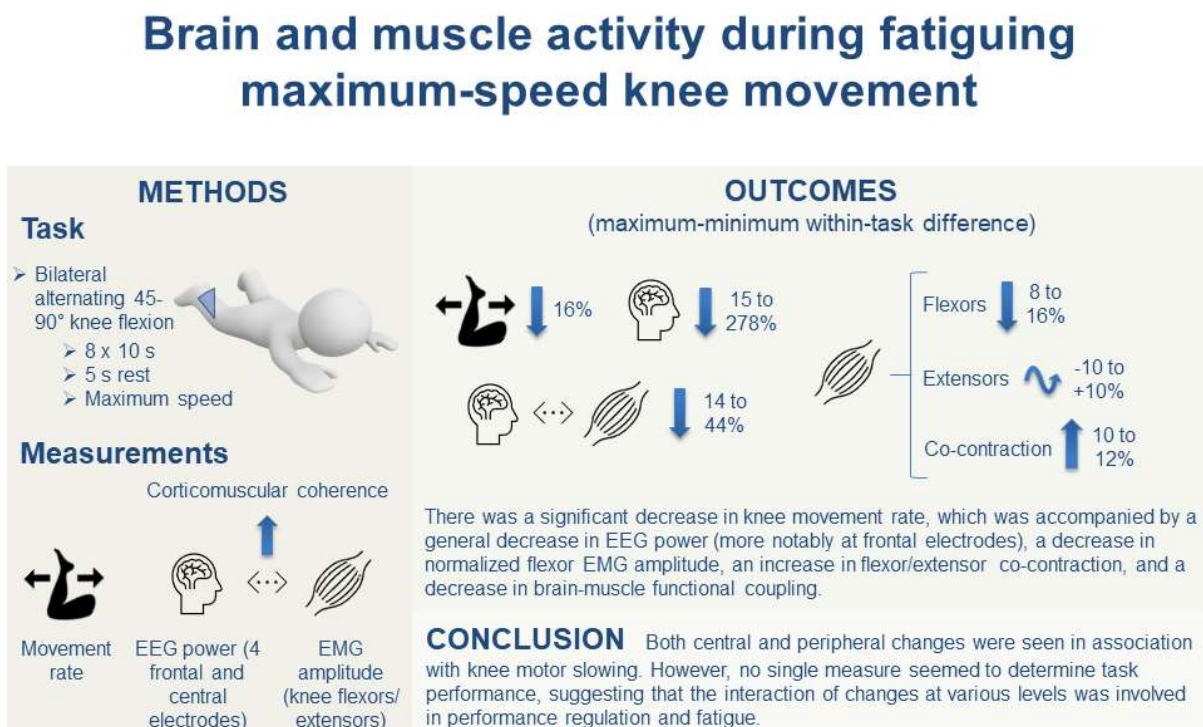
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Witvrouw Erik

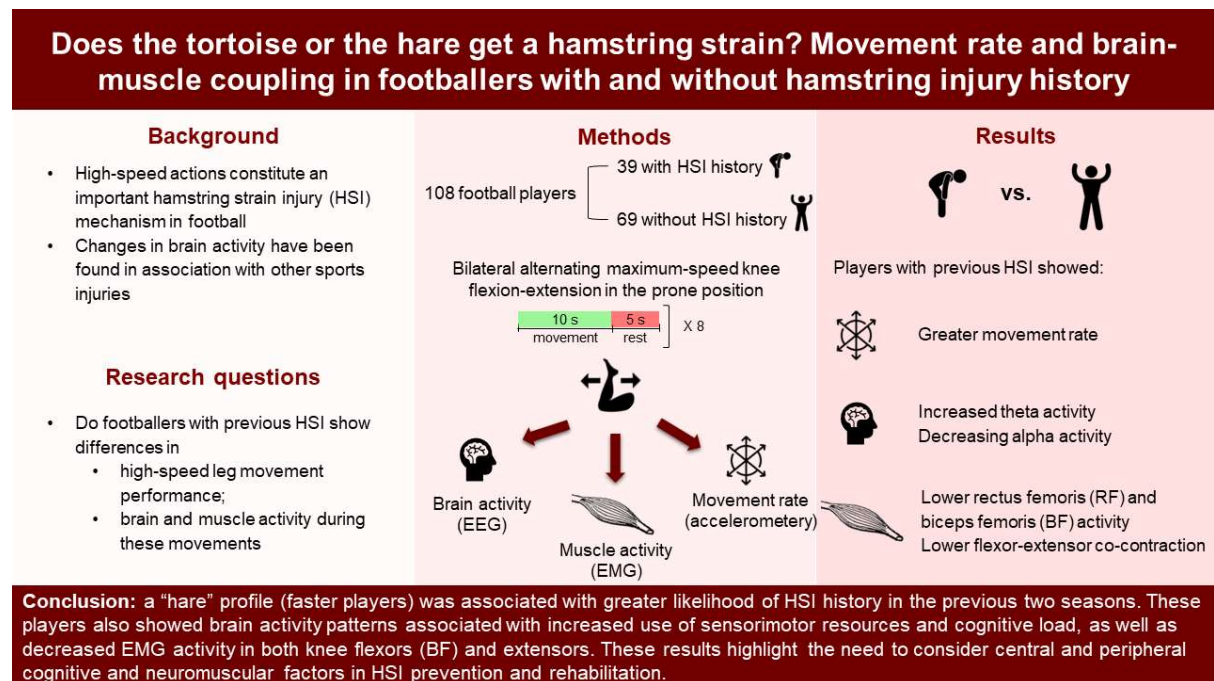
Appendix 2. Graphical abstract of the “Range of motion remains constant as movement rate decreases during a repetitive high-speed knee flexion-extension task” study.



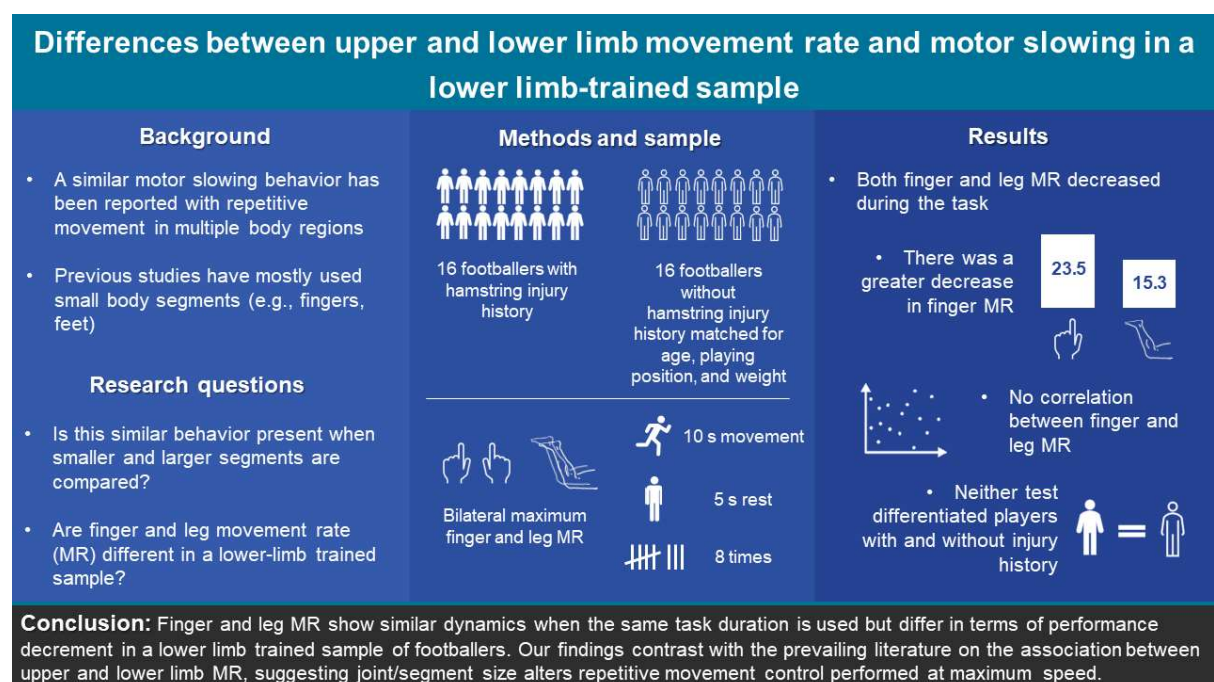
Appendix 3. Graphical abstract of the “Brain and muscle activity during fatiguing maximum-speed knee movement” study.



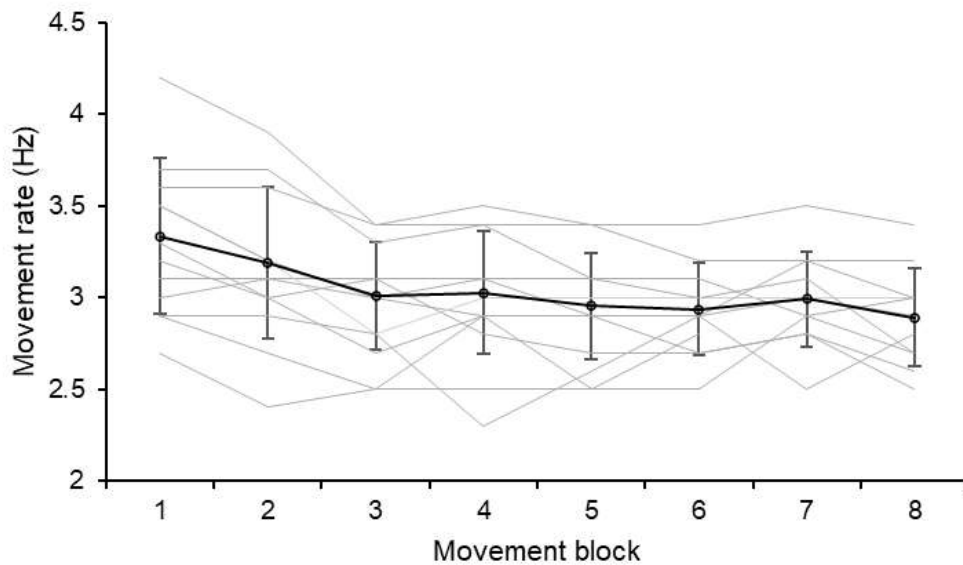
Appendix 4. Graphical abstract of the “Does the tortoise or the hare get a hamstring strain? Movement rate and brain-muscle coupling in football players with and without hamstring injury history” study.



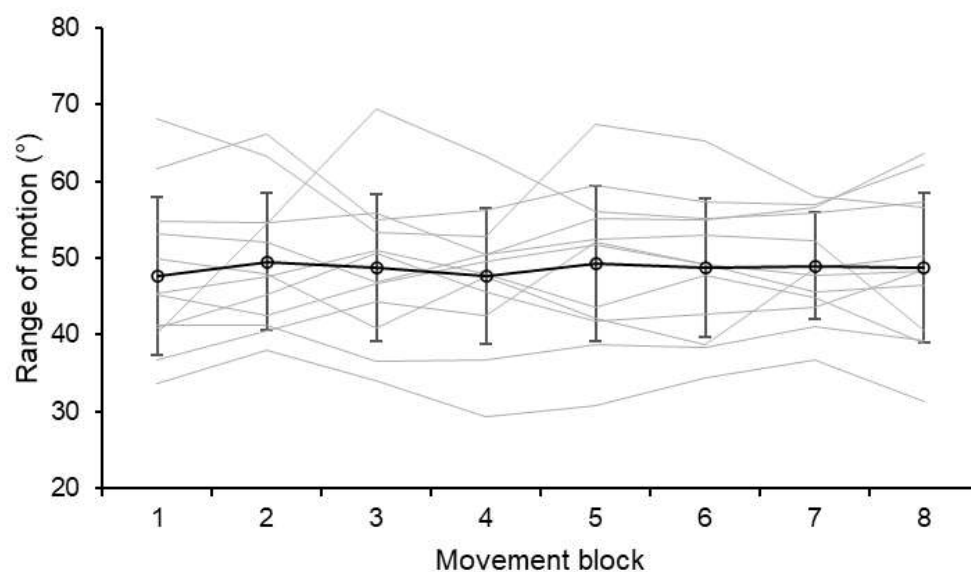
Appendix 5. Graphical abstract of the “Differences between upper and lower limb movement rate and motor slowing in a lower limb-trained sample” study.



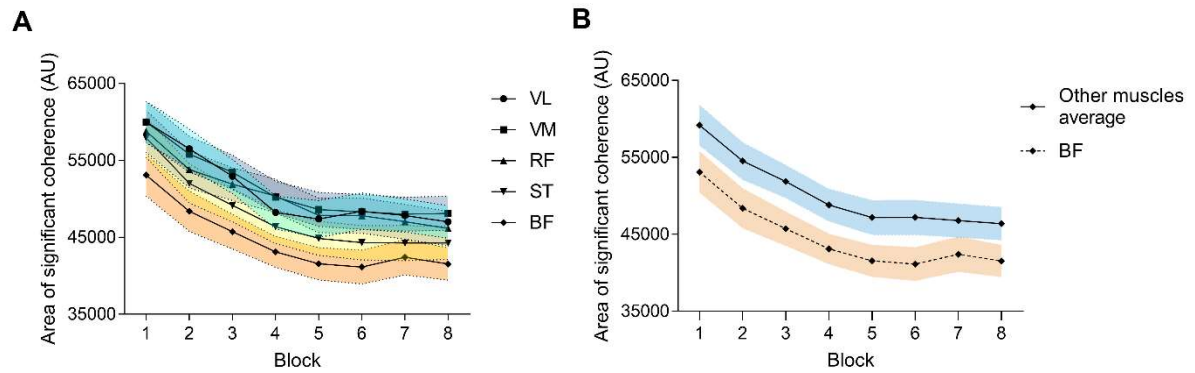
Supplementary figure 1. Individual and mean movement rate in each block. The black line represents the mean movement rate with the standard deviation on the error bars. Grey lines represent each individual's values.



Supplementary Figure 2. Individual and mean range of motion in each block. The black line represents the mean range of motion with the standard deviation on the error bars. Grey lines represent each individual's values.



Supplementary Figure 3. Comparison of changes in corticomuscular coherence between the BF and other muscles in footballers.



Supplementary Table 1. Relative EEG power findings

Electrode	Band		Block								Within subjects			Between subjects			Interaction		
			1	2	3	4	5	6	7	8	p	ηp^2	Power	p	ηp^2	Power	p	ηp^2	Power
F4	Theta	HSI	0.33	0.40	0.39	0.35	0.41	0.44	0.46	0.43	0.073	0.026	0.68	0.285	0.015	0.186	0.060	0.027	0.70
		No HSI	0.36	0.35	0.37	0.36	0.36	0.35	0.37	0.34									
	Alpha	HSI	0.24	0.21	0.21	0.23	0.21	0.21	0.21	0.21	0.648	0.009	0.28	0.56	0.004	0.088	0.007	0.036	0.90
		No HSI	0.2	0.21	0.22	0.23	0.22	0.23	0.24	0.24									
	Beta	HSI	0.31	0.28	0.29	0.30	0.27	0.25	0.24	0.26	0.013	0.035	0.85	0.40	0.009	0.13	0.49	0.011	0.31
		No HSI	0.31	0.30	0.29	0.31	0.30	0.29	0.27	0.31									
	Gamma	HSI	0.12	0.11	0.11	0.12	0.11	0.11	0.09	0.11	0.63	0.008	0.23	0.36	0.010	0.15	0.76	0.006	0.18
		No HSI	0.12	0.13	0.12	0.12	0.13	0.13	0.12	0.12									
F3	Theta	HSI	0.31	0.36	0.36	0.35	0.40	0.43	0.43	0.41	0.22	0.017	0.50	0.23	0.018	0.23	0.031	0.030	0.78
		No HSI	0.34	0.32	0.35	0.33	0.32	0.33	0.33	0.31									
	Alpha	HSI	0.24	0.23	0.22	0.21	0.22	0.20	0.21	0.21	0.93	0.004	0.13	0.63	0.003	0.08	0.007	0.037	0.90
		No HSI	0.20	0.20	0.22	0.23	0.22	0.23	0.24	0.25									
	Beta	HSI	0.33	0.29	0.29	0.30	0.27	0.25	0.26	0.27	0.017	0.034	0.83	0.26	0.016	0.20	0.35	0.014	0.39
		No HSI	0.33	0.33	0.31	0.32	0.32	0.31	0.30	0.31									
	Gamma	HSI	0.13	0.12	0.13	0.13	0.11	0.12	0.11	0.12	0.66	0.008	0.21	0.49	0.006	0.11	0.43	0.12	0.32
		No HSI	0.13	0.14	0.13	0.13	0.14	0.14	0.13	0.13									
C4	Theta	HSI	0.30	0.36	0.34	0.34	0.39	0.42	0.43	0.41	0.008	0.038	0.89	0.077	0.039	0.42	0.10	0.022	0.74
		No HSI	0.30	0.29	0.30	0.31	0.30	0.32	0.32	0.30									
	Alpha	HSI	0.25	0.23	0.22	0.21	0.22	0.21	0.22	0.23	0.62	0.009	0.28	0.82	0.001	0.056	0.039	0.028	0.77
		No HSI	0.21	0.21	0.22	0.23	0.24	0.23	0.24	0.24									
	Beta	HSI	0.32	0.30	0.32	0.32	0.28	0.26	0.25	0.27	0.001	0.049	0.95	0.11	0.031	0.35	0.53	0.010	0.36
		No HSI	0.35	0.36	0.33	0.33	0.33	0.32	0.31	0.33									
	Gamma	HSI	0.13	0.12	0.12	0.13	0.11	0.11	0.10	0.10	0.065	0.026	0.69	0.11	0.033	0.37	0.58	0.009	0.27
		No HSI	0.14	0.15	0.14	0.14	0.14	0.14	0.13	0.13									
C3	Theta	HSI	0.28	0.35	0.33	0.32	0.37	0.39	0.42	0.38	0.082	0.024	0.65	0.22	0.019	0.24	0.085	0.024	0.68
		No HSI	0.31	0.29	0.31	0.32	0.30	0.30	0.32	0.30									
	Alpha	HSI	0.23	0.21	0.21	0.21	0.21	0.20	0.21	0.21	0.49	0.011	0.34	0.98	<0.001	0.050	0.083	0.024	0.68
		No HSI	0.19	0.19	0.20	0.21	0.22	0.22	0.23	0.23									
	Beta	HSI	0.33	0.30	0.31	0.32	0.29	0.27	0.26	0.28	0.008	0.040	0.88	0.17	0.024	0.28	0.44	0.012	0.32
		No HSI	0.35	0.35	0.33	0.32	0.34	0.32	0.31	0.32									
	Gamma	HSI	0.15	0.14	0.14	0.15	0.13	0.14	0.12	0.13	0.33	0.014	0.40	0.29	0.014	0.18	0.51	0.011	0.30
		No HSI	0.15	0.17	0.15	0.15	0.15	0.16	0.15	0.15									

HSI, hamstring strain injury

Supplementary Table 2. Normalized EEG power findings

Electrode	Band		Block								Within subjects			Between subjects			Interaction		
			1	2	3	4	5	6	7	8	p	η^2	Power	p	η^2	Power	p	η^2	Power
F4	Theta	HSI	1	1.68	2.02	1.67	2.31	3.36	3.00	3.62	0.004	0.056	0.90	0.021	0.08	0.64	0.013	0.047	0.83
		No HSI	1	1.47	1.67	1.53	1.50	1.21	1.57	1.47									
	Alpha	HSI	1	1.19	1.35	1.10	1.13	1.47	1.78	1.97	0.004	0.046	0.91	0.44	0.008	0.12	0.24	0.018	0.47
		No HSI	1	1.29	1.34	1.12	1.21	1.09	1.37	1.35									
	Beta	HSI	1	1.18	1.31	1.05	0.97	1.06	1.25	1.46	0.010	0.040	0.86	0.47	0.007	0.11	0.58	0.009	0.25
		No HSI	1	1.23	1.22	1.01	0.98	0.92	0.99	1.16									
F3	Theta	HSI	1	1.16	1.16	0.95	0.96	0.98	1.11	1.36	0.049	0.030	0.69	0.56	0.004	0.090	0.63	0.008	0.21
		No HSI	1	1.32	1.30	1.13	1.19	1.03	1.07	1.24									
	Alpha	HSI	1	2.14	1.62	1.65	2.14	2.97	2.59	3.21	0.064	0.032	0.63	0.11	0.036	0.36	0.21	0.021	0.43
		No HSI	1	1.52	1.98	1.34	1.43	1.06	1.57	1.91									
	Beta	HSI	1	1.20	1.24	0.92	1.00	1.29	1.35	1.45	0.14	0.022	0.56	0.64	0.003	0.075	0.45	0.012	0.31
		No HSI	1	1.38	1.68	1.20	1.23	1.02	1.24	1.33									
C4	Theta	HSI	1	1.15	1.20	0.99	0.94	1.06	1.20	1.48	0.020	0.035	0.80	0.80	0.001	0.060	0.48	0.011	0.29
		No HSI	1	1.22	1.31	1.12	0.98	0.91	0.99	1.21									
	Gamma	HSI	1	1.16	1.14	0.96	0.98	1.02	1.13	1.41	0.005	0.046	0.89	0.90	<0.001	0.052	0.46	0.012	0.29
		No HSI	1	1.22	1.21	1.02	1.07	1.00	0.99	1.19									
	Alpha	HSI	1	1.67	1.31	1.06	1.35	1.96	2.31	2.44	0.093	0.031	0.63	0.67	0.003	0.071	0.042	0.038	0.74
		No HSI	1	1.49	2.00	1.81	1.63	1.36	1.42	1.52									
C3	Beta	HSI	1	1.08	1.31	0.98	1.06	1.42	1.81	2.03	0.004	0.052	0.90	0.63	0.003	0.076	0.079	0.028	0.62
		No HSI	1	1.33	1.45	1.31	1.09	1.11	1.35	1.36									
	Gamma	HSI	1	1.15	1.31	1.03	0.95	1.11	1.29	1.60	0.009	0.046	0.84	0.514	0.006	0.099	0.21	0.019	0.43
		No HSI	1	1.23	1.19	1.08	1.04	0.97	0.92	1.24									
	Alpha	HSI	1	1.08	1.13	0.92	0.92	0.90	1.03	1.31	0.012	0.043	0.82	0.43	0.008	0.12	0.33	0.015	0.35
		No HSI	1	1.34	1.28	1.13	1.09	1.04	0.93	1.20									
C3	Theta	HSI	1	1.97	1.68	1.60	1.98	2.77	2.82	2.95	0.004	0.057	0.91	0.13	0.036	0.33	0.17	0.025	0.52
		No HSI	1	1.47	1.94	1.56	1.43	1.32	1.71	2.05									
	Alpha	HSI	1	1.14	1.32	0.96	1.03	1.45	1.59	1.69	0.022	0.036	0.79	0.95	<0.001	0.050	0.22	0.019	0.46
		No HSI	1	1.40	1.71	1.28	1.11	1.10	1.26	1.43									
	Beta	HSI	1	1.10	1.25	0.99	0.93	1.06	1.19	1.49	0.009	0.043	0.85	0.94	<0.001	0.051	0.60	0.008	0.21
		No HSI	1	1.26	1.33	1.09	1.08	0.96	1.01	1.36									
	Gamma	HSI	1	1.15	1.19	1.05	0.97	0.99	1.08	1.39	0.011	0.041	0.84	0.62	0.003	0.079	0.59	0.009	0.22
		No HSI	1	1.37	1.27	1.26	1.11	1.03	0.99	1.31									

HSI, hamstring strain injury

Supplementary Table 3. Significant corticomuscular coherence findings

Block										Within subjects			Between subjects			Interaction		
Pair		1	2	3	4	5	6	7	8	p	ηp^2	Power	p	ηp^2	Power	p	ηp^2	Power
C3-VL	HSI	62545	60012	53277	49726	49991	49592	49149	48495	<0.001	0.28	>0.99	0.15	0.22	0.30	0.53	0.009	0.31
	No HSI	58648	54661	52744	47438	46026	47764	47155	46234									
C3-RF	HSI	60531	57339	52751	51424	49706	49866	49109	47092	<0.001	0.23	>0.99	0.17	0.021	0.28	0.64	0.007	0.22
	No HSI	57890	52008	51494	49812	46907	46757	45953	45665									
C3-VM	HSI	62634	59047	54069	52082	49601	47784	48288	48438	<0.001	0.25	>0.99	0.33	0.011	0.16	0.25	0.014	0.48
	No HSI	58615	54109	53141	49287	48107	48576	47861	47955									
C3-BF	HSI	55386	50437	46194	44074	42799	44091	44883	43126	<0.001	0.23	>0.99	0.17	0.021	0.28	0.70	0.007	0.23
	No HSI	51916	47329	45508	42616	40932	39613	41148	40718									
C3-ST	HSI	60811	53077	49908	48290	46585	45775	46024	46198	<0.001	0.28	>0.99	0.18	0.019	0.27	0.90	0.004	0.14
	No HSI	56455	51452	48772	45408	43984	43544	43343	43277									

VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus; HSI, hamstring strain injury.

Supplementary Table 4. EMG variables findings

		Block								Within subjects			Between subjects			Interaction		
Variable		1	2	3	4	5	6	7	8	p	ηp^2	Power	p	ηp^2	Power	p	ηp^2	Power
VL	HSI	1	1.20	1.16	1.19	1.16	1.15	1.06	1.27	0.013	0.036	0.83	0.79	0.001	0.058	0.64	0.007	0.20
	No HSI	1	1.37	1.30	1.22	1.19	1.15	1.02	1.19									
RF	HSI	1	1.04	0.96	0.92	0.86	0.84	0.79	0.90	<0.001	0.067	0.97	0.029	0.050	0.60	0.088	0.023	0.55
	No HSI	1	1.08	1.08	1.03	1.01	0.98	0.98	1.09									
VM	HSI	1	1.05	0.92	0.85	0.74	0.70	0.72	0.79	<0.001	0.135	>0.99	0.13	0.026	0.33	0.43	0.011	0.29
	No HSI	1	1.10	1.04	0.98	0.89	0.83	0.84	0.97									
BF	HSI	1	0.94	0.88	0.87	0.83	0.77	0.74	0.79	<0.001	0.183	>0.99	0.023	0.056	0.63	0.26	0.015	0.41
	No HSI	1	1.07	1.02	0.95	0.91	0.88	0.84	0.89									
ST	HSI	1	0.98	0.91	0.90	0.82	0.78	0.76	0.81	<0.001	0.134	>0.99	0.058	0.039	0.48	0.28	0.014	0.41
	No HSI	1	1.00	1.01	0.94	0.91	0.91	0.84	0.89									
CCI _{lat}	HSI	34.58	29.44	31.02	32.35	32.83	33.65	33.49	33.84	<0.001	0.098	0.98	0.091	0.034	0.39	0.62	0.006	0.13
	No HSI	35.32	32.07	33.94	34.95	35.57	35.68	35.90	36.00									
CCI _{med}	HSI	36.56	35.63	35.05	35.86	35.69	36.67	37.24	37.97	0.16	0.021	0.41	0.020	0.060	0.65	0.57	0.007	0.16
	No HSI	40.65	38.49	39.14	39.68	40.48	39.89	39.96	40.26									

VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; BF, biceps femoris; ST, semitendinosus; CCI, co-contraction index; HSI, hamstring strain injury.