Universidade de Lisboa

Faculdade de Motricidade Humana

Chronology of neuromuscular adaptations to strength training: the role of intermuscular coordination

Paulo Duarte Guia dos Santos

Orientador: Professor Doutor Pedro Luís Camecelha de Pezarat Correia

Co-orientador: Professor Doutor João Pedro Casaca da Rocha Vaz

Tese especialmente elaborada para obtenção do grau de Doutor em Motricidade Humana na Especialidade de Comportamento Motor

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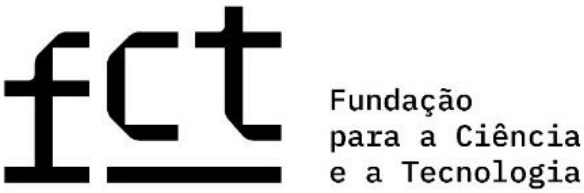

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como for, fica para mim, no final desta etapa, o grande exemplo como professor, coordenador e investigador, mas sobretudo como pessoa, e mesmo que este vínculo mais formal esteja a chegar ao fim, sei que o seu acompanhamento não se esgotará e que as suas palavras sábias e amigas se manterão.

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ABSTRACT

Neural adaptations in intermuscular coordination are not fully understood, although the underlying mechanisms may be determinant to strength gains following strength training. Thus, the purpose of this dissertation is to bring new insights into the acute, short-term and long-term adaptations in intermuscular coordination to strength training. Specifically, it is presented a set of 6 studies that allowed to understand changes in intermuscular coordination concerning i) the acute responses following fatiguing protocols, ii) the short-term adaptations following 6 weeks of a squat training program, and iii) the long-term adaptations regarding the comparison between individuals with different training status.

Study I aimed to reflect the state of the art regarding the different neural mechanisms in the control of agonist, antagonist and synergist muscles between untrained and highly trained individuals. Generally increased neural input to the agonist muscles during maximal contractions and a more efficient recruitment during submaximal tasks was observed for the long-term trained individuals, who have also presented different control of the antagonist muscle as well as different strategies of global coordination during complex motor tasks. Study II reflected the state of the art regarding the acute adaptations in intermuscular coordination following fatiguing protocols, namely concerning intermuscular coherence (IMC), which allowed to infer about the motor unit synchronization in different muscles. The coupling between muscles at different frequency-bands allowed to better understand the acute central responses to compensate fatigue. Study III was designed to understand the acute adaptations to fatigue during maximal force production in individuals with different training background. The long-term trained individuals presented greater maximal and rapid force, and IMC at beta-band between vastus lateralis and rectus femoris than the untrained individuals. After fatigue, different responses concerning the rate of activation of rectus femoris were observed, representing the relevance of the role of biarticular muscles during force production in multi-joint tasks. Studies IV-VI allowed to understand the 6-week short-term and/or long-term training adaptations in intermuscular coordination regarding i) maximal isometric force production during multi-joint exercises, ii) submaximal isometric torque production during knee extension and iii) dynamic strength during squats with different loads. Changes in coupling following the 6 weeks of squat training were observed

between muscles with different functional roles during maximal and submaximal isometric contractions. In addition, 6 weeks of training impacted the load-velocity profile of the squat, with parallel changes in the spatial component of the synergic recruitment of lower limb muscles. On its turn, long-term trained individuals have also presented different coupling between muscles in maximal and submaximal isometric contractions compared to short-term trained and untrained individuals, associated mainly to differences concerning the recruitment of rectus femoris. Furthermore, long-term trained individuals presented adapted spatial and temporal synergy components during dynamic squats at different intensities. This thesis presents novel insights into the neural adaptations in intermuscular coordination, suggesting that specific adaptations emerge at different timings during the training process.

Neuromuscular adaptations to strength training are vastly described. It is usually accepted that initial gains in strength are caused by neural adaptations while muscular adaptations present a major role at the long-term. However, recent research suggests that muscular adaptations may emerge earlier and that neural adaptations remain evolving at later training stages.

Keywords: resistance training, intermuscular coherence, muscle synergy, fatigue, neural adaptations

RESUMO

As adaptações na coordenação intermuscular ainda não são completamente compreendidas, embora os mecanismos subjacentes possam representar um elevado potencial explicativo para os ganhos de força após um período de treino. O propósito desta dissertação é procurar entender quais as adaptações agudas, de curta-duração e de longa-duração ao treino de força na coordenação intermuscular. Especificamente, é apresentado um conjunto de 6 estudos que permitiram uma melhor compreensão sobre alterações na coordenação intermuscular no que diz respeito: i) às respostas agudas a estímulos fatigantes, ii) às adaptações de curta-duração após um período de treino de agachamento de 6 semanas, e iii) às adaptações de longa-duração relativas à comparação de grupos com diferente experiência de treino.

O Estudo I procurou retratar o estado de arte relativamente aos diferentes mecanismos de controlo dos agonistas, sinergistas e antagonistas da ação muscular entre indivíduos destreinados e experientes. Durante contrações máximas foi observado, de forma geral, um maior *input* neural para os músculos agonistas, enquanto que durante contrações submáximas se verificou uma maior eficiência no recrutamento para os indivíduos experientes, que também apresentaram um diferente controlo dos músculos antagonistas assim como diferentes estratégias de controlo da coordenação global durante tarefas motoras complexas. O Estudo II retratou o estado de arte sobre as adaptações agudas na coordenação intermuscular após protocolos fatigantes, nomeadamente no que diz respeito à coerência intermuscular (IMC), permitindo inferir sobre a sincronização de unidades motoras em músculos diferentes. O recrutamento sincronizado de dois músculos em diferentes bandas de frequências permitiu uma melhor compreensão sobre as respostas centrais agudas para compensar a fadiga. O Estudo III foi protocolado de forma a possibilitar uma melhor compreensão sobre as adaptações agudas à fadiga durante contrações máximas em indivíduos com diferente experiência de treino. Os indivíduos experientes apresentaram valores superiores de força máxima e rápida, e de IMC na banda-beta entre o vasto externo e o reto femoral do quadricípite. Após a fadiga, diferentes respostas dos dois grupos foram observadas na taxa de ativação do reto femoral do quadricípite, representando a importância do controlo dos músculos biarticulares durante a produção de força em tarefas multiarticulares. Os Estudos IV-VI permitiram perceber as adaptações ao treino de força de

curta-duração (6 semanas) e/ou de longa-duração na coordenação intermuscular em i) tarefas multiarticulares (*leg-press*) durante produção de força isométrica máxima, ii) extensões do joelho durante produção de força isométrica submáxima e iii) tarefas dinâmicas durante agachamentos com diferentes cargas. Alterações no recrutamento sincronizado após 6 semanas de treino de agachamento foram observadas entre músculos com diferentes funções durante contrações isométricas máximas e submáximas. Para além disso, 6 semanas de treino modificaram o perfil carga-velocidade de agachamento, com alterações paralelas na componente espacial do recrutamento sinérgico dos músculos do membro inferior. Por sua vez, indivíduos com experiência de longa-duração também apresentaram um diferente acoplamento entre músculos em tarefas isométricas máximas e submáximas quando comparados com indivíduos com experiência de curta-duração ou destreinados, sendo isso maioritariamente associado ao recrutamento do reto femoral do quadricípite. Os indivíduos mais experientes mostraram ainda adaptações nas componentes espaciais e temporais das sinergias neuromusculares durante agachamentos dinâmicos a diferentes intensidades. Esta tese apresenta resultados pertinentes no estudo das adaptações neurais na coordenação intermuscular, sugerindo adaptações específicas em fases cronologicamente distintas do processo de treino.

Palavras-chave: treino de força, coerência intermuscular, sinergia neuromuscular, fadiga, adaptações neurais

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ABBREVIATIONS

1RM – 1-repetition maximum;

ANOVA – Analysis of variance;

BF – Biceps femoris:

BSL – Baseline;

CMC – Corticomuscular coherence;

CNS – Central nervous system;

CV – Co-variance;

DOF – Degrees of freedom;

EMG – Electromyography;

EMD – Electromechanical delay;

GM/Gmax – Gluteus maximum;

GL – Gastrocnemius lateralis;

H – Heavy loads;

ICC – Intraclass correlation coefficient;

IMC – Intermuscular coherence;

L – Light loads;

LD0 – Theoretical maximal load;

LT – Long-term trained individuals;

LVP – Load-velocity profile;

MCV – Mean concentric velocity;

MEP – Motor evoked potentials;

MH – Moderate-heavy loads;

ML – Moderate-light loads;

MVC – Maximum voluntary contraction;

POS – Post-training;

PF – Peak force;

PRFD – Peak rate of force development;

RER – Rate of electromyographic rise;

RF – Rectus femoris;

RFD – Rate of force development;

RT – Resistance trained individuals;

RTD – Rate of torque development;

SEM – Standard error of measurement;

SICI – Short-interval intracortical inhibition;

ST – Short-term trained individuals;

TA – Tibialis anterior;

TMS – Transcranial magnetic stimulation;

UT – Untrained individuals;

V0 – Theoretical maximal velocity;

VL – Vastus lateralis;

VM – Vastus medialis;

VAF – Variance accounted for;

W0 – Training beginning;

W2 – Week 2 of training;

W4 – Week 4 of training.

Chapter 1

Introduction

OUTLINE OF THE THESIS

The present dissertation is a collection of six research articles published or presently submitted in peer-reviewed journals with ISI Impact Factor in the field of sports science or applied physiology. The novel insights from the articles contribute to the body of literature regarding aspects related to the neuromuscular adaptations to strength training. The present document is organized as follows:

Chapter 1 provides a general introduction presenting the state of the art concerning neuromuscular adaptations to training and what is known about the role of intermuscular coordination. In this chapter are presented the main purposes of the thesis as well as the general methodological procedures applied across studies.

Chapter 2 and Chapter 3 present the first and second studies of this thesis. Both studies are systematic reviews intending to organize the current knowledge regarding the differences in coordinative patterns between trained and untrained individuals during force production tasks, as well as the acute adaptations in intermuscular coordination assessed by the calculation of intermuscular coherence.

Chapter 4 presents a study that allowed to establish the differences between groups with different training background in intermuscular coherence during multi-joint isometric maximal force production, as well as the respective acute adaptations to a fatiguing protocol.

Chapter 5, 6 and 7 allow to understand the adaptations in intermuscular coordination to strength training overtime. It was intended to establish the effects of a strength training program of 6 weeks in the coordinative patterns during i) isometric maximal tasks, ii) isometric submaximal tasks, and iii) dynamic tasks with different intensities. Additionally, the effects of the short-term training program were compared to the coordinative characteristics of individuals highly specialized in strength-related tasks, allowing to understand the chronology of the adaptations.

Chapter 8 presents the general discussion of the results of the 6 studies, providing a comprehensive understanding of the chronology of adaptations in intermuscular coordination, namely regarding i) acute, ii) short-term and iii) long-term strength training adaptations, as well as the implications and perspective for future research.

LIST OF ARTICLES

The present Doctoral thesis resulted in the following publications/submissions:

1) **Santos, P. D. G.**, Vaz, J. R., Correia, J., Neto, T., & Pezarat-Correia, P. (2023). Long-term neurophysiological adaptations to strength training: A systematic review with cross-sectional studies. J Strength Cond Res, 37(10), 2091-2105. https://doi.org/10.1519/jsc.0000000000004543

2) **Santos, P.D.G.**, Correia, J.P., Vaz, J.R. & Pezarat-Correia, P. (2024). Changes in intermuscular coherence with fatigue: a systematic review [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

3) **Santos, P.D.G.**, Vaz, J.R., Gomes, M., Barão, G., Infante, J. & Pezarat-Correia, P. (2024). Fatigue-related changes in muscle activation and coordination after an acute squat protocol in resistance trained and untrained individuals [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

4) **Santos, P.D.G.**, Vaz, J.R., Gomes, M., Infante, J. & Pezarat-Correia, P. (2024). Chronology of adaptations to strength training: muscle activation and coordination during maximal force production [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

5) **Santos, P.D.G.**, Vaz, J.R., Gomes, M., Oliveira, J., Infante, J. & Pezarat-Correia, P. (2024). Chronology of neural adaptations to strength training: intermuscular coordination during isometric submaximal torque production [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

6) **Santos, P.D.G.**, Vaz, J.R., Gomes, M., Fitas, A., Arrenega, C., Oliveira, J., & Pezarat-Correia, P. (2024). Chronology of adaptations to strength training: muscle coordination during load-velocity profiling [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

INTRODUCTION

It is widely known that regular practice of strength training is associated to increases in maximal strength, changes in neuromuscular function and muscle morphology (Folland & Williams, 2007; Sale, 1988).

At the muscle level, strength training promotes an increase of the cross-sectional, mainly through the hypertrophy of muscle fibers with increased myofibrillar size and number (Franchi et al., 2018; Mobley et al., 2018). This phenomenon is associated with proliferation and fusion of satellite cells with existing fibers which consequently increase in numerical density of myonuclei. Other morphological adaptations, such as changes in muscle architecture (pennation angle and fascicle length) (Blazevich, Gill, Bronks, & Newton, 2003; Timmins et al., 2016; Wells et al., 2014), in fiber type and in tendons structure may occur (Folland & Williams, 2007).

However, neural adaptations to strength training occur earlier than muscle adaptations and the initial gains in strength are not accompanied by increases in muscle size. Changes in the neural drive to the muscle have been inferred from surface electromyography (EMG) studies, showing increased neural drive to the agonist muscles during the first weeks of training (Duchateau, Semmler, & Enoka, 2006; Folland & Williams, 2007; Moritani & deVries, 1979; Sale, 1988). The increased neural drive to agonist muscles reflects increased motor unit recruitment or firing frequency, while being sensitive to changes in synchronization (Folland & Williams, 2007). Strength training leads to a greater recruitment of fast-twitch muscle fibers innervated by higher threshold motoneurons which results in an increased motor unit firing rate, particularly at the onset of ballistic contractions, and thus promoting greater rate of force development. Furthermore, motor unit recruitment thresholds are reduced in response to training (Folland & Williams, 2007; Griffin & Cafarelli, 2005; Sale, 1988), and cortical adaptations, like primary motor cortex changes in movement representation and increased corticospinal excitability, nerve conduction velocity, reflex function and motoneuron excitability may be other neurological adaptations promoted by strength training (Carson, 2006; Griffin & Cafarelli, 2005; Sale, 1988).

The nervous system must adapt itself to the specific required movements and it involves the ability to develop qualitative changes in coordinative patterns of muscle activation, with the

optimization of coordination between agonists, antagonists and synergists being essential to produce the desired movement output concerning angular amplitudes and velocities of the involved joints. Thus, the optimized motor output following strength training regarding neural adaptations in intermuscular coordination arises generally from three mechanisms: a more efficient activation of the agonist muscle, a generally decreased antagonist activation (although it may depend on the task, muscle group, velocity, type of muscle contraction, intensity and joint angle, as it will be assessed through this thesis) and optimized patterns between synergists concerning the order, intensity and timing of activation (Rutherford & Jones, 1986). The coordination between muscles allows to produce the required joint moments in the intended direction to perform specific movements (Duchateau et al., 2006; Folland & Williams, 2007; Griffin & Cafarelli, 2005; Sale, 1988).

Regarding the described mechanisms of neuromuscular adaptations to strength training, it is plausible to conclude that morphological adaptations become the dominant factor in later training stages and that neural factors are determinant in the initial voluntary strength increment (Moritani & deVries, 1979; Sale, 1988). Strength gains in advanced training stages are associated to continued muscle adaptations. However, regarding to coordination during complex movements, the role of long-term training in the refinement of these tasks and the possible timings of skill improvement are issues that remain unexplored.

MUSCLE COORDINATION

The control of movement that enables the performance of coordinated actions implies the existence of functional relations between all the components of the system, i.e., muscles and other structures organize themselves to perform complex movements. However, there is more than one way that the central nervous system (CNS) can adopt to perform one motor task, and this redundancy associated to motor control refers to the degrees of freedom problem, proposed by Bernstein (1967). The musculoskeletal system has many solutions to perform an action, regarding how the elements of the system interact with each other. Also, it has been demonstrated that the human body has more elements than it should be necessary to perform a particular motor task (Latash, Scholz, & Schöner, 2007).

Thus, according to Bernstein (1967), when learning some new skill, the neuromuscular system adapts to the motor possibilities manipulating the degrees of freedom (DOF) and promoting an approach that leads to an optimal solution constructed to minimize the cost to the CNS (Hirashima & Oya, 2016). During skill acquisition an intermittent reduction and release of DOF may be observed. In early stages of this process the CNS will reduce the number of DOF, stiffening the movement but controlling the excess of DOF that could possibly add to much variability to the system. With practice, some of these DOF are released, smoothing the movement and increasing its efficiency (Latash et al., 2007)

The abundance of DOF allows to the neuromuscular system to ensure stability of important performance variables and flexibility to adapt to internal and external changes of the environment, and the redundancy of DOF may be used to compensate errors that arise from unpredictable acting forces (Latash, Krishnamoorthy, Scholz, & Zatsiorsky, 2005; Latash et al., 2007). In other words, the permanent elimination of DOF does not occur. Instead, those alternative DOF are used to minimize changes of the movement and to promote a functional adapted motor control. We can assume that coordination regards to the interaction between all the components of neuromusculoskeletal system. Thus, the control of locomotive system is achieved through the refinement of redundant DOF that group themselves and allow the system to perform coordinated movements. In response to practicing and training many elements of the nervous system may adapt and therefore produce specific coordinative

patterns, and namely strength training may allow to optimize muscle recruitment during performance.

It should be noted that strength training induces some supraspinal adaptations, which ensure that the task is performed in the most efficient way possible. For example, a reduction in cortical activation and therefore a decrease in the interference of other areas of the brain with the execution of movement will be observed. With the increase of force production capacity of muscles fewer descending fibers will be activated for a given task, controlling the muscle in a more effective way. In other words, with training the relation between brain activity and force production will change resulting in less brain activity being necessary for the same kinetic output (Carson, 2006). Also, during skill acquisition, neural connections between primary motor cortex and other areas (long term potentiation of synapses), and between corticospinal neurons and motoneurons will be altered (Carroll, Riek, & Carson, 2001; Carson, 2006). The choice and adjustment of DOF by the CNS, the combination of joint angles to produce the required movement or the selection of individual motor units and the consequent muscular output, are problems referring fewer constraints than elements, helping to reduce DOF that the nervous system must control (Latash et al., 2005). Thus, it appears the concept of functional synergies, ensembles of elements forming coordinative structures that allow the performance of coordinated movements (Latash et al., 2007).

Muscle synergies represent a mechanism organizing a system with high number of elements, reducing the cost for the CNS and simplifying motor control. Thus, the coordination of different elements of musculoskeletal system, i.e., various muscles, can be recruited by a single neural command, representing just one variable that may be controlled. The contribution of various elements to each synergy reveals its sharing character and ensure that one alteration in the function of one element will be compensated by other, which means that synergies adapt themselves to different tasks even when recruiting the same elements (Latash et al., 2007). The combination of recruitment of multiple synergies will result in the production of a wide range of possible movements, and highly complex tasks can be achieved by modulating neural commands specifying spatiotemporal patterns of muscle activation that can produce natural motor behaviors (Safavynia, Torres-Oviedo, & Ting, 2011; Ting & McKay, 2007).

Muscle patterns of activation are the result of simultaneous and independent recruitment of muscle synergies, that are combined, scaled in amplitude and shifted in time (d'Avella, Saltiel, & Bizzi, 2003). The simplification of motor control is related to shared muscle synergies across tasks. In other words, a variety of motor behaviors may be achieved through combination of small number of the same low-level discrete elements, being them explicative of a large fraction of the variation of data (Bizzi & Cheung, 2013; d'Avella & Bizzi, 2005; Prevete, Donnarumma, d'Avella, & Pezzulo, 2018). Namely, freely moving frogs presented small number of synchronous and time-varying muscle synergies that represented the variation across swimming, jumping and walking tasks, reflecting the inherent shared structure of neural modulation, and implementing behavior specific modules to efficiently achieve the biomechanical requirements of the task (d'Avella & Bizzi, 2005; d'Avella et al., 2003). It is important to emphasize that synergies may be synchronous, representing fixed spatial relation of muscle activation in a given time, or time-varying, denoting stereotypical temporal activation profiles shared across muscles during the whole movement. The combination of these two types of low-level circuits that implement descending motor commands and reflex contributions leads to coordinated muscle activity and release the higher structures of the CNS, namely in the brain, to operate on other specific variables of the task (Delis, Hilt, Pozzo, Panzeri, & Berret, 2018).

Muscle synergies origin has been suggested as being neural, recruited by functional units of spinal interneurons that request specific activation of muscles and a consequent motor output. The combination of these motor modules allows the performance of an unlimited number of movements (Bizzi & Cheung, 2013). Chemical and electric stimulation in several vertebral species have been the main approaches to study the representation of muscle synergies in spinal cord (Bizzi & Cheung, 2013). The simultaneous electrical stimulation of two sites of the spinal cord in frogs resulted in equivalent generated forces when compared to the summation of each of the two sites stimulated separately (Mussa-Ivaldi, Giszter, & Bizzi, 1994). Neuronal discharges in the spinal cord gray of frogs at the L2/L3 zone activated motor primitives rather than individual muscles (Hart & Giszter, 2010). Premotor interneurons in the primate cervical spinal cord showed spatiotemporal properties correlated with muscle synergies during voluntary hand movements (Takei, Confais, Tomatsu, Oya, & Seki, 2017). Chemical stimulation with N-methyl-D-aspartate (NMDA), agonist of glutamate NMDA

excitatory receptors, by application of iontophoresis in the interneuronal regions of the lumbar spinal cord of frogs, elicited EMG patterns that revealed to be grouped in muscle synergies (Saltiel, Wyler-Duda, D'Avella, Tresch, & Bizzi, 2001). In cats, muscle synergies identified by cluster analysis were the same before and after spinal transection, revealing, however, differences in timing of certain synergies and suggesting the importance of afferent inputs for the expression of some muscle synergies (Desrochers, Harnie, Doelman, Hurteau, & Frigon, 2019). Intracortical microstimulation applied to motor cortical areas of macaques evoked hand movements, revealing muscular activations reducible to summations of few basic patterns representing muscle synergies (Overduin, d'Avella, Carmena, & Bizzi, 2012), and similar synergistic organization of the brain was verified for grasping different objects (Hao et al., 2017).

Regarding the studies mentioned above, muscle synergies have been proposed to be structured in brainstem and spinal cord (Bizzi & Cheung, 2013; Bruton & O'Dwyer, 2018), activated through supraspinal commands that control activity in spinal circuits and regulated by sensory feedback refining the pattern of locomotor output (Grillner & Jessell, 2009). As such, muscle synergies are commonly associated with central pattern generators, ensembles of oscillatory neurons that produce rhythmic motor patterns during locomotion (Zehr, 2005). These modules remain similar in frogs during swimming and jumping before and after deafferentation, altering, however, the amplitude and temporal patterns of muscle synergies and suggesting that sensory feedback regarding the specificity of the task may modulate the activation of centrally organized synergies (d'Avella & Bizzi, 2005). The absence of sensory and/or descending modulation during fictive locomotion in neonates results in lack of specific activation pattern on foot contact (Dominici et al., 2011). In adult humans, some studies corroborate the above mentioned. For instance, the composition of synergies of the unaffected and affected arm of mildly to moderately impaired stroke survivors with lesions in motor cortical areas were similar, despite differences in motor output, which can be due faulty activation of spinal modules by altered descending commands (Cheung et al., 2009), and merging of unaffected arm muscle synergies correlated with the severity of motor impairment (Cheung et al., 2012).

The main approach to study muscle synergies suggesting indirectly evidence of neural control in humans is to measure EMG from a large number of muscles and to apply statistical analyses to group the activation of muscles (Tresch & Jarc, 2009). However, not all studies suggested muscle synergies as having a neural origin, suggesting in contrast that muscle synergies appear to reflect task-related biomechanical constraints, and a model predicting musculotendon length changes on estimating muscle activity (through EMG records) could control feedback-related synergies, even though this model is not currently feasible (Kutch & Valero-Cuevas, 2012). For example, these authors attribute the results reported by Cheung and colleagues (Cheung et al., 2009) as being consequent of similar task constraints and upper-limbs biomechanical structure. Furthermore, addition of new muscle patterns of activation from neonates to toddlers reveals the importance of neural adaptation to biomechanical changes, incorporating information about biomechanical properties in the characteristics of motor modules activation and imposing specific highly calibrated motor performance (Bizzi & Cheung, 2013; Dominici et al., 2011). Thus, origin of muscle synergies remains a controversial topic. Nevertheless, the concept of a neural origin of muscle synergies is not incompatible with the idea that biomechanical properties of the limb are incorporated in their structure (Bizzi & Cheung, 2013).

As previously stated, coordination refers to the distribution of muscle activation among individual muscles to produce a given combination of joint moments. Since surface EMG is mainly related to the number of activated motor units and their discharge rates, it is one adequate tool to understand how different muscles are recruited in a motor task and how they can be coordinated to optimize the intended mechanical output. In any motor task, different muscles present different functional roles, and the adaptations in intermuscular coordination arise from the interaction between agonist, synergist and antagonist muscles. In this way, in the study of muscle coordination, we can process the EMG signals in three ways (Hug, 2011): 1) analyzing the individual EMG profile in a certain task, performing a rectification, smoothing and amplitude normalization; 2) extracting muscle synergies, allowing us to understand the behavior of a combination of muscles that present related activity during the movement (muscles with similar EMG profiles that are activated together), and presenting spatial (muscle synergy vectors) and temporal components (synergy activation coefficients); 3) processing the signal in the frequency domain, namely with the calculation of

intermuscular coherence (IMC), allowing to understand the CNS shared neural input to two muscles.

Muscle synergy extraction has been used in clinics, robotics and sports (Singh, Iqbal, White, & Hutchinson, 2018; Taborri et al., 2018). Regarding strength training tasks few studies have been conducted and the training adaptations overtime are still not fully understood. Considering bench press at different velocities, trained subjects showed similar temporal patterns of muscle activation, although individualized weightings of each muscle within the synergies were reported (Samani & Kristiansen, 2018). Across conditions, the synergy associated to eccentric phase showed muscle vectors with greater intra-subject than inter-subject similarity for slow velocity, being more individualized across conditions than shared across subjects when performed slowly. However, regarding concentric phase synergy, the activation coefficient presented greater inter-subject similarity at fast velocity than intra-subject similarity across conditions, i.e., synergy timing varied more between conditions than between subjects when performed quickly (Samani & Kristiansen, 2018). Between powerlifters and untrained subjects, the powerlifters showed larger inter-subject variability in the concentric phase activation coefficient, while the weightings of each muscle within the synergies were less variable in powerlifters (Kristiansen, Madeleine, Hansen, & Samani, 2015). After a five-week bench press training program, the untrained subjects presented post-training muscle vectors significantly different from pre-training, corroborating the results from the previous study (Kristiansen, Samani, Madeleine, & Hansen, 2016). Additionally, a study encompassing 4 weeks of wobble board sensorimotor training concluded that, after training, the experimental group presented modified modular organization in the early landing phase, with separation of the synergy that comprised plantar flexors and ankle evertors, which was accompanied with a reduction in secondary muscle activation (Silva, Oliveira, Mrachacz-Kersting, & Kersting, 2018). Furthermore, when analyzing whole body complex tasks as weightlifting movements, different intermuscular coordination strategies were observed between groups with different training expertise, with different timings of activation of the synergies as well as the muscle weighting within the synergies (Santos et al., 2021). In addition, although the modular organization of muscle synergies during loaded exercises is not affected by the external load (Kenville, Clauß, & Maudrich, 2024), greater activity of specific muscles within the synergies may play an important role, especially

during high-loads (~90% RM), to differentiate the highly skilled individuals mechanisms (Hakariya, Kibushi, & Okada, 2023).

Although muscle synergy analysis may provide important general information about how the CNS controls the neuromusculoskeletal system redundancy, another approach has been used to understand the interactions between cortical, subcortical and spinal mechanisms during movement, the coherence analysis (Grosse, Cassidy, & Brown, 2002). This analysis has been used considering that IMC may provide comparable information to corticomuscular coherence, namely regarding the descending cortical drives to the muscle (Brown, Farmer, Halliday, Marsden, & Rosenberg, 1999; Grosse et al., 2002), and that motor unit synchronization is not only present within a muscle, but also between synergistic muscles recruited functionally during certain tasks (De Luca & Erim, 2002; De Luca, Roy, & Erim, 1993; Farina, Merletti, & Enoka, 2014) . Thus, the IMC or EMG-EMG coherence aims to investigate neural mechanisms of motor control, evaluating the relation between the EMG of two muscles (two data time series).

While muscle synergy extraction relates only to temporal domain, IMC analysis may be a powerful tool to detect changes in the EMG power spectrum during dynamic and static contractions and then to assess synchrony between central mechanisms of motor control and the movement production (De Marchis, Severini, Castronovo, Schmid, & Conforto, 2015; Kenville et al., 2020). Additionally, the IMC approach has shown to be particularly sensitive to changes in neuromuscular control during fatiguing tasks. It is well known that fatigue, defined as a loss of force or power in response to contractile activity that is secondary to physiological disequilibrium at multiple levels of functioning (Kent-Braun, Fitts, & Christie, 2012), can promote a decline of median frequency of the EMG signals power spectrum (Contessa, Adam, & De Luca, 2009; Correia, Oliveira, Vaz, Silva, & Pezarat-Correia, 2016), changing the distribution of the signal frequencies across the whole spectrum. The physiological foundation as well as the acute responses in IMC to strength training will be developed in Chapter 3.

AIMS OF THE THESIS

The general purpose of this thesis is to better understand what the role of intermuscular coordination in the chronology of strength training adaptations is, and how does coordinative patterns of muscle recruitment change overtime. Thus, we intend to provide a general comprehensive overview of the state of the art concerning 1) the differences between chronically resistance-trained and untrained individuals in neural mechanisms regarding the motor control of agonist, antagonist and synergist muscles, and 2) the acute adaptations in muscle coupled organization after a fatiguing traditional strength session. Furthermore, we designed experimental studies that allowed to examine:

1) The acute adaptations in intermuscular coupling assessed through intermuscular coherence calculations in groups with different training expertise.
2) The short-term adaptations to strength training in isometric submaximal and maximal contractions as well as dynamic contractions with different loads following 6 weeks of training.
3) The long-term adaptations to strength training in isometric submaximal and maximal contractions as well as dynamic contractions with different loads.

The secondary aims of each study will be presented in the respective chapter as well as the hypotheses based on the current research.

GENERAL METHODOLOGY

This section will provide general information about the methods concerning data collection and processing. The specific methodology applied in each study should be consulted in the respective chapter.

Participants

Untrained and resistance-trained individuals were included in the experimental studies of this thesis. General information of the participants is overviewed in Table 1.1.

Table 1.1 Summary of the participants characteristics.

Group	N	Age (years)	Height (cm)	Weight (kg)
UT	11	26.2 ± 3.6	173.0 ± 7.2	66.6 ± 8.2
ST	11	22.6 ± 3.1	176.4 ± 7.9	70.5 ± 14.9
LT	10	28.0 ± 6.1	174.7 ± 6.7	83.1 ± 9.2

UT – untrained individuals; ST – Short-term trained individuals involved in the longitudinal study; LT – Long-term trained powerlifters/weightlifters

The sample was composed of untrained individuals (UT) who were unexperienced in strength-related tasks, long-term trained individuals (LT) who were experienced powerlifters or weightlifters with at least 2 years of regular practice of strength training and short-term trained individuals who were involved in the longitudinal studies, namely being comprised in 6 weeks of squat training.

The general description of the participants visits to the laboratory is described in Figure 1.1.

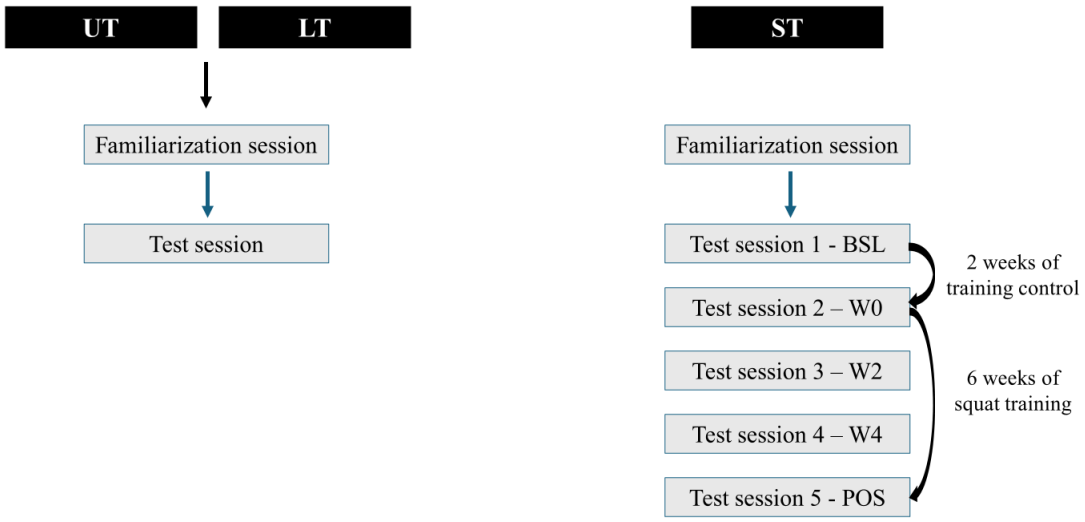

Figure 1.1 Flowchart of the participants visits to the laboratory.

Each ST participant was requested to go to the laboratory in six occasions. The first session was used to familiarize the participants with the testing tasks as well as with the back-squat exercise. The remaining five sessions were used to evaluate the coordinative mechanisms or to assess squat 1RM. The first of these sessions took place one week after the familiarization session and was used as baseline (BSL), after which the participants were instructed to maintain their regular physical activity without adding strength training exercises. After two weeks of strength training abstinence, the participants were evaluated again, with this session accounting as the beginning of the training period (W0). After W0, the participants started the training program and were evaluated every two weeks. Thus, the third, fourth and fifth evaluation sessions were conducted after two (W2), four (W4) and six weeks of training (POS), respectively. The evaluation session after the sixth week was the final session that evaluated training adaptations corresponding to the training program end.

The strength training program performed by the ST lasted six weeks with three training sessions per week, which resulted in 18 training sessions. The strength training program consisted in 5 sets of 10 repetitions of back-squats with 2 minutes of rest between sets. The exercise intensity was targeted to 75% of 1RM of the back-squat. The participants were instructed to perform the exercise with the concentric phase following a controlled eccentric phase. In the final repetitions of the last sets the researcher could spot the participants, and in

sets at which the researcher help was needed in 2 or more repetitions, the load was decreased by 2,5kg for the subsequent set. During the training program the relative load was maintained, with absolute load progressions each two weeks relatively to the back-squat 1RM determined during the evaluation sessions.

Each UT and LT participant was requested to go to the laboratory in two occasions. The first session was used to familiarize the participants with the testing tasks. The second session was used to evaluate the coordinative mechanisms concerning the evaluated tasks.

The experimental studies methods may be overviewed in Figure 1.2. The specific materials and test session procedures regarding data collection, data processing and statistical analysis are presented in the respective chapter.

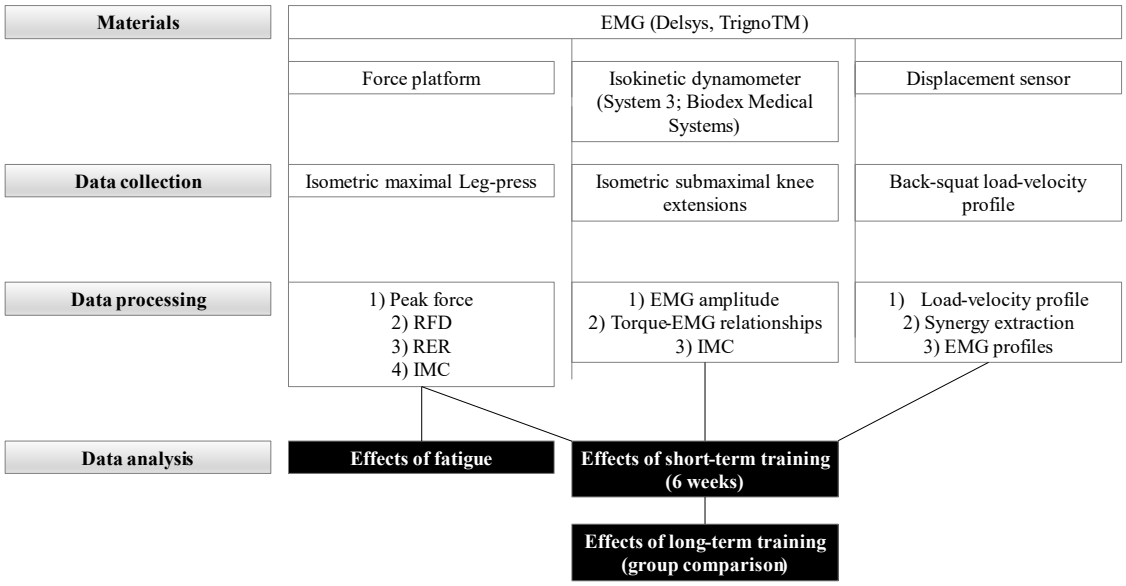

Figure 1.2 Flowchart of the experimental studies materials and methods. EMG – Electromyography; IMC – Intermuscular coherence; RER – Rate of EMG Rise; RFD – Rate of force development.

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Chapter 2

Long-Term Neurophysiological Adaptations to Strength Training: A Systematic Review With Cross-Sectional Studies

Santos, P. D. G., Vaz, J. R., Correia, J., Neto, T., & Pezarat-Correia, P. (2023). Long-Term Neurophysiological Adaptations to Strength Training: A Systematic Review With Cross-Sectional Studies. J Strength Cond Res, 37(10), 2091-2105.
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ABSTRACT

Neuromuscular adaptations to strength training are an extensively studied topic in sports sciences. However, there is scarce information about how neural mechanisms during force production differ between trained and untrained individuals. The purpose of this systematic review is to better understand the differences between highly trained and untrained individuals to establish the long-term neural adaptations to strength training. Three databases were used for the article search (PubMed, Web of Science, and Scopus). Studies were included if they compared groups of resistance-trained with untrained people, aged 18–40 year, and acquired electromyography (EMG) signals during strength tasks. Twenty articles met the eligibility criteria. Generally, strength-trained individuals produced greater maximal voluntary activation, while reducing muscle activity in submaximal tasks, which may affect the acute response to strength training. These individuals also presented lower co-contraction of the antagonist muscles, although it depends on the specific training background. Global intermuscular coordination may be another important mechanism of adaptation in response to long-term strength training; however, further research is necessary to understand how it develops over time. Although these results should be carefully interpreted because of the great disparity of analyzed variables and methods of EMG processing, chronic neural adaptations seem to be decisive to greater force production. It is crucial to know the timings at which these adaptations stagnate and need to be stimulated with advanced training methods. Thus, training programs should be adapted to training status because the same stimulus in different training stages will lead to different responses.

Key Words: strength training, electromyography, muscle activation, coactivation, neuromuscular performance, physical fitness expertise

INTRODUCTION

It is widely known that regular practice of strength training leads to increases in maximal strength, through adaptation at the neuromuscular system. At the morphological level, strength training promotes increases in the cross-sectional area of the muscle, mainly through the hypertrophy of muscle fibers (increase in myofibrillar size and number) (Franchi et al., 2018; Mobley et al., 2018). Other morphological adaptations, such as changes in muscle architecture (e.g. pennation angle and fascicle length) (Blazevich, Gill, Bronks, & Newton, 2003; Timmins et al., 2016; Wells et al., 2014), in cross-sectional areas of fast-twitch fibers and in the tendons' structure may occur following strength training (Folland & Williams, 2007). Neural adaptations have been shown to occur earlier than morphological adaptations which appears to explain the initial strength improvement that is not accompanied by increases in muscle size (Folland & Williams, 2007; Sale, 1988). Specifically, an increase in the agonist muscle activation is commonly observed during the first weeks of training, reflecting increases in motor unit recruitment and/or firing frequency (Duchateau, Semmler, & Enoka, 2006; Moritani & deVries, 1979; Sale, 1988, 2003). Furthermore, the central nervous system can control unwarranted co-contraction of the antagonists, which can lead to a reduced power output. Indeed, strength training has previously shown to decrease antagonists' activation and to adjust synergists' degree and timing of activation (Arabatzi & Kellis, 2012; Balshaw, Massey, Maden-Wilkinson, Lanza, & Folland, 2019; Griffin & Cafarelli, 2005; Häkkinen et al., 1998). Altogether, these neural adaptations contribute to the development of maximal force/torque capacity, and to the ability to produce force/torque in a short amount of time (i.e. rate of force/torque development) (Folland & Williams, 2007; Maffiuletti et al., 2016), a crucial element in sports and daily life activities.

Strength training related research has extensively investigated the changes that occur at the muscular level (Blazevich et al., 2003; Folland & Williams, 2007; Timmins et al., 2016; Wells et al., 2014). While substantial research supports the aforementioned neural adaptations, an integrated look at the neural adaptations is needed to provide a more comprehensive understanding of the strength training related adaptations. Most of the previous research focused on the adaptations of the agonist's activity throughout the first weeks of training (Del Balso & Cafarelli, 2007; Del Vecchio, Casolo, et al., 2019; Jenkins,

Housh, Buckner, Bergstrom, Cochrane, et al., 2016). The agonist's activity level, however, provides very limited information, as neural adaptations occur at different sites of the Central Nervous System (CNS). More precisely, neural adaptations to strength training may emerge from the spinal cord, from the motor cortex or from the synapses that converge into the motoneurons (Škarabot, Brownstein, Casolo, Del Vecchio, & Ansdell, 2021), and that will lead to changes in the motor unit recruitment within the agonist, antagonist, or synergist muscles. Regardless the sites of adaptation, the integrated control of muscles with different functional roles within the CNS will allow to increase the mechanical output in strength tasks. Different methods and technologies allow the assessment of neural adaptations at different sites from brain centers to motor units (e.g. standard electromyography (EMG), percutaneous electrical nerve stimulation, transcranial magnetic stimulation (TMS) or non-invasive high-density EMG). Despite the important contributions of these different technologies to the comprehension of the adaptation's sites, the current research lacks to describe and explain how these emerge in the global motor control. In other words, an important question remains unanswered: how does the central nervous system adapt to organize the large number of muscles (i.e., intermuscular coordination patterns) as a result of strength training? In fact, the understanding of the intermuscular coordination mechanisms has been carried out mainly through the study of adaptations in antagonist activation, but also through the extraction of muscle synergies (Hug, 2011). The extraction of muscle synergies through algorithms like Non-Negative Matrix Factorization or Principal Component Analysis allows to understand how the central nervous system controls complex patterns of movement and has been used to analyze the synergistic behavior of muscles. Only a couple of studies used this comprehensive approach in the field of strength training (Kristiansen, Samani, Madeleine, & Hansen, 2016; Silva, Oliveira, Mrachacz-Kersting, & Kersting, 2018). Additionally, the effects of strength training in coordination were evaluated by coherence analysis between the cortex and muscles (Elie, Barbier, Ido, & Cremoux, 2021) or within muscles (Walker et al., 2019) which may also provide insights into the muscle synergy theory. This approach is usually applied to investigate neural mechanisms of motor control between pairs of agonist-agonist or agonist-antagonist muscles. Namely, it has been suggested that intermuscular coherence allows to identify common corticospinal drives shared between motoneurons innervating different muscles (Farina, Merletti, & Enoka, 2014). Moreover, this approach has

shown to be particularly sensitive to changes in neuromuscular control during fatiguing tasks (Castronovo, De Marchis, Schmid, Conforto, & Severini, 2018; Charissou, Vigouroux, Berton, & Amarantini, 2016; Semmler, Ebert, & Amarasena, 2013).

Although several research report the neural adaptations after a strength training protocol, these are typically limited to short- (< 6 weeks) and medium-term (7-23 weeks) effects (Ashton et al., 2020; Pearcey, Alizedah, Power, & Button, 2021). Therefore, there is scarce information about the long-term (>23 weeks or >1 year) adaptations. Given the limitations of collecting data across several years, the information we currently have about long-term strength training arise from cross-sectional designed studies that compare chronically resistance-trained (RT) with untrained (UT) individuals (Pearcey et al., 2021). Despite the well-known short-term neural adaptations that explain the increases in force production, neural adaptations remain to occur in the long-term (Pearcey et al., 2021; Sale, 1988).

This review aims to elucidate about strength training chronic neural adaptations in muscles with different functional roles in strength tasks. First, we aimed to elucidate which different neural mechanisms adapt to strength training resulting in a greater recruitment of agonist muscles during maximal tasks and how is muscle activity modulated during submaximal tasks. Second, we intended to define how the activity of the antagonist muscles is modulated in chronically strength-trained individuals. Third, we aimed to clarify how the motor control of agonist, antagonist and synergist muscles is integrated, characterizing the intermuscular coordination processes that are poorly investigated. This will be accomplished by comparing highly experienced and untrained individuals through the analysis of cross-sectional studies.

METHODS

This systematic review was conducted according to the PRISMA statement (Preferred Report Items for Systematic Reviews and Meta-analysis), where we specified and registered all the methodological aspects (PROSPERO registration number: CRD42021279394).

Eligibility criteria and search strategy

For the present review there was no limit for the year of publication. The articles should meet the following criteria: (i) cross-sectional study comparing a group of experienced RT participants with at least 2 years of regular practice of strength training and a control group of untrained individuals during strength-related tasks (types of contraction included: isometric or dynamic; maximal or submaximal; explosive or ramp; voluntary or elicited); (ii) included samples of adults with less than 40 years old; (iii) acquisition of EMG signals during the tasks with outcomes of muscle activation. We did not include studies using balance tasks or referring to adaptations in proprioception or clinical outcomes. Reviews and case studies were also excluded.

We conducted a search of peer-reviewed articles until October 2021 in three databases: PubMed, Web of Science and Scopus. All the databases were screened with the following keywords and respective combination: (“strength training” OR “resistance training” OR “strength program” OR “muscle strength” OR “Weight training” OR “Resistance exercise” OR “resistive exercise” OR “Long-term strength training”) AND (“electromyography” OR “EMG” OR “muscle activity” OR “muscle activation” OR “EMG amplitude and duration” OR “electromyogram”) AND (“neural adaptation” OR “neural adaptations” OR “neuromuscular adaptations” OR “neuromuscular adaptation” OR “neuromuscular variables” OR “intermuscular coordination” OR “muscle coordination” OR “coordination” OR “neural drive” OR “agonist” OR “antagonist” OR “synergist” OR “agonist and antagonist muscles” OR “motor modules” OR “muscle synergies” OR “neuromuscular performance” OR “coactivation” OR “Agonist-antagonist co-activation”). A manual search (i.e. list of references of articles) was performed as complement to the electronic search to find further eligible articles.

Data extraction

The titles and abstracts of the studies resulting from the search were screened by two authors (P.S. & J.C.). Consensus was reached between the two authors. Duplicate entries were removed and a first screening regarding the title and abstract of the articles was made. Finally, we extracted the information about each article (authors and year of publication), participants (sample size and training experience), compared tests (task, type and intensity of contraction), electromyographic assessment (monitored muscles, calculated variables) and neurophysiological outcomes. Uncertainties were resolved by consensus.

The information extracted from each study was summarized by study characteristics (participants, task, electromyographic measures), differences in strength, differences in agonist activation, differences in antagonist activation, agonist-antagonist relationship and differences in synergist activation.

Quality assessment and data synthesis

To assess study quality, we used the quality assessment tool developed by the Effective Public Health Practice Project (EPHPP), and we evaluated five of the six proposed methodological domains: selection bias, study design, confounders, data collection methods and withdrawals and dropouts (Thomas, Ciliska, Dobbins, & Micucci, 2004). We did not assess the sixth item of the original scale, namely the blinding of the participants, because it is not possible to blind participants regarding their maximum force production capacity or the maximum tolerance to resistive exercises. Based on the scores of each component, three levels were used to classify the global methodological quality of the studies: strong, moderate and weak. Two authors independently rated the five domains (P.S. & J.C.) reaching consensual results.

RESULTS

Study selection and characteristics

The search in the three databases (PubMed, Web of Science and Scopus) resulted in 2624 publications. Detailed information is presented in Figure 2.1. Twenty articles respecting all the inclusion criteria were then included in this review.

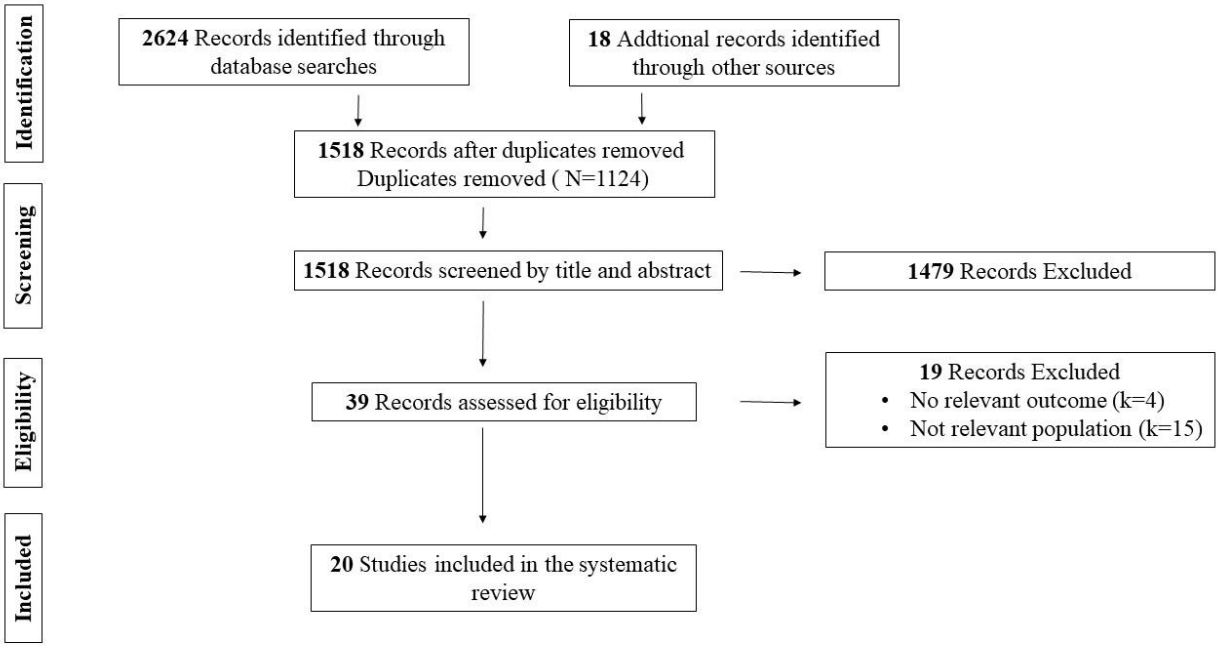

Figure 2.1 Flowchart of the search strategy and results.

The characteristics and the summary of all the included studies are reported in Table 2.1. All studies were cross-sectional, with exception of one study that although it presented data regarding strength training over 12 weeks (Balshaw et al., 2019), we did not use this information for the present review. Also, one study compared the RT and the untrained participants with endurance trained athletes (Charissou et al., 2016), which was not used in this review as well as the information of another study that compared the adult population with other age groups (comparing with older population) (Orssatto, Wiest, Moura, Collins, & Diefenthaeler, 2020). All studies reported the inclusion of male individuals only, with exception for Viitasalo and colleagues (Viitasalo, Salo, & Lahtinen, 1998) who did not refer if the participants were male or female. The most common sample size corresponded to 8-15

participants in each group, with a total of 204 evaluated RT (age: 24.85 ± 3.34 years; height: 179.4 ± 2.6 cm; body mass: 86.3 ± 6.4 kg) and 249 UT (age: 24.20 ± 2.48 years; height: 177.8 ± 2.9 cm; body mass: 76.1 ± 5.08 kg). The experienced participants were engaged in different types of training with the vast majority performing strength training as their main activity or performing strength training complementary to other activities as athletics or team sports (Charissou et al., 2016; Tillin, Jimenez-Reyes, Pain, & Folland, 2010; Viitasalo et al., 1998). Nevertheless, RT participants included in all the 20 studies were engaged in strength training programs for at least 2 years (with the mean minimum strength training time of practice of 3,5 years).

All the studies assessed strength training tasks with collection of EMG signals from agonist and/or antagonist and/or synergist muscles, with 5 studies evaluating acute neuromuscular responses to training (Ahtiainen & Häkkinen, 2009; Charissou et al., 2016; Hartman, Ryan, Cramer, & Bemben, 2011; Pick & Becque, 2000; Ye, Beck, & Wages, 2015). In what regards to mechanical measures, differences in maximum force production capacity, power or rate of force development were reported. The EMG outputs encompassed variables across i) agonist muscles (such as EMG amplitude in different tasks (Ahtiainen & Häkkinen, 2009; Balshaw et al., 2019; Pick & Becque, 2000; Stastny, Lehnert, Zaatar, Svoboda, & Xaverova, 2015; Viitasalo et al., 1998; Ye et al., 2015), median or mean power frequency (Tillin et al., 2010; Ye et al., 2015), slope EMG-torque (Amarantini & Bru, 2015; Balshaw et al., 2019), electromechanical delay (Del Vecchio et al., 2018; Tillin et al., 2010), conduction velocity (Del Vecchio et al., 2018) and evoked responses to peripheral nerve stimulation (Hartman et al., 2011; Orssatto et al., 2020; Škarabot, Balshaw, et al., 2021; Tallent, Goodall, Hortobágyi, St Clair Gibson, & Howatson, 2013; Tillin et al., 2010) or transcranial magnetic stimulation (del Olmo, Reimunde, Viana, Acero, & Cudeiro, 2006; Lahouti, Lockyer, Wiseman, Power, & Button, 2019; Pearcey, Power, & Button, 2014; Philpott, Pearcey, Forman, Power, & Button, 2015; Tallent et al., 2013)), ii) antagonist muscles (co-contraction indexes (Amarantini & Bru, 2015; Balshaw et al., 2019; Pearcey et al., 2014)) and iii) synergist muscles (degree of activation (Stastny et al., 2015), intermuscular coherence (Charissou et al., 2016) and muscle synergies (Kristiansen, Madeleine, Hansen, & Samani, 2015; Santos et al., 2021)). Within the selected studies, some evaluated tasks for the lower limb (N=11) (Ahtiainen & Häkkinen, 2009; Amarantini & Bru, 2015; Balshaw et al., 2019; Charissou et

al., 2016; Hartman et al., 2011; Orssatto et al., 2020; Pick & Becque, 2000; Stastny et al., 2015; Tallent et al., 2013; Tillin et al., 2010; Viitasalo et al., 1998) and other for the upper limb (N=6) (del Olmo et al., 2006; Del Vecchio et al., 2018; Lahouti et al., 2019; Pearcey et al., 2014; Philpott et al., 2015; Ye et al., 2015), while one study evaluated both (Škarabot, Balshaw, et al., 2021) or whole-body muscle synergies (N=2) (Kristiansen et al., 2015; Santos et al., 2021).

The methodological quality of each study is presented in Table 2.2 with details of each domain of the scale. Almost all studies were rated as "moderate" with exception of one study that was rated as "strong" (Balshaw et al., 2019). This is justified by the classification in selection bias domain where the 19 studies were classified as "weak". In these studies, it was not stated what percentage of the population the sample represents, and it is plausible that even if this was defined, it would be a low participation rate within the selected populations because studies that evaluate neuromuscular function with time-consuming methodologies normally present small samples, rarely exceeding the 15 participants. The same studies were classified as "moderate" in what concerns to study design, while the remaining study was classified as "strong" in these two domains. Regarding the confounders, one study did not differentiate the gender of the participants were considered "moderate" (Viitasalo et al., 1998) while all others were considered "strong". For the data collection method and withdrawals, all studies were considered "strong".

Table 2.1 Summary of the studies comparing the neural output of experienced and untrained individuals during strength training tasks.

Reference	Participants	Evaluated tasks	Evaluated muscles	EMG variables	Strength differences	Agonist activation differences	Antagonist activation differences	Agonist-activation relationship	Synergist activation differences
Ahtiainen & Häkkinen (2009)	4 male powerlifters or weightlifters - RT (32 ± 7y) , 4 UT (27 ± 4y)	Maximal isometric KE; KE dynamic protocols	VL, VM and RF	Averaged iEMG of all muscles	↑ KE MVC;	When performing a forced repetition protocol, UT continued to increase while RT decreased during the forced repetitions	-	-	-
Amarantini & Bru (2015)	5 male RT (24.6 ± 3.25y) and 5 UT (21.8 ± 2.28y)	KE and KF MVC and ramp contractions	GA, VM, RF, BF	EMG-moment relationship; Co-activation	↑ KE and KF MVC;	EMG-moment relationship with linear fitting for RT and curvilinear fitting for UT	EMG-moment relationship with linear fitting for RT and curvilinear fitting for UT	↓ Co-activation during KE and KF MVC	-
Balshaw et al. (2019)	14 male RT (22 ± 2y) and 29 UT (25 ± 2y)	KE and KF MVC, KE isometric contractions at 20, 40, 60 and 80%MVC, muscle size, muscle electrode difference	VL, VM, RF, BF and ST	EMG amplitude, slope torque-agonist, slope torque-antagonist	↑ KE and KF MVC, quadriceps cross-sectional area	↑ activation during MVC; ↓ activation at higher common torque within all the participants	↓ KE slope antagonist-torque and EMG at higher common torque	↓ slope antagonist/agonist	-
Charissou et al. (2016)	10 male RT rugby players (23.6 ± 2.9y) and 9 UT (25.4 ± 5.3y)	KE MVC; Fatigue protocol of 10 x 40%MVC until failure	VM and RF	Wavelet coherence analysis; beta IM	↑ KE MVC; ↓ decrease in 40%MVC KE holding time	-	-	-	↓ IM before fatigue; after fatigue IM remained stable in RT while decrease in UT
del Olmo et al. (2006)	10 male RT (20 ± 4y) and 10 UT (19 ± 3y)	EF MVC and isometric contractions at 10, 20, 30, 40, 50, 60, 70, 80 and 90%MVC	BB and TB	EMG amplitude, MEP	↑ EF MVC; ↓ evoked force at each target force				

Table 2.1 *Cont.*

Reference	Participants	Evaluated tasks	Evaluated muscles	EMG variables	Strength differences	Agonist activation differences	Antagonist activation differences	Agonist-activation relationship	Synergist activation differences
Del Vecchio et al. (2018)	8 male RT (22.2 ± 2.5y) and 8 UT (23.4 ± 3.1y)	EF MVC and EF explosive contractions at 75%MVC	BB HDsEMG	Conduction velocity, EMD	↑ EF MVC; ↑ absolute torque at 50, 100, 150 and 200ms, relative torque at 50 and 100ms, absolute and normalized RTD 0-50ms; ↓ normalized RTD 50-100 and 100-150ms	↑ Muscle fiber conduction velocity at MVC;	-	-	-
Hartman et al. (2011)	8 male RT (25.7 ± 4.2y) and 6 UT (25.8 ± 4.9y)	PF MVC; Fatigue protocol at 40%MVC	SOL and GM	Voluntary activation, EMG amplitude	↑ PF MVC	Only UT decreased central activation ratio	-	-	-
Kristiansen et al. (2015)	10 male powerlifters – RT (28.6 ± 5.8y) and 9 UT (25.5 ± 3.4y)	Bench Press 3-RM, 60%3-RM	PM, LD, ES, AD, TB, VL, BB, SOL, IT	Muscle synergies	↑ 3-RM strength	-	-	-	↑ inter-subject variability in the activation coefficient during the concentric phase corresponding synergy; ↓ inter-subject variability of the muscle vectors in the same synergy
Lahouti et al. (2019)	8 male RT (27.5 ± 7.6y) and 8 UT (29.1 ± 3.2y)	EF MVC, submaximal isometric contractions at 15, 25 and 40%MVC	BB	Mmax, MEP and SICI	↑ EF MVC	↓ SICI at 25 and 45%MVC and active motor threshold	-	-	-

Table 2.1 *Cont.*

Reference	Participants	Evaluated tasks	Evaluated muscles	EMG variables	Strength differences	Agonist activation differences	Antagonist activation differences	Agonist-activation relationship	Synergist activation differences
Orssatto et al. (2020)	14 male RT (26.7y) and 14 UT (26.2y)	KE MVC, explosive contractions at 80%MVC and octet elicited contractions	VL, VM and RF	Average EMG amplitude	↑ KE MVC, Absolute (at 50, 100 and 150ms) and normalized (at 50ms) torque; ↑ octet peak torque, absolute and normalized octet at 50ms, and toque at 50ms/octet torque at 50ms	↑ EMG amplitude at all time windows	-	-	-
Pearcey, Power & Button (2014)	8 male RT (24.3 ± 2.03y) and 7 UT (22.5 ± 5.99y)	EF MVC and isometric contractions at 10, 20, 30, 40, 50, 60, 70, 80 and 90%MVC	BB and TB	MEP, CMEP, Mmax, EMG amplitude	↑ EF MVC	↓ MEP at 60, 70, 90 and 100%MVC, lower ratio MEP or CMEP/force, EMG/force ratio	-	↓ triceps/biceps ratio at all intensities	
Philpott et al. (2015)	7 male RT (22.9 ± 3.5y) and 6 UT (22.0 ± 2.2y)	Non-dominant EF MVC and isometric contractions at 25, 50, 75 and 90%MVC	BB	MEP, CMEP, Mmax	↑ EF MVC	↑ CMEP amplitude at 50 and 75%MVC	-	-	-
Pick & Becque (2000)	9 male RT (22.5 ± 0.8y) and 7 UT (23.7 ± 2.62y)	Squat 1-RM; Set until failure with 85% 1-RM (SUF)	VL and VM	EMG amplitude	↑ Squat 1-RM and number of repetitions performed with 85% 1-RM	↑ VM and combined VM and VL activation during 1-RM; ↑ VL activation at 40, 60 and 80% of the SUF and iEMG of the SUF exceeded 1-RM iEMG; UT did not increase VM activation until 60% of the SUF, not surpassing 75% of 1-RM iEMG at the end of the SUF, while RT increased VM activation until near the 1-RM iEMG having higher VL and VM combined activation at the end of the SUF	-	-	-

Table 2.1 *Cont.*

Reference	Participants	Evaluated tasks	Evaluated muscles	EMG variables	Strength differences	Agonist activation differences	Antagonist activation differences	Agonist-activation relationship	Synergist activation differences
Santos et al. (2021)	7 male weightlifters – RT (30.7 ± 9.3y) and 10 UT (24.8 ± 2.0y)	Power clean 5-RM, 70% 5-RM	TS, PM, LD, BB, TB, EDC, FDS, ES, RA, OE, Gmax, VL, BF, ST, GL, TA	Muscle synergies	↑ Power clean 5-RM	-	-	-	↑ interindividual variability in weightlifters in the #3 synergy; Fractionation of the synergy #1 of UT into synergy #1 and #3 of weightlifters and consequent lower values of similarity of the vectors; UT anticipated synergies #1 and #2 while retarded synergy #3
Škarabot et al. (2021)	EF: 15 male RT (22 ± 4y) and 14 UT (22 ± 3y); KE: 14 male RT (22 ± 2y) and 49 UT (25 ± 2y)	KE and EF MVC	BB long head, BB short head, 2 x VL, 2 x VM and 2 x RF	EMG amplitude	↑ EF and KE MVC, BB thickness and cross-sectional area	↑ BB short head EMG, Mmax and Mmax corrected to muscle-electrode distance; ↑ KE muscles EMG, Mmax and Mmax corrected to muscle-electrode distance	-	-	-
Stastny et al. (2015)	14 male RT (30.02 ± 5.60y) and 14 UT (28.35 ± 5.71y)	KE, KF and HAbd MVC; Ipsilateral and contralateral walking lunges and stationary split squats 5-RM	VL, VM, Gmed and BF	EMG amplitude	↑ range of motion during the ipsilateral and contralateral walking lunges in KE/KF and in hip flexion in ipsilateral walking lunges	↑ Eccentric VL amplitude during contralateral walking lunges	-	-	↑ Eccentric Gmed amplitude in walking lunges and split squats
Tallent et al. (2013)	10 male RT (22 ± 2y) and 9 UT (26 ± 3y)	DF MVC and isokinetic contractions (15, 25, 50 and 80%MVC)	TA	MEP, Mmax, H-reflex and V-wave	↑ Absolute DF MVC	-	-	-	-

Table 2.1 *Cont.*

Reference	Participants	Evaluated tasks	Evaluated muscles	EMG variables	Strength differences	Agonist activation differences	Antagonist activation differences	Agonist-activation relationship	Synergist activation differences
Tillin et al. (2010)	9 male power athletes – RT (21 ± 3y) and 10 UT (22 ± 4y)	KE and KF MVC, KE explosive contractions	VL, VM, RF and BF long head	Tetanic contractions, EMD, EMG amplitude, median frequency	↑ KE MVC, force at 50, 100 and 150ms, absolute and normalized RTD at 0-50ms, tetanic twitch tension and absolute RTD at 0-50 and 100-150ms; ↓ normalized RTD at 50-100ms	↑ EMG during the 0-50ms for each muscle, mean quadriceps rate of change in EMG during 0-25ms, median frequency of VL and average of all quadriceps muscles; ↓ mean quadriceps rate of change in EMG during 25-75ms	-	-	-
Viitasalo et al. (1998)	7 power trained – RT (27.6 ± 3.6y) and 11 UT (20.6 ± 2.6y)	Drop jump (40 and 80cm)	VL, RF, GL and BF	EMG amplitude	↑ jump height, average and peak vertical ground reaction force; ↓ contact times; UT with knee angle at deepest position more bent and ankle angle at touch down and take-off more extended	↑ EMG pre-activity in VL and GL, and general EMG activity during pre-contact and braking phases	-	-	-
Ye, Beck & Wages (2015)	13 male RT (24 ± 4y) and 12 UT (23 ± 4y)	EF MVC; 6 x 10 concentric or eccentric isokinetic contractions at 60º/s	BB	EMG amplitude, mean frequency	↑ EF MVC; Eccentric training induced greater strength decline in UT	-	-	-	-

Abbreviations: ↑, resistance trained individuals presented greater; ↓ resistance trained individuals presented lower; AD, *anterior deltoideus*; BB, *biceps brachii*; BF, *biceps femoris*; CMEP, cervicomedullary evoked potentials; DF, dorsiflexion; EDC, *extensor digitorum communis*; EE, elbow extension; EF, elbow flexion; EMD, electromechanical delay; EMG, electromyography; ES, *erector spinae*; FDS, *flexor digitorum superficialis*; GA, *gastrocnemius*; GM, *gastrocnemius medialis*; Gmax, *gluteus* maximus; Gmed, *gluteus medius*; HAbd, hip abduction; HDsEMG, high-density surface electromyography; iEMG, electromyographic integral; IM, intermuscular interactions; IT, *inferior trapezius*; KE, knee extension; KF, knee flexion; LD, *latissimus dorsi*; MEP, motor evoked potential; MVC, maximum voluntary contraction; OE, *obliquus externus;* PF, plantarflexion; PM, *pectoralis major*; RA, *rectus abdominis*; RF, *rectus femoris*; RT, resistance-trained individuals; RTD, rate of torque development; SICI, short-interval cortical inhibition; SM, semimembranosus; SOL, *soleus*; ST, *semitendinosus*; TA, *tibialis anterior*; TB, *triceps brachii*; TS, *trapezius superior*; UT, untrained individuals; VA%, voluntary activation; VM, *vastus medialis*; VL, *vastus lateralis*; WF, wrist flexion.

Table 2.2 Quality assessment of all included studies.

Reference	Selection Bias	Study Design	Confounders	Data Collection Method	Withdrawals	Global
Ahtiainen & Häkkinen (2009)	1	2	3	3	3	Moderate
Amarantini & Bru (2015)	1	2	3	3	3	Moderate
Balshaw et al. (2019)	3	3	3	3	3	Strong
Charissou et al. (2016)	1	2	3	3	3	Moderate
del Olmo et al. (2006)	1	2	3	3	3	Moderate
Del Vecchio et al. (2018)	1	2	3	3	3	Moderate
Hartman et al. (2011)	1	2	3	3	3	Moderate
Kristiansen et al. (2015)	1	2	3	3	3	Moderate
Lahouti et al. (2019)	1	2	3	3	3	Moderate
Orssatto et al. (2020)	1	2	3	3	3	Moderate
Pearcey, Power & Button (2014)	1	2	3	3	3	Moderate
Philpott et al. (2015)	1	2	3	3	3	Moderate
Pick & Becque (2000)	1	2	3	3	3	Moderate
Santos et al. (2021)	1	2	3	3	3	Moderate
Škarabot et al. (2021)	1	2	3	3	3	Moderate
Stastny et al. (2015)	1	2	3	3	3	Moderate
Tallent et al. (2013)	1	2	3	3	3	Moderate
Tillin et al. (2010)	1	2	3	3	3	Moderate
Viitasalo et al. (1998)	1	2	2	3	3	Moderate
Ye, Beck & Wages (2015)	1	2	3	3	3	Moderate

Agonist activity

Agonist EMG activity in strength tasks. During isometric knee extension MVC, greater absolute activity was found for the RT in comparison with UT individuals (Balshaw et al., 2019), finding also greater agonist activation during elbow flexion MVC. Orssatto and colleagues (2020) looked at specific time intervals but also found greater activation at all intervals for RT (0-50ms, 50-100ms and 100-150ms) (Orssatto et al., 2020). Tillin and colleagues (2010) had previously reported similar findings for the 0-50ms interval. However, in this study the rate of EMG change was greater for RT participants at the 0-25ms time window while greater for UT participants at the 25-75ms time window (Tillin et al., 2010). These differences in activation resulted in different rate of torque development (RTD). Generally, RT showed greater absolute RTD and greater RTD in the initial phase of

contraction (0-50ms) (Del Vecchio et al., 2018; Orssatto et al., 2020; Tillin et al., 2010). However, UT presented greater relative RTD at 50-100ms in two studies (Del Vecchio et al., 2018; Tillin et al., 2010). More details are presented in Table 1. Additionally, Skarabot and colleagues (2021) found greater absolute Mmax corrected to muscle electrode distance in RT participants during elbow flexion and knee extension (Škarabot, Balshaw, et al., 2021).

Regarding EMG frequency analysis during isometric MVC contractions, RT showed greater agonist median frequency during knee extension (Tillin et al., 2010). During elbow flexion MVC, RT showed higher muscle fiber conduction velocity (Del Vecchio et al., 2018).

When performing submaximal isometric tasks, RT participants presented a linear EMG-moment relationship in knee extension, while UT participants presented a curvilinear relationship (Amarantini & Bru, 2015), and RT participants presented a lower activation at highest common torque between groups (Balshaw et al., 2019). Also, RT participants presented lower agonist activation during submaximal isometric elbow flexion from 10 to 90%MVC (Pearcey et al., 2014). Additionally, RT participants showed to reach greater relative activation during submaximal dynamic exercises, which led to different acute training adaptations (Ahtiainen & Häkkinen, 2009; Pick & Becque, 2000).

In other strength-related tasks, RT participants showed greater vastus medialis and combined (vastus medialis and vastus lateralis) activation during maximum dynamic squat (Pick & Becque, 2000), greater eccentric vastus lateralis amplitude during contralateral walking lunges (Stastny et al., 2015), and greater vastus lateralis and gastrocnemius lateralis pre-activity during pre-contact of drop jumps (Viitasalo et al., 1998).

Motor evoked potentials. Pearcey and colleagues (2014) found lower motor evoked potentials (MEP) in biceps brachii at 60, 70, 90 and 100% MVC in RT participants, as well as lower MEP or cervicomedullary motor evoked potentials (CMEP)/force and EMG/force (Pearcey et al., 2014). Additionally, Philpott and colleagues (2015) found higher CMEP at 50 and 75%MVC (Philpott et al., 2015), whereas Labouti and colleagues (2019) reported lower short-interval cortical inhibition (SICI) of the RT participants when performing elbow flexion contractions at 25 and 40%MVC, and lower active motor threshold (Lahouti et al., 2019).

Antagonist activity

During isometric submaximal contractions, RT participants presented a linear EMG-moment relationship in knee extension antagonist muscles, while UT participants presented a curvilinear relationship (Amarantini & Bru, 2015), with lower antagonist EMG-moment slope and lower EMG amplitude at higher common torque between groups (Balshaw et al., 2019).

Only three studies applied mathematical functions that related agonist and antagonist activation. During isometric MVC, RT participants presented lower antagonist/agonist ratio in knee extension and knee flexion (Amarantini & Bru, 2015) as well as during knee extension submaximal isometric contractions presented a lower antagonist/agonist slope than UT (Balshaw et al., 2019). Also, during elbow flexion the antagonist/agonist ratio was lower for RT participants at all intensities from 10 to 90%MVC (Pearcey et al., 2014).

Intermuscular Coordination

RT participants presented higher gluteus medius activity during eccentric phase of walking lunges and split squats, and presented lower intermuscular interactions between vastus medialis and rectus femoris during knee extension isometric MVC (Stastny et al., 2015). However, after fatigue, only the UT participants presented decreased intermuscular interactions, while RT interaction remained the same (Charissou et al., 2016).

Two studies also evaluated intermuscular coordination extracting muscle synergies from EMG signals. The first one evaluated bench press muscle synergies from 9 muscles, reporting that powerlifters present more interindividual variability in the activation coefficients and less interindividual variability in the muscle vectors (Kristiansen et al., 2015). In the second study, Santos and colleagues extracted power clean muscle synergies from 16 muscles, finding greater interindividual variability in weightlifters synergies and differences in the muscle synergy components (Santos et al., 2021).

DISCUSSION

The purpose of this systematic review was to summarize the neural adaptations to long-term strength training by analyzing cross-sectional designed studies comparing highly experienced individuals with untrained ones. Twenty studies were included. Generally, RT showed greater voluntary activation of the agonist muscles in maximal tasks, while decreasing the degree of activation in submaximal intensities. RT also presented lower antagonist activation, although these results should be interpreted with caution. Global intermuscular coordination was also chronically altered with long-term strength training, and combined, all these chronic adaptations result in different acute responses to training that may be adapted to the individual training stage.

Generally, during maximal tasks, RT individuals' trend to present greater agonist muscle activity, which is an important contributor to develop higher strength values. Also, these individuals present greater conduction velocity and greater initial muscle activation which results in greater RTD in the first 50ms of torque production, while the UT individuals may present greater results in later intervals of RTD analysis in result of delayed muscle activation.

In the evaluated studies, surface EMG revealed an increased agonist activity during isometric MVC in RT individuals (Balshaw et al., 2019; Grosprêtre, Gimenez, & Martin, 2018; Škarabot, Balshaw, et al., 2021) while other studies report no differences (Ahtiainen & Häkkinen, 2009; Lattier, Millet, Maffiuletti, Babault, & Lepers, 2003; Wang et al., 2019). Additionally, RT showed to have greater agonist EMG amplitude than UT (Pick & Becque, 2000; Sbriccoli et al., 2010; Viitasalo et al., 1998). Increased EMG amplitude is related to greater neural drive to the muscle (Häkkinen et al., 1998; Sale, 1988) and, together with muscle volume and pre-training MVC, has shown to explain the variance in MVC changes with training (Balshaw et al., 2017). Furthermore, one study showed a greater median frequency in the RT (Sozen, Erdogan, Ince, & Soylu, 2019; Tillin et al., 2010), while other did not (Quinzi, Bianchetti, Felici, & Sbriccoli, 2018; Ye et al., 2015). Namely, Tillin and colleagues (2010) interpreted greater values of median frequency for the RT during the first 150ms of contraction as greater recruitment of fast twitch fibers, and hence an increased conduction velocity. Additionally, 4 weeks of dorsiflexion isometric training resulted not

only in decreased normalized recruitment-thresholds of the tibialis anterior, but also in increased discharge rate during the plateau of isometric contractions (Del Vecchio, Casolo, et al., 2019). Thus, RT individuals presented greater force production capacity than UT with the increases in maximal strength being in part associated to neural adaptations overtime.

As for rapid force production tasks, power athletes showed greater values of change in agonist EMG during the first 25ms than UT individuals (Tillin et al., 2010) resulting in greater normalized RTD during the first 50ms of the contraction. Also, greater ratio between voluntary torque at 50ms and octet torque at 50ms was found for RT individuals (Orssatto et al., 2020). In addition, Tillin and colleagues (2010) presented greater activation of the trained group during the first 50ms and reported a strong correlation ($r2 = 0.75$-0.83) between agonist activation and initial torque output (Tillin et al., 2010). This is in line with previous evidence that associate early phase RTD with neural mechanisms (Cossich & Maffiuletti, 2020), such as increased discharge rate of motor units (Del Vecchio, Negro, et al., 2019; Van Cutsem, Duchateau, & Hainaut, 1998) or greater conduction velocity during the initial phase of contraction (Del Vecchio et al., 2018). Additionally, longitudinal studies with strength training interventions found increased EMG activation or increased rate of EMG rise during the initial phase of the contraction after 4 weeks of low-load or high-load elbow flexion strength training (Jenkins, Housh, Buckner, Bergstrom, Smith, et al., 2016), 10 weeks of lower limb strength training (Marshall, McEwen, & Robbins, 2011) or 14 weeks of lower limb strength training (Aagaard, Simonsen, Andersen, Magnusson, & Dyhre-Poulsen, 2002).

On the other hand, the UT individuals presented greater increase in EMG only during a delayed time window between 25ms and 75ms (Tillin et al., 2010), which possibly caused the greater normalized RTD during the 50-100ms (Del Vecchio et al., 2018; Tillin et al., 2010). However, Folland and colleagues found different time windows for muscle activation, reporting that agonist activation mainly accounted for rapid force production at the 50ms time point (Folland, Buckthorpe, & Hannah, 2014). Conversely, Johnson and colleagues (2015) reported recurrent inhibition and V-wave as important predictors of RTD in plantarflexion not only in the early time intervals (until the 100ms of contraction) but also during the time intervals of 0-200ms and 0-250ms (Johnson, Kipp, Norcross, & Hoffman, 2015). These differences and lags in time windows that can be found in the literature may be

related with the studied muscles having different functional characteristics, and EMG signal procedures (e.g., filtering).

Regarding electromechanical delay (EMD) and conduction velocity, most of the studies report no differences in EMD (Del Vecchio et al., 2018; Paasuke, Ereline, & Gapeyeva, 1999; Tillin et al., 2010) and a greater conduction velocity for RT (Del Vecchio et al., 2018; Quinzi et al., 2018; Sbriccoli et al., 2010). It has been shown a strong correlation between conduction velocity and fiber diameter (Sadoyama, Masuda, Miyata, & Katsuta, 1988), and since individuals that perform resistance training present a greater fiber diameter (Folland & Williams, 2007; Franchi et al., 2018; Mobley et al., 2018) it is also plausible that they present also greater conduction velocity. Additionally, Mmax was greater in RT and was also related to muscle size (Škarabot, Balshaw, et al., 2021). In this study, although different results considering the analyzed muscle group (knee extensors and elbow flexors) were found in EMG with the RT presenting greater amplitude in knee extensors but not in the elbow flexors, there were no differences when the results were normalized to Mmax. Thus, RT performance in maximal tasks appeared to be mostly modulated by peripheral muscle morphology rather than voluntary EMG activity (Škarabot, Balshaw, et al., 2021). It is essential to ensure that the normalization procedure is suitable for the analyzed data in each study and these possibly confounding influences should be considered when interpreting EMG studies since it may lead to a vast disparity of results.

The central mechanisms associated to strength training have been studied to differentiate the origin of neural adaptations. The use of peripheral nerve stimulation and transcranial magnetic stimulation remain the primary methodologies to study the adaptations of the different paths used by the CNS. Although this topic is not the main purpose of this review, it is important to understand the exercise-induced neuroplasticity when applied to voluntary force production. Spinal and supraspinal adaptations contribute to greater force production in RT, and although the research around this topic is still limited, spinal motoneurons and intra-cortical circuits plasticity appear to represent the main adaptations in the corticospinal pathway (Pearcey et al., 2021).

Two of the analyzed studies reported differences between RT and UT regarding MEP (representing supraspinal excitability) and CMEP (representing spinal excitability) in the

biceps brachii. Although one study reported reduced MEP and maintained CMEP for the RT (Pearcey et al., 2014), the other did not show any difference in MEP while presenting increased CMEP for the RT (Philpott et al., 2015). The results of the two studies are different, however, both indicate increased spinal excitability of dominant and non-dominant upper limb, and this is probably due to motoneuron neuroplasticity resulting in decreased CMEP amplitude for the same force production intensity (Pearcey et al., 2021; Pearcey et al., 2014). Generally, MEP amplitude have been unchanged after acute-resistance training (Pearcey et al., 2021), and RT individuals present no differences when compared to UT individuals (del Olmo et al., 2006; Tallent et al., 2013). Additionally, V-waves, representing a command from the cortical centers, are generally greater in strength or power-trained athletes (Grosprêtre, Bouguetoch, & Martin, 2020; Grosprêtre et al., 2018; Škarabot, Brownstein, et al., 2021). The assumptions regarding the site of the adaptations may be done with caution because motoneuron excitability have different contributions (McNeil, Butler, Taylor, & Gandevia, 2013; Škarabot, Brownstein, et al., 2021). Also, the relation between motor evoked potentials and H-reflexes was greater in power athletes than UT individuals and the authors attributed these results to decreased spinal excitability despite greater corticospinal excitability (Grosprêtre et al., 2020). Studies evaluating not just RT individuals but traceurs whose activity also demands great power production have shown that regarding spinal excitability, measured by H-reflexes, these athletes present lower values at rest than untrained individuals (Grosprêtre et al., 2018). However, these results were only found for soleus and not for gastrocnemius medialis, and the different anatomic and functional characteristics of the muscles as well as the type of training may lead to different adaptations.

Studies using TMS also evaluated responses in intra-cortical circuits to strength training. Namely, Lahouti and colleagues (2019) have shown that SICI resulting from the activation of intracortical inhibitory circuits was lower in RT individuals, as well as the active motor threshold representing the lowest TMS intensity that elicited a MEP and a possible enhanced excitability of the corticospinal pathway (Lahouti et al., 2019). Besides decreasing SICI, short-term strength training has also shown to decrease the silent period (Mason et al., 2020; Siddique et al., 2020).

Although RT individuals can increase the maximal neural output during maximal isometric or dynamic tasks, during submaximal tasks the neural strategies adopted by them lead to a reduced muscle activity. This greater efficiency of the neuromuscular system, demanding lower muscle activity for the same mechanical output or the same muscle activity for a greater mechanical output, may be an adequate mechanism to delay fatigue. Considering that during strength training it is common the prescription of submaximal loads, the level of experience of the individual must be considered to an adequate neurophysiological response.

As previously reported, the maximum EMG activity in a muscle may represent increased neural drive, but the functional activity of muscles during submaximal tasks has shown to decrease after a strength training program (Mangine et al., 2015; Rabita, Pérot, & Lensel-Corbeil, 2000) as well as it is lower in RT individuals when compared to UT (Pearcey et al., 2014). Specifically, a downward shift of the EMG-moment slope with training has been shown in the knee extensor muscles demonstrating interindividual variability in the extent of this adaptation (Rabita et al., 2000). This relation between muscle activity and force production was also different in athletes with different athletic background (David, Mora, & Pérot, 2008). Furthermore, already RT individuals included in a strength training program seem to decrease the knee extensor agonist muscles EMG-load slopes during squats independently of the training intensity (70% vs 90%RM) (Mangine et al., 2015).

Amarantini and colleagues (2015) found a linear relationship between EMG and torque for RT individuals, while a curvilinear relationship was found for UT (Amarantini & Bru, 2015). However, Balshaw and colleagues (2019) found a linear relationship for all the individuals (Balshaw et al., 2019). This may be related with the way of collection of the data, with one study reporting 10 points relative to a ramp contraction (Amarantini & Bru, 2015) while the other collected contractions at 20%, 40%, 60% and 80%MVC (Balshaw et al., 2019). In the study of Balshaw and colleagues (2019), although the relation was equal independently of the training status, the RT individuals presented lower activation at the highest common torque of 196Nm, with the EMG-torque relationship presenting a downward shift (less activity needed for each relative force output) (Balshaw et al., 2019). These results are adjusted not only for UT individuals but also for a group that trained for 12 weeks, which is representative of the continued adaptations with long-term strength training (Balshaw et al.,

2019). Generally, strength training allows that trained individuals reduce muscle activity for the same relative intensities of force production.

Moreover, during traditional strength training sessions using submaximal loads, the use of advanced methods, namely the forced repetitions method allowed different levels of acute fatigue in RT and UT. The UT continued to increase muscle activity which could be interpreted as the fatigue emerging due to peripheral factors rather than neural origin. Conversely, RT decreased muscle activity in the last repetitions, which could represent neural fatigue, suggesting that UT are unable to activate the same amount of motor units not reaching fatigue at the neural level (Ahtiainen & Häkkinen, 2009). RT also demonstrated to have the ability to achieve their maximum neural output during squats until failure, while UT do not (Pick & Becque, 2000). Thus, the acute responses to strength training are also different regarding training status, and different training methods may be more adjusted to one population than the other (Counts et al., 2017; Krzysztofik, Wilk, Wojdała, & Gołaś, 2019).

The long-term adaptations in the antagonist muscles recruitment is a topic that present divergent results. Although most results point to a reduction of antagonist activity after strength training, we cannot discard the specific adaptations to particular tasks or training modalities. Thus, while traditional strength training practices, as isometric or dynamic submaximal tasks, usually lead to a reduction of the antagonist activity, in some cases it may be useful to maintain or even increase the activity of the antagonist muscle.

As previously described, the adaptations in the antagonist muscle are not yet fully understood. Some studies did not find differences in antagonist activity after strength training programs (Aagaard, 2002; Andersen et al., 2005; Remaud, Cornu, & Guével, 2010; Seynnes, De Boer, & Narici, 2007). Furthermore, studies where traditional strength training with controlled concentric and eccentric phases also presented increased antagonist activity in strength training tasks increasing joint stability (Arabatzi & Kellis, 2012; Sampson & Groeller, 2016). However, different training modes revealed specific adaptations in antagonist activation as an increase after stretch-shortening training and a decrease after rapid concentric training (Sampson & Groeller, 2016) or after Olympic weightlifting training (Arabatzi & Kellis, 2012). Besides these studies, the vast majority report decreased activity

of the antagonist muscles after concentric or eccentric strength training (Krentz & Farthing, 2010; Mason et al., 2020; Pensini, Martin, & Maffiuletti, 2002; Tillin, Pain, & Folland, 2011).

RT individuals present lower activity of the antagonist muscles (Amarantini & Bru, 2015; Grosprêtre et al., 2018; Pearcey et al., 2014; Wang et al., 2019), although there are results reporting differences in antagonist muscles only in submaximal contractions but not in maximal contractions (Balshaw et al., 2019). The training background of the evaluated individuals is determinant when interpreting the results. For example, one study evaluating gymnasts revealed a decreased co-activation of the antagonist muscles during elbow extension, shoulder flexion and elbow flexion, and increased co-activation in shoulder extension (Kochanowicz, Niespodziński, Mieszkowski, Kochanowicz, & Sawczyn, 2018). The specificity of training may imply those specific neural adaptations, as reported by Sbriccoli and colleagues (2010) that found increased antagonist activation in a specific karate task (Sbriccoli et al., 2010). For instance, when compared to endurance training, strength training revealed higher suppression of β corticomuscular oscillations accompanied with lower activation of the antagonist muscles (Dal Maso, Longcamp, & Amarantini, 2012) indicating stronger activation of the primary motor cortex (Dal Maso et al., 2012; Patino, Chakarov, Schulte-Mönting, Hepp-Reymond, & Kristeva, 2006; Salmelin, Hämäläinen, Kajola, & Hari, 1995) and different mechanisms of control of muscles with different function, namely in the relationship between agonist and antagonist muscles (Dal Maso, Longcamp, Cremoux, & Amarantini, 2017). Also, badminton players presented greater β-band intermuscular coherence on antagonist muscles with accompanied with lower activity of antagonist muscle, which may represent a more efficient way to ensure joint stability (Wang et al., 2019).

Regarding submaximal isometric tasks, Balshaw and colleagues (2019) reported differences in the slope of the antagonist muscle during submaximal contractions from 20% to 80% MVC, presenting evidence showing lower antagonist activation in response to strength training (Balshaw et al., 2019). Furthermore, the slope of the regression between antagonist EMG and torque as well as the slope between antagonist EMG and agonist EMG decreased after 12 weeks of strength training and remained to adapt with continued decrease in RT individuals (Balshaw et al., 2019). Also, the analysis of a wide spectrum of intensities

between 10% and 90%MVC revealed that with the decreased agonist activity, the activity of the antagonist muscle also decreased in RT individuals (Pearcey et al., 2014).

The adaptations in antagonist activity may be carefully inferred by the studies because in addition to all the EMG limitations (Farina et al., 2014), the presentation of the data in different studies relies on different calculations of the antagonist activation. Namely, there are studies reporting the normalized values (Amarantini & Bru, 2015; Kochanowicz et al., 2018), co-activation indexes (Arabatzi & Kellis, 2012; Mason et al., 2020), agonist-antagonist slopes (Amarantini & Bru, 2015; Balshaw et al., 2019), phase synchronization index between antagonist muscles (Wang et al., 2019), corticomuscular and intermuscular coherence (Dal Maso et al., 2017; Mohr, von Tscharner, Whittaker, Emery, & Nigg, 2019), which can make it difficult to interpret results.

The quantification of intermuscular coordination is not always easy because it usually relies on mathematical algorithms that present limitations on the interpretation of physiological mechanisms of motor control. The evidence presented in the studies included in this review are based in some main methodological approaches: differences in the degree of activation, timings of activation, muscle synergy extraction and intermuscular coherence analysis. RT individuals present specific patterns of muscle coordination in strength training tasks, revealing specific adaptations in the coupling between synergist muscles, but also in global coordination presenting spatiotemporal adaptations in the recruitment of muscle synergies and individual EMG profiles.

Intermuscular coherence has been used to study common synaptic inputs and synchronization between two muscles (Farina et al., 2014). The analysis of intermuscular interactions allows to distinguish bands of frequencies representing cortical, subcortical or spinal neural inputs (Grosse, Cassidy, & Brown, 2002), and β activity in the 15-35Hz band has been extensively studied since it reflects intermuscular coupling and the possible modulation of muscle synergies (Charissou et al., 2016; De Marchis, Severini, Castronovo, Schmid, & Conforto, 2015). Time-frequency analysis revealed that although RT and endurance trained individuals present lower β intermuscular interactions between synergist muscles (VM and RF) than UT, these interactions remain stable after fatigue which may also be related to corticospinal adaptations to training (Charissou et al., 2016). After fatiguing protocols in UT, synergist

knee extensor (Chang et al., 2012) and elbow flexor muscles (Semmler et al., 2013) showed to increase β-band coherence. However, a dynamic leg extension protocol until failure revealed a modification of the synergistic recruitment of the quadriceps muscles with decreased synchronism between muscles (Castronovo et al., 2018), as it was previously assessed for UT individuals (Charissou et al., 2016). In young people, strength training also appeared to increase the 40-60Hz band coherence at specific submaximal intensities (70%MVC) but not at maximal contractions, reflecting oscillations during voluntary contractions in steadiness tasks (Walker et al., 2019). Strength training appeared not to influence lower-frequency bands (<15Hz) (Walker et al., 2019).Coherence analysis has been linked to the extraction of muscle synergies (De Marchis et al., 2015), but muscle synergy analysis of itself can be used to characterize general muscle coordination during tasks involving several muscles (Frère & Hug, 2012; Santos et al., 2021; Turpin, Guével, Durand, & Hug, 2011). The simplification of motor control is related to shared muscle synergies across tasks. In other words, a variety of motor behaviors may be achieved through combination of small number of the same low-level discrete elements, explaining some of the variation of data (Bizzi & Cheung, 2013; d'Avella & Bizzi, 2005; Safavynia, Torres-Oviedo, & Ting, 2011). Some studies have shown these elements to be from neural origin (Desrochers, Harnie, Doelman, Hurteau, & Frigon, 2019; Hart & Giszter, 2010; Mussa-Ivaldi, Giszter, & Bizzi, 1994; Saltiel, Wyler-Duda, D'Avella, Tresch, & Bizzi, 2001), while others link the existence of muscle synergies to biomechanical contexts (Dominici et al., 2011; Kutch & Valero-Cuevas, 2012). Independently from its origin that is discussed elsewhere (Bizzi & Cheung, 2013; Bruton & O'Dwyer, 2018), several studies have applied mathematical algorithms to extract muscle synergies from EMG signals overtime and thus explore the patterns of muscle activation during a wide range of tasks. Namely, in sports field, muscle synergies have been extracted comparing athletes with UT individuals concerning postural tasks (Kim, Kim, Kim, & Yoon, 2018), rowing (Turpin et al., 2011), breaststroke swimming (Vaz et al., 2016) or badminton (Matsunaga & Kaneoka, 2018).

Regarding strength training two studies have compared RT with UT individuals (Kristiansen et al., 2015; Santos et al., 2021). Kristiansen and colleagues (2015) have investigated muscle coordination in powerlifters and UT, extracting muscle synergies and showing that powerlifters exhibited larger inter-subject variability in muscle vectors of concentric phase

of bench press when compared to UT individuals (Kristiansen et al., 2015), corroborating these results with a five-week training protocol of UT individuals (Kristiansen et al., 2016). Also, four weeks of wobble board training appeared to modify modular organization in the early landing phase of a single-leg drop-landing with separation of the synergy comprising plantar flexors and ankle evertors while the activation of secondary muscles was reduced (Silva et al., 2018). Furthermore, Santos and colleagues (2021) evaluated muscle synergies in a more complex loaded motor task, the power clean, and found that weightlifters present different intermuscular strategies to perform the task concerning temporal and spatial components of muscle synergy analysis (Santos et al., 2021). Although muscle synergies in the power clean have shown to be reliable across sets and days, UT individuals with strength training background presented more stable muscle vectors between days, probably reflecting a greater flexibility in adapting muscles synergies when performing new tasks (Santos et al., 2020).

Besides muscle synergy analysis, other studies evaluated the degree of activation in intermuscular coordination. Differences in degree of activation were assessed with surface EMG for hip adduction exercises (Serner et al., 2014). Also, the influence of the synergist muscles was different in similar exercises with different ipsilateral or contralateral carrying conditions (Stastny et al., 2015). Strength training also modified the activation of the stabilizer muscles during elbow flexion (Buckthorpe, Erskine, Fletcher, & Folland, 2015), and free-weight bench press training resulted in different activation of the stabilizers while constrained pathway bench press training did not (Cacchio et al., 2008). Tillin and colleagues (2010) also presented information regarding the synchronism of the agonist muscles during knee extension (vastus lateralis, vastus medialis and rectus femoris), demonstrating that RT individuals activated all of them in half the time of the UT, and suggesting that intermuscular coordination may be one factor that influence the RTD (Tillin et al., 2010).

This review present EMG-based results from 20 articles. The dependent variables analyzed in these studies are so vast that we cannot stablish main variables common to some of the studies. This problem in the literature comprehension is exacerbated by the EMG collection and processing procedures that are distinct across the vast majority of the studies, which can be related with contradictory study outputs (e.g. co-contraction calculations). Even so, the

studies included in this review allow us to draw some conclusions. Namely, it was generally shown that the EMG output in the agonist muscles in voluntary maximal tasks is greater in resistance chronically trained individuals. This is accompanied by greater V-waves and reduced SICI, which underpin alterations in cortical and/or subcortical structures (Škarabot, Brownstein, et al., 2021). Also, strength training promoted lower muscle activity during equalized submaximal intensities of force production. Together, this evidence suggests different acute responses to strength training bouts because although the training loads may be adjusted, the implied muscle activity to the same relative intensities regarding training status will be differently modified during training sessions. Training status and the applied training methods also appear to have huge influence in co-contraction of the antagonist muscles. Generally, strength-trained individuals show lower co-contraction indexes (independently how they are calculated), but contradictory results may be found, often in studies evaluating populations with specific training backgrounds. Additionally, the coordination between synergistic muscles has shown to adapt with strength training, modulating the patterns of muscle activity during strength training tasks. Furthermore, the global intermuscular coordination may be one important mechanism to increase strength not only in an initial training phase but also in later stages of training experience.

The topic around the long-term adaptations to strength training is still matter of debate in the sports science field. Scientific studies regarding strength training usually present interventions with durations limited to a few weeks or months. However, in sports practice the athletes develop their physical skills during decades, which does not allow us to perfectly establish the long-term adaptations to training. Scientific research comparing trained athletes with years of training with untrained or short-term trained individuals is the actual evidence that allow us to have a better comprehension of the physiological adaptations to long-term training. Although there is evidence regarding chronic neural adaptations to strength training, the model presented by Sale (1988) present some gaps, as it can be depicted from Pearcey and collegues work (Pearcey et al., 2021; Sale, 1988). Neural adaptations to strength training, namely in what concerns to intermuscular coordination are not confined to the initial training stage. Thus, it is important to clearly understand what neural adaptations are achieved with few weeks of strength training and what continue to evolve with long-term training. The study design adopted by Balshaw and colleagues (2019) may be one clever strategy to better

understand this (Balshaw et al., 2019). Future research around this topic should focus on the chronology of neural adaptations to strength training, which may be useful to understand the specific timings of adaptations and how long they can last until a training plateau, allowing to introduce variation and advanced methods while preventing stagnation.

Despite the use of cross-sectional studies in this review allow us to better understand the chronic adaptations to strength training, we should look with caution at the data because the years of strength training of the RT individuals were not monitored and surely were different between them. Thus, RT individuals did not complete a consistent and standardized training program, and some of the neural adaptations observed in the studies may emerge from their different training background. Additionally, it cannot be ruled out that the RT individuals were not equivalent to the UT in the neural strategies used in tasks requiring maximal or explosive force production before starting the strength training practice. Inherent physiological characteristics, as muscle anatomy, fiber composition of the muscles or greater capacity to recruit motor units, may have predisposed the RT individuals to the practice of strength training.

As a limitation of the analyzed studies, all of them evaluated only men, with exception of one study that did not specify the participants' sex (Viitasalo et al., 1998). Therefore, it is important to carefully look for these results when generalizing for women, because differences between men and women have previously been reported. For example, women present greater co-activation (Krishnan & Williams, 2009), greater neural drive when compared to strength matched men (Inglis & Gabriel, 2020) and present different patterns of coordination (Kipp et al., 2014).

It is also important to clarify that all the studies included in this review reported valid procedures for EMG recording and the EMG normalization procedures were also described. However, and although all studies report the precise methods of normalization they used, these procedures are not equal across the studies. This may limit our interpretation because different normalization procedures may lead to different results. In this review we included studies that reported EMG values normalized to the MVC (Amarantini & Bru, 2015; Balshaw et al., 2019; del Olmo et al., 2006; Hartman et al., 2011; Orssatto et al., 2020; Pearcey et al., 2014; Stastny et al., 2015; Tillin et al., 2010; Viitasalo et al., 1998; Ye et al., 2015), to the

M-max (Lahouti et al., 2019; Philpott et al., 2015; Škarabot, Balshaw, et al., 2021; Tallent et al., 2013; Tillin et al., 2010), to the maximal value in the evaluated dynamic task (Ahtiainen & Häkkinen, 2009; Kristiansen et al., 2015; Pick & Becque, 2000; Santos et al., 2021; Viitasalo et al., 1998), to the muscle-electrode distance (Balshaw et al., 2019; Škarabot, Balshaw, et al., 2021) or without normalization in specific cases of coherence analysis (Charissou et al., 2016) or HDsEMG utilization (Del Vecchio et al., 2018). Thus, we may interpret the data with caution, with particular emphasis to studies that report more than one way of EMG normalization, normally with the normalization of the agonist muscle being different to that used to normalize the antagonist or synergist muscles (Balshaw et al., 2019; Škarabot, Balshaw, et al., 2021; Tillin et al., 2010; Viitasalo et al., 1998).

Also, as referred before, the relationship between the activity of agonist and antagonist muscles is not easy to address mainly because of the inconsistency of the processing methods used in studies. Some studies present indexes of co-activation while others only present the values of the normalized EMG of the antagonist muscles. For example, a study that reports a decreased co-activation index after training may result from i) decreased activity of the antagonist muscle with unchanged or increased agonist muscle activity; ii) maintained activity of the antagonist muscle with increased agonist activity; iii) decreased activity of the antagonist and agonist muscles with greater decrease of the antagonist muscle, or iv) increased activity of the antagonist and agonist muscles with greater increase of the agonist muscle. Nevertheless, these indexes allow us to have a global perspective of the relationship between muscles with two functional roles and should be presented together with the results of each muscle separately. Additionally, we should consider that studies reporting information related to antagonist muscles, usually only focus on one muscle. For instance, antagonist muscles of knee extension are biceps femoris (long and short head), semitendinosus, semimembranosus, popliteus, plantaris, gastrocnemius (medialis and lateralis), gracilis and sartorius. Usually, only the long head of biceps femoris is assessed with EMG, which may represent a poor representation of overall antagonist activity.

PRACTICAL APPLICATIONS

This review elucidates about the neurophysiological long-term adaptations to strength training and how does that contribute to a greater mechanical output. By understanding the differences between experienced and unexperienced individuals, strength and conditioning coaches may adapt their approaches to achieve the optimal muscle stimuli to create the desired adaptations. On the one hand, when evaluating UT, since they are not able to reach the maximal full potential of motor unit recruitment, the maximal lifted load will be undervalued. On the other hand, the prescription of maximal tasks for UT may be inadequate because of lack of capacity to achieve the recruitment of all motor units. Thus, UT and RT individuals will activate the agonist muscles differently in maximal as well as submaximal tasks. Namely, in submaximal tasks the UT will present a greater muscle activation than RT. This means that to reach the same relative stimulation, UT and RT will need different training volume and intensity, particularly when the objective is to achieve fatigue of the higher threshold motor units. Therefore, advanced strength training methods as forced repetitions are not adequate to UT since they do not represent the same physiological response as in already RT.

As a final thought, it is also important that coaches should guide individuals in an initial stage of strength training but also already trained ones into the development of individually effective patterns of intermuscular coordination, since proper activation of agonist, antagonist and synergist muscles seems to be one way to increase strength. This should consider the specificity of the sport since specific sport movements may elicit different demands of muscle coordination. For instance, the intensity of the activation of the antagonist muscle during specific sport tasks may demand the prescription of training exercises that contribute in a greater extent to a reduction or an increase of co-activation depending on the needing of performing explosive or joint stability actions, respectively. Also, the synchronism between the synergists or specific sequences of global muscle coordination must be considered when prescribing strength training programs.

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Chapter 3

Changes in intermuscular coherence with fatigue: a systematic review

Santos, P.D.G., Correia, J.P., Vaz, J.R. & Pezarat-Correia, P. (2024). Changes in intermuscular coherence with fatigue: a systematic review [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

ABSTRACT

The acute neuromuscular adaptations following fatiguing protocols are extensively studied in sports sciences. However, the specific adaptations in intermuscular coordination are not fully understood, although some studies have investigated the impact of fatigue in intermuscular coherence (IMC). Thus, the purpose of this review is to better understand what are the adaptations in IMC at several frequency-bands in response to fatigue. Three databases were used for the article search (PubMed, Web of Science, and Scopus). Studies were included if they evaluated acute changes in neuromuscular performance due to fatigue in people aged 18–40 years old, while acquiring EMG data from at least two muscles and calculating IMC. Thirteen articles met the eligibility criteria. Generally, the fatiguing protocols elicited specific changes in IMC, concerning the frequency-band: delta-band (0-5 Hz) IMC was generally increased although it depends on the evaluated tasks; alpha- (5-15 Hz) and beta-band IMC increased in some studies while maintaining or even decreasing in other studies, which was attributed to different methodological approaches, namely, the evaluated task and fatiguing protocol, the collected muscles, the intensity of the contractions or the training status; gamma-band (>40 Hz) IMC was generally unchanged, depending especially from on the intensity of the contraction or the type of contraction (static or dynamic). Although caution should be taken, concerning the limitations of the use of IMC analysis, concerning the evaluated populations, collected muscles, evaluated tasks and processing methods, these results can provide valuable insights into the central control of muscles with different functional roles (agonists, antagonist or synergists) and what neural strategies in intermuscular coordination are adopted after fatiguing protocols.

Key words: electromyography, antagonist muscles, synergist muscles, intermuscular coordination, muscle fatigue

INTRODUCTION

The control of movement that enables the performance of coordinated actions implies the existence of functional relations between all the components of the system. However, the central nervous system (CNS) adopts multiple strategies to perform adjusted motor tasks, and this muscle redundancy associated to motor control refers to the degrees of freedom (DOF) problem, proposed by Bernstein (Bernstein, 1967). The musculoskeletal system has abundant solutions to perform an action regarding how the elements of the system interact with each other (Latash, Scholz, & Schöner, 2007). Practice and training lead to multiple CNS adaptations and therefore produce specific patterns of muscle activation to minimize the cost of CNS processing (Hirashima & Oya, 2016; Prilutsky & Zatsiorsky, 2002).

During skill acquisition, neural connections between the primary motor cortex and other areas (long-term potentiation of synapses), and between corticospinal cells and motoneurons, undergo changes (Carroll, Riek, & Carson, 2001; Carson, 2006). These adaptations will lead to an optimal control of agonist, antagonist, and synergist muscles that interact to produce a specific torque output at a given joint (Zajac, Neptune, & Kautz, 2002). The choice and adjustment of DOF by the CNS, the combination of joint angles to produce the required movement, or the selection of individual motor units and the consequent muscular output, are problems whose elicited solutions refer fewer constraints than elements, helping to reduce the DOFs that the motor system must control (Bernstein, 1967; Latash, Krishnamoorthy, Scholz, & Zatsiorsky, 2005). Thus, the concept of functional synergies, consisting of ensembles of elements forming coordinative structures that allow the performance of coordinated movements, was proposed (Latash et al., 2007).

There is still scarce information about how muscles are coordinated to develop strength, namely regarding complex tasks involving a great number of DOFs. Intermuscular coordination has been studied through the decomposition of surface EMG recordings into muscle synergies (Hug, 2011) across a variety of complex movements (Frère & Hug, 2012; Kristiansen, Samani, Madeleine, & Hansen, 2016; Santos et al., 2021). Each synergy integrates the combination of multiple muscles, and the combination of multiple synergies results in the production of a wide range of possible complex movements. Thus, specific tasks can be achieved by modulating neural commands that specify patterns of muscle

activation, resulting in the production of natural motor behaviors (Bizzi & Cheung, 2013; Safavynia, Torres-Oviedo, & Ting, 2011; Ting & McKay, 2007).

Although muscle synergy analysis may provide important general information about how the CNS controls the neuromusculoskeletal system redundancy, coherence analysis has been used to understand the interactions between cortical, subcortical, and spinal mechanisms during movement (Grosse, Cassidy, & Brown, 2002; Liu, Sheng, & Liu, 2019). This analysis has been used considering that motor unit synchronization is present both within and between muscles recruited during a task (De Luca & Erim, 2002; De Luca, Roy, & Erim, 1993; Farmer, 1998). It has been suggested that synergistic muscles are innervated by motoneurons sharing common corticospinal drives (Boonstra, 2013; Conway et al., 1995; Farmer, 1998; Salenius, Portin, Kajola, Salmelin, & Hari, 1997). Thus, the electromyographic (EMG)-EMG coherence or intermuscular coherence (IMC) aims to investigate neural mechanisms of motor control, evaluating the functional time-frequency coupling between EMG signals of two muscles.

The IMC approach has shown to be particularly sensitive to changes in neuromuscular control during fatiguing tasks, in contrast to the muscle synergy analysis. Fatigue is defined as a loss of force or power in response to contractile activity that is secondary to physiological disequilibrium at multiple levels and is characterized by changes from the cortex to motor units (Kent-Braun, Fitts, & Christie, 2012). At the motor unit level, in addition to an increase in motor unit recruitment (Adam & De Luca, 2003; Carpentier, Duchateau, & Hainaut, 2001; Stock, Beck, & Defreitas, 2012), fatigue may induce a decline in the discharge frequency of the motor neuron pool (Aoki, Uchida, & Inoue, 2005; Carpentier et al., 2001; Contessa, Adam, & De Luca, 2009; Cowling, Harwood, Copithorne, & Rice, 2016; Kuchinad, Ivanova, & Garland, 2004) which will lead to a decline in the median frequency of the EMG power spectrum (Cardozo, Gonçalves, & Dolan, 2011; Contessa et al., 2009; Correia, Oliveira, Vaz, Silva, & Pezarat-Correia, 2016). Additionally, intermuscular coordination changes with fatigue have been demonstrated (McLean & Goudy, 2004; Rudroff, Barry, Stone, Barry, & Enoka, 2007), without corresponding changes in muscle synergy components (Turpin, Guével, Durand, & Hug, 2011). However, Smale et al. (Smale, Shourijeh, & Benoit, 2016) combined a time-frequency analysis with muscle synergy extraction and detected changes in the spectral characteristics of most of the analyzed muscles. Thus, while muscle synergy

analysis relates only to temporal domain, IMC analysis may be a powerful tool to detect changes in the EMG power spectrum during dynamic and static contractions and to assess the synchrony between central mechanisms of motor control and movement production.

IMC is directly associated with corticomuscular coherence (CMC). These two approaches are complementary, and the combination of both allows to differentiate neural pathways to the motoneurons (Boonstra, 2013). The oscillations in different frequency bands observed in these approaches allow for a better understanding of the origin of central control of movement and force production: the delta band (0-5 Hz) is referred to as the 'common drive' and is related to postural tasks (De Luca & Erim, 1994; Obata, Abe, Masani, & Nakazawa, 2014); the alpha band (5-15 Hz) is associated with physiological tremor (McAuley & Marsden, 2000) and also reflects cortical and subcortical activity as well as peripheral integration (Erimaki & Christakos, 2008; Klass, Lévénez, Enoka, & Duchateau, 2008; McAuley & Marsden, 2000); finally, the beta (15-35 Hz) and gamma bands (40-60 Hz) are both linked to the corticospinal pathway. While the beta-band is associated with precise force maintenance tasks, the gamma band is associated with stronger and/or dynamic contractions (Gwin & Ferris, 2012; Mima, Steger, Schulman, Gerloff, & Hallett, 2000).

Fatigue-induced effects on IMC have been studied and provided further insights into how the CNS controls neuromusculoskeletal redundancy under extreme conditions, more precisely when one part of the system (i.e., one or more muscles) reaches failure. However, different tasks lead to different acute adaptations within the CNS, resulting in different IMC outputs with fatigue. Namely, different changes in the aforementioned frequency bands may reveal how the CNS adapts during fatiguing tasks. Additionally, the impact of fatigue in muscles with variable functional relevance will be different, namely referring to unilateral synergist and antagonist muscles, or even bilateral homologous muscles. Thus, this review aims to organize the known evidence about the acute IMC responses to fatigue and to elucidate how the CNS adapts and coordinate its DOFs under this condition. Furthermore, we intend to understand what factors may affect IMC calculations and how they may influence the physiological interpretations. To accomplish this purpose, we systematically analyzed all published literature that evaluated IMC before and after a fatigue protocol in healthy people.

METHODS

This systematic review was conducted according to the PRISMA statement (Preferred Report Items for Systematic Reviews and Meta-analysis), where we specified and registered all the methodological aspects (PROSPERO registration number: CRD42024505973).

Eligibility criteria and search strategy

For the present review there was no limit for the year of publication. The articles met the following criteria: (i) including samples of healthy adults <40 years old; (ii) evaluating acute changes in neuromuscular performance due to fatigue; (iii) acquiring EMG data of at least two muscles and calculating IMC between the tested muscles.

We conducted a search of peer-reviewed articles until July 2022 in three databases: PubMed, Web of Science and Scopus. All the databases were screened with the following keywords and respective combination: ("electromyography" OR "EMG" OR "muscle activity" OR "muscle activation" OR "EMG amplitude and duration" OR "electromyogram") AND ("coherence" OR "intermuscular coupling" OR "intermuscular interactions" OR "beta band" OR "alpha band" OR "gamma band" OR "EMG-EMG" OR "intermuscular synchronization") AND ("neuromuscular performance" OR "fatiguing contraction" OR "fatigue" OR "task failure" OR "exhaustion" OR "exhausting exercise").

Data extraction

The titles and abstracts of the studies resulting from the search were screened by two authors (P.S. & J.C.). Duplicate entries were removed and a first screening regarding the title and abstract of the articles was made. Finally, we extracted information about authors and year of publication, participants (sample size and age), task parameters (pre- and post-task fatigue evaluation, intensity of fatiguing task), EMG assessment (monitored muscles, IMC algorithm, analyzed frequency bands) and pre- to post-fatigue changes in each frequency band. Uncertainties were resolved by consensus.

The information extracted from each study was summarized by study characteristics (participants, task, coherence calculations), as well as by changes in delta, alpha, beta, and gamma bands after fatigue.

Quality assessment and data synthesis

To assess study quality, we used the quality assessment tool developed by the Effective Public Health Practice Project (EPHPP), and we evaluated five of the six proposed methodological domains: selection bias, study design, confounders, data collection methods, and withdrawals and dropouts (Thomas, Ciliska, Dobbins, & Micucci, 2004). We did not assess the sixth item of the original scale, the blinding of the participants, since it is not possible to blind participants regarding their maximum force production capacity or the maximum tolerance to resistive exercises. Based on the scores of each component, three levels were used to classify the global methodological quality of the studies: strong, moderate, and weak. Two authors independently rated the five domains.

RESULTS

The search in the three databases (PubMed, Web of Science, and Scopus) resulted in 266 publications. Detailed information is presented in Figure 3.1. Thirteen articles fulfilling all the inclusion criteria were ultimately included in this review.

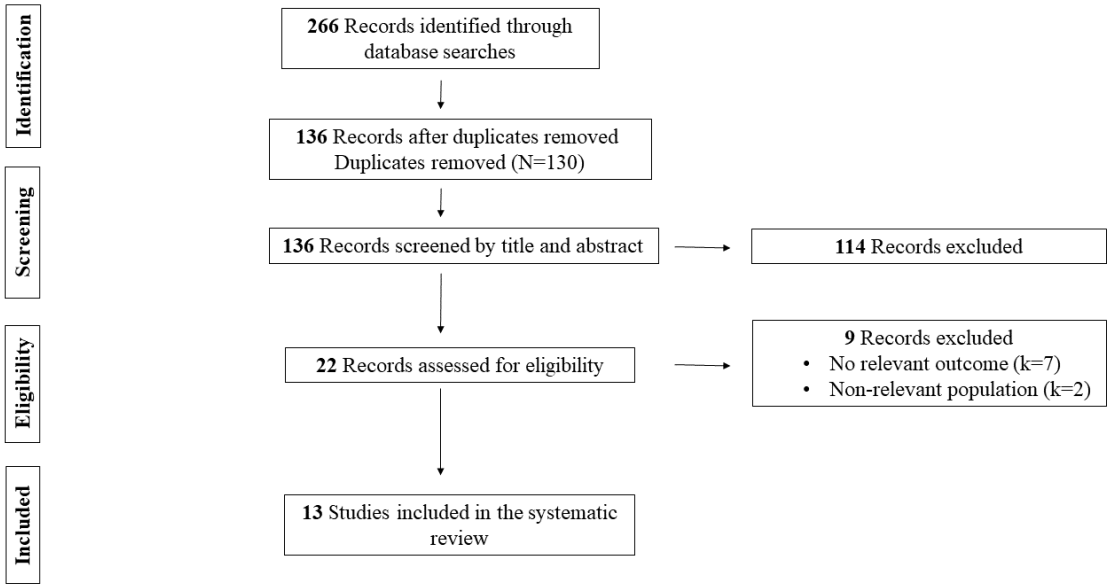

Figure 3.1 Flowchart of the search strategy and results.

Characteristics of the included studies

The characteristics and the summary of all the included studies are reported in Table 3.1. All studies evaluated IMC before and after a fatiguing protocol or during the early and late stages of the protocol. All studies reported the inclusion of male individuals, with seven studies only evaluating males (Boonstra et al., 2008; Charissou, Vigouroux, Berton, & Amarantini, 2016; Rossato et al., 2022; Semmler, Ebert, & Amarasena, 2013; Wang et al., 2011; Wang et al., 2015; Watanabe, Saito, Ishida, Tanabe, & Nojima, 2018), and the remaining six studies evaluating both males and females (Boonstra, Daffertshofer, van As, van der Vlugt, & Beek, 2007; Castronovo, De Marchis, Schmid, Conforto, & Severini, 2018; Chang et al., 2012; Danna-Dos Santos et al., 2010; Dos Santos et al., 2020; Kattla & Lowery, 2010). Each study evaluated between 10 and 15 healthy participants, with exception of two studies; one that

evaluated 26 participants divided into three groups (resistance-, endurance-, and recreationally-trained individuals) (Charissou et al., 2016), and other that evaluated 24 participants divided into two groups (younger and older individuals) (Dos Santos et al., 2020). A total of 180 participants were evaluated in the studies included in this review (age: 28.3 ± 5.0 years; height: 174.6 ± 5.2 cm; body mass: 71.2 ± 6.4 kg).

All studies assessed fatiguing tasks with collection of EMG signals from agonist and antagonist or synergist muscles. IMC was evaluated during isometric maximal tasks (Charissou et al., 2016); isometric submaximal tasks (Boonstra et al., 2007; Boonstra et al., 2008; Danna-Dos Santos et al., 2010; Kattla & Lowery, 2010; Rossato et al., 2022; Semmler et al., 2013; Wang et al., 2011; Wang et al., 2015); quiet standing (Watanabe et al., 2018); and dynamic tasks as walking (Dos Santos et al., 2020), dynamic knee extensions (Castronovo et al., 2018) or stepping exercise (Chang et al., 2012). The fatiguing protocols used across studies consisted in isometric submaximal tasks (Boonstra et al., 2007; Boonstra et al., 2008; Charissou et al., 2016; Danna-Dos Santos et al., 2010; Kattla & Lowery, 2010; Rossato et al., 2022; Wang et al., 2011; Wang et al., 2015), sit-to-stand tasks (Dos Santos et al., 2020), eccentric contractions (Semmler et al., 2013), dynamic knee extensions (Castronovo et al., 2018), heel raises (Watanabe et al., 2018) or stepping exercise (Chang et al., 2012). IMC was calculated using magnitude-squared coherence in all but one study that used wavelet coherence analysis (Charissou et al., 2016). Some studies opted by rectifying EMG signals before IMC analysis (Boonstra et al., 2007; Boonstra et al., 2008; Chang et al., 2012; Dos Santos et al., 2020; Semmler et al., 2013; Wang et al., 2015; Watanabe et al., 2018) while others used the non-rectified signals (Castronovo et al., 2018; Charissou et al., 2016; Danna-Dos Santos et al., 2010; Kattla & Lowery, 2010; L. Wang et al., 2011), which may be an important consideration when interpreting the results.

Seven studies evaluated lower limb muscles (Boonstra et al., 2008; Castronovo et al., 2018; Chang et al., 2012; Charissou et al., 2016; Dos Santos et al., 2020; Rossato et al., 2022; Watanabe et al., 2018), while six evaluated upper limb muscles (Boonstra et al., 2007; Danna-Dos Santos et al., 2010; Kattla & Lowery, 2010; Semmler et al., 2013; Wang et al., 2011; Wang et al., 2015). All studies evaluated pairs of agonist muscles (synergist muscles during the task) with exception of one study that evaluated only a pair of agonist-antagonist muscles

(Wang et al., 2015) and other study that evaluated only bilateral homologous muscles (Boonstra et al., 2007). One study evaluated a pair of agonist muscles and a pair of agonist-antagonist muscles (Dos Santos et al., 2020) and two others evaluated intralimb and interlimb coherence (Boonstra et al., 2008; Watanabe et al., 2018). Regarding the bands of interest provided by IMC analysis, 4 studies evaluated the common drive to the collected muscles (Danna-Dos Santos et al., 2010; Rossato et al., 2022; Semmler et al., 2013; Watanabe et al., 2018), 9 studies evaluated IMC in alpha-band (Boonstra et al., 2007; Boonstra et al., 2008; Chang et al., 2012; Danna-Dos Santos et al., 2010; Kattla & Lowery, 2010; Semmler et al., 2013; Wang et al., 2011; Wang et al., 2015; Watanabe et al., 2018), 9 studies evaluated IMC in beta-band (Chang et al., 2012; Charissou et al., 2016; Danna-Dos Santos et al., 2010; Dos Santos et al., 2020; Kattla & Lowery, 2010; Semmler et al., 2013; Wang et al., 2011; Wang et al., 2015; Watanabe et al., 2018) and 7 evaluated IMC in gamma-band (Castronovo et al., 2018; Chang et al., 2012; Danna-Dos Santos et al., 2010; Kattla & Lowery, 2010; Semmler et al., 2013; Wang et al., 2011; Wang et al., 2015).

The methodological quality of each study is presented in Table 3.2 with details of each domain of the scale. All studies were rated as “moderate”. The “weak” classification concerning the selection bias of all studies is justified by the non-stated percentage of the population the sample represents, and it is plausible that even if it was defined, this percentage would be low, as experimental studies evaluating neuromuscular variables with time-consuming methodologies usually present a small sample size. All studies were classified as “moderate” in what concerns to study design and “strong” concerning the data collection method. Regarding the confounders, six studies that evaluated males and females without differentiation were classified as “moderate”.

Table 3.1 Summary of the studies evaluating pre- and post-fatigue intermuscular coherence (IMC) across the delta, alpha, beta, and gamma bands.

Reference	Participants	Evaluated tasks for coherence calculation	Fatigue protocol	Coherence analysis procedures	Muscles	Effects of fatigue in delta band (0-5Hz)	Effects of fatigue in alpha band (5-15Hz)	Effects of fatigue in beta band (15-35Hz)	Effects of fatigue in gamma band (35-60Hz)
Dos Santos et al. (2020)	healthy younger (n = 12, 20–25 y) and older (n = 12, 66–77 y) participants	Walking at 1.2m/s	Repeated sit-to-stand until failure or until 30min	Magnitude squared coherence	VL, RF, BF, ST, GL, SOL, TA, PL	-	-	↑ GL-SL in swing phase for older (+23%); ↓ GL-SL in swing phase for younger (-23%); ↓ RF-BF in late swing (-20%); ↑ TA-PL in early stance phases (+16%)	-
Semmler et al. (2013)	10 healthy males (24 ± 6 years)	First and last 30 s of EF at 30%MVC until failure	EF at 30%MVC until failure; Sets of 10 eccentric EF contractions with 40%MVC until MVC drop >40%	Magnitude squared coherence	BB, BR, Bra (intramuscular), TB	↑ BB-Bra, BB-BR, BR-Bra in the last 30s	↑ BB-Bra, BB-BR, BR-Bra in the last 30s	No changes	No changes
Boonstra et al. (2007)	11 healthy males and females (23, 22-27 y)	EF and EE at 20 and 40%MVC over time	3 trials of 90 s of EF and EE at 20 and 40%MVC	Magnitude squared coherence	BBlh, BBsh, BR, Bra, TLlh, TLlath, TLmh	-	↑ BB left – BB right and TB left – TB right with stronger synchronization at 40%MVC	-	-
Castronovo et al. (2018)	11 healthy individuals (27 ± 5 y, 3 females)	First and last set of 10 repetitions of leg extension at 20% vs 70%RM	Sets of 10 repetitions of leg extension at 20% vs. 70%RM until failure	Magnitude squared coherence	RF, VM, VL	-	-	-	↓ 30-100Hz pooled and pairwise coherence in the 70%RM task

Table 3.1 *Cont.*

Kattla & Lowery (2010)	15 healthy, right-hand dominant participants (10 males and 5 females, 25 y, 25–34 y)	Index finger flexion at 10%MVC; First and second half of the fatigue protocol	Index finger flexion at 30%MVC until failure	Magnitude squared coherence	FDI, FDS	-	↑ during protocol at 30%MVC; No changes at post-fatigue at 10%MVC	No changes during protocol at 30%MVC; ↑ at post-fatigue at 10%MVC	No changes during protocol at 30%MVC; ↑ at post-fatigue at 10%MVC
Boonstra et al. (2008)	12 healthy male students, (22y, 20-25y)	Consecutive windows of 15 s during the trials of the fatiguing protocol	Experiment 1: 3 trials of 90 s knee extension contractions at 90º, 120º and 150º; Experiment 2: 3 trials of 60s knee extension contractions at 10%, 35% and 60%MVC	Magnitude squared coherence	VM, RF, TA, BF, GM	-	↑ intra- and interlimb at 6-11Hz; No changes in 13-18Hz in time	-	-
Watanabe et al. (2018)	13 healthy males (22.2 ± 0.73 y)	Quiet standing on a platform	Heel raises until exhaustion	Magnitude squared coherence	MG, SOL (bilateral)	↓ homologous muscles coherence; ↓ MG-SOL coherence	↓ homologous muscles coherence (marginal effects); No changes in MG-SOL coherence	No changes in MG-SOL coherence	-
Wang et al. (2011)	10 healthy males (27.3 ± 2.6 y)	First and second half of the fatigue protocol	EF at 50%MVC until failure	Magnitude squared coherence	BB, BR	-	No changes	↑ BB-BR coherence	No changes
Wang et al. (2015)	15 healthy males (23.2 ± 2.51 y)	First and second half of the fatigue protocol	EF at 20%MVC until failure	Magnitude squared coherence	BB, TB	-	↑ BB-TB coherence	↑ BB-TB coherence	No changes

Table 3.1 *Cont.*

Charissou et al. (2016)	26 healthy males: 10 strength-trained (23.6 ± 2.9 y); 7 endurance-trained (37.1 ± 13.6 y); 9 recreationally active (25.4 ± 5.3 y)	KE MVC	10 isometric KE at 40%MVC until exhaustion with 1 min of rest between them	Wavelet coherence analysis	VM, RF	-	-	↓ coherence only for the recreationally active and not for the strength- and endurance-trained	-
Danna-Dos Santos et al. (2010)	8 healthy adults (27 ± 6 y)	First and last quarter of the fatigue protocol	Grip at 40%MVC until exhaustion	Magnitude squared coherence	12 hand muscles (intramuscular)	↑ coherence for all muscle pairs combined	↑ coherence for all muscle pairs combined	↑ coherence for all muscle pairs combined	No changes
Chang et al. (2012)	11 healthy adults (23.6 ± 3.2 y)	First and last four step cycles of the fatigue protocol	Stepping exercise until exhaustion	Magnitude squared coherence	VL, VM, RF	-	No changes	↑ RF-VM coherence in the ascent phase of the step; ↑ RF-VL coherence in the descent phase of the step	No changes
Rossato et al. (2022)	14 healthy men for triceps surae protocol (28.8 ± 7 y); 15 healthy adults for quadriceps protocol (27.7 ± 6.3 y)	Trapezoid contractions at 30%MVC before and after the fatiguing protocol; beginning and ending of the fatiguing protocol	KE and Plantarflexion at 30%MVC until exhaustion	Magnitude squared coherence	RF, VL, VM, GM, GL, SOL (High-density EMG)	↑ VL-VM and GL-GM coherence	-	-	-

MVC – maximum voluntary contraction; EE – elbow extension; EF – elbow flexion; KE – knee extension; RM – repetition maximum; RF – rectus femoris; VL – vastus lateralis; VM – vastus medialis; GL – gastrocnemius lateralis; GM – gastrocnemius medialis; SOL – soleus; BB – biceps brachii (sh – short head; lh – long head); TB – triceps brachii (lath – lateral head; lh – long head; mh – medial head); BR – brachioradialis; BF – biceps femoris; TA – tibialis anterior; FDI – first dorsal interosseus; FDS – flexor digitorum superficialis; Bra – brachialis; PL – peroneus longus; ST – semitendinosus; EMG – electromyography; RMS – root mean square; Age is presented as mean ± SD or mean, minimum-maximum, depending on the presentation of the respective study.

Table 3.2 Quality assessment of all included studies.

Reference	Selection Bias	Study Design	Confounders	Data Collection Method	Withdrawals	Global
Dos Santos et al. (2020)	1	2	2	3	2	Moderate
Semmler et al. (2013)	1	2	3	3	3	Moderate
Boonstra et al. (2007)	1	2	3	3	2	Moderate
Castronovo et al. (2018)	1	2	3	3	2	Moderate
Kattla & Lowery (2010)	1	2	3	3	2	Moderate
Boonstra et al. (2008)	1	2	3	3	3	Moderate
Watanabe et al. (2018)	1	2	3	3	3	Moderate
Wang et al. (2011)	1	2	3	3	3	Moderate
Wang et al. (2015)	1	2	3	3	3	Moderate
Charissou et al. (2016)	1	2	3	3	3	Moderate
Danna-Dos Santos et al. (2010)	1	2	3	3	2	Moderate
Chang et al. (2012)	1	2	3	3	2	Moderate
Rossato et al. (2022)	1	2	3	3	3	Moderate

IMC adaptations to fatigue

In the delta band (0-5 Hz), usually associated with the common drive to muscles, three studies found increased IMC between synergist muscles after fatigue (Danna-Dos Santos et al., 2010; Rossato et al., 2022; Semmler et al., 2013), while one study reported decreased IMC (Watanabe et al., 2018). Namely, increasing IMC during isometric submaximal contractions from 30 to 40% of MVC has been reported in elbow flexors (Semmler et al., 2013), knee extensors and plantarflexors (Rossato et al., 2022), and the combination of hand muscles during a grip task (Danna-Dos Santos et al., 2010). On the other hand, the study reporting reduced IMC between unilateral and bilateral synergist muscles in this band, used a quiet standing position to evaluate the acute effects of a dynamic heel raise fatiguing protocol (Watanabe et al., 2018).

In the alpha band (5-15 Hz), most studies reported increased IMC. Greater IMC between synergistic muscles was reported, namely, between elbow flexors (Semmler et al., 2013), bilateral homologous elbow flexors and extensors (Boonstra et al., 2007), index finger flexors (Kattla & Lowery, 2010), knee extensors (Boonstra et al., 2008), and the combination of hand muscles during a grip task (Danna-Dos Santos et al., 2010). All these studies evaluated IMC during isometric submaximal contractions from 20 to 60% of MVC. Moreover, when analyzing IMC between antagonist muscles, one study reported increased IMC after fatigue (Wang et al., 2015). Three studies evaluating IMC between

synergists did not find significant differences after the respective fatiguing protocols during isometric submaximal contractions at 50% MVC (Wang et al., 2011), dynamic stepping exercise (Chang et al., 2012), and quiet standing only with unilateral plantarflexor muscles (Watanabe et al., 2018). However, the last study found that after the heel raise fatiguing protocol, IMC during quiet standing decreased between homologous bilateral plantarflexors (Watanabe et al., 2018).

In the beta band (15-35 Hz), some studies showed that IMC between synergist muscles increases after fatigue of the elbow flexors at 50% MVC (Wang et al., 2011), for the combination of hand muscles during a grip task (Danna-Dos Santos et al., 2010), and for different combinations of synergist muscles during a stepping task, more precisely with rectus femoris – vastus medialis IMC increasing during the ascendant phase of the step and rectus femoris – vastus lateralis IMC increasing during the descendant phase of the step (Chang et al., 2012). Other studies did not present any change regarding this band of interest, either for elbow flexors after eccentric exercise (Semmler et al., 2013), for unilateral plantarflexors during quiet standing after a dynamic heel raise protocol (Watanabe et al., 2018), or for the second half of an exhausting isometric submaximal index finger flexion at 30% MVC, although in this study IMC increased in a lower force level of 10% MVC measured after the fatiguing task (Kattla & Lowery, 2010). Still regarding synergistic muscles, one study found decreased IMC during knee extension MVC after the exhausting protocol only for recreationally active individuals and not in strength- or endurance-trained athletes (Charissou et al., 2016). Another study reported apparently contradictory results concerning the studied groups; namely, after an exhausting sit-to-stand task, older individuals presented increased IMC of the plantarflexors during the swing phase of walking, while younger individuals presented reduced IMC of the same muscles during the same phase of the task (Dos Santos et al., 2020). Regarding antagonist muscles, the same study reported that during walking, IMC between thigh muscles, namely rectus femoris – biceps femoris, decreased during the swing phase, while IMC between shank muscles, namely tibialis anterior – peroneus longus, increased during the early stance phase (Dos Santos et al., 2020). One other study reported increased biceps brachii – triceps brachii IMC at the end of isometric submaximal elbow flexion at 20% MVC (Wang et al., 2015).

In the gamma band (35-60 Hz), most studies reported no changes in IMC after fatigue either between synergistic muscles during isometric submaximal contractions (Danna-

Dos Santos et al., 2010; Semmler et al., 2013; Wang et al., 2011) or between antagonistic muscles (Wang et al., 2015). As seen for the beta-band IMC, gamma-band IMC between synergistic muscles remained unchanged during the second half of a fatiguing isometric submaximal index finger flexion at 30% MVC, although it increased at 10% MVC measured after the fatiguing task (Kattla & Lowery, 2010). Regarding dynamic tasks, no changes were also observed when IMC was calculated during stepping exercise (Chang et al., 2012), while decreased IMC was observed during dynamic knee extensions only at 70%RM (Castronovo et al., 2018).

DISCUSSION

The purpose of this review was to summarize the acute responses to exhausting force production tasks in IMC by analyzing studies that evaluated EMG of healthy people before and after a fatiguing protocol. Thirteen studies were included. In this review, we reported results concerning all the usually studied frequency bands. Delta band IMC increased with fatigue in most studies, although differences concerning the used tasks may be found. Alpha and beta bands also increased in some studies for synergist and antagonist muscles while not changing or even decreasing in other reports. Gamma band IMC was generally unchanged, although decreased IMC may be found when performing dynamic strong contractions.

Delta band (0-5Hz)

Most of the analyzed studies reported increased delta band IMC between synergistic muscles after fatigue. Our findings suggest that fatigue leads to increased synchronization of muscle activity between synergistic muscles in the delta frequency band. This band is associated with the common drive to muscles (De Luca & Erim, 1994; De Luca, LeFever, McCue, & Xenakis, 1982), and the synchronous modulation of motor unit firing rates (Lowery, Myers, & Erim, 2007). The increased IMC may be related to the number of shared projections from the CNS to the motoneurons and consequently greater common synaptic input (Castronovo, Negro, Conforto, & Farina, 2015; Rossato et al., 2022). This mechanism is particularly seen if the analyzed muscles share anatomical and functional characteristics as vastus lateralis - vastus medialis or gastrocnemius lateralis – gastrocnemius medialis (Rossato et al., 2022).

Furthermore, greater IMC in this band may be associated to greater co-activation to compensate for fatigue, and this has been shown in older individuals when compared to a younger population (Degani, Leonard, & Danna-Dos-Santos, 2017) as well as in patients with cortical or capsular strokes, which may be associated with a source outside the corticospinal system (Farmer, Bremner, Halliday, Rosenberg, & Stephens, 1993; Grosse et al., 2002). Thus, the contribution of sensory mechanisms should not be discarded, as the common drive between motor units has been shown during stance slow oscillations and may result from the activity of muscle spindles and Golgi tendon organs

(De Luca & Erim, 2002; De Luca, Gonzalez-Cueto, Bonato, & Adam, 2009; Degani et al., 2017).

Additionally, when analyzing IMC to investigate the correlation between motor unit discharges, either through high-density EMG or intramuscular EMG, greater synchronization after fatigue has also been found in tibialis anterior (Castronovo et al., 2015), first dorsal interosseus (McManus, Hu, Rymer, Suresh, & Lowery, 2016) or vastus lateralis (Contessa et al., 2009) following isometric submaximal contractions, and in biceps brachii after eccentric training (Dartnall, Nordstrom, & Semmler, 2008) as is also demonstrated when analyzing IMC (Semmler et al., 2013).

However, one study reported decreased IMC between unilateral and bilateral synergistic muscles in the delta band during a quiet standing position after a fatiguing protocol (Watanabe et al., 2018). This discrepancy may be due to differences in the fatiguing protocol and task demands. Contrary to the previous reported studies, this study did not evaluate an isometric submaximal task, and it has been the only study where dynamic concentric contractions were performed as part of the fatiguing protocol. The stance task involves the contribution of many antigravitational muscles, and the authors suggest that compensation with greater activation of other involved muscles may be used as response to fatigue (Davidson, Madigan, Nussbaum, & Wojcik, 2009; Watanabe et al., 2018).

Alpha band (5-15Hz)

Regarding alpha band IMC, most studies have reported increased IMC between synergistic muscles after fatigue. The analyzed studies suggest that fatigue enhances the synchronization of muscle activity between synergistic muscles in the alpha frequency band. Also, using intramuscular EMG, greater coherence in the alpha band has been shown after fatigue between motor units of the first dorsal interosseus (Christou, Rudroff, Enoka, Meyer, & Enoka, 2007; McManus et al., 2016), which suggests that synchronization between motor units is a physiological mechanism of motor control within and between muscles.

Alpha band IMC is usually associated not only with greater motor unit synchronization but also with physiological tremor (Boonstra et al., 2008; McAuley & Marsden, 2000). Although the origin of oscillations around this frequency band have been attributed to

oscillatory activity at 13-18 Hz present particularly in the paramedian lobule of the primate cerebellar cortex (Pellerin & Lamarre, 1997), as well as to oscillatory activity from olivocerebellar neurons (McAuley & Marsden, 2000; Welsh, Lang, Suglhara, & Llinás, 1995) or thalamo-cortical loops (Gross et al., 2002; Marsden, Ashby, Limousin-Dowsey, Rothwell, & Brown, 2000), physiological tremor around 10 Hz appears to be multifactorial, and it may be divided according to the type of muscle action (McAuley & Marsden, 2000). Thus, the generally increased coherence in this band may be caused by cortical or subcortical loops, but also by spinal reflex arcs from afferent stretch receptors (Erimaki & Christakos, 2008; Klass et al., 2008; McAuley & Marsden, 2000).

Two studies also found that alpha-band IMC increased after fatigue between homologous muscles of contralateral limbs (Boonstra et al., 2007; Boonstra et al., 2008). This means that the common input for motor units of contralateral limbs is greater after an exhausting task, since the afferent fibers may modulate the spinal interneurons but not the motoneurons of the contralateral homologous muscle as suggested by Boonstra and colleagues (Arya, Bajwa, & Edgley, 1991; Boonstra et al., 2008; Harrison & Zytnicki, 1984; McCrea, 2001). Furthermore, these authors (Boonstra et al., 2007) showed greater IMC of bilateral extensor than flexor muscles of the upper limb.

In unilateral contractions, an increased ipsilateral primary motor cortex activation and a decreased intracortical inhibition resulting from reduced interhemispheric contralateral inhibition (Cabibel, Hordacre, & Perrey, 2020), and it has been shown that at high force levels there is an increase of contralateral irradiation (Arányi & Rösler, 2002; Zijdewind & Kernell, 2001). This interhemispheric communication is an important mechanism in motor control of bilateral tasks (MacDonald, Laksanaphuk, Day, Byblow, & Jenkinson, 2021) and although the oscillations between contralateral limbs appear to be independent (Conway et al., 1995; McAuley & Marsden, 2000), it is suggested that interhemispheric connectivity between both motor cortices exists during submaximal tasks (Oda, 1997). It has also been shown that after an unilateral fatiguing task, there is increased contralateral physiological tremor (Morrison, Kavanagh, Obst, Irwin, & Haseler, 2005). Additionally, and although this was not the case in the analyzed studies, it is important to note the existence of a bilateral strength deficit in maximal force production, in which the transcallosal connections may inhibit activity of the contralateral motor cortex, resulting in a common drive between motor cortices that modulates muscle contraction of homologous muscles (Oda & Moritani, 1995; Škarabot, Cronin, Strojnik, & Avela, 2016).

On the other hand, three studies found unaltered IMC between ipsilateral synergistic muscles (Chang et al., 2012; Wang et al., 2011; Watanabe et al., 2018) and one found decreased interlimb coherence after fatigue (Watanabe et al., 2018). Chang et al. (2012) evaluated IMC during a dynamic stepping exercise. The different task characteristics when compared with the previous referred studies that evaluated IMC during isometric submaximal tasks may be a key factor for the absence of significant IMC changes and the associated postural tremor after fatigue. Watanabe et al. (2018) have also evaluated the participants after a dynamic fatiguing protocol during a postural task, and the IMC of ipsilateral muscles remained unchanged after fatigue, despite the decrease in interlimb IMC, which is contrary to the results presented in the previous discussed studies that evaluated effortful tasks (Boonstra et al., 2007; Boonstra et al., 2008). Postural tasks do not elicit strong voluntary contraction of the muscles, and the authors suggest that these results may be related with decreased neural input from the subcortical system to homologous plantar flexor muscles (Watanabe et al., 2018).

In addition to synergistic muscles, increased IMC has also been reported between antagonist muscles after fatigue. Wang et al. (2015) found greater IMC between the biceps brachii and triceps brachii at the end of an isometric submaximal elbow flexion task after fatigue. These findings suggest that fatigue affects the coordination between antagonist muscles, changing motor control during effortful tasks. The increased alpha band IMC between antagonistic muscles may be linked to postural tremor of antagonistic muscles as a result of fatigue in the activity of peripheral Ia afferents as well as subcortical and cortical mechanisms with a particular role played by olivocerebellar neurons (S. Hansen, Hansen, Christensen, Petersen, & Nielsen, 2002; McAuley & Marsden, 2000; Wang et al., 2015).

Beta band (15-35Hz)

This is the most studied IMC frequency band, and it is usually associated with the corticospinal pathway (Baker, Olivier, & Lemon, 1997; Farmer et al., 1993; Kattla & Lowery, 2010; Mima & Hallett, 1999), namely with the fastest corticospinal fibers (Ibáñez, Del Vecchio, Rothwell, Baker, & Farina, 2021). A positive linear relationship between the IMC in this band and motor unit synchronization has been reported (Farmer et al., 1993; Lowery et al., 2007). Furthermore, suppressed beta band activity has been

shown in patients with incomplete spinal cord lesion (N. L. Hansen et al., 2005) or with unilateral stroke (Nielsen et al., 2008). Additionally, beta-band has been linked to oscillations within the sensorimotor cortex and its communication with other cortical and subcortical structures as well as the integration of sensory information via Ia afferents and Renshaw cells (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013; Ushiyama et al., 2011).

In the analyzed studies, the findings regarding the effects of fatigue in IMC in this band are mixed. Some studies have reported increased IMC between synergistic muscles after fatigue, namely between hand muscles during a griping task (Danna-Dos Santos et al., 2010), between elbow flexors during isometric submaximal contractions (Wang et al., 2011) or between knee extensors during a stepping task concerning specific synergistic pairs of muscles in specific stepping phases (Chang et al., 2012). Considering the physiological foundation of the beta band, these results suggest that fatigue can modulate motor unit recruitment enhancing the synchronization between synergistic muscles in this band, possibly implying an increased common corticospinal drive. Other studies did not find increases in beta-band IMC between synergistic muscles. Unaltered IMC was found after an eccentric elbow flexor fatiguing protocol (Semmler et al., 2013). The authors suggest that the unchanged IMC may be due to the weaker corticospinal connections of proximal muscles (Brouwer & Ashby, 1990; Phillips & Porter, 1964; Semmler et al., 2013; Ushiyama, Takahashi, & Ushiba, 2010). For example, greater IMC in the index finger flexors measured after a fatiguing task was observed in a submaximal contraction at 10% MVC (Kattla & Lowery, 2010), while decreased CMC of the elbow flexors was found in the second half of a submaximal contraction at 30% MVC (Yang et al., 2009). However, in the study of Kattla et al. (2010) unchanged IMC was found at 30% MVC, while increased IMC between elbow flexors was shown after an isometric submaximal contraction at 50% MVC (Wang et al., 2011), which means that differences between studies may be due to the tested muscles as well as the relative intensity of the used protocols. Also, as observed for the alpha band in plantar flexors during a quiet standing task, IMC also remained unchanged after fatigue (Watanabe et al., 2018), which may have been result of a compensatory strategy involving a greater contribution of hip rather than ankle muscles (Davidson et al., 2009). It has been shown that during exhausting tasks, the main agonist activation may be reduced and compensated by an increased activation of

surrounding muscles, although those coordinative strategies may depend on interindividual variability (Contessa, Letizi, De Luca, & Kline, 2018).

Furthermore, two studies found decreased IMC after fatigue during isometric maximal knee extension force production (Charissou et al., 2016) and during the swing phase of walking only for the plantar flexors of younger people, while older people showed an increase in the IMC of the same muscles (Dos Santos et al., 2020). The first of these studies was the only one that evaluated isometric maximal contractions, and different responses in IMC may be attributed to different levels of contraction. However, in this study, only recreationally active individuals presented decreased IMC, while strength- and endurance-trained individuals presented unchanged IMC (Charissou et al., 2016). Interestingly, the trained athletes presented lower IMC without fatigue, maintaining the coordinative patterns after fatigue (Charissou et al., 2016). Additionally, ballet dancers and weightlifters have also shown to present lower CMC than untrained individuals specially in the lower limb muscles (Ushiyama et al., 2010). Differences between populations have also been demonstrated concerning age, with younger people presenting greater IMC between knee extensors in submaximal contractions, suggesting intact corticospinal tract function, although no differences were shown in maximal contractions (Walker et al., 2018). Additionally, in response to fatigue, older individuals presented increased IMC of the plantar flexors during the swing phase of walking after a sit-to-stand protocol, while younger individuals presented decreased IMC, which may be related to greater co-contraction of the older individuals and possible compensatory strategies adopted by younger participants (Dos Santos et al., 2020).

The relation between the analyzed muscles also influences IMC. For example, the IMC between intrinsic hand muscles during a grip task is greater than IMC between an intrinsic and an extrinsic hand muscle before and after fatigue (Danna-Dos Santos et al., 2010), suggesting that the CNS binds the neural drive of functionally identical muscles, as suggested previously for the 0-5 Hz band (Rossato et al., 2022). Additionally, the coupling between muscles elicited by the CNS depends on the muscle synergies recruited during a specific motor behavior, since they can be shared and flexibly adapt (Bizzi & Cheung, 2013; d'Avella & Bizzi, 2005). Chang et al. (2012) found specific increases in paired synergistic muscles depending on the phase of a dynamic stepping task (ascendant or descendant). This may imply that the recruitment of different muscle synergies along the movement cycle maintains its structure after fatigue (Turpin et al., 2011) while

modulating their components, namely with the increase of corticospinal drive to the muscles. These adjustments allow for an effective motor control during coordinated movements (Hug, 2011; Latash et al., 2007). Furthermore, during rhythmic movement, as in the stepping exercise used by Chang et al. (2012), central pattern generators, which are ensembles of oscillatory interneurons encoded in the spinal cord, may be modulated by integrating descending commands and sensory feedback to establish an appropriate locomotor rhythm (Desrochers, Harnie, Doelman, Hurteau, & Frigon, 2019; Grillner & Jessell, 2009). Additionally, it has been proposed that beta oscillations are supported by the recruitment of muscle synergies that are in a first instance represented in the primary motor cortex, connecting other nuclei to the muscle and integrating the information from somatosensory pathways in the primary motor cortex again (Aumann & Prut, 2015).

Previous studies demonstrated that the increased activity of agonist muscles, as demonstrated by greater EMG amplitude, is accompanied by increased activation of antagonist muscles (Balshaw, Massey, Maden-Wilkinson, Lanza, & Folland, 2019; Santos, Vaz, Correia, Neto, & Pezarat-Correia, 2023). The magnitude of this relation depends on population characteristics, as the ratio of antagonistic co-contraction is usually greater for untrained individuals than for trained ones (Amarantini & Bru, 2015; Balshaw et al., 2019; L. Wang et al., 2019) and for older rather than young individuals (Chen, Kwon, Fox, & Christou, 2014; Hortobágyi & Devita, 2006; Macaluso et al., 2002). Previous research on an animal model showed closely grouped antagonistic corticospinal pathways (Ethier, Brizzi, Giguère, & Capaday, 2007), although this control appears to be modulated at supraspinal and spinal levels, with the supraspinal pathways being controlled separately (Duchateau & Baudry, 2014; Lévénez, Garland, Klass, & Duchateau, 2008). Nevertheless, increased co-activation between agonist and antagonist muscles has been found after fatigue (Psek & Cafarelli, 1993), with significant agonist-antagonist oscillatory coupling (Dal Maso, Longcamp, Cremoux, & Amarantini, 2017; Wang et al., 2015).

The acute responses to exhausting exercise between antagonistic muscles in the beta band show that IMC tends to increase, revealing greater co-contraction between agonist and antagonist muscles, possibly relying on a greater corticospinal drive from the motor cortex to the motoneurons, which may indicate a closely related organization of corticospinal connections between antagonistic muscles (Wang et al., 2015). However, increased IMC after fatigue in this band has been only noted in stroke patients and not in

healthy participants in another study (Wang et al., 2020), which may be a result of the higher contraction intensity of the testing protocol as well as of the low efficiency of motor control attributed to motor impairment (Wang et al., 2020). Nevertheless, the increased beta-band IMC between antagonist muscles suggests that corticospinal pathways are modulated after fatigue (Wang et al., 2015).

Gamma band (>35Hz)

In addition to the beta band, gamma band oscillations are also associated with the corticospinal drive (Conway et al., 1995; Mima & Hallett, 1999). Moreover, coherence in this frequency band and around 40 Hz (corresponding to the Piper rhythm), has been associated with attentional focus and efferent drive during strong isometric voluntary contractions or dynamic effort (Brown, 2000; Brown, Salenius, Rothwell, & Hari, 1998; Gwin & Ferris, 2012; Mima, Simpkins, Oluwatimilehin, & Hallett, 1999). In the analyzed studies, gamma band IMC remained unchanged after fatigue in almost every study. These results are relative to IMC between synergist muscles (Danna-Dos Santos et al., 2010; Semmler et al., 2013; Wang et al., 2011) as well as antagonist muscles (Wang et al., 2015) during isometric submaximal contractions. The absence of differences in gamma-band IMC across studies may be due to the isometric submaximal force tasks used (Brown et al., 1998; Mima et al., 1999) since it has been demonstrated that the shift of corticospinal oscillations toward the gamma band mainly occurs during dynamic contractions, allowing the rapid integration of sensorial information (Gwin & Ferris, 2012; Omlor, Patino, Hepp-Reymond, & Kristeva, 2007).

However, Kattla et al. (2010) presented greater IMC after fatigue at 10% MVC but not at 30% MVC, as also reported for the beta band. Although the gamma-band IMC increment at 10% MVC may be justified by the increased neuromuscular drive necessary to perform a contraction at the same intensity after fatigue, which may represent a higher percentage of the post-fatigue MVC, the same result would be expected at 30% MVC. On the one hand, at 30% MVC, gamma-band IMC remained the same while an increased alpha-band IMC was reported, while on the other hand, at 10% MVC, alpha band IMC remained the same while beta and gamma band IMC increased. According to the physiological meaning of each band, these results may be interpreted as greater intensities eliciting peripheral fatigue, which in turn causes physiological tremor, which is related to alpha

band IMC (Bigland-Ritchie, Furbush, & Woods, 1986; Burnley, Vanhatalo, & Jones, 2012), while lower intensities should lead to a greater extent of central fatigue associated with the corticospinal drive (Eichelberger & Bilodeau, 2007; Smith, Martin, Gandevia, & Taylor, 2007).

Considering the previous paragraphs, we may interpret the results of the study of Castronovo et al. (2018) that evaluated dynamic knee extension at 20% and 70% RM finding decreased gamma-band IMC only at the higher intensity. These results suggest that gamma band IMC is only affected by dynamic contractions at greater intensities, which elicit decreased corticospinal oscillations after fatigue, while weaker dynamic contractions do not change IMC within this band (Castronovo et al., 2018; Chang et al., 2012). Additionally, adaptations within this band after 14 weeks of strength training have been also demonstrated only during strong isometric contractions at 70% MVC (Walker et al., 2018).

Limitations

Although the results reported in this review have a physiological interpretation concerning each of the analyzed frequency bands, caution should be taken when comparing studies.

First, it is important to understand what populations are being analyzed even when considering healthy people, as age and training status may influence motor control as it was seen during this review (Dal Maso et al., 2017; Dos Santos et al., 2020; Walker et al., 2018). Additionally, most studies evaluated male and female individuals, which can be a confounding variable, since differences in IMC have been reported (Kipp et al., 2014), namely in what concerns to IMC during dynamic single-leg squats (Mohr, von Tscharner, Whittaker, Emery, & Nigg, 2019).

Second, the muscle selection for analysis may be determinant to the results. As we have seen throughout this review, the muscle pairing for the IMC calculation is determinant, as muscles with different functional roles will present different levels of coupling during the analyzed tasks. Even muscles whose main function is similar, for example vastus lateralis and rectus femoris, may be centrally coupled differently than vastus medialis and vastus intermedius, despite their common knee extension action. The anatomical

configuration of a muscle, as seen in the mono- or bi-articular anatomy of the previous example, may determine the common neural drive during a given task. Additionally, most studies only consider the spectral relationship between two muscles, which may not be representative of what is happening in the studied joint, since various muscles act to produce a given torque and compensatory strategies may rely on specific muscles that may not be studied, namely when studying fatigue adaptations.

Third, the processing methods influence the results. The rectification of the signals prior to coherence calculation is an ongoing debate, and as we can observe by the methods of the studies included in this review, there is a great disparity concerning the use of rectified or non-rectified signals. Rectification prior to coherence analysis, as well as other nonlinear transformations, amplifies the signal power, allowing to identify interactions in frequency bands that were not present in the original signal (Farina, Merletti, & Enoka, 2014). Furthermore, rectified EMG signals include noise derived from amplitude cancellation. This phenomenon increases with the increased neural drive to the muscle, which means that muscle contractions at higher intensities will lead to increased amplitude cancellation. Thus, coherence may be amplified only if this noise is sufficiently small, which does not happen during strong contractions, suggesting that rectification may be useful mainly for low-force contractions.

Fourth, almost every study included in this review adopted the magnitude squared coherence for the IMC calculation. However, Charissou and colleagues (2016) calculated the interactions in the time-frequency domain, quantifying the magnitude using wavelet coherence analysis. Although both methods are suitable, wavelet coherence provides insights about the frequency bands over time, while magnitude squared coherence presents an overall value of correlation between the signals. Additionally, the low and high limits of the frequency bands of interest present some variability across studies. For example, there are studies that consider alpha band between 8 and 12 Hz and others that consider from 5 to 15 Hz, which may lead to slightly different results. These differences in the calculation methods and in the frequency band definition should be considered when comparing studies.

This review organized the current knowledge about changes in coordination, measured by IMC, in response to exhausting protocols. This is an important step to better understand how the CNS controls muscle activity and flexibly adapt to exhaustion, and what relationships modify between muscles with different functional roles during

fatiguing force production (agonist, antagonist, and synergist muscles, in unilateral and bilateral contractions). Although there is some research around this topic which resulted in the inclusion of 13 studies in this review, we cannot extrapolate the present results to all situations. Namely, future research should focus on stablishing the effects of different protocols in IMC at all bands, clearly identifying different patterns of acute adaptations 1) following dynamic concentric vs dynamic eccentric vs isometric training, 2) following high-force vs low-force protocols, for example below and above the critical torque, 3) following high-load vs low-load dynamic protocols, 4) between muscles with different functional roles, since the muscle pairing in the reported studies usually concerns to agonist-agonist and few studies observing agonist-antagonist or pairs of synergist muscles acting at different joints, 5) in different evaluation tasks as dynamic complex movements that may allow to understand specific and more practical applications for training prescription or rehabilitation.

CONCLUSION

This review presented IMC changes after fatiguing protocols from 13 studies. IMC analysis may be a sensitive tool to understand how muscle coordination is modified in the presence of fatigue. This approach allows us to better understand how the CNS modulates motor control, since differences in delta, alpha, beta, and gamma bands may rely on different origins of acute adaptations. Analyses in the frequency domain of EMG signals may be especially affected by the drawbacks of surface EMG, as the location of the electrode, mechanical noise, crosstalk, or signal cancellation. Additionally, caution should be taken concerning the populations evaluated in the studies, since differences considering age, sex, training status or clinical condition have shown to lead to different coordination patterns, as well as the IMC calculation method and the use of rectified or non-rectified signals. However, and considering these possible limitations, it is possible to state that changes in IMC relate to physiological responses to fatigue. In this review, we organized the available information about fatigue adaptations in IMC across the aforementioned frequency bands.

Delta-band IMC generally increased after fatigue, revealing a general greater common drive, although different compensation strategies may be found namely regarding postural tasks. Alpha- and beta-band IMC also increased in some studies between unilateral synergist and antagonist muscles as well as bilateral homologous muscles. However, other studies revealed an absence of changes or even decreased IMC, which may be due to the different analyzed tasks and fatigue protocols. Moreover, the collected muscles have great impact in the calculated IMC, since differences between proximal and distal, flexor and extensor, upper and lower limb, or mono- and bi-articular muscles have been demonstrated. The intensity of contraction is also determinant for IMC. The only study evaluating IMC in beta band during maximal contractions after fatigue showed decreased IMC only for previously untrained individuals, suggesting that previously trained participants adopted specialized motor control neural strategies. Additionally, gamma-band IMC was found to be unchanged after fatigue in almost every study, with exception of one study that revealed that IMC in this band is sensitive to strong and dynamic contractions. All these results together reveal that changes in IMC can provide valuable insights into the effects of muscle fatigue on intermuscular coordination.

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Chapter 4

Fatigue-related changes in muscle activation and coordination after an acute squat protocol in resistance trained and untrained individuals

Santos, P.D.G., Vaz, J.R., Gomes, M., Barão, G., Infante, J. & Pezarat-Correia, P. (2024). Fatigue-related changes in muscle activation and coordination after an acute squat protocol in resistance trained and untrained individuals [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

ABSTRACT

Acute adaptations to fatiguing conditions may be altered concerning training background. Muscle activation and coordination are affected by fatigue, although differences between subjects with different training status remains unclear. This study investigated differences between strength-trained (ST) and untrained individuals (UT) in leg-press isometric maximum voluntary contraction before and after a back-squat fatiguing protocol. Peak force (PF), rate of force development (RFD), electromyographic (EMG) amplitude of 7 lower-limb muscles, rate of EMG rise (RER) of agonist muscles and intermuscular coherence between synergist or antagonist pairs of muscles were evaluated. ST presented greater PF, maximal RFD and RFD at 150-200ms. All force-related variables decreased with fatigue for both groups, and PF decreased to a greater extent for ST. EMG amplitude of vastus medialis and rectus femoris increased in both groups, and RER of rectus femoris increased for ST while decreasing for UT. Additionally, coherence analysis revealed greater beta-band coherence between rectus femoris and vastus medialis for UT, while fatigue affected coherence across bands of interest differently concerning the functional relation of the paired muscles. Different training status imply different acute responses to fatigue relying on changes in activation of agonist muscles as well as coordination between pairs of synergist and/or antagonist muscles.

Keywords: resistance training, electromyography, fatigue, neuromuscular performance, physical fitness expertise

INTRODUCTION

Strength-trained individuals (ST) present greater maximal strength than untrained individuals (UT), and long-term strength training has revealed to induce chronic adaptations in the neuromechanics of force production (Folland & Williams, 2007; Sale, 1988; Škarabot, Brownstein, Casolo, Del Vecchio, & Ansdell, 2021). Several studies compared ST and UT individuals and it is consensual that ST reach higher values of force in maximal voluntary contractions (MVC) (Ahtiainen & Häkkinen, 2009; Balshaw, Massey, Maden-Wilkinson, Lanza, & Folland, 2019; Del Vecchio et al., 2018; Lahouti, Lockyer, Wiseman, Power, & Button, 2019; Tillin, Jimenez-Reyes, Pain, & Folland, 2010) or greater dynamic strength values (Kristiansen, Madeleine, Hansen, & Samani, 2015; Lysenko, Popov, Vepkhvadze, Sharova, & Vinogradova, 2020; Pick & Becque, 2000; Santos et al., 2021). Additionally, ST individuals has shown to present greater values of rate of torque development (RTD) which is the rate at which the torque-time curve ascends in explosive contractions, and namely in what concerns to the initial phase of torque production from 0 to 50ms, differences are reported regarding training background with the ST presenting greater values than UT (Del Vecchio et al., 2018; Orssatto, Wiest, Moura, Collins, & Diefenthaeler, 2020; Tillin et al., 2010). This initial phase in rapid force production has been associated to neural adaptations to strength training since it is related to greater firing frequency of motor units and faster recruitment of high-threshold fibers (Del Vecchio et al., 2019; Del Vecchio et al., 2018; Maffiuletti et al., 2016; Pearcey, Alizedah, Power, & Button, 2021), greater rate of agonist muscle activation (Aagaard, Simonsen, Andersen, Magnusson, & Dyhre-Poulsen, 2002; Cossich & Maffiuletti, 2020; Orssatto et al., 2020; Tillin et al., 2010), recurrent inhibition and V-wave (Johnson, Kipp, Norcross, & Hoffman, 2015). Other adaptations in the central nervous system (CNS) are induced by strength training, namely in what concerns to muscle coordination as decreased antagonist co-contraction (Arabatzi & Kellis, 2012; Balshaw et al., 2019; Griffin & Cafarelli, 2005; Häkkinen et al., 1998) or altered synergist activation (Kristiansen et al., 2015; Kristiansen, Samani, Madeleine, & Hansen, 2016; Santos et al., 2021). On the other hand, late RTD has greater correlation with MVC and depends greatly on muscular variables as muscle thickness, cross-sectional area and muscle architecture (Andersen, Andersen, Zebis, & Aagaard, 2010; Cossich & Maffiuletti, 2020; D'Emanuele et al., 2021; Folland, Buckthorpe, & Hannah, 2014).

Concerning the acute responses to strength training, it is widely evaluated the decline of MVC in consequence of neuromuscular fatigue (D'Emanuele et al., 2021). Neuromuscular fatigue is defined as a loss of force or power in response to contractile activity and results from nervous, mechanical and biochemical factors (for review see (Kent-Braun, Fitts, & Christie, 2012)). Interest has been given to changes in RTD to the study of fatigue, which in turn, has shown to be more sensitive than MVC in studies evaluating neuromuscular acute responses to strength training fatiguing protocols (D'Emanuele et al., 2021). Early RTD showed to be particularly sensitive to identify neuromuscular fatigue in a greater extent than late RTD (D'Emanuele et al., 2021). As referred previously, early RTD is mainly associated to neural mechanisms, and fatigue has revealed to promote changes along the corticospinal pathway from the cortex to motor units (Kent-Braun et al., 2012). Studies employing surface electromyography (EMG) have depicted the central control of the agonist muscles in response to fatigue, revealing an impairment in the recruitment of motor units as well as a decline in its firing frequency (Ahtiainen & Häkkinen, 2009; Kent-Braun et al., 2012; Pick & Becque, 2000). Additionally, differences in responses to fatigue have been shown between ST and UT individuals, with the ST achieving nearly the maximal neuromuscular potential and reaching voluntarily neural fatigue (Ahtiainen & Häkkinen, 2009; Pick & Becque, 2000). It is also known that neuromuscular fatigue affects intermuscular coordination (Castronovo, De Marchis, Schmid, Conforto, & Severini, 2018; McLean & Goudy, 2004; Rudroff, Barry, Stone, Barry, & Enoka, 2007; Semmler, Ebert, & Amarasena, 2013). However, to our knowledge only one study has shown between-group differences regarding intermuscular coherence (IMC) changes in response to fatiguing protocols, revealing that ST present lower intermuscular coherence than UT individuals although they are less affected with fatigue (Charissou, Vigouroux, Berton, & Amarantini, 2016). This approach may be an useful tool to study coordination adaptations to fatigue since it relays on the assumption that synergistic muscles are innervated by motoneurons sharing common corticospinal drives (Conway et al., 1995; Farmer, 1998; Salenius, Portin, Kajola, Salmelin, & Hari, 1997). Thus, coherence analysis allows to detect changes in the EMG power spectrum, assessing the synchrony between the central mechanisms of motor control and the movement production (Boonstra, 2013; Semmler et al., 2013).

Thus, this study aims to understand how force-time curve characteristics presented by two populations with different strength training background can be in partly explained by different patterns of muscle activation, namely in what concerns to agonist activation but also in the pairing between agonists, agonist-antagonist and synergists acting in different joints. Additionally, we intend to understand if the decline in isometric force production induced by a fatiguing protocol may be linked with neurophysiological changes specific to training background. Thereby, ST and UT participants will perform maximal rapid isometric contractions before and after a squat protocol with a load based on each one maximal dynamic strength. It was hypothesized that ST participants may present greater capacity to produce maximal and rapid force associated with faster muscle activation and greater agonists and synergists coherence as well as lower co-contraction from the antagonists. Additionally, we hypothesize that with fatigue, both groups should decrease the maximal and rapid force production capacity, with the resistance-trained possibly being 1) relatively more affected regarding the neural drive to the muscle, which may be justified by the greater full neural activation during the 1-repetition maximum (1RM) determination and during the protocol and the subsequent greater neural fatigue, 2) less affected in what concerns to intermuscular interactions, maintaining global coordination.

METHODS

Participants

Twenty-eight participants, 19 unexperienced (UT) and 9 strength-trained (ST) were included in this study. The participants were healthy men without history of musculoskeletal injuries within the last 6 months. ST were powerlifters or weightlifters with at least two years of regular practice (age: 27.1 ± 6.0 years; height: 173.6 ± 6.4 cm; weight: 81.8 ± 8.0 kg), while UT were active and were not involved in strength training exercises (age: 25.7 ± 3.8 years; height: 173.3 ± 6.9 cm; weight: 66.8 ± 7.9 kg). This study was approved by the Faculty's Ethics Committee (CEIFMH N.º: 24/2021) and all procedures adhered to the Declaration of Helsinki.

Data collection

Experimental approach. Aiming to assess the effect of expertise in the ability of the neuromuscular system to generate force and to assess muscle activation and coordination differences between different training-level groups during a fatiguing condition, each UT performed three sessions, while ST performed two. The first UT session purpose was to familiarize the participants with the task and with the testing equipment. In this familiarization all the UT experienced one session of technical learning of the task. The subsequent session for the UT and the first one of the ST aimed to determine the squat 1RM. Finally, the last session aimed to assess the neural strategies associated to maximal isometric force production and the effect of fatigue in each group of participants.

1RM Determination. For the squat 1RM determination, we used a progressive loading squat test. The squat was performed with a high-bar position, and an 80-90º squat depth was used. Participants started to perform 5 repetitions with the unloaded barbell (20kg), incrementing 10-20kg each time. After, participants performed 3 repetitions with each load until the load was challenging, and finally, they performed sets of 1 repetition with smaller load increases (~5kg) until the 1RM determination.

Testing procedures. The evaluation session started with a 5-minute cycle ergometer (Monark Exercise AB, Sweden) warm-up. After, participants were evaluated in isometric maximal

bilateral leg press (extension of the hip, knee and ankle). A horizontal leg press machine with custom-build force platform (Faculty of Human Kinetics) was used to assess lower limb maximal strength. The leg press machine was adjusted so the participants knee-angle was approximately 110º (107º according to Peltonen and colleagues (2018)). Three MVC were performed by each participant. Participants were asked to perform each repetition as fast and forceful as possible and to maintain the maximal force during 3-5s. Repetitions presenting a visible initial countermovement were excluded and one more repetition was asked. All strength tests were accompanied by verbal encouragement. Thereafter, the participants performed one squat training simulation with 5 sets of 10 repetitions with 75% 1RM determined in the previous session. Between sets, 2' rest were given. With the progression of the sets, if participants could not perform the last repetitions by themselves, the researcher could spot them, and in sets at which the researcher help was needed in 2 or more repetitions, the load was decreased by 2,5kg for the subsequent set. Finally, 30 seconds after the ending of the last set of squats, the participants performed two leg press MVC separated by 1 minute, with the same feedback as the ones performed previously.

EMG collection. All tests were accompanied by data collection of myoelectrical signals. These signals were recorded on 7 muscles of the right side of the body: gluteus maximus (Gmax), vastus lateralis of quadriceps (VL), rectus femoris of quadriceps (RF), vastus medialis of quadriceps (VM), biceps femoris long head (BF), lateral gastrocnemius (GL) and tibialis anterior (TA). The muscles were selected so we could assess the lower limb agonist muscles during the triple extension of the lower limb, and so that we could assess agonist-antagonist pairs of muscles of the knee and ankle. The electrodes were placed according to SENIAM (Surface EMG for Non-Invasive Assessment of Muscles). Before the placement of the electrodes, the skin was shaved and cleaned with alcohol to minimize skin impedance. Surface EMG was acquired using seven bipolar surface electrodes (EMG Delsys, TrignoTM), fixed with specially designed adhesive interface, aligned with the muscle fibers (Hermens et al., 2000) and then additionally fixed with tape to avoid movement artefacts. EMG signals were preamplified and band-pass filtered between 20 and 450Hz, while digitized at 1000 samples/s. After, the EMG signals were corrected for the 48-ms delay inherent to the Trigno EMG system.

Data processing

Force data. The leg press isometric MVC peak force (PF) was defined as the highest value of force achieved in each repetition. Absolute rate of force development (RFD) for the leg press MVC was calculated as the slope of the force-time curve (Δforce/ Δtime) in incremental epochs of 50ms (0-50ms; 50-100ms; 100-150ms; 150-200ms) starting from the onset of contraction. The onset of contraction was defined as the time point where the force exceed the baseline by 10 N. Peak RFD (PRFD) was defined as the maximum force-time slope at time windows of 20ms (Rodríguez-Rosell et al., 2017). At each time interval where RFD was computed, we also calculated the normalized RFD to MVC to assess the percentage of force exerted at each time point. We selected and analyzed the repetition with highest PRFD if the PF value was >95% of the highest PF value. The post-exercise leg press isometric MVC was analyzed in the same way.

EMG processing. Raw EMG signals were band-pass filtered (20-450Hz), rectified, smoothed with a low-pass filter (12Hz, 4th order Butterworth). Normalization was made to the average value of the 100ms across the EMG peak of the pre-exercise leg press isometric MVC. Average EMG values of all muscles were calculated at each isometric MVC during leg press in a time window from 1500ms to 2500ms from the onset of force production to ensure signal stability. Additionally, rate of EMG rise (RER) of VL, RF and VM was determined as the EMG increase calculated from the onset of electrical activity to the point that maximal rate of MVC force development will occur in the torque/force recording (Del Balso & Cafarelli, 2007). RER in time intervals of 0-50ms and 50-100ms was also calculated. The onset of electrical activity was defined as the time point where the EMG will exceed the baseline by 3 standard deviations (Jenkins et al., 2014).

IMC. Coherence analysis was performed using Matlab 2018a (Mathworks, Natick, MA, United States). Previous to data analysis, all data files were visually inspected to detect possible artifacts. In the cases where signals demonstrated some disruption or noise the repetitions were excluded from the analysis. IMC analysis was performed during 2500ms of each repetition, starting from 500ms after the onset of force production. A total of 7.5 seconds and 5 seconds for the pre- and post-fatigue MVC were analyzed, respectively. Before IMC analysis, EMG signals were full wave rectified (Boonstra et al., 2008; Walker et al., 2019; L.

Wang et al., 2015), and data was divided into non-overlapping windows of 500 samples in length. The signals were subjected to fast Fourier transform, which gave a frequency resolution of 2Hz. IMC was calculated as the cross-spectrum normalized by the auto-spectrum:

$$C_{xy}(f) = \frac{\left|P_{xy}(f)\right|^2}{P_{xx}(f)P_{yy}(f)}$$

where $C_{xy}(f)$ is the magnitude squared coherence between two rectified EMG signals, $x(t)$ and $y(t)$, for a given frequency f. $P_{xy}(f)$ is the cross-spectrum and $P_{xx}(f)$ and $P_{yy}(f)$ are the auto-spectrum of $x(t)$ and $y(t)$, respectively. Coherence above Z was considered significant (Rosenberg, Amjad, Breeze, Brillinger, & Halliday, 1989; Walker et al., 2019):

$$Z = 1 - \alpha^{1/(L-1)}$$

where *L* is the total number of sections and the significance level α was set to 0.05. The pre-fatigue *L*-value was 15, while the post-fatigue value was 10.

IMC was computed for the follow pairs of muscles: VL-VM, VL-RF, VM-RF (knee extensor agonists), VL-Gmax (knee extensor and hip extensor, synergists in the evaluated tasks), VL-GL (knee extensor and plantar flexor, synergists in the evaluated tasks), VL-BF, RF-BF and GL-TA (agonist-antagonist pairs). Total coherence was averaged across subjects in each group before and after fatigue for 3-100Hz, as well as coherence sectioned into 3-7, 8-14, 15-35, 40-60 and 60-100 Hz bands. Within 15-35 Hz band representing beta band, two additional 15-24, 25-35 Hz bands were separated. Average coherence within each band was used to compare groups (RT and UT) and conditions (before and after fatigue).

Statistics

All variables were statistically analyzed using SPSS software version 25 (IBM, New York, NY, United States). Normality was verified through the Shapiro–Wilk test using a significance level of $p < 0.05$ for all variables. When sphericity was not assumed, a Greenhouse-Geisser correction was made. PF, PRFD, absolute and normalized RFD in time intervals, average EMG of each muscle, RER of each knee extensor muscle were compared

between groups and within each subject condition before and after fatigue. Average coherence within each band was not normally distributed, so to allow parametric tests to be performed IMC values were log 10 transformed. A mixed ANOVA (between groups and within participant at 2 time points: 2 group x 2 time) was used on all the variables described before. Bonferroni adjustments were used in *Post hoc* tests.

RESULTS

Force production. Force-related variables values are presented in Table 4.1. ST showed greater PF than UT ($p < 0.001$), as well as greater maximal RFD ($p = 0.038$), absolute RFD at 100-150ms and 150-200ms ($p = 0.040$ and $p = 0.019$, respectively). However, early absolute RFD values at 0-50ms and 50-100ms were not different between groups as well as all normalized RFD values at 50, 100, 150 and 200ms (Figure 4.1). After fatigue, all variables decreased significantly for both groups, and PF presented significant *time x group* interaction, with the ST decreasing in a greater extent than UT ($p = 0.018$; Figure 4.2).

Table 4.1 Force variables for the untrained (UT) and strength-trained individuals (ST) before and after the fatiguing protocol.

Variable	UT		ST	
	Pre-fatigue	Post-fatigue	Pre-fatigue	Post-fatigue
PF (N) * # §	2555.3 ± 616.1	2085.8 ± 548.4	3884.3 ± 916.6	2961.2 ± 632.0
RFDmax (N/ms) * #	9.9 ± 2.2	6.1 ± 2.4	12.7 ± 4.3	8.4 ± 4.1
RFD0-50ms (N/ms) *	5.7 ± 1.8	3.3 ± 1.5	6.5 ± 2.3	5.4 ± 2.6
RFD50-100ms (N/ms) *	9.0 ± 2.4	5.4 ± 2.3	10.9 ± 4.2	8.2 ± 4.1
RFD100-150ms (N/ms) * #	8.3 ± 1.8	5.6 ± 2.2	11.4 ± 4.8	8.0 ± 3.9
RFD150-200ms (N/ms) * #	5.6 ± 1.6	4.6 ± 1.7	8.7 ± 3.7	6.5 ± 2.9
MVC50ms (%) *	14.0 ± 4.4	9.5 ± 3.5	10.2 ± 5.0	8.4 ± 4.0
MVC100ms (%) *	35.3 ± 10.0	22.7 ± 7.5	26.2 ± 11.7	20.8 ± 9.3
MVC150ms (%) *	54.9 ± 13.6	36.3 ± 10.8	42.2 ± 17.6	33.5 ± 13.3
MVC200ms (%) *	68.3 ± 15.2	47.3 ± 12.5	54.0 ± 20.2	44.0 ± 15.1

PF – Peak force; RFD – Rate of force development; MVC – Maximum voluntary contraction. * $p < 0.05$ between before and after conditions, # $p < 0.05$ between groups, § $p < 0.05$ time x group interactions

Muscle activation. Average normalized amplitude of EMG signals of all the analyzed muscles did not show any between-group difference. However, after fatigue two of the three heads of quadriceps femoris showed increased activity (vastus medialis: $p = 0.005$; rectus femoris: $p = 0.039$) as it is depicted in Figure 4.3. Additionally, rectus femoris RER from the onset of electrical activity to the point at maximal RFD presented *time x group* interactions ($p = 0.024$), as well as RER measured at time intervals of 0-50ms ($p = 0.025$) and 50-100ms ($p = 0.006$), as it is observed in Figure 4.4, increasing for the ST and decreasing for UT.

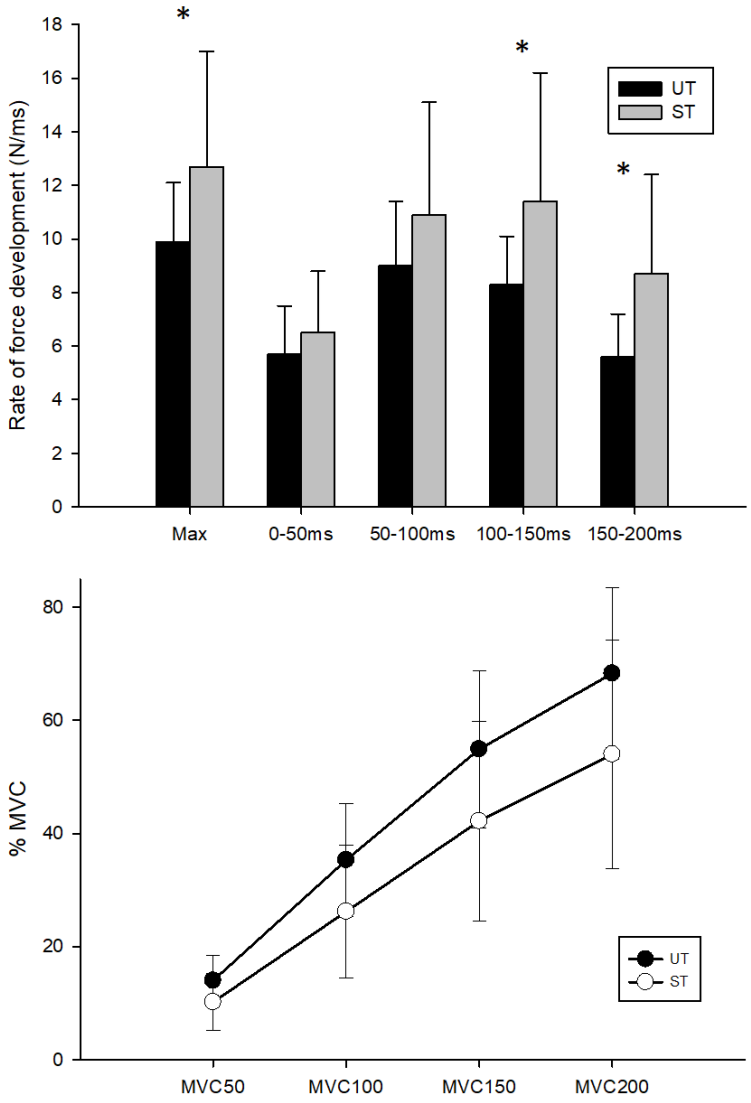

Figure 4.1 Rapid force comparison between the untrained (UT) and strength-trained individuals (ST). Upper panel: Absolute rate of force development; Lower panel: normalized rate of force development. * $p < 0.05$ between groups.

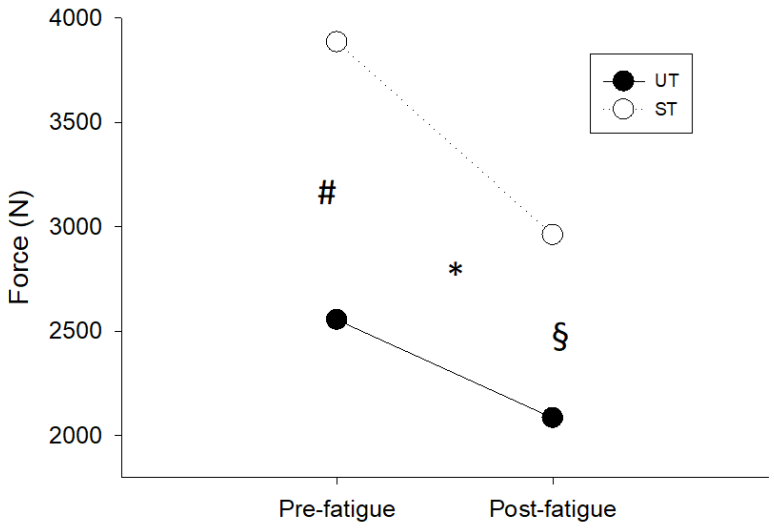

Figure 4.2 Maximal force decrements comparison between the untrained (UT) and strength-trained individuals (ST). * $p < 0.05$ between before and after conditions, # $p < 0.05$ between groups, § $p < 0.05$ time x group interactions.

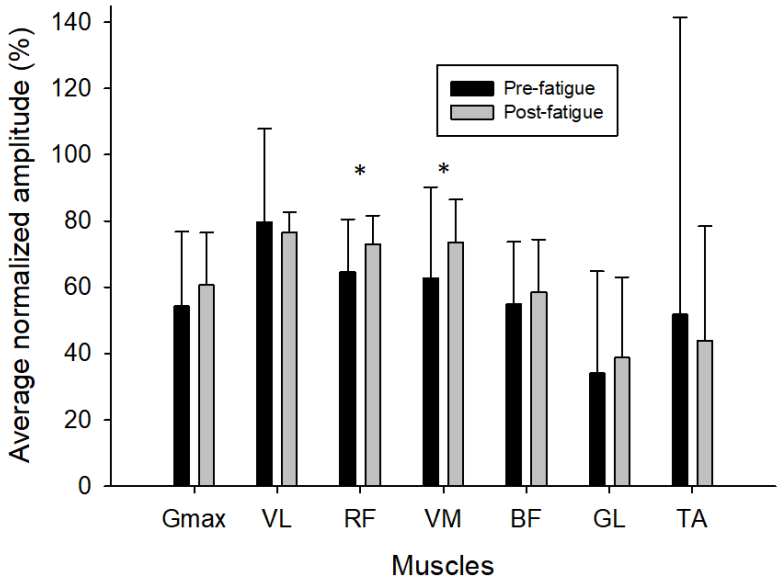

Figure 4.3 Average normalized amplitude of lower limb muscles before and after fatiguing protocol. Gmax – gluteus maximum; VL – vastus lateralis; RF – rectus femoris; VM – vastus medialis; BF – bíceps femoris; GL – gastrocnemius lateralis; TA – tibialis anterior. * $p < 0.05$ between groups.

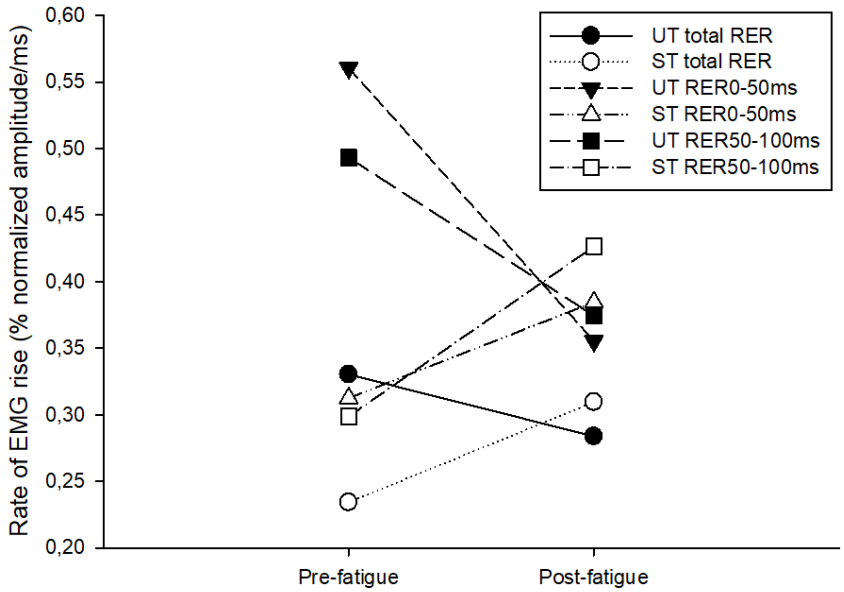

Figure 4.4 Rate of EMG rise changes comparison between the untrained (UT) and strength-trained individuals (ST). * $p < 0.05$ between before and after conditions, # $p < 0.05$ between groups, § $p < 0.05$ time x group interactions.

Intermuscular coherence. Figure 4.5 shows between-group comparison of all the analyzed pairs of muscles before fatigue. Particularly, coherence between rectus femoris and vastus medialis was different between UT and ST, with the ST presenting greater mean coherence value at beta-band (15-35 Hz). Additionally, a visual inspection of the coherence data series revealed that coherence in the higher values of beta-band (> 30 Hz) presented significant peaks for all agonist-agonist pairs (VL-VM, VL-RF and VM-RF) for both groups. Agonist-antagonist GL-TA pair also showed significant peaks of coherence in the same band of interest for both groups, and VL-BF showed significant peaks of coherence only for ST although the band average did not show any significant between-group difference. Additionally, coherence in lower frequencies (3-7Hz) was significant for all muscle pairs in both groups.

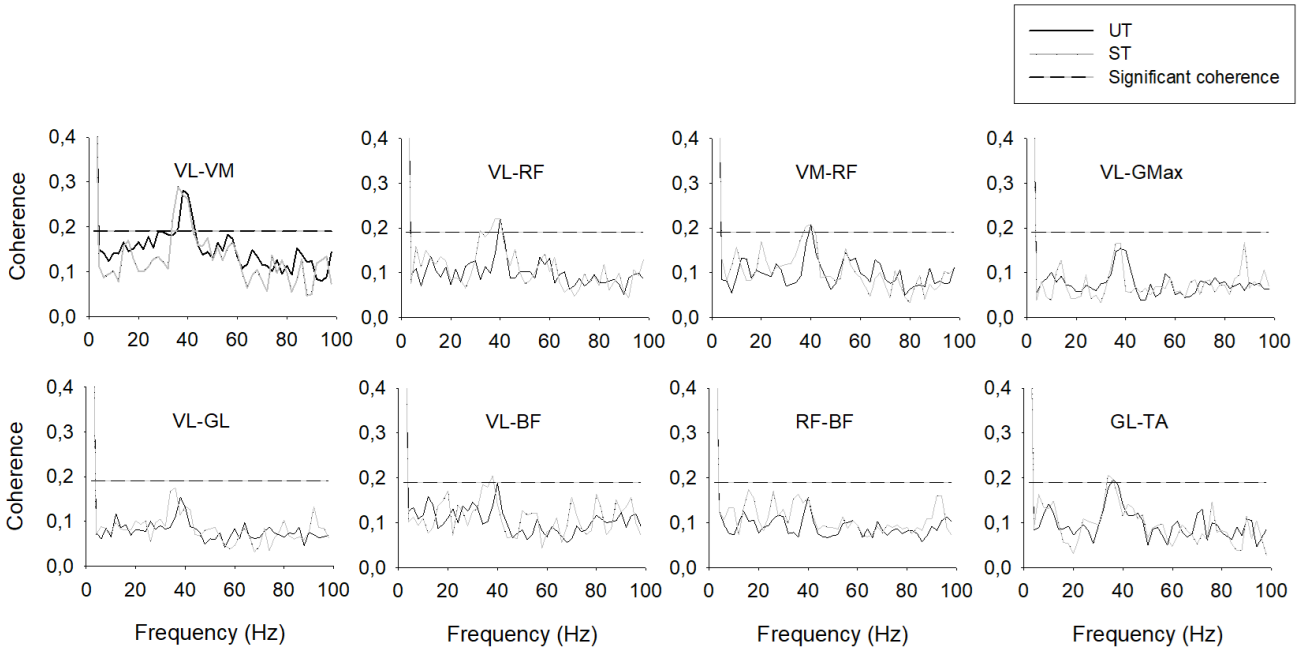

Figure 4.5 Coherence of the analyzed pairs of muscles for the untrained (UT) and strength-trained individuals (ST) between 0 and 100 Hz. The horizontal line represents significant coherence Gmax – gluteus maximum; VL – vastus lateralis; RF – rectus femoris; VM – vastus medialis; BF – bíceps femoris; GL – gastrocnemius lateralis; TA – tibialis anterior.

After fatigue, coherence was affected in specific bands for the different muscle pairs. As example, Figure 4.6 shows how coherence between RF and VM changed with fatigue for both groups. As this pair of muscles was the only which showed different coherence in beta-band before fatigue, we analyzed separately both groups (Figure 4.7). Nevertheless, both groups presented greater total coherence as well as coherence in high-gamma band (> 60 Hz), while UT also presented greater coherence in 3-7 Hz band after fatigue. All other pairs of muscles were analyzed for all participants since there was not between-group differences or time x group interactions. Percentage change and significance values for this and the other pairs of muscles are presented in Table 4.2. Total coherence as well as coherence at high-gamma-band increased for all pairs of muscles. VL and VM also demonstrated increased alfa and low-beta bands coherence. VL also increased coherence with synergist muscles acting in

other lower limb joints, as Gmax (at all bands > 15 Hz) and GL (at low-beta and gamma bands). GL and TA also presented greater coherence at beta- and gamma-bands. An example of agonist-antagonist (VL-BF) coherence within each band is presented in Figure 4.8. These two muscles also increased coherence after fatigue in beta, gamma and high-gamma bands, as well as total coherence.

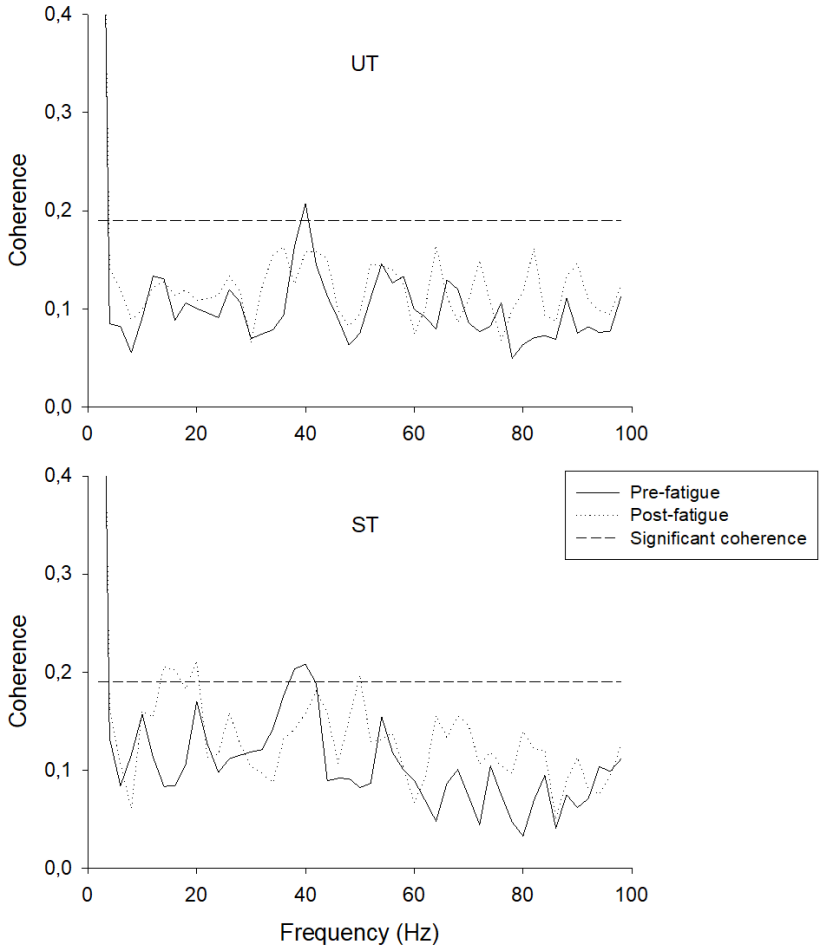

Figure 4.6 Coherence between vastus medialis and rectus femoris muscles before and after the fatiguing protocol for the untrained (UT; upper panel) and strength-trained individuals (ST; lower panel).

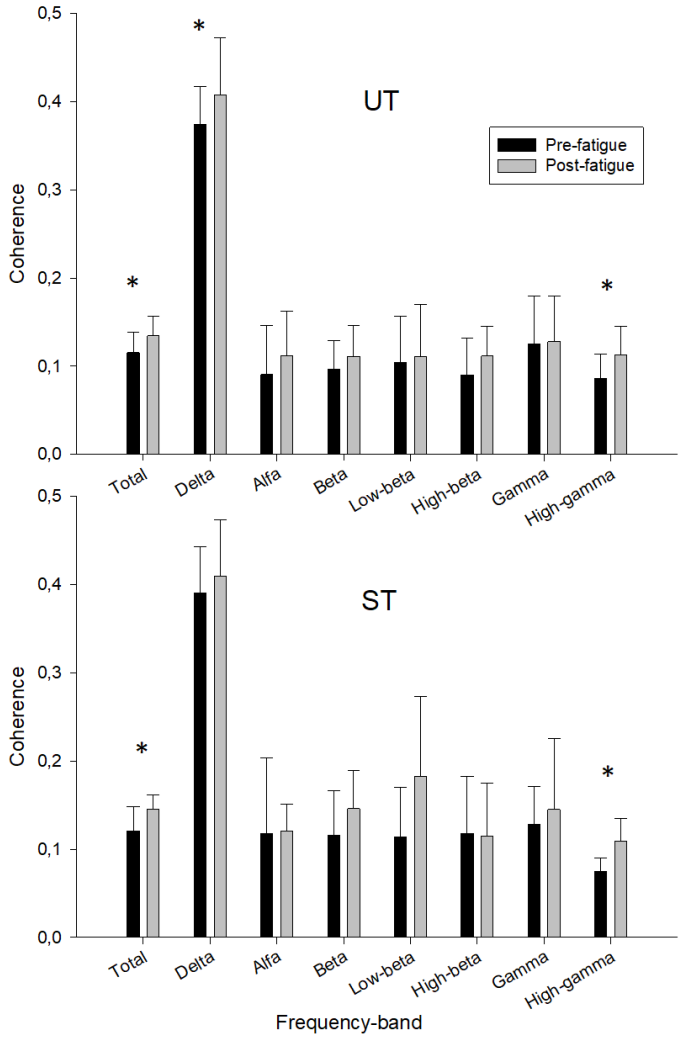

Figure 4.7 Coherence between vastus medialis and rectus femoris within each frequency-band before and after the fatiguing protocol for the untrained (UT; upper panel) and strength-trained individuals (ST; lower panel). * $p < 0.05$ between before and after conditions.

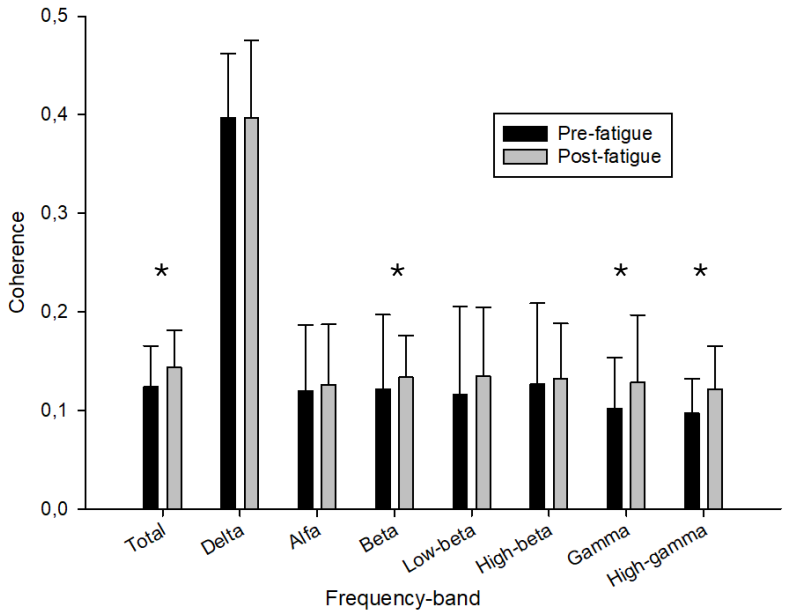

Figure 4.8 Coherence between vastus lateralis and biceps femoris within each frequency-band before and after the fatiguing protocol for all participants. * $p < 0.05$ between pre- and post-fatigue conditions.

Table 4.2 Percentage of change (before and after fatigue) of coherence values of the analyzed pairs of muscles for all the participants. Positive values mean coherence increased while negative values mean coherence decreased. Presented *p-values* refer to ANOVAs' main effect for Time factor. * $p < 0.05$ between pre- and post-fatigue conditions.

Band of interest	VL - VM		VL - RF		VM - RF		VL - Gmax		VL - GL		VL - BF		RF - BF		GL - TA	
	%	*p*	%	*p*	%	*p*	%	*p*	%	*p*	%	*p*	%	*p*	%	*p*
Total	12	**0.006***	13	**0.001***	18	**0.001***	41	**<0.001***	24	**0.001***	16	**0.001***	15	**0.003***	27	**<0.001***
Delta	2	0.297	0	0.611	8	0.101	4	0.097	5	0.139	0	0.96	3	0.365	8	0.167
Alfa	19	**0.042***	0	0.89	16	0.086	19	0.211	16	0.159	6	0.386	41	0.102	29	0.108
Beta	6	0.076	11	0.062	20	0.073	53	**<0.001***	21	0.054	10	**0.033***	4	0.216	24	**0.009***
Low-beta	16	**0.042***	12	0.233	27	0.126	56	**0.003***	33	**0.027***	16	0.134	0	0.8771	49	**0.021***
High-beta	-1	0.246	10	0.244	14	0.342	51	**0.001***	12	0.2	5	0.158	7	0.305	10	0.531
Gamma	3	0.202	4	0.299	6	0.531	49	**<0.001***	41	**0.017***	26	**0.018***	11	0.126	34	**0.006***
High-gamma	32	**<0.001***	31	**0.001***	35	**<0.001***	64	**<0.001***	39	**<0.001***	25	**0.008***	32	**0.002***	38	**<0.001***

Gmax – gluteus maximum; VL – vastus lateralis; RF – rectus femoris; VM – vastus medialis; BF – biceps femoris; GL – gastrocnemius lateralis; TA – tibialis anterior. * $p < 0.05$ between pre- and post-fatigue conditions.

DISCUSSION

The present study demonstrated that individuals with strength training background present different neuromechanical mechanisms of force production and may present specific responses following acute bouts of strength training. In this study, ST presented greater PF, maximal RFD and absolute RFD at time intervals of 100-150ms and 150-200ms, while there were not differences in normalized RFD values. These differences in force variables were accompanied by different coherence in beta-band between VM and RF. After fatigue, maximal and rapid force production were affected in both groups, with the ST being affected in a greater extent in what concerns to maximal strength. Activation of VM and RF increased, and RER of RF was the only electromyographic variable that changed differently in the two groups, decreasing in UT and increasing in ST after fatigue. Both groups presented changes with fatigue in coherence across the analyzed bands, with specific changes concerning the functional role of the muscles within each of the analyzed pairs.

Between-group differences.

Strength training has been previously established as an adequate method to increase maximal capacity of force production as well as rapid force production usually measured as the RFD produced in isometric tasks (Aagaard et al., 2002; Cadore et al., 2014; Peltonen, Walker, Lähitie, Häkkinen, & Avela, 2018; Vila-Chã, Falla, & Farina, 2010). In this study, ST also presented greater values of PF and maximal RFD, which is line with other studies that also measured these mechanical variables (Del Vecchio et al., 2018; Orssatto et al., 2020; Tillin et al., 2010). Previous studies that analyzed RFD at time intervals of 50ms reported increased rate of torque development (RTD) for ST individuals in the earlier intervals (usually < 50ms) which is related with greater neural input to the muscles (Del Vecchio et al., 2019; Del Vecchio et al., 2018; Maffiuletti et al., 2016; Pearcey et al., 2021). Additionally, it has been shown that UT may present greater RTD during the 50-100ms time interval (Del Vecchio et al., 2018; Tillin et al., 2010), which is possibly justified by greater EMG increases only after 25ms from the onset of muscle activation (Tillin et al., 2010), although these results are not consistent because of the disparity of methodologies used to determine onsets of force production and/or muscle activation (Folland et al., 2014; Johnson et al., 2015). However, in this study we found that although there is a trend to greater absolute RFD at 0-50ms and 50-

100ms for ST these results are not significant in contrast to absolute RFD at 100-150ms and 150-200ms that were statistically greater to ST. These results were unexpected and since late RFD is related with maximal force (Cossich & Maffiuletti, 2020; Maffiuletti et al., 2016) we may associate these results to a clear between-group difference concerning PF. Additionally, the ST were heavier than UT, which is a consequence of greater muscle mass, and cross-sectional area or muscle thickness are correlated with RFD at later time intervals (Andersen et al., 2010; Cossich & Maffiuletti, 2020; D'Emanuele et al., 2021; Folland et al., 2014). However, when RFD at time intervals was normalized there were not significant differences although UT presented a trend to reach higher relative values at each time point which may be due lower PF values. Also, we may not discard the fact that in the previously cited studies (Cossich & Maffiuletti, 2020; Orssatto et al., 2020; Tillin et al., 2010) the analyzed tasks only involved knee extension and not the triple extension of lower limb joints. The fact that we used a multi-joint exercise may result in different neuromechanical patterns of force production, and previous studies showed different neural input to the muscle when comparing single-joint and multi-joint exercises (Ema, Sakaguchi, Akagi, & Kawakami, 2016) as well as closed chain (as the leg press machine) and open chain kinetics (as the knee extension extension) (Boccia, Martinez-Valdes, Negro, Rainoldi, & Falla, 2019; Irish, Millward, Wride, Haas, & Shum, 2010). Namely, synaptic input measured as discharge rate to VM and VL of the quadriceps in contractions > 50% MVC was higher in single-joint knee extension exercises compared to leg press tasks (Boccia et al., 2019). Finally, these results may also be justified with lack of specificity in the evaluated task since the ST individuals did not perform isometric leg press tasks in their training programs.

In this study we did not identify between-group differences in the EMG activity of any muscle. However, we normalized all EMG signals to the maximum of each muscle in pre-exercise leg press isometric MVC. Although for the quadriceps muscles it may be an ideal way to normalize EMG signals since the task has a predominant knee extension action and do not present differences in EMG amplitude when compared to single-joint knee extension (Alkner, Tesch, & Berg, 2000), for muscles as BF, Gmax, GL or TA, this normalization procedure may not be the ideal when studying degree of activation. For example, BF relative activity to its maximum in a knee flexion task may be decreased in ST individuals compared to UT as it is suggested by previous studies (Amarantini & Bru, 2015; Pearcey, Power, &

Button, 2014), and the approach we used is not adequate to assess relative differences in the referred muscles since it only supplies information regarding the maximum achieved in the evaluated task and not the real maximum muscle ability to activate (Bolgla & Uhl, 2007; Knutson, Soderberg, Ballantyne, & Clarke, 1994). However, there is also evidence suggesting that between-group differences in antagonist muscle activity may be only present in submaximal contractions but not in maximal contractions (Balshaw et al., 2019).

IMC analysis identifies interactions between pairs of muscles allowing to distinguish signal input frequencies common between those muscles and to infer about the neural origin of motor initiation (Grosse, Cassidy, & Brown, 2002). In this study, IMC analysis revealed that only one pair of agonist-agonist muscles (VM and RF) presented differences regarding training status. Namely, ST individuals presented greater coherence in beta-band (15-35 Hz) than UT. These results are contradictory with those presented by Charissou and colleagues (2016) that found greater coherence in beta-band between VM and RF for UT when compared with ST and endurance trained individuals (Charissou et al., 2016). However, caution should be taken when interpreting these results. On the one hand, IMC analysis provided by the authors of the study relies on coherence analysis through wavelet transformation, and not cross-spectrum coherence as we determined. On the other hand, the performed task was a single-joint knee extension which require different neural input than leg press, as discussed previously. Additionally, although we did not find between-group differences in VM-VL coherence, strength training has shown to possibly change it in young and older people in single-joint knee extensions (Walker et al., 2019). Namely, the younger participants of this study presented increased coherence in gamma band (40-60 Hz) in submaximal 70% MVC contractions after 14 weeks of strength training. Although there were not changes in average coherence within each band, authors referred sporadic significant but non-systematic increases in some frequency bins during 100% MVC.

We observed for both groups peaks within the beta band for all three pairs of quadriceps muscles (VL, VM and RF), which is in line with previous studies that associate this frequency-band with the corticospinal pathway (Farmer, Bremner, Halliday, Rosenberg, & Stephens, 1993; Kattla & Lowery, 2010; Mima & Hallett, 1999) with particular emphasis to the fastest corticospinal fibers (Ibáñez, Del Vecchio, Rothwell, Baker, & Farina, 2021).

Additionally, communication between sensorimotor cortex and other cortex areas as well as the periphery has been attributed to beta oscillations (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013). Also, positive linear correlations have been demonstrated between motor unit synchronization and coherence in this band and in the 0-5 Hz band reflecting a common drive to motor units by a subcortical origin (Farmer et al., 1993; Lowery, Myers, & Erim, 2007). In this study, these results are corroborated by significant coherence for all muscle pairs at 3-7 Hz band.

Regarding agonist-antagonist activity, we have also observed significant GL-TA coherence peaks within the beta-band for both groups. These results are supported by Wang and colleagues (2019) that compared badminton players and UT in plantar flexion isokinetic contractions (Wang et al., 2019). However, in this study badminton players presented greater beta-band GL-TA coherence during isokinetic dorsiflexion contractions. Although we did not measure a dorsiflexion task, we could also expect this behavior, since ST individuals training involve plantar flexion in a greater extent than dorsiflexion actions as well as for the badminton activity that also involve plantar flexion action in ground support and change of direction. VL and BF coherence also showed a significant peak only for ST, although differences in average beta-band coherence were not statistically significant. Previous research using corticomuscular coherence has also showed different mechanisms between ST and endurance trained without experience in strength training regarding the motor control of agonist and antagonist muscles with the ST revealing stronger activation of motor cortex (Dal Maso, Longcamp, Cremoux, & Amarantini, 2017). ST presented greater suppression of beta-band corticomuscular oscillations accompanied with lower activation of the antagonist muscles (Dal Maso, Longcamp, & Amarantini, 2012).

Fatigue effects.

After the squat fatiguing protocol, both groups decreased their force production capacity regarding maximal and rapid force. Beyond decreased PF, both groups decreased absolute RFD as well as normalized RFD. As it is known, fatigue relies on neurophysiological changes that impair the capacity to maintain a given intensity of muscle contraction (D'Emanuele et al., 2021; Kent-Braun et al., 2012). In this study, ST presented greater decrease in PF when compared to UT. As it was previously showed, UT are not able to recruit the total amount of

muscle fibers within a muscle (Grosprêtre, Gimenez, & Martin, 2018; Orssatto et al., 2020). This means that UT 1RM may be undervalued because of not reaching the full activation potential of the muscles and as consequence they start the fatiguing protocol in a lower level of relative intensity than the ST which do not lead to the same amount of decrease in PF. This happens because according to Henneman principle they can add new motor units with greater diameter during the squat protocol (Ahtiainen & Häkkinen, 2009; Pick & Becque, 2000). On the other hand, ST can reach greater voluntary activation of muscle fibers during testing (Del Balso & Cafarelli, 2007; Jenkins et al., 2016; Orssatto et al., 2020), starting the squat protocol in a greater level of relative intensity of recruitment, meaning that fast twitch fibers with greater diameter (Del Vecchio et al., 2018; Hakansson, 1956) and more fatigable (Bagley et al., 2017; Thorstensson & Karlsson, 1976) may reach exhaustion in an earlier phase and consequently be unable to be recruited in post-fatigue assessments.

From pre- to post-fatigue leg press measurements, VM and RF activation increased independently the group. As it is known, fatigue leads to increased amplitude of EMG activity of the agonist muscles (Kattla & Lowery, 2010; Pick & Becque, 2000; L. Wang et al., 2015). Although the increase in EMG amplitude is usually seen in submaximal tasks, as we used a multi-joint task, we may expect different patterns of muscle coordination derived from the incapacity to reach the pre-fatigue force-values. The observed increase in muscle activity may represent effects of fatigue in VM and RF muscles that are two of the three primary recruited muscles during squat. Although other studies evaluating lower limb triple extension observed increased activity of the three muscles (Miranda et al., 2018) we did not find changes in VL activity. Also, activity of Gmax and BF remained unchanged, which was expected since parallel squat do not induce strong activity of both muscles (Caterisano et al., 2002; Schoenfeld, 2010). Interestingly, neither of the quadriceps muscles showed significant declines over time regarding contraction velocity assessed by RER. However, RER of the RF showed a time x group interaction, increasing in ST and decreasing in UT. Since RF is a knee extensor and a hip flexor, we should speculate that with fatigue ST are capable to recruit it in a more effective way as an agonist of knee extension contributing to the output of the vasti muscles, and then increasing the ability to produce force explosively. On the other hand, UT do not seem to be capable of maintain the effectiveness of force transmission from the hip to the knee by RF in rapid force contractions.

Total coherence (3-100 Hz) increased in all pairs of the analyzed muscles. This may represent increased general synchronization of the muscles and a greater common origin of inputs of the CNS (Farina, Merletti, & Enoka, 2014). After an acute bout of strength training the increases in coherence of synergistic as well as antagonist muscles may be a neural strategy to attenuate neuromuscular failure maintain the global muscle coordination (Chang et al., 2012). Additionally, coherence within high-gamma frequencies (> 60 Hz) increased across all pairs of muscles independently their functional role in lower limb extension. These results were previously attributed to the recruitment of new motor units in submaximal exhausting stepping exercise (Chang et al., 2012). In this study, although EMG amplitude increased only in VM and RF after fatigue, greater coherence may arise from greater synchronization at higher frequencies to compensate possible drops in discharge rate (Aoki, Uchida, & Inoue, 2005; Hwang, Lin, Huang, & Chen, 2020).

Regarding coordination of knee extensor synergistic muscles, we did not observe any increase in coherence between RF and VL or VM within all the other analyzed frequency-bands (< 60 Hz). However, VL and VM coherence within these bands increased after fatigue. Since VM and VL are two single-joint acting muscles with greater role in knee extension force and power production (Escamilla et al., 2001; Schoenfeld, 2010), it is plausible that after fatigue there is a modulation of motor unit recruitment by corticospinal pathway which is congruent with greater coherence in beta-band (Farmer et al., 1993; Kattla & Lowery, 2010; Mima & Hallett, 1999). In our case, VM and VL presented greater coherence in lower beta band frequencies (15-25 Hz) and in alpha band (8-14 Hz). Beta band coherence is usually studied to assess neural responses to fatigue, and increased coherence within this band has been previously demonstrated in elbow flexor (Semmler et al., 2013), finger flexors (Kattla & Lowery, 2010) as well as synergistic knee extensors (Chang et al., 2012). In this last study, only RF-VL and RF-VM coherence increased while VM-VL coherence remained unchanged, which is contrary to our results. The different task that elicited fatigue may have resulted in different adaptations within the Central Nervous System. Namely, in our study the loaded squats with 75% 1RM are a completely different effort regarding muscle recruitment in comparison with unloaded stepping exercises (Chang et al., 2012) which may result in the different acute response observed concerning beta-band coherence. However, single-joint knee extensions with submaximal 70% 1RM loads resulted in decreased

coherence for all pairs within quadriceps muscles (VL, VM and RF) (Castronovo et al., 2018). These results derive from different methodological approaches adopted by the authors, namely with the coherence analysis being performed in the non-rectified EMG signals. Regarding alpha band coherence, the higher values observed after fatigue may as well as beta band be related to greater motor unit synchronization but are also attributed to physiological tremor (Boonstra et al., 2008; McAuley & Marsden, 2000). Although the origin of alpha-band coherence has been attributed to oscillatory activity at 13-18 Hz present particularly in the paramedian lobule of primate cerebellar cortex (Pellerin & Lamarre, 1997), physiological tremor around 10 Hz appears to be multifactorial and it may be divided concerning the type of muscle action (McAuley & Marsden, 2000). In our case, the maximal isometric contractions used to assess fatigue effects in coherence elicited higher amplitude tremors which are related to increased motor unit synchronization as consequence of firing rate modulation (McAuley & Marsden, 2000). Increased alpha band coherence after exhausting protocols has been shown (Kattla & Lowery, 2010; Semmler et al., 2013), although other did not report any differences possibly because postural tremor of synergist muscles is not associated with the development of fatigue (Chang et al., 2012).

In this study, we also found increased coherence within beta- and gamma-bands between VL and two muscles acting primarily in the hip and ankle joint (Gmax and GL). Increased coherence in these bands between those muscles is an interesting finding since it points at a possible global control of muscles, aligned with muscle synergy theory. Muscle synergies represent a mechanism organizing a high number of elements – the degrees of freedom implied during the action of each muscle – in a more simplified way of control for the CNS (Hirashima & Oya, 2016; Safavynia, Torres-Oviedo, & Ting, 2011). Thus, the recruitment of a small number of muscle synergies allows the production of a wide variety of motor behaviors since they can be shared and flexibly adapt to specific tasks (Bizzi & Cheung, 2013; d'Avella & Bizzi, 2005). In our case, the greater coupling between muscles acting primarily in different joints may reflect an adaptation in the recruitment of lower limb muscle synergies, namely adjusting the synchronization between them to efficiently adapt to a fatigue condition. However, when interpreting the data in this way, we may have caution concerning the coupling between VL and GL since GL is also a knee flexor and the differences in coherence may emerge from its role as a knee extension antagonist.

The analysis between agonist and antagonist muscles also revealed increased coherence within specific bands. Although coherence between BF and RF increased only concerning total and high-gamma-band coherence, coherence between BF and VL increased within beta- and gamma-band. The differences in RER and mean activity found in RF after fatigue may imply a specific coordination adaptation of the muscle regarding its role in the hip and in the knee. On the other hand, the increased coherence between VL and BF within beta and gamma bands may rely on a greater corticospinal drive from motor cortex to the muscles reflecting stronger coupling between motor cortical neurons and motor units of both muscles (Kattla & Lowery, 2010; Wang et al., 2015), indicating closely related organization of corticospinal connections between antagonist muscles (Wang et al., 2015). However, there is evidence suggesting that increased coherence after fatigue may be only present in stroke patients and not in healthy ones (Wang et al., 2020). The authors justified this apparently contradicting results to the higher intensity of contraction of the testing protocol as well as the low efficiency of motor control attributed to motor impairment, suggesting that changes in antagonist muscles coupling is linked to the degree of central fatigue (L. J. Wang et al., 2020). Although previous research on animal model showed that antagonist corticospinal neurons are closely grouped (Ethier, Brizzi, Giguère, & Capaday, 2007) the control of agonist and antagonist muscles appears to be modulated by supraspinal and spinal levels with the supraspinal pathways being controlled separately (Duchateau & Baudry, 2014). Nevertheless, the increased coherence in beta- and gamma-bands observed in this study support previous findings suggesting modulation of corticospinal pathways after fatigue (Wang et al., 2015). However, the same study showed increased alpha-band coherence which may be linked to postural tremor of the antagonist muscles with fatigue possibly caused by peripheral factors of Ia afferents and central mechanisms (Hansen, Hansen, Christensen, Petersen, & Nielsen, 2002). We did not find the same results in alpha-band, possibly because of the intensity of the fatiguing protocol which was clearly greater that the one used in the study of Wang and colleagues (2015). Additionally, coherence between GL and TA increased within the same bands, possible reflecting the greater coupling between antagonist muscles around the ankle joint.

CONCLUSION

The greater capacity of force production of ST individuals is determined by different neuromechanical strategies while performing rapid maximal contractions. Greater maximal and absolute RFD in specific time intervals and greater peak force in ST individuals may be justified by neural mechanisms as greater beta-band coherence between VM and RF muscles. ST were more affected in maximal force production, revealing a different acute response in RF RER which may be related to a specific pattern of control of the RF as a bi-articular muscle important to the efficiency of the lower limb kinetic chain. After fatigue, there were not between-group differences in intermuscular coherence. Coherence between muscles increased in both groups with particularly increases within each band of interest concerning the functional relation between the compared muscles. This study brings new insight into the study of fatigue-related adaptations in groups with different training backgrounds and may be useful to understand specific neurophysiological responses to strength training concerning the level of practice of the individuals, namely, concerning the interactions between agonist, synergist and antagonist muscles. Further research should focus on the understanding of these interactions during the heavy dynamic strength training protocols in populations with different expertise in complex tasks, and how does this relate with changes in temporal and/or spatial components resulting from muscle synergy analysis.

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Chapter 5

Chronology of adaptations to strength training: muscle activation and coordination during maximal force production

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ABSTRACT

Previously untrained individuals tend to increase maximal and rapid strength during the initial strength training stages. Muscle activation and coordination are neural mechanisms contributing to the increased mechanical output. However, how the force production characteristics are accompanied by changes in activation of agonist muscles as well as coordination of muscles with different functional roles is not fully understood. This study investigated the time course of adaptations following 6 weeks of strength training, evaluating every two weeks a leg-press isometric maximum voluntary contraction. Peak force (PF), rate of force development (RFD), rate of EMG rise (RER) of the agonist muscles and intermuscular coherence between synergist or antagonist pairs of muscles were evaluated. In result of a dynamic squat program, the maximal and rapid leg-press isometric force increased after the 6-week period (p = 0.011 and p = 0.015, respectively), although improvements at specific intervals of RFD at specific time points were observed. Regarding knee extensor activation, generally decreased RER was observed only for rectus femoris and not for the monoarticular portions of quadriceps. Additionally, intermuscular coherence analysis revealed increased coupling between rectus femoris and the monoarticular portions of quadriceps after training, and adaptations between agonist muscles acting in different joints as well as between agonist and antagonist muscle at specific time points were observed concerning specific bands. This study brings new insights into the neural mechanisms of muscle recruitment following strength training in what concerns to coordinative strategies in the control of muscles with different functional roles.

Keywords: resistance training, electromyography, neural adaptations, neuromuscular performance, intermuscular coherence

INTRODUCTION

Strength training induces increased capacity of force production that emerges from neuromuscular adaptations. Previously untrained individuals present lower maximal (Balshaw, Massey, Maden-Wilkinson, Lanza, & Folland, 2019; Škarabot et al., 2021) or rapid force (Del Vecchio et al., 2018; Orssatto, Wiest, Moura, Collins, & Diefenthaeler, 2020; Tillin, Jimenez-Reyes, Pain, & Folland, 2010) than trained ones, which has been shown to be related to muscular adaptations, such as changes in muscle size (Franchi et al., 2018; Mobley et al., 2018) and architecture (Blazevich, Gill, Bronks, & Newton, 2003; Timmins et al., 2016; Wells et al., 2014), but also to neural factors. More precisely, strength trained individuals have shown to be capable of producing greater voluntary activation of muscles during maximal force production (Balshaw et al., 2019; Orssatto et al., 2020; Santos, Vaz, Correia, Neto, & Pezarat-Correia, 2023; Škarabot et al., 2021) presenting adaptations spanning from the cortex to the spinal cord, as reduced intracortical inhibition and changed corticospinal pathway (Kidgell, Bonanno, Frazer, Howatson, & Pearce, 2017; Lahouti, Lockyer, Wiseman, Power, & Button, 2019), or motor unit recruitment with increased discharge rate (Del Vecchio, Casolo, et al., 2019; Del Vecchio, Negro, et al., 2019).

During the first weeks of training, adaptations seem to be mainly related to neural mechanisms, while muscular adaptations present greater relevance after 6-8 weeks of training (Folland & Williams, 2007; Sale, 1988). For example, during this initial training stage, increased corticospinal excitability and reduced short-interval cortical inhibition as well as reduced activation of the antagonist muscles were observed after only 2 weeks of isotonic wrist flexion training (Mason et al., 2020). Also, changes in the activation of stabilizers during elbow flexions after 3 weeks (Buckthorpe, Erskine, Fletcher, & Folland, 2015), increased voluntary activation and rate of activation of the plantar flexors (Del Balso & Cafarelli, 2007) or decreased recruitment threshold of motor units and increased discharge rate (Del Vecchio, Casolo, et al., 2019) after 4 weeks were observed. However, how these specific adaptations emerge overtime is still not entirely understood, and it may be crucial to a more effective strength training prescription. For example, different methods of strength training have demonstrated to promote different acute adaptations in muscle activity assessed by electromyography (EMG) in groups with different training background (Ahtiainen &

Häkkinen, 2009) which may lead to distinct long-term adaptations. Additionally, strength adaptations of untrained individuals during initial strength training stages seem to be influenced by the pre-existing strength level (James et al., 2018).

The use of heavy loads is recommended to increase maximal strength (Jenkins et al., 2017; Schoenfeld, Grgic, Ogborn, & Krieger, 2017). Additionally, it has been suggested that training programs with heavy loads promote increases not only in maximal capacity of force production but also in rapid force production measured by rate of force development (RFD) which is the rate at which the force-time curve increases in explosive contractions (Pareja-Blanco, Alcazar, Cornejo-Daza, et al., 2020; Tøien, Haglo, Unhjem, Hoff, & Wang, 2018; Vila-Cha, Falla, & Farina, 2010). Also, when analyzing specific time points of this curve, it is possible to distinguish the origin of adaptations. On one hand, the initial 50 to 100ms have been related to neural adaptations as greater firing frequency (Del Vecchio, Casolo, et al., 2019; Del Vecchio, Negro, et al., 2019; Maffiuletti et al., 2016; Pearcey, Alizedah, Power, & Button, 2021) or greater rate of agonist muscle activation (Aagaard, Simonsen, Andersen, Magnusson, & Dyhre-Poulsen, 2002; Cossich & Maffiuletti, 2020; Orssatto et al., 2020; Tillin et al., 2010). On the other hand, muscular adaptations as muscle thickness, cross-sectional area and muscle architecture (Andersen, Andersen, Zebis, & Aagaard, 2010; Cossich & Maffiuletti, 2020; D'Emanuele et al., 2021; Folland, Buckthorpe, & Hannah, 2014) seem to be associated to adaptations in late RFD.

As previously described, although several studies have characterized the input from the Central Nervous System (CNS) to the agonist muscle during strong contractions, few studies have evaluated the intermuscular coordination patterns during force production. Changed agonist-antagonist relationship has been demonstrated following a period of strength training, with the antagonist muscle usually decreasing its activity (Arabatzi & Kellis, 2012; Balshaw et al., 2019; Häkkinen et al., 1998) although it depends on the elicited task and the mode of contraction (Santos et al., 2023). Furthermore, global coordination has been assessed through the extraction of muscle synergies, namely with the comparison of individuals with and without strength training experience (Kristiansen, Madeleine, Hansen, & Samani, 2015; Santos et al., 2021), although only one study has observed the effects of a strength training program (Kristiansen, Samani, Madeleine, & Hansen, 2016). Nevertheless, other approach

has been used to assess specific neural mechanisms of motor control between pairs of muscles, the intermuscular coherence (IMC). This method of analysis of EMG signals refers to the cross-correlation between the frequency power spectrum of two muscles and allows to understand how the analyzed muscles may share common corticospinal drive to the motoneurons (Farmer, 1998; Farmer, Bremner, Halliday, Rosenberg, & Stephens, 1993; Salenius, Portin, Kajola, Salmelin, & Hari, 1997). Strength trained individuals have presented lower IMC in beta band (15 – 35 Hz) between synergist muscles (Charissou, Vigouroux, Berton, & Amarantini, 2016) as well as lower corticomuscular coherence (Ushiyama, Takahashi, & Ushiba, 2010). Additionally, one study evaluating the adaptations in IMC between synergist muscles with 14 weeks of strength training showed that during submaximal contractions (70% maximum voluntary contraction (MVC)) increased IMC in gamma band (> 40 Hz) may be found, as well as sporadic peaks at MVC (Walker et al., 2019). Concerning the relationship between agonist and antagonist muscles, strength trained individuals showed higher suppression of corticomuscular oscillations in beta band than endurance trained ones (Dal Maso, Longcamp, & Amarantini, 2012), although there is lack of research around this topic.

Current research still lacks to describe the adaptations with strength training in agonist-antagonist IMC during maximal force production, and even relationships between synergist muscles are not fully understood. Additionally, the timings of these adaptations during the initial stages of strength training are not known, and it may be useful to understand how different mechanisms contribute differently overtime. Thus, the main purpose of this study is to establish the time course of adaptations in muscle activation and coordination in maximal and rapid strength of untrained individuals during the initial stage of strength training. To characterize the neural mechanisms involved in changes concerning maximal and rapid force production, muscle activation and coordination measured by IMC between synergist as well as antagonists during a maximal isometric task will be assessed. We hypothesize that maximal and rapid force production will increase with training and that the associated mechanisms will likely be explained by an increased initial activation of knee extensor muscles as well as changed IMC between muscles with different functional roles, which may reflect an adaptation in global motor control during maximal force production.

METHODS

Participants.

Eleven participants were included in this study (age: 22.6 ± 3.1 years; height: 176.4 ± 7.9 cm; weight: 70.5 ± 14.9 kg). The participants were healthy men without history of musculoskeletal injuries within the last 6 months. Although all participants were active physical education students, they did not have any strength training background. All participants provided informed written consent. This study was approved by the Faculty's Ethics Committee (CEIFMH N.º: 24/2021) and all procedures adhered to the Declaration of Helsinki.

Data collection.

Experimental approach. Aiming to assess the effect of strength training in the ability of the neuromuscular system to generate force and to assess the time course of intermuscular coordination adaptations, participants were included in a high-bar back-squat training program.

Each participant was requested to go to the laboratory in six occasions. The first session was used to familiarize the participants with the testing tasks as well as with the back-squat exercise. The remaining five sessions were similar between them and were used to evaluate the mechanical and neuromuscular outputs. The first of these sessions took place one week after the familiarization session and was used as baseline (BSL), after which the participants were instructed to maintain their regular physical activity without adding strength training exercises. After two weeks of strength training abstinence, the participants were evaluated again, with this session accounting as the beginning of the training period (W0). After W0, the participants started the training program and were evaluated every two weeks. Thus, the third, fourth and fifth evaluation sessions were conducted after two (W2), four (W4) and six weeks of training (POS), respectively. The evaluation session after the sixth week was the final session that evaluated training adaptations corresponding to the training program end.

Strength training. The training program lasted six weeks with three training sessions per week, which resulted in 18 training sessions. The strength training program consisted in 5 sets of 10 repetitions with 2 minutes of rest between sets (Izquierdo et al., 2011) of back-

squats. The exercise intensity was set at 75% of 1 repetition maximum (RM) of the back-squat. The participants were instructed to perform the exercise with the concentric phase following a controlled eccentric phase. In the final repetitions of the last sets the researcher could spot the participants, and in sets at which the researcher help was needed in 2 or more repetitions, the load was decreased by 2,5kg for the subsequent set. During the training program the relative load was maintained, with absolute load progressions every two weeks relatively to the back-squat 1RM determined during the evaluation sessions.

1RM Determination. For the squat 1RM determination, we used a progressive loading squat test. The squat was performed with a high-bar position, and a squat depth corresponding to a knee angle of 80-90º. Participants started to perform 5 repetitions with the unloaded barbell (20kg), incrementing 10-20kg each time. Afterwards, participants performed 3 repetitions with each load until the load was challenging, and finally, they performed sets of 1 repetition with smaller load increases (~5kg) until the RM determination.

Testing procedures. The evaluation session started with a 5-minute cycle ergometer (Monark Exercise AB, Sweden) warm-up. Subsequently, participants were evaluated in isometric maximal bilateral leg press (extension of the hip, knee and ankle). A horizontal leg press machine with custom-build force platform (Faculty of Human Kinetics) was used to assess lower limb maximal strength. The leg press machine was adjusted so the participants knee-angle was approximately 110º (107º according to Peltonen and colleagues (Peltonen, Walker, Lähitie, Häkkinen, & Avela, 2018)). Three maximal voluntary contractions (MVC) were performed by each participant. Participants were asked to perform each repetition as fast and forceful as possible and to maintain the maximal force during 3-5s. Repetitions presenting a visible initial countermovement were excluded and one more repetition was performed. Thereafter, the 1RM of the participants was assessed. All strength tests were accompanied by verbal encouragement.

EMG collection. All tests were accompanied by data collection of myoelectrical signals. These signals were recorded on 7 muscles of the right side of the body: gluteus maximus (GM), vastus lateralis of quadriceps (VL), rectus femoris of quadriceps (RF), vastus medialis of quadriceps (VM), biceps femoris long head (BF), lateral gastrocnemius (GL) and tibialis anterior (TA). The muscles were selected so we could assess the lower limb agonist muscles

during the triple extension of the lower limb, and so that we could assess agonist-antagonist pairs of each lower limb joint. The electrodes were placed according to SENIAM (Surface EMG for Non-Invasive Assessment of Muscles). Before the placement of the electrodes, the skin was shaved and cleaned with alcohol to minimize skin impedance. Surface EMG was acquired using 7 bipolar surface electrodes (EMG Delsys, TrignoTM), fixed with specially designed adhesive interface, aligned with the muscle fibers (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000) and then additionally fixed with tape to avoid movement artefacts. EMG signals were preamplified and band-pass filtered between 20 and 450Hz, while digitized at 1000 samples/s. After, the EMG signals were corrected for the 48-ms delay inherent to the Trigno EMG system.

Data processing

Force data. Initially, force data was low pass filtered (12Hz, 4th order Butterworth). The leg press isometric MVC peak force (PF) was defined as the highest value of force achieved in each repetition. Absolute rate of force development (RFD) for the leg press MVC was calculated as the slope of the force-time curve (Δforce/ Δtime) in incremental epochs of 50ms (0-50ms; 50-100ms; 100-150ms; 150-200ms) starting from the onset of contraction. The onset of contraction was defined as the time point where the force exceeded the baseline by 10 N. Peak RFD (PRFD) was defined as the maximum force-time slope at time windows of 20ms (Rodríguez-Rosell, Pareja-Blanco, Aagaard, & González-Badillo, 2018). At each time interval where RFD was computed, we also calculated the normalized RFD to MVC to assess the percentage of force exerted at each time point. We selected and analyzed the repetition with the highest PRFD if the PF value was >95% of the highest PF value across the three repetitions.

EMG processing. Raw EMG signals of VL, RF and VM were band-pass filtered (20-450Hz), rectified and smoothed with a low-pass filter (12Hz, 4th order Butterworth). Normalization was made to the average value of the 100ms across the EMG peak of the leg press isometric MVC. Rate of EMG rise (RER) of VL, RF and VM was determined as the EMG increase calculated from the onset of electrical activity to the point correspondent to PRFD (Del Balso & Cafarelli, 2007). RER in time intervals of 0-50ms and 50-100ms was also calculated. The

onset of electrical activity was defined as the time point where the EMG exceeded the baseline by 3 standard deviations.

Intermuscular coherence (IMC). Coherence analysis was performed using Matlab 2018a (Mathworks, Natick, MA, United States). Before data analysis, all data files were visually inspected to detect possible artifacts. In the cases where signals demonstrated some disruption or noise the repetitions were excluded from the analysis. IMC analysis was performed during 2500ms of each repetition, starting from 500ms after the onset of force production. A total of 7.5 seconds were analyzed. Before IMC analysis, raw EMG signals were full wave rectified (Boonstra et al., 2008; Walker et al., 2019; Wang et al., 2015), and data was divided into non-overlapping windows of 500 samples in length. The signals were subjected to fast Fourier transform, which gave a frequency resolution of 2Hz. IMC was calculated as the cross-spectrum normalized by the auto-spectrum:

$$C_{xy}(f) = \frac{\left|P_{xy}(f)\right|^2}{P_{xx}(f)P_{yy}(f)}$$

where $C_{xy}(f)$ is the magnitude squared coherence between two rectified EMG signals, $x(t)$ and $y(t)$, for a given frequency f. $P_{xy}(f)$ is the cross-spectrum and $P_{xx}(f)$ and $P_{yy}(f)$ are the auto-spectrum of $x(t)$ and $y(t)$, respectively. Coherence above Z was considered significant (Rosenberg, Amjad, Breeze, Brillinger, & Halliday, 1989; Walker et al., 2019):

$$Z = 1 - \alpha^{1/(L-1)}$$

where L is the total number of sections and the significance level α was set to 0.05. The L-value was 15.

IMC was computed for the follow pairs of muscles: VL-VM, VL-RF, VM-RF, VL-GM, VL-GL, VL-BF, RF-BF and GL-TA. Total coherence between 3-100Hz was averaged across participants at each timing of evaluation, as well as coherence sectioned into 3-7, 8-14, 15-35, 40-60 and 60-100 Hz bands. Within 15-35Hz band representing beta band, two additional 15-24, 25-35 Hz bands were separated. Average coherence within each band was used to compare the evaluation timings (BSL, W0, W2, W4 and POS).

Statistics

Statistical analysis was made using jamovi software version 2.3.28.0 (Sydney, Australia). We verified normality through the Shapiro-Wilk test. A repeated measures ANOVA with four levels (W0, W2, W4 and POS time-points) was used to assess differences during the time course of the training program. When normality was not assumed, a Friedman test was used, and when sphericity was not assumed, a Greenhouse-Geisser correction was made. Tukey adjustments were used in *Post hoc* tests of ANOVA, and Durbin-Conover adjustments were used in *Post hocs* of Friedman test. The previously described analysis was made to all variables (PF, PRFD, absolute and normalized RFD in time intervals, RER of each knee extensor muscle as well as average coherence within each band). As IMC values within each band were not normally distributed, we applied a log 10 transformation to allow parametric tests to be performed.

We assessed the relative reliability of the measurements between the BSL and W0 time points by calculating two-way mixed-effects intraclass correlation coefficients [ICC(3,1)] (Koo & Li, 2016), with 95% confidence interval. ICC values were considered: poor, <0.5; moderate, 0.5-0.75; high, 0.75-0.9; excellent, >0.9. Additionally, we calculated standard error of measurement [SEM] as an absolute reliability measurement (Weir, 2005). All statistical analyses were performed using a significance level of $p < 0.05$. Data is presented as mean ± *SD*. Cohen' *d* was calculated as measure of effect size. Effect size was considered small, medium or large for Cohen' *d* of 0.2 – 0.5, 0.5 – 0.8 and > 0.8, respectively.

RESULTS

Reliability. Most mechanical variables regarding force production (PF, PRFD, absolute RFD at time intervals and %MVC at 50ms) revealed high to excellent reliability between BSL and W0 ($0.85 < ICC < 0.98$), with exception of %MVC at 100ms that was moderate (ICC = 0.73) and poor at 150 and 200ms (ICC = 0.37 and 0.29, respectively). The SEM of the variables with high to excellent reliability was consequently low, with the SEM of %MVC at 100, 150 and 200ms, that presented poor to moderate reliability varying from 4.69 to 7.34%.

Regarding muscle activation, there were variables presenting high (RER of RF, RER of RF between 0 and 50ms and between 50 and 100ms), moderate (RER of VL and VM, RER of VL and VM between 0 and 50ms) and poor (RER of VL and VM between 50 and 100ms) relative reliability. The SEM values for RER of VL, VM and RF were similar ranging from 0.07 to 0.08 %/ms, and the RER at time intervals for the three muscles ranging from 0.12 to 0.18 %/ms.

For the IMC analysis, ICC values revealed that most of the 64 variables (8 pairs of muscles x 8 bands of interest) present moderate to excellent reliability (moderate, 42.2% of the variables; high, 14.1%; excellent, 4.7%), although 39.1% of the variables present poor reliability.

Force production. A time effect was shown for PF during the leg press, with the final moment of evaluation (POS) being significantly different from the first (W0; $p = 0.011$ and $d = 0.944$). Although there was a trend for a progressive increment of PF along the weeks, there were not significant differences in post hoc comparisons between W0 and W2 or W4 even with medium effect sizes ($p = 0.064$; $d = 0.516$ and $p = 0.073$; $d = 0.583$, respectively). Concerning PRFD, only differences between W0 and POS were found ($p = 0.015$ and $d = 0.888$). Absolute and relative RFD only presented differences in post hoc comparisons between W2 and POS for absolute RFD between 50 and 100ms that was greater after training ($p = 0.048$; $d = 0.302$), and in the overall ANOVA for the relative RFD represented by %MVC at 200ms ($p = 0.013$; $d = 0.917$) that tended to reduce with training. Results are detailed in Table 5.1.

Table 5.1. Force and muscle activation related variables.

Variable	W0	W2	W4	POS
Force Production				
PT (N) *	2514 ± 578	2885 ± 836	2877 ± 705	2964 ± 664 #
PRFD (N/ms)	9.98 ± 2.13	9.94 ± 0.92	10.30 ± 1.97	11.20 ± 2.70 #
RFD0-50ms (N/ms)	5.36 ± 1.82	5.30 ± 1.56	5.05 ± 2.13	5.78 ± 2.84
RFD50-100ms (N/ms)	8.97 ± 2.01	8.96 ± 1.49	9.05 ± 2.05	9.60 ± 2.60 §
RFD100-150ms (N/ms)	8.63 ± 2.00	8.87 ± 1.02	8.96 ± 1.60	9.57 ± 2.47
RFD150-200ms (N/ms)	6.14 ± 2.67	6.41 ± 1.67	6.10 ± 2.43	6.93 ± 3.40
%MVC50ms	12.28 ± 4.23	10.55 ± 4.09	9.91 ± 4.61	11.27 ± 5.40
%MVC100ms	31.53 ± 8.93	27.41 ± 8.90	26.58 ± 9.80	28.73 ± 10.80
%MVC150ms	49.58 ± 10.09	43.68 ± 11.06	42.75 ± 11.36	45.67 ± 11.64
%MVC200ms *	62.07 ± 9.64	55.03 ± 11.60	53.43 ± 10.97	57.51 ± 10.01
Muscle Activation				
RER_VL (%/ms)	0.43 ± 0.08	0.39 ± 0.16	0.41 ± 0.09	0.43 ± 0.12
RER_RF (%/ms) *	0.36 ± 0.13	0.29 ± 0.11	0.26 ± 0.08 ###	0.29 ± 0.09
RER_VM (%/ms)	0.44 ± 0.08	0.41 ± 0.13	0.43 ± 0.16	0.43 ± 0.19
RER_VL0-50ms (%/ms)	0.75 ± 0.17	0.65 ± 0.37	0.70 ± 0.22	0.76 ± 0.30
RER_RF0-50ms (%/ms)	0.73 ± 0.31	0.46 ± 0.26 ##	0.44 ± 0.24 ###	0.51 ± 0.21
RER_VM0-50ms (%/ms)	0.79 ± 0.17	0.61 ± 0.32	0.73 ± 0.37	0.74 ± 0.42
RER_VL50-100ms (%/ms)	0.74 ± 0.24	0.61 ± 0.25	0.74 ± 0.19	0.66 ± 0.19
RER_RF50-100ms (%/ms)	0.70 ± 0.24	0.53 ± 0.23	0.48 ± 0.26 ###	0.60 ± 0.18
RER_VM50-100ms (%/ms)	0.70 ± 0.17	0.67 ± 0.22	0.65 ± 0.21	0.55 ± 0.28

EMG – Electromyography; MVC – Maximum voluntary contraction; PF – Peak force; POS – Ending of training; PRFD – Peak rate of force development; RER – Rate of EMG rise; RF – Rectus Femoris; RFD – Rate of force development; W0 – Training beginning moment; W2 – Week 2 of training; W4 – Week 4 of training; VM – Vastus Medialis; VL – Vastus Lateralis. * $p < 0.05$ in overall repeated measures ANOVA; # $p < 0.05$ in post hoc comparisons between W0 and POS; ## $p < 0.05$ in post hoc comparisons between W0 and W4; ### $p < 0.05$ in post hoc comparisons between W0 and W2; § $p < 0.05$ in post hoc comparisons between W2 and POS;

Knee extensor activation. Muscle activation measured by RER from the onset of electrical activity to the point at PRFD showed to be unchanged for VM and VL. For RF, the ANOVA revealed a significant decreasing effect of training overtime ($p = 0.045$; $d = 0.777$) with post hoc comparisons presenting differences between W0 and W4 ($p = 0.030$; $d = 0.904$).

Regarding RER at time intervals for VM and VL there was not any significant training effect. For RF, although there were not significant overall differences, there was post hoc differences between W0 and W2 for RER between 0 and 50ms (p = 0.044; d = 0.904) and between W0 and W4 for RER between 0 and 50ms (p = 0.020; d = 1.005) as well as between 50 and 100ms (p = 0.028; d = 0.863), with all the significant differences representing a decreased activation. Results are detailed in Table 1.

Intermuscular coherence. Figure 5.1 shows all the analyzed muscle pairs at each time point. A visual inspection of the coherence data series revealed that IMC at 25 to 45 Hz, encompassing the higher beta band as well as the initial frequencies of gamma band, presented significant peaks between VL and VM. IMC between VM and RF has also presented a significant peak at this frequency only at W0. Significant peaks at occasional time points have been shown between VL and BF at 8 to 14 Hz and 15 to 35 Hz bands, and between GL and TA at 25 to 45 Hz only at the two first evaluations (W0 and W2).

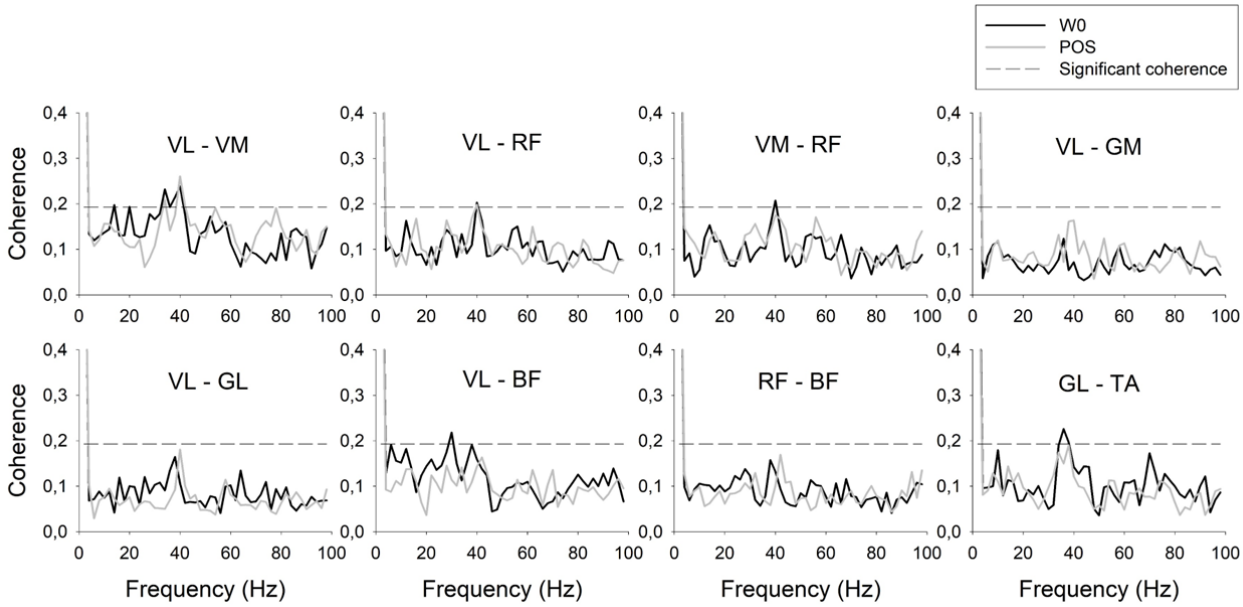

Figure 5.1. Intermuscular coherence of the analyzed pairs of muscles at W0 and POS between 0 and 100 Hz. The horizontal line represents significant coherence. BF – biceps femoris; GL – gastrocnemius lateralis; GM – gluteus maximum; POS – Ending of training; RF – rectus femoris; TA – tibialis anterior; VM – vastus medialis; VL – vastus lateralis; W0 – Training beginning moment.

The overall result of the ANOVA for each pair of muscles at each time point did not show any significant effect of training in IMC with exception of GL and TA IMC between 3 to 100 Hz that tended to be reduced with training (p = 0.025; d = 0.963). However specific differences between time points have been revealed by post hoc comparisons. Concerning agonist-agonist pairs, increased IMC between VM and RF at 3 to 7 Hz (p = 0.012; d = 0.922) and between VL and RF at 15 to 24 Hz (p = 0.017; d = 0.857) was shown between W0 and POS. Regarding synergist pairs acting at different joints, VL and GL presented decreased IMC at 25 to 35 Hz after the six weeks of training (p = 0.047; d = 0.784), and a significant occasional increase between VL and GM at 8 to 14 Hz has been shown between W2 and W4 (p = 0.041; d = 0.784). Agonist-antagonist pairs have also revealed occasional differences, with decreased IMC between VL and BF after the first two weeks of training at 8 to 14 Hz (p = 0.045; d = 0.467) and 15 to 24 Hz (p = 0.017; d = 0.567) bands, although these changes had not been maintained during the subsequent weeks. Additionally, decreased IMC at 3 to 100 Hz frequency range has been shown between RF and BF between W4 and POS (p = 0.008; d = 0.065) and between GL and TA between W2 and W4 (p = 0.048; d = 0.725).

DISCUSSION

The present study assessed adaptations in lower limb muscle activation and coordination following a 6-week strength training period, describing the time course of those adaptations. Training may lead to adaptations in the mechanics of force production as result of specific changes in muscle activation and coordination strategies. Maximal force production during a leg press task tended to increase during the training period, although PF and PRFD have only increased significantly after the six weeks of training. The assessment of RER revealed reduced RF activation, and the IMC analysis showed significant peaks between pairs of agonists as well as between pairs of agonist-antagonist muscles. Although the IMC reliability was moderate to high for most variables, there was also some variables presenting only poor reliability, and caution should be taken when interpreting results. Nevertheless, there was coupling changes across the analyzed bands, with muscles with different functional roles presenting specific adaptations overtime.

First, it is important to consider the reliability calculations that involved the experimental group as its own control. The mechanical data presented promising reliability values. PF, PRFD, absolute RFD and relative RFD at 50ms presented high to excellent reliability. This is in line with previous research considering the plantar flexor muscles that found also high to excellent reliability with exception for the initial 50ms of contraction that seems to present greater intersession variability (Oranchuk, Storey, Nelson, Neville, & Cronin, 2022; Tavakkoli Oskouei et al., 2021). In our study we found high to excellent reliability in these early RFD measurements. The automated definition of the onset, as we measured may be more reliable than in studies using manual detection (Thompson et al., 2012). However, we have just found poor to moderate reliability in relative RFD at time points from 100ms onwards, which may be corroborated by a previous study also assessing the leg press and presenting unreliable measurements (Sleivert & Wenger, 1994). Additionally, the calculation of the mentioned variables considers the PF of the day, and as we used the MVC repetition with the highest PRFD unless it did not reach 95% of the maximum of the day, it may present more variation namely at later intervals. Concerning muscle activation measured from the EMG-time curve, results from poor to excellent reliability have been shown previously, depending on the studied muscle as well as the task (Clark, Cook, & Ploutz-Snyder, 2007;

Sleivert & Wenger, 1994; Tavakkoli Oskouei et al., 2021) which are in line with our results. Regarding IMC measurements, although most variables presented moderate to high reliability, some variables only presented poor reliability. Previous research has shown that monopolar current measurements may be preferable during tasks without impacts (as the isometric leg-press) or between muscles far enough to avoid crosstalk (Mohr, Schön, von Tscharner, & Nigg, 2018). Nevertheless, bipolar electrodes, as the ones used in the present study, may be used to study IMC, although they can be less sensitive to detect changes in IMC than the monopolar current systems. Bipolar electrodes also revealed good reliability between vastus lateralis and vastus medialis (Mohr et al., 2018). Additionally, we cannot discard the hypothesis that untrained individuals may present higher interday variability in IMC.

Maximal and rapid strength

Six weeks of squat training led to increased PF. Previous research showed increased isometric MVC PF following six weeks of dynamic strength training (Jenkins et al., 2017; Knight & Kamen, 2001; Pelzer, Ullrich, & Pfeiffer, 2017; Vila-Cha et al., 2010). Although the sample size is small and caution should be taken when interpreting the results, it is interesting that our results only demonstrated a training effect after the sixth week of training. Previous studies reported increased isometric knee extension PF following only 3 weeks of training but only when training is performed with high loads (80% 1RM) (Jenkins et al., 2017). The same study showed that PF continued to increase until the completion of the 6 weeks for the group who trained with high loads, and that significant increases in PF with low loads were only achieved after 6 weeks. Others also found increases in isometric knee extension torque/force after 10 days (Seynnes, De Boer, & Narici, 2007) or 3 weeks of dynamic knee extension training (Falvo, Sirevaag, Rohrbaugh, & Earhart, 2010), in isometric wrist flexion after 3 weeks of biceps curl training (Mason et al., 2017) or 2 weeks of dynamic wrist flexion training (Mason et al., 2020). However, 2 weeks did not seem enough to increase isometric strength following dynamic elbow flexion training, with significant increases being observed after 4 weeks only with high loads (Jenkins, Housh, Buckner, Bergstrom, Cochrane, et al., 2016). Although significant results were only observed at the final evaluation, a progressive trend to an increase may be observed. This progressive trend

to an increase may also be observed after 2 (Knight & Kamen, 2001) and 3 weeks of strength training (Vila-Cha et al., 2010) although significant results were only achieved after the sixth week. The study of Knight and Kamen (Knight & Kamen, 2001) has shown that individuals without training background present an increase in isometric force due to familiarization even without training. The familiarization session and the previously BSL session performed in our study may have helped to minimize the magnitude of this learning effect, although BSL and W0 measurements have shown good reliability. Additionally, it has been shown that neuromuscular adaptations are task-specific, and that dynamic training programs will tend to promote greater gains in dynamic than in isometric strength (Buckthorpe et al., 2015).

We have also found greater PRFD after six weeks of training. Previous research showed increased RFD after 6 weeks of dynamic strength training (Nicholson, Ispoglou, & Bissas, 2016; Vila-Cha et al., 2010). In our study we did not find differences in 0-50ms interval, but a trend for increased 50-100ms absolute RFD was observed. Previously, the 0-50ms interval in RFD analysis have shown to be greater in strength trained individuals when compared to untrained ones, although the 50-100ms interval may be increased for the untrained individuals possibly because of delayed activation of the agonist muscles (Del Vecchio et al., 2018; Orssatto et al., 2020; Tillin et al., 2010). These intervals are related to greater neural input to the muscles, namely greater firing frequency of motor units and muscle fiber conduction velocity (Del Vecchio et al., 2018; Del Vecchio, Negro, et al., 2019). The fact that we only verified significant results at 50-100ms time window may suggest that 6 weeks led to increased neural output to the muscles, although this activation may be delayed when comparing with long-term trained individuals. Concerning later intervals, our results have also shown decreased relative RFD at 200ms. The later intervals are related with cross-sectional area or muscle thickness, as well as PF (Cossich & Maffiuletti, 2020; Maffiuletti et al., 2016). Although we do not present muscular adaptations to the 6-week training program, it is plausible that the load dynamics adopted in this study led to gains in muscle mass. The decreased relative RFD at 200ms may be surprising, although it results from an unchanged absolute RFD at 150-200ms time interval, and a great magnitude increase in PF during the training period.

Furthermore, dynamic strength training programs have shown to increase RFD at specific time windows. Increased maximal rate of torque development of knee extensor and flexor muscles was observed after 10 weeks of barbell deadlift training, but also at time windows of 50 and 200ms (Thompson et al., 2015). Similar results were also achieved after 14 weeks of heavy lower limb training (Aagaard et al., 2002). Also, heavy leg press training (90% 1RM) for 8 weeks led to increased RFD at early and later time windows when performed with or without eccentric overload (Tøien et al., 2018). It is important to note that specific results may be found in current research. For example, 8 weeks of bench press training have also increased early RFD at 50ms during a bench press, but only when the velocity loss during the training program was 0%, while greater velocity losses resulted in increased later RFD (Pareja-Blanco, Alcazar, Cornejo-Daza, et al., 2020). Additionally, velocity losses above 20% have shown to decrease the early 50ms RFD in isometric squat following 8 weeks of squat training (Pareja-Blanco, Alcazar, Sánchez-Valdepeñas, et al., 2020). One study comparing 1 vs 4 vs 8 exhausting squat sets also found decreased RFD at all time intervals (Marshall, McEwen, & Robbins, 2011). The previous cited studies observed differences in previously trained men, and as it was stated above, different training background will lead to different neuromuscular adaptations. Also, differences in study design may lead to different results.

Knee extensor activation

Muscle activation was measured by RER, and it was observed that the monoarticular portions of the quadriceps remained similar from W0 to POS, while RF decreased its activation overtime. This may be surprising, since RF is agonist of knee extension, and it was expected a greater activation of the knee extensors. Previous studies have found increased activation during the initial epochs of the contraction of plantar flexors following 4 weeks of isometric plantar flexion training (Del Balso & Cafarelli, 2007), knee extensors of strength trained athletes during the initial 25ms of contraction (Tillin et al., 2010), elbow flexors during the initial 30ms only after 2 weeks of dynamic elbow flexion training (Jenkins, Housh, Buckner, Bergstrom, Smith, et al., 2016), VL during a jump squat after 10 weeks of power training only for a stronger group (James et al., 2018), or knee extensors during isometric knee extension after 14 weeks of heavy lower limb training (Aagaard et al., 2002). The fact that

the participants of the present study did not have any strength training experience may be related to the absence of adaptations concerning VL and VM activation, as suggested by James et al. (2018). Also, the remaining enumerated studies evaluated single-joint while in our study we have evaluated a multi-joint exercise. This fact may have resulted in different neuromechanical patterns of force production since there is evidence of different neural input to agonist muscles between single- and multi-joint exercises (Ema, Sakaguchi, Akagi, & Kawakami, 2016) as well as between closed (as the leg press) and open kinetic chain (as knee extension) (Boccia, Martinez-Valdes, Negro, Rainoldi, & Falla, 2019; Irish, Millward, Wride, Haas, & Shum, 2010). Indeed, the decreased activation of RF observed in the present study may be related with better efficiency of RF activation as a biarticular muscle, agonist of knee extension and antagonist of hip extension. Activity of RF during closed chain exercises has been demonstrated to be lower when compared to open chain exercises (Ema et al., 2016; Stensdotter, Hodges, Mellor, Sundelin, & Häger-Ross, 2003). Additionally, when knee extension is performed with concomitant hip extension, RF activation has decreased when compared to knee extension without hip extension, which may contribute to increased hip extension torque (Ema et al., 2016). In previous work of our group, although strength trained individuals did not present significantly different RF RER from untrained ones, acute responses to training were different between the two groups, showing possible modulation of RF activation by the trained ones (Santos et al., 2024). Also, RF presents specific regional recruitment (Watanabe, Vieira, Gallina, Kouzaki, & Moritani, 2021), also depending on hip flexion angle (Mitsuya, Nakazato, Hakkaku, & Okada, 2023), and at long-term different adaptations may result from the consecutive solicitations of the muscle in specific conditions, and the fact that the training program only included squats may have led to these adaptations during an isometric leg press task.

Intermuscular coherence

Muscle coordination has been assessed through muscle coupling between pairs of muscles with distinct functional roles. Namely, IMC analysis distinguishes signal input frequencies common between a pair of muscles, and concerning the correlation between the respective power spectral densities it allows to infer about the neural origin of movement control (Grosse, Cassidy, & Brown, 2002).

Concerning agonist coupling, in this study, we identified at W0 significant IMC peaks between 25 and 45Hz between the single-joint portions of quadriceps and between VM and RF. This frequency range encompasses frequencies of beta (15 – 35 Hz) and gamma (> 40 Hz) bands usually associated with corticospinal pathway (Baker, Olivier, & Lemon, 1997; Conway et al., 1995; Farmer et al., 1993; Kattla & Lowery, 2010; Mima & Hallett, 1999). Beta band has also been linked to oscillations within the sensorimotor cortex and the integration of information from other cortical and subcortical structures as well as Ia afferents or Renshaw cells (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013; Ushiyama et al., 2011), while gamma band has been associated to attentional focus and efferent drive during strong isometric voluntary contractions or dynamic effort (Brown, 2000; Brown, Salenius, Rothwell, & Hari, 1998; Gwin & Ferris, 2012; Mima, Simpkins, Oluwatimilehin, & Hallett, 1999). The peaks observed in IMC between VL and VM have remained after training. On the other hand, IMC between VL and RF increased within the 15-24 Hz frequency range. The fact that rate of activation has decreased but coupling between VL and RF increased at this band may have been an adapting process to better allow the kinetic output transmission from proximal to distal joints. Additionally, greater IMC below 7 Hz was observed between VM and RF, which is associated to greater common drive to the muscles (De Luca & Erim, 1994; De Luca, LeFever, McCue, & Xenakis, 1982) and a greater synchronization in firing rate of motor units modulated by the CNS (Castronovo, Negro, Conforto, & Farina, 2015; Rossato et al., 2022). Namely, since RF is antagonist at hip joint, its rate of activation may be decreased to facilitate an increase in torque development at that joint. Concurrently, augmenting common corticospinal input may be more effective to allow a better synchronization with the monoarticular powerful muscles of quadriceps. In our previous work, we have also observed greater IMC at beta band between VM and RF in strength trained individuals (Santos et al., 2024), which means that the greater coupling between RF and the monoarticular knee extensors may be a neural adaptation to optimize maximal force production. On the contrary, one study has found lower beta band IMC between VM and RF in strength trained individuals (Charissou et al., 2016). However, in this study the method of calculation of IMC was based on wavelet analysis, and the evaluated task was an isometric knee extension which requires different patterns of muscle activation as discussed previously. Furthermore, lower IMC at gamma band was observed between RF and VM or VL than

between VM and VL during squats which may suggest a specific mechanism of control of biarticular and monoarticular muscles during dynamic tasks (Maudrich et al., 2022). Nevertheless, no significant changes were observed between VM and VL, which is in line with previous research that did not find differences in IMC between those muscles at any band following 14 weeks of strength training, although greater IMC at gamma band has been found during submaximal contractions at 70% MVC (Walker et al., 2019). Furthermore, it is interesting that corticomuscular coherence, measured between electroencephalographic and EMG of lower limb muscles as the BF, TA and soleus, was lower in ballet dancers and weightlifters than in untrained individuals, which reveals a non-synchronized discharge of corticospinal cells in chronically trained athletes, which suggests that long-term training leads to fine postural adjustments dependent on specific temporal sequences (Ushiyama et al., 2010).

Regarding synergist muscles acting at different joints, we have also found differences concerning the neural input between VL and GL as well as VL and GM, although VL and GM IMC was an occasional event that resulted from increased IMC of three participants. In its turn, VL and GL showed a trend to a decreased IMC at higher beta band (25 – 35 Hz). As we mentioned before, this band may be associated to corticospinal pathway, and the decreased IMC observed after training may arise from greater efficiency in muscle recruitment to produce joint moments. The fact that we observed altered patterns concerning the integration of RF during the task may also be applied to GL, considering its role as a biarticular muscle, antagonist of knee extension and agonist of plantarflexion. The reduced common corticospinal input to VL and GL after 6 weeks of training may be related to an adaptive role of GL as an ankle stabilizer during lower limb extension tasks (Schoenfeld, 2010; Smale, Shourijeh, & Benoit, 2016), providing a more efficient force transmission. Additionally, the changes in the shared neural input to both muscles may be the result of a flexible adaptation in the recruitment of muscle synergies (Bizzi & Cheung, 2013; d'Avella & Bizzi, 2005), supporting the beta oscillations from cortex to muscles (Aumann & Prut, 2015).

Regarding the agonist-antagonist analyzed pairs, GL and TA showed significant peaks between 25 and 45 Hz (encompassing frequencies from beta and gamma bands). General

IMC (3– 100 Hz) was reduced after the 6 weeks of training. These results may suggest that both muscles share corticospinal projections that tend to be decreased by training, thus reducing co-activation. However, different neural strategies may be adopted concerning the task and the training mode. For example, badminton players presented higher GL and TA synchronization than untrained individuals, although reducing EMG amplitude of the GL during an isokinetic dorsiflexion, which may be interpreted as a more effective control strategy while maintaining ankle stability (Wang et al., 2019). Additionally, it has been shown that distal muscles have stronger corticospinal connections than proximal ones (Brouwer & Ashby, 1990; Semmler, Ebert, & Amarasena, 2013; Ushiyama et al., 2010) with weaker Renshaw cell inhibitory feedback (Rossi & Mazzocchio, 1991; Williams & Baker, 2009) and greater number of muscle spindles in some muscles as TA or soleus compared to RF or BF (Banks, 2006; Ushiyama et al., 2010), which suggest that modulation of those mechanisms may contribute to adaptations in IMC after training.

We have also observed that pre-training IMC peaks at alpha and beta band between VL and BF decreased after two weeks of training, although this behavior has not been maintained. This may have been a compensatory neural strategy to overcome initial muscle soreness. Previous research focusing on adaptations following eccentric training reported that biceps brachii muscle soreness only dissipated after two weeks of training (Krentz & Farthing, 2010). Although these findings should not be directly transposed to our study, given our concentric training program, we can assume that muscle soreness was present in the first weeks of training and that the respective prolonged fatigue led to altered agonist-antagonist coordination. Namely, decreased IMC at lower beta (15 – 24 Hz) and alpha (8 – 14 Hz) band may be a consequence of lower corticospinal connectivity, but also from afferent feedback associated to alpha band (Erimaki & Christakos, 2008; Klass, Lévénez, Enoka, & Duchateau, 2008; McAuley & Marsden, 2000). Alpha band is linked to physiological tremor, and although its origin is multifactorial, the modulation of afferent feedback appears to be one mechanism contributing to IMC in this band (McAuley & Marsden, 2000). It has been observed that afferent feedback modulation during an acute fatiguing state affects the CNS control of muscle recruitment (Finn, Kennedy, Green, & Taylor, 2020; Sidhu et al., 2018). Thus, the initial weeks of training may have led to prolonged fatigue that elicited specific agonist-antagonist connectivity modulated by the integration of corticospinal and sensory

information. On the other hand, the decreased general IMC between RF and BF after W4, suggests that initial neural adaptations after 2 weeks of training may be transitional adjustments until the system becomes more efficient with task-specific optimization of central commands achieved with long-term training (Ushiyama et al., 2010). Furthermore, long-term strength trained individuals have shown different mechanisms of motor control of agonist and antagonist muscles, with lower activation and greater corticomuscular beta band suppression of the antagonist muscles (Dal Maso et al., 2012; Dal Maso, Longcamp, Cremoux, & Amarantini, 2017).

The results of this study should be interpreted with caution. First, although valid, the general limitations of the applied data processing methods should be considered when confronting the results with previous research. For example, onset definition of force and EMG may have impact in the results concerning RFD or RER, respectively. Second, muscle selection is determinant for IMC analysis results, as well as the evaluated task. Third, the rectification of EMG signals prior to IMC calculation is still a matter of debate. Rectification is highly recommended for low-force contractions (Farina, Merletti, & Enoka, 2014), although it was not the case of our study. We opted by rectifying EMG signals to a better comparison with relevant studies although both options may be found in the literature. Fourth, the methods of IMC calculation can lead to different conclusions, although most studies calculate magnitude squared coherence as it was done in this study. Finally, it is important to consider that some IMC variables presented only poor reliability between BSL and W0, which may represent interday variability of untrained individuals, and that the significant results should be interpreted with caution because of the small sample size and generally low effect sizes in IMC adaptations.

CONCLUSION

Six weeks of training led to increased maximal and rapid force production of previously untrained individuals. However, mechanical variables during intermediate evaluations were unchanged, which was probably caused by the different tasks used in evaluation and in training. Increased PF, maximal RFD and specific changes in time intervals were achieved with concomitant changes in neural mechanisms concerning agonist muscle activation as well as lower limb muscles coordination. Activation of RF was reduced after training, which may be caused by its role as a biarticular muscle. This adaptation may have resulted in specific coordination patterns involving the RF as it was observed by changes in IMC between RF and the monoarticular portions of the quadriceps. Additionally, adaptations between synergist muscles acting in different lower limb joints as well as agonist-antagonist control were observed, suggesting that training led to neuromechanical strategies to enhance the capacity of maximal and rapid force production. This study brings new insights into the training adaptations of previously untrained individuals and may be useful to understand the specific neurophysiological responses during an initial training stage, namely concerning the interactions between agonist, synergist and antagonist muscles. Further research should focus on changes in coordination with different training methods in populations with strength training background, so it may be possible to understand if these interactions between muscles remain adapting even during later training stages. Additionally, better understanding on how coordination during dynamic complex tasks evolves in temporal and/or spatial components resulting from synergy extraction and EMG profiling analysis is needed.

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Chapter 6

Chronology of neural adaptations to strength training: intermuscular coordination during isometric submaximal torque production

Santos, P.D.G., Vaz, J.R., Gomes, M., Oliveira, J., Infante, J. & Pezarat-Correia, P. (2024). Chronology of neural adaptations to strength training: intermuscular coordination during isometric submaximal torque production [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

ABSTRACT

Strength training induces neural adaptations that lead to changed muscle activity during maintained isometric torque production at submaximal intensities. Namely, with training muscle activity is decreased for the same torque level, and this concerns to the agonist as well as the antagonist muscle, although the adaptations may manifest at different timings. Nevertheless, it is not fully understood what happens in muscles with different functional roles and how they are coordinated at different intensities. Two experiments were conducted to understand: i) how these adaptations emerge following 6 weeks of strength training, and ii) what adaptations are presented by long-term trained individuals when compared to short-term trained and untrained individuals. Electromyography (EMG) during knee extensions at 20-80% MVC was collected from vastus lateralis (VL), rectus femoris (RF), vastus medialis (VM) and biceps femoris (BF). Torque-EMG as well as agonist-antagonist relationships were calculated. Additionally, to understand the coupling between muscles, intermuscular coherence (IMC) between agonist muscles and between agonist-antagonist pairs was calculated. Six weeks of squat training did not alter the relationships between torque and EMG, although a general increase in IMC at beta- and gamma-bands was observed between agonist muscles, namely between VL and RF. The long-term trained individuals presented lower general activity of the agonist muscles and generally lower IMC between agonists but also between agonist-antagonist pairs, especially at gamma-band during strong contractions. This study brings novel insights concerning the motor control of muscles with different functional roles during submaximal torque production, suggesting transitional adjustments in coordination at initial training stages, and continued adaptations at the long-term allowing greater neuromuscular efficiency.

Keywords: strength training, electromyography, agonist-antagonist relationship, intermuscular coherence, torque-EMG relationship, physical fitness expertise

INTRODUCTION

The relationship between torque at submaximal contractions and muscle activity measured by electromyography (EMG) is vastly explored. This relationship shows an increased EMG activity at greater torque levels. In isometric contractions this relationship has been reported as being linear, non-linear or quadratic (Amarantini & Bru, 2015; Onishi et al., 2000; Pincivero & Coelho, 2000; Tillin, Pain, & Folland, 2011; Watanabe & Akima, 2009), depending on several factors as the methodological approach to determine the relationship, which includes EMG data collection and processing, the torque range or the force direction (Amarantini & Bru, 2015; Anders, Brose, Hofmann, & Scholle, 2008; Paquin & Power, 2018; Pincivero & Coelho, 2000) and the evaluated muscle and the respective torque-angle relationship, muscle type or co-contraction of the antagonist muscles (Amarantini & Bru, 2015; S. H. Brown & McGill, 2008; Pincivero & Coelho, 2000). Nevertheless, this relationship emerges from the well-known Henneman's size principle which states that at greater torque production levels the number of motor units recruited is also greater.

Strength training influences the torque-agonist relationship, as resistance trained individuals present greater linearity of the torque-agonist relationship and lower co-activation of the antagonist muscles than untrained individuals (Amarantini & Bru, 2015). Nevertheless, this is influenced by the methodological approach as stated before, and linear fitting of the torque-agonist relationship has shown to be representative (Balshaw, Massey, Maden-Wilkinson, Lanza, & Folland, 2019). Additionally, in this study it was demonstrated that long-term strength training induces a shift towards less agonist activity at same absolute torque level although short-term training is not enough to induce significant changes (Balshaw et al., 2019). Additionally, 4 weeks of strength training are not enough to change torque-agonist relationship at different submaximal contractions changing only at longer training periods (Häkkinen & Komi, 1983; Narici et al., 1996; Tillin et al., 2011). These results may be interpreted as the interaction between muscles with different functional roles adapts with strength training and that specific coordination patterns contributes differently to a more efficient force production during the time course of training adaptations (Pearcey, Alizedah, Power, & Button, 2021; Santos, Vaz, Correia, Neto, & Pezarat-Correia, 2023).

However, when assessing muscle recruitment during submaximal contractions it is not well understood how different muscles with different functional roles are coordinated. It was shown that coordination between agonist and antagonist muscles may change with training. The slope of the torque-antagonist relationship was different between untrained, short-term and long-term trained individuals, being progressively lower with training experience, although agonist-antagonist relationship was different for untrained individuals but not differing between short-term and long-term trained individuals (Balshaw et al., 2019). Additionally, 4 weeks of strength training appears to be enough to change agonist-antagonist relationship (Tillin et al., 2011). Also, the coupling changes with training between agonist muscles with different anatomical and functional roles, as the coordination between biarticular and monoarticular muscles is not well understood.

One possible way to assess coordination adaptations with training, not only between agonist and antagonist muscles but also between synergist muscles with different functional roles, as between rectus femoris and the monoarticular portions of the quadriceps, is the intermuscular coherence (IMC) analysis. This analysis provides the cross-correlation between the frequency power spectrum of two muscles and allows to infer about shared neural pathways from the cortex to the motoneurons (Farmer, 1998; Farmer, Bremner, Halliday, Rosenberg, & Stephens, 1993; Salenius, Portin, Kajola, Salmelin, & Hari, 1997). Resistance trained individuals presented lower corticospinal connections between synergist muscles in an isometric maximal voluntary contraction (MVC), inferred by lower IMC at beta band between 15 and 35 Hz (Charissou, Vigouroux, Berton, & Amarantini, 2016), as well as between cortex and agonist muscles at 30% MVC, inferred by lower corticomuscular coherence (Ushiyama, Takahashi, & Ushiba, 2010). Furthermore, 14 weeks of strength training has shown to induce IMC changes in young adults synergist muscles, with reduced IMC at 18-20 Hz at 20% MVC, increased IMC at 22-24 Hz as well as 36-64 Hz at 70% MVC and sporadic increases at 100% MVC (Walker et al., 2019). To the best of our knowledge, this is the only study evaluating IMC before and after a strength training program. Additionally, there is lack of research concerning agonist-antagonist IMC after strength training, although there is evidence that resistance trained individuals present higher suppression of corticomuscular connections in beta band than endurance trained individuals (Dal Maso, Longcamp, & Amarantini, 2012).

Current research still lacks to describe how do neural adaptations in intermuscular coordination emerge overtime and what can be its specific role in strength gains at early and later training stages. Thus, two experiments were conducted to better understand the short-term and the long-term training adaptations in intermuscular coordination during isometric submaximal contractions. Therefore, the main purposes of Experiment 1 were 1) to understand how the torque-EMG relationship of different muscles with different functional roles during knee extensions is affected by short-term strength training and 2) to understand how coordination between agonists and between agonist-antagonist muscles is changed by training at different submaximal intensities of contraction. In turn, the main purposes of Experiment 2 were 1) to compare the torque-EMG relationship of different muscles with different functional roles during knee extensions between untrained, short-term trained and long-term trained individuals, and 2) to understand how coordination during submaximal contractions at different intensities may be modulated by training background. We hypothesize that torque-EMG relationship of the agonist as well as the antagonist muscles will present a less steep slope for the long-term trained, while the short-term training may not lead to significant differences, although this may depend on the muscle role in the contraction. Additionally, we hypothesize changes in coherence reflecting adapted coordination patterns between rectus femoris and the monoarticular portions of the quadriceps as well as between the knee extensors and biceps femoris, which may arise from a central adaptation in global motor control.

METHODS

Participants

Experiment 1

Eleven participants were included in this experiment (age: 22.6 ± 3.1 years; height: 176.4 ± 7.9 cm; weight: 70.5 ± 14.9 kg). The participants were healthy men without history of musculoskeletal injuries within the last 6 months. Although all participants were active physical education students, they did not have any strength training background. All participants provided informed written consent. This study was approved by the Faculty's Ethics Committee (CEIFMH N.º: 24/2021) and all procedures adhered to the Declaration of Helsinki.

Experiment 2

A total of 32 participants were included in this experiment. Eleven of them were untrained (UT: age: 26.2 ± 3.6 years; height: 173.0 ± 7.2 cm; weight: 66.6 ± 8.2 kg) and 10 were long-term trained (LT: age: 28.0 ± 6.1 years; height: 174.7 ± 6.7 cm; weight: 83.1 ± 9.2 kg). Although all UT were active physical education students, they did not have any strength training background, while LT were powerlifters or weightlifters with at least two years of regular practice. The remaining 11 participants were the participants that assigned to Experiment 1. This group was originally similar to UT and trained for 6 weeks, which was considered to characterize the participants as short-term trained (ST). The participants were healthy men without history of musculoskeletal injuries within the last 6 months.

Data collection

Experiment 1

Experimental approach. Aiming to assess the effect of strength training in the ability of the neuromuscular system to generate force at submaximal intensities and to assess the time course of intermuscular coordination adaptations, untrained participants were included in a high-bar back-squat training program.

Each participant was requested to go to the laboratory in six occasions. The first session was used to familiarize the participants with the testing tasks as well as with the back-squat exercise. The remaining five sessions were used to evaluate the coordinative mechanisms during isometric submaximal knee extensions or to assess squat 1RM. The first of these sessions took place one week after the familiarization session and was used as baseline (BSL), after which the participants were instructed to maintain their regular physical activity without adding strength training exercises. After two weeks of strength training abstinence, the participants were evaluated again, with this session accounting as the beginning of the training period (W0). After W0, the participants started to train and returned to the laboratory each two weeks to reevaluate squat 1RM to adjust the training loads (third and fourth sessions). The fifth evaluation session was conducted at sixth week of training (POS). This evaluation session was the final session that evaluated training adaptations corresponding to the training program ending.

Strength training. The training program lasted six weeks with three training sessions per week, which resulted in 18 training sessions. The strength training program consisted in 5 sets of 10 repetitions of back-squats with 2 minutes of rest between sets. The exercise intensity was targeted to 75% of RM of the back-squat. The participants were instructed to perform the exercise with an explosive concentric phase following a controlled eccentric phase. In the final repetitions of the last sets the researcher could spot the participants, and in sets at which the researcher help was needed in 2 or more repetitions, the load was decreased by 2,5kg for the subsequent set. During the training program the relative load was maintained, with absolute load progressions each two weeks relatively to the back-squat 1RM determined during the evaluation sessions.

1RM Determination. For the squat RM determination, we used a progressive loading squat test. The squat was performed with a high-bar position, and an 80-90º squat depth was used. Participants started to perform 5 repetitions with the unloaded barbell (20kg), incrementing 10-20kg each time. After, participants performed 3 repetitions with each load until the load was challenging, and finally, they performed sets of 1 repetition with smaller load increases (~5kg) until the RM determination.

EMG collection. All tests were accompanied by data collection of myoelectrical signals. These signals were recorded on 4 muscles of the right side of the body: vastus lateralis of quadriceps (VL), rectus femoris of quadriceps (RF), vastus medialis of quadriceps (VM) and biceps femoris long head (BF). The muscles were selected so we could assess the knee extensor muscles and so that we could assess the agonist-antagonist relationship during knee extensions. The electrodes were placed according to SENIAM (Surface EMG for Non-Invasive Assessment of Muscles). Before the placement of the electrodes, the skin was shaved and cleaned with alcohol to minimize skin impedance. Surface EMG was acquired using four bipolar surface electrodes (EMG Delsys, TrignoTM), fixed with specially designed adhesive interface, aligned with the muscle fibers (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000) and then additionally fixed with tape to avoid movement artefacts. EMG signals were preamplified while digitized at 1000 samples/s. After, the EMG signals were corrected for the 48-ms delay inherent to the Trigno EMG system.

Testing procedures. After the EMG electrodes placement, the participants began with a warm-up consisting of 5 minutes of unloaded cycle ergometry (Monark Ergomedic 828 E cycle ergometer; Monark Exercise AB, Vansbro, Sweden). After, participants were seated on an isokinetic dynamometer (System 3; Biodex Medical Systems, Shirley, NY). The dynamometer chair was positioned with the hip at 85º (supine position = 0º) and the participants were strapped around their chest, hip and distal thigh to minimize extraneous movement. The center of rotation of the knee was carefully aligned with the dynamometer axis of rotation, and the lever arm of the dynamometer was firmly attached to the lower leg with inextensible straps 2cm above de medial malleolus. These procedures were followed by a specific warm-up encompassing 6 submaximal isokinetic contractions at $60^{o}.s^{-1}$ and 2 near maximal isometric contractions.

It was provided online visual feedback on a computer screen. Maximum voluntary contraction (MVC) was assessed for knee extension and flexion. The knee extension MVC was assessed at an angle of 70° (Pincivero, Salfetnikov, Campy & Coelho, 2004), while the flexion MVC was assessed at an angle of 30° (Timmins et al., 2015). Three extension MVC and three flexion MVC were performed, ensuring 1-minute of rest between repetitions. We excluded repetitions presenting an initial countermovement in the torque-time curve or pre-

tension before the onset of torque production. After, the participants performed one submaximal knee extension contraction at four target torque (at 20%, 40%, 60% and 80% MVC). The participants were instructed to maintain torque, matching it with a target bar superimposed on a computer screen. Each contraction lasted 10s with 1 minute of rest between them.

Experiment 2

Experimental approach. Aiming to assess the effect of strength training in the ability of the neuromuscular system to generate force at submaximal intensities, UT individuals were compared to ST (who trained for 6 weeks) and to LT (who trained for at least 2 years). Each UT and LT participant was requested to go to the laboratory in two occasions. The first session was used to familiarize the participants with the testing tasks. The second session was used to evaluate the submaximal isometric contractions and the respective coordinative mechanisms. The remaining procedures concerning data collection were the same presented in Experiment 1.

Data processing

EMG pre-processing. Raw EMG signals were band-pass filtered (20-450Hz), rectified and smoothed with a low-pass filter (12Hz, 4th order Butterworth). Normalization of VL, RF and VM was made regarding the average value of the 500ms between 1s and 1.5s after the onset of the knee extension isometric MVC, while normalization of BF was made regarding the average value of the 500ms between 1s and 1.5s after the onset of the knee flexion isometric MVC. Electromyographic amplitude of each muscle at each contraction intensity from 20 to 80% was calculated as the average value from 3s to 9s after the onset of the contraction, defined manually. Visual inspection of all repetitions allowed to guarantee that the analyzed window corresponded to the target torque. Relationships between the normalized amplitudes of the recorded muscles and relative torque were plotted. Those relationships were linearly fitted and the slope of each one of them was calculated. Additionally, the relationship between agonist and antagonist muscles was also plotted. Relationships between normalized

VL and BF, and between normalized RF and BF were linearly fitted and the slope of each one of them was calculated.

Intermuscular coherence (IMC). Coherence analysis was performed using Matlab 2018a (Mathworks, Natick, MA, United States). Before data processing and analysis, all data files containing raw EMG signals were visually inspected to detect possible artifacts. In the cases where signals demonstrated some disruption or noise, the repetitions were excluded from the analysis. IMC analysis was calculated at each contraction intensity from 20 to 80%, from 3s to 9s after the onset of the contraction, defined manually. A total of 6s were analyzed at each intensity. Before IMC analysis, raw EMG signals were full wave rectified (Boonstra et al., 2008; Walker et al., 2019; Wang et al., 2015), and data was divided into windows of 500 samples in length with an overlapping of 50%. The signals were subjected to fast Fourier transform, which gave a frequency resolution of 2Hz. IMC was calculated as the cross-spectrum normalized by the auto-spectrum:

$$C_{xy}(f) = \frac{\left|P_{xy}(f)\right|^2}{P_{xx}(f)P_{yy}(f)}$$

where $C_{xy}(f)$ is the magnitude squared coherence between two rectified EMG signals, $x(t)$ and $y(t)$, for a given frequency f. $P_{xy}(f)$ is the cross-spectrum and $P_{xx}(f)$ and $P_{yy}(f)$ are the auto-spectrum of $x(t)$ and $y(t)$, respectively. Coherence was considered significant considering the steps provided by Kattla and Lowery (2010) and adapted from Terry and Griffin (2008).

IMC was computed for the follow pairs of muscles: VL-VM, VL-RF, RF-VM, VL-BF and RF-BF. Total coherence between 3-100Hz was averaged across participants at each timing of evaluation, as well as coherence sectioned into 3-7 (common drive band), 8-14 (alpha band), 15-35 (beta band), 40-60 (gamma band) and 60-100 Hz bands (high-gamma band). Within 15-35 Hz band representing beta band, two additional 15-24, 25-35 Hz bands were separated. Average coherence within each band was used to compare the evaluation timings (BSL, W0, and POS) at each intensity (20%, 40%, 60% and 80% MVC).

Statistics

Experiment 1

Statistical analysis was made using jamovi software version 2.3.28.0 (Sydney, Australia). We verified normality through the Shapiro-Wilk test. A repeated measures t-test was used to assess if there were differences from the beginning (W0) to the ending (POS) of the training program, with a Wilcoxon test used when normality was not assumed. The previously described analysis was made to all variables at each intensity (EMG amplitude, slope of the established relationships, IMC). As IMC values within each band were not normally distributed we applied a log 10 transformation to allow parametric tests to be performed. Additionally, a two-way ANOVA with two within factors (time and intensity) was used to assess time x intensity interactions for EMG amplitude of each muscle, and a two-way ANOVA with two within factors (time and muscle) was used to assess time x muscle interactions for EMG amplitude at each intensity. Tukey adjustments were used as *Post hoc* tests.

We assessed the relative reliability of the measurements between the BSL and W0 time points by calculating two-way mixed-effects intraclass correlation coefficients (ICC(3,1)) (Koo & Li, 2016), with 95% confidence interval. ICC values were considered: poor, <0.5; moderate, 0.5-0.75; high, 0.75-0.9; excellent, >0.9. Additionally, we calculated standard error of measurement (SEM) as an absolute reliability measurement (Weir, 2005). All statistical analyses were performed using a significance level of $p < 0.05$. Data is presented as mean ± *SD*. Cohen' *d* was calculated as measure of effect size. Effect size was considered small, medium or large for Cohen' *d* of 0.2 – 0.5, 0.5 – 0.8 and > 0.8, respectively.

Experiment 2

A one-way ANOVA with three levels (UT, ST and LT groups) was used to assess between group differences for all variables (EMG amplitude, slope of the established relationships, IMC). When normality was not assumed, a Kruskal-Wallis test was used, and when Levene's homogeneity of variances was not assumed, a Welch correction was made. Tukey adjustments were used in *Post hoc* tests of ANOVA, and Dwass-Steel-Critchlow-Fligner adjustments were used in *Post hocs* of Kruskal-Wallis test. Additionally, a mixed ANOVA

was used to assess intensity (within-group factor) x group (between-groups factor) interactions for EMG amplitude of each muscle, and a mixed ANOVA was used to assess muscle (within-group factor) x group (between-group factor) interactions for EMG amplitude at each intensity. Tukey adjustments were used as Post hoc tests.

RESULTS

Experiment 1

Reliability. The EMG amplitude-related variables presented moderate to excellent relative reliability, with the ICC varying from 0.53 to 0.92. From the 22 variables encompassing VL, RF, VM and BF amplitude at each intensity and the slopes of the established relationships, 45.5% presented moderate, 40.9% presented high and 13.6% presented excellent reliability. Concerning the EMG amplitude, the SEM calculations representing absolute reliability, respectively to the 20%, 40%, 60% and 80% MVC intensities were: for VL, 2.90%, 5.27%, 5.76% and 7.18%; for RF, 7.08%, 8.98%, 11.43% and 17.58%; for VM, 4.31%, 4.67%, 11.61% and 17.36%; and for BF, 1.61%, 2.61%, 4.13% and 6.22%.

For the IMC analysis, ICC values revealed that most of the 160 variables (5 pairs of muscles x 8 bands of interest x 4 intensities of contraction) present moderate to excellent reliability (moderate, 43.1% of the variables; high, 34.4%; excellent, 4.4%) although 18.1% of the variables present poor reliability.

Amplitude analysis. Concerning EMG amplitude, no differences were found from W0 to POS at any intensity of contraction neither regarding the slopes of the established relationships. The ANOVA analyzing time x intensity interactions for each muscle showed an intensity effect for all muscles (all $p < 0.001$), with amplitude increasing with increased intensity and with the multiple comparisons revealing differences between every intensity. Additionally, the ANOVA analyzing time x muscle interactions at each intensity showed a muscle effect for all intensities (all $p < 0.001$), with the amplitude of BF differing from other muscles as revealed by post hoc comparisons.

Intermuscular coherence. A visual inspection of the IMC data revealed specific frequencies of significant coherence. Regarding agonist pairing, at W0 coherence between RF and the monoarticular portions of quadriceps presented a peak encompassing the 8-14 Hz and initial frequencies of lower beta-band at 60% MVC, although slightly significant coherence emerged only between RF and VM at 40% and 80% MVC at the same band. Additionally, a peak at > 55 Hz frequencies appeared at the higher intensities of 60% and 80% MVC. Coherence between VL and VM was significant from 8-14 Hz band to > 40 Hz at > 40% MVC, and continued significant toward ~60 Hz only at 80% MVC. The contraction at 20%

MVC has only shown one peak at 8-14 Hz band. Regarding antagonist pairing, coherence between VL and BF presented peaks at 8-14 Hz band and lower frequencies of beta-band at 40% and 60% MVC, and at 40-60 Hz band only at 80% MVC. Also, coherence between RF and BF presented one peak at 8-14 Hz band at 60% MVC and at 40-60 Hz band at 80% MVC. Concerning POS, coherence patterns were similar, although with some adjustments. Coherence between VL and VM was also significant above 8-14 Hz to ~60 Hz, but in this case at all contractions > 40% MVC. Coherence between RF and VM maintained similar, and coherence between VL and RF was significant at 8-14 Hz and initial frequencies of lower beta-band at > 40% MVC with a peak at ~60 Hz at 80% MVC. Coherence between VL and BF presented peaks at 8-14 Hz band and lower frequencies of beta-band at > 40% MVC, with peaks at 40-60 Hz band at > 40% MVC. Coherence between RF and BF was similar to W0, although with significant at 8-14 Hz at all intensities > 40% MVC.

Concerning the repeated measures t-test, differences between W0 and POS were found at: 20% MVC, decreasing between VL and VM at 15-35 Hz band ($p = 0.042$, $d = 0.697$); 60% MVC, increasing between VL and BF at 3-100 Hz ($p = 0.025$, $d = 0.791$) and 40-60 Hz ($p < 0.001$, $d = 1.570$), RF and BF at 15-35 Hz ($p = 0.022$, $d = 0.819$) and specifically at 15-25 Hz ($p = 0.004$, $d = 1.130$), and VL and VM at 40-60 Hz ($p = 0.042$, $d = 0.697$); 80% MVC, increasing between VL and RF at 40-60 Hz ($p = 0.019$, $d = 0.841$) and between VL and BF at > 60 Hz ($p = 0.031$, $d = 0.757$). The ANOVA analyzing time x intensity interactions for each pair of muscles showed a general intensity effect for all pairs of muscles in the analyzed bands ($p < 0.05$) with a trend to increasing coherence with increased intensity, with exception of coherence between VL and RF at > 60 Hz, RF and VM at 8-14 Hz and > 60 Hz, VL and BF at 3-7 Hz and RF and BF at 8-14 Hz, 25-35 Hz and > 60 Hz. Additionally, time x intensity interactions were significant between VL and VM at 15-35 Hz ($p = 0.003$, $d = 1.077$) and specifically at 15-25 Hz ($p = 0.021$, $d = 0.867$) and between VL and RF at 40-60 Hz ($p = 0.015$, $d = 0.908$). A time effect was also observed between RF and BF at 15-35 Hz ($p = 0.026$, $d = 1.172$) and specifically at 15-25 Hz ($p = 0.033$, $d = 1.102$). Figure 6.1 depicts the time x intensity changes.

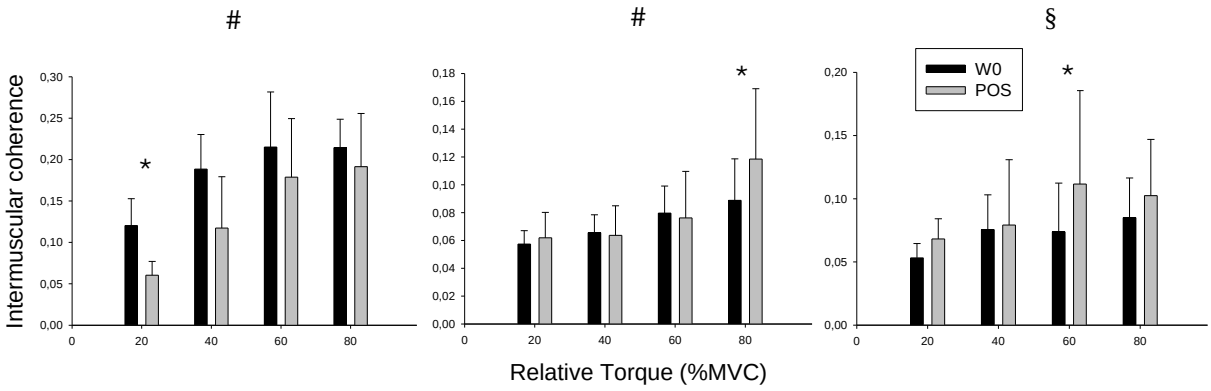

Figure 6.1 – Changes in intermuscular coherence from W0 to POS evaluations at different submaximal torque levels. The graphs represent changes in 15-35 Hz band between VL and VM (left panel), 40-60 Hz between VL and RF (central panel) and 15-35 Hz between RF and BF (right panel). * $p < 0.05$ between W0 and POS, # $p < 0.05$ time x intensity interaction, § $p < 0.05$ time effect.

Experiment 2

Amplitude analysis. Concerning EMG amplitude, the ANOVA showed between-group differences for VL at 20 ($p = 0.022$. $d = 0.775$), 40 ($p = 0.029$, $d = 0.645$) and 60% MVC ($p = 0.022$, $d = 0.640$) with post hoc differences revealing lower amplitude for LT when compared to UT ($p = 0.018$, $d = 0{,}399$; $p = 0.018$, $d = 0.509$; and $p = 0.034$, $d = 0.997$, respectively). The ANOVA has also shown that RF amplitude was different between groups at 20 ($p = 0.041$, $d = 0.714$), 40 ($p = 0.039$, $d = 0.723$) and 80% MVC ($p = 0.002$, $d = 1.042$), with post hoc differences revealing greater amplitude for UT when compared to ST at 20 and 40% MVC ($p = 0.033$, $d = 0.130$ and $p = 0.042$, $d = 1.047$, respectively) and for UT when compared to ST ($p = 0.009$, $d = 3.829$) or LT ($p = 0.004$, $d = 0.243$) at 80% MVC. Figure 6.2 and 6.3 show the group-differences in torque-VL and torque-RF relationships, respectively. VM did not differ between groups at any intensity. The antagonist activity of BF has also shown between-group differences at 20% ($p = 0.021$, $d = 0.700$) and 40% MVC ($p = 0.036$, $d = 0.635$), with post hoc comparisons only revealing greater amplitude for UT compared to ST at 20% MVC ($p = 0.025$, $d = 1.071$). Additionally, the ANOVA showed differences in RF-torque relationship ($p = 0.009$, $d = 0.893$), namely with a steeper slope for UT compared to LT ($p = 0.007$, $d = 2.574$).

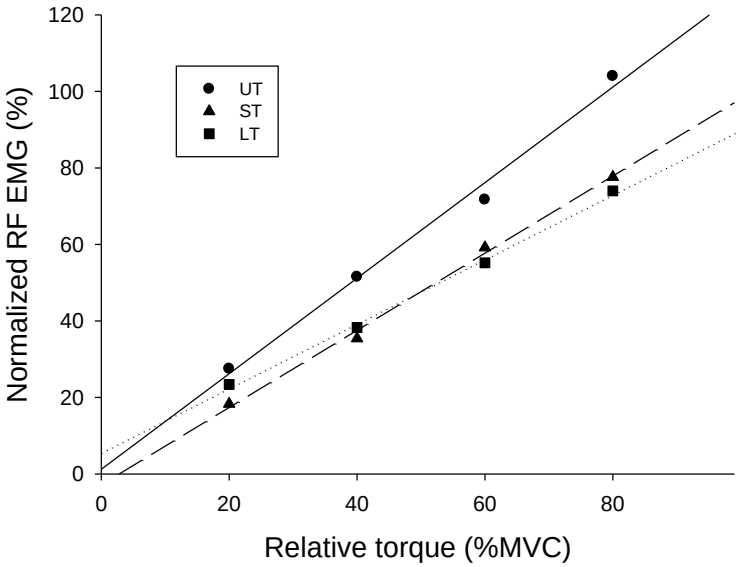

Figure 6.2 – Group comparison of RF activity at different submaximal torque levels. The straight, dashed and dotted lines represent the linear relationship of UT, ST and LT, respectively.

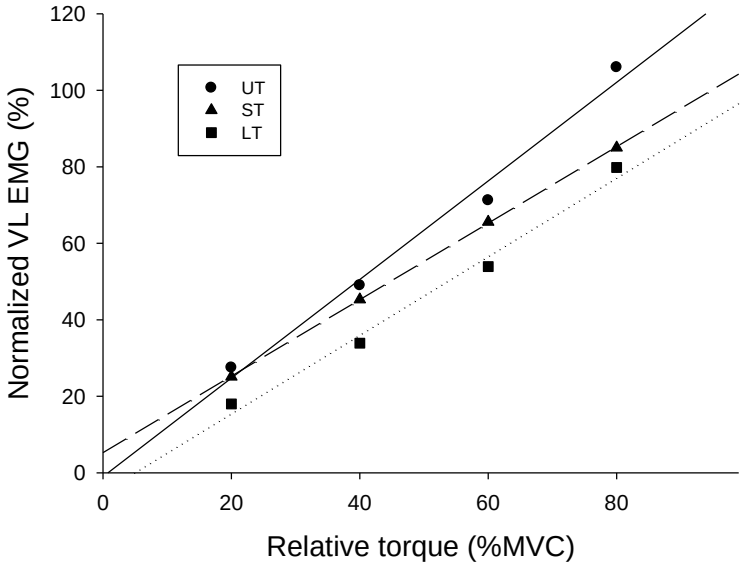

Figure 6.3 – Group comparison of VL activity at different submaximal torque levels. The straight, dashed and dotted lines represent the linear relationship of UT, ST and LT, respectively.

The mixed ANOVA analyzing group x intensity interactions for each muscle showed an intensity effect for all muscles (all $p < 0.001$), with amplitude increasing with increased intensity and with the multiple comparisons revealing differences between every intensity. Group interactions were only observed for RF ($p = 0.013$; $d = 0.854$) with UT presenting greater amplitude than ST ($p = 0.023$, $d = 0.010$) and LT ($p = 0.028$, $d = 0.012$), although greater amplitude was also shown regarding VL post hoc comparisons for UT compared to LT ($p = 0.039$, $d = 0.024$). Group x intensity interactions were also significant concerning VL ($p = 0.047$, $d = 0.566$) and RF ($p = 0.001$, $d = 0.758$). On its turn, the mixed ANOVA analyzing group x muscle interactions for each intensity of contraction showed a muscle effect for all muscles (all $p < 0.001$), with the amplitude of BF differing from other muscles as revealed by post hoc comparisons. Group interactions were observed at 80% MVC ($p = 0.016$, $d = 0.825$) with multiple comparisons showing greater amplitude for the UT compared to LT ($p = 0.014$, $d = 0.028$), although greater amplitude was also shown regarding 40% MVC comparisons for UT compared to LT ($p = 0.018$, $d = 0.170$). Group x muscle interactions were also significant concerning 20% MVC ($p = 0.016$, $d = 0.631$).

Intermuscular coherence. As described in Experiment 1, a visual inspection of the IMC data revealed specific frequencies of significant coherence. The UT coherence patterns were very similar to the ones observed for the group analyzed in Experiment 1 at W0. The ST correspond to the POS evaluation of the group analyzed in Experiment 1 (see section 3.1 – Intermuscular coherence). On its turn, the LT presented significant peaks from the 8-14 Hz band to the initial frequencies of lower beta-band at > 40% MVC (with the peaks with greater magnitude at 60% MVC) in all pairs. In addition, only coherence between VL and VM showed peaks slightly above significance line at 40-60 Hz band, with all the other pairs not presenting any significant peak.

Between-group differences were found at: 20% MVC between VL and VM ($p = 0.043$, $d = 0.827$; post hoc comparisons showing greater coherence for ST than LT, $p = 0.037$, $d = 0.121$) and VL and BF ($p = 0.033$, $d = 0.603$; post hoc comparisons showing greater coherence for ST than UT, $p = 0.025$, $d = 0.100$) at 3-7 Hz, between VL and VM at 8-14 Hz ($p = 0.012$, $d = 0.864$; post hoc comparisons showing greater coherence for UT than LT, $p = 0.012$, $d = 3.100$) and at 40-60 Hz ($p = 0.030$, $d = 0.755$; post hoc comparisons showing greater

coherence for ST than LT, $p = 0.041$, $d = 0.120$); 40% MVC between VL and VM ($p = 0.022$, $d = 0.793$; post hoc comparisons showing greater coherence for UT than LT, $p = 0.020$, $d = 4.937$) and VL and RF ($p = 0.014$, $d = 0.779$; post hoc comparisons showing greater coherence for UT than LT, $p = 0.014$, $d = 0.264$) at 15-35 Hz with specific differences between VL and VM at 15-25 Hz ($p = 0.003$, $d = 1.011$; post hoc comparisons showing lower coherence for LT than UT, $p = 0.003$, $d = 0.177$, and ST, $p = 0.022$, $d = 2.611$), and between RF and BF at > 60 Hz ($p = 0.027$, $d = 0.676$; without any significant post hoc comparisons); 60% MVC between VL and RF at 3-7 Hz ($p = 0.031$, $d = 0.654$; without any significant post hoc comparisons) and at 8-14 Hz ($p = 0.020$, $d = 0.803$; post hoc comparisons showing lower coherence for UT than LT, $p = 0.028$, $d = 2.780$), between VL and VM ($p = 0.013$, $d = 0.884$; post hoc comparisons showing greater coherence for ST than LT, $p = 0.006$, $d = 3.639$), VL and BF ($p = 0.038$, $d = 0.762$; post hoc comparisons showing lower coherence for UT than ST, $p = 0.040$, $d = 4.276$) and RF and BF ($p = 0.006$, $d = 0.943$; post hoc comparisons showing greater coherence for ST than LT, $p = 0.005$, $d = 0.171$) at 40-60 Hz; 80% MVC between VL and VM at 3-7 Hz ($p = 0.010$, $d = 0.961$; post hoc comparisons showing greater coherence for ST than UT, $p = 0.017$, $d = 0.140$, and LT, $p = 0.044$, $d = 0.111$) and 8-14 Hz ($p = 0.009$, $d = 0.897$; post hoc comparisons showing greater coherence for ST than UT, $p = 0.007$, $d = 2.006$), and between RF and BF at > 60 Hz ($p = 0.042$, $d = 0.714$; post hoc comparisons showing greater coherence for UT than LT, $p = 0.039$, $d = 0.131$).

The mixed ANOVA analyzing group x intensity interactions for each pair of muscles showed a general intensity effect for all pairs of muscles in the analyzed bands ($p < 0.05$) with a trend to increasing coherence with increased intensity, with exception of coherence between VL and RF at 8-14 Hz, RF and VM at 3-7 Hz and 8-14 Hz, VL and BF at 3-7 Hz and RF and BF at 3-7 Hz. Group interactions were observed between VL and VM at 3-100 Hz ($p = 0.035$, $d = 0.736$), 3-7 Hz ($p = 0.003$, $d = 1.017$) and 40-60 Hz ($p = 0.009$, $d = 0.895$), between VL and BF ($p = 0.032$, $d = 0.747$) and between RF and BF ($p = 0.031$, $d = 0.749$) at 40-60 Hz. Group x intensity interactions were also significant between VL and VM at 8-14 Hz ($p < 0.001$, $d = 1.004$) and 15-25 Hz ($p = 0.027$, $d = 0.599$), between VL and RF at 8-14 Hz ($p = 0.017$, $d = 0.626$) and 15-25 Hz ($p = 0.039$, $d = 0.578$) and between RF and BF at 25-35 Hz ($p = 0.048$, $d = 0.564$).

DISCUSSION

The present study assessed the chronology of training adaptations in muscle activity and coordination during isometric submaximal contractions at different torque levels. Our study supports previous findings suggesting that short-term strength training is not enough to induce changes in torque-agonist relationship. However, differences between short-term trained and untrained groups in RF activity shows that we should not discard the possibility that muscle recruitment may present some innate component while presenting modulation in muscles with specific functional roles. Additionally, long-term trained individuals presented a general lower activity of agonist and antagonist muscles. Concerning muscle coordination, 6 weeks of training revealed changes in IMC of the agonist muscles at beta and gamma bands, namely concerning the coupling between RF and the monoarticular portions of the quadriceps as well as between VL and VM at specific torque levels. Also, agonist-antagonist coupling was changed at the higher torque levels (> 60% MVC) at gamma band. The group comparison showed that long-term trained individuals present differences between VM and VL at all torque levels at specific bands, and between RF and VL at specific bands. Additionally, coordination between agonist and antagonist muscles showed more pronounced changes at the higher torque levels, supporting the results observed after short-term training.

Amplitude analysis

Six weeks of squat training did not change EMG amplitude at any torque level in all the analyzed muscles, as well as the relationships between torque and EMG of agonist and antagonist muscles or between the EMG of muscles with different functional roles. This is in line with previous studies demonstrating that short-term strength training is not enough to induce changes in torque-agonist EMG relationship (Balshaw et al., 2019; Häkkinen & Komi, 1983; Tillin et al., 2011). For example, 4 weeks of training did not result in any change concerning absolute torque-agonist relationship when individuals performed a squat program (Häkkinen & Komi, 1983) or either a more specific isometric knee extension program (Tillin et al., 2011). Even 12 weeks of isometric training were not enough to observe significant adaptations in absolute torque-agonist relationship (Balshaw et al., 2019). However, even with the absence of changes in Experiment 1, the results of Experiment 2 point to a difference

between UT and ST who performed the training program, namely regarding RF activity. In a first instance this may look contradictory, however, we should consider the interindividual variability. Previous research has reported that there is a strong relation between the estimated % of type II fibers (Johnson, Polgar, Weightman, & Appleton, 1973) with the coefficient of variation of muscle thickness, reflecting that interindividual variability in peripheral factors depends on the myotypology (Wakahara et al., 2010). Also, the proportion of fiber types present large interindividual variability in the VL with type I fibers ranging from 15% to 85% (Simoneau & Bouchard, 1989). However, both studies evaluated individuals with different training background which may have increased the variability of the data. On the other hand, one study suggested that muscle myotypology is not the main influence in the torque-agonist EMG, with fiber type dominance not being significantly related to the non-linearity of torque-EMG relationship (Amarantini & Bru, 2015). Nevertheless, and in line with the suggestion of Amarantini and Bru, the interindividual variability in peripheral factors should not be completely discarded (Stebbings, Morse, Williams, & Day, 2014), considering specifically the anatomical properties of RF muscle that influence the moment arm of the muscle and consequently the force production (Duda, Brand, Freitag, Lierse, & Schneider, 1996). Also, neural factors may be responsible for interindividual variability in EMG adaptations namely concerning synergist muscles, for example in cycling tasks (Crouzier et al., 2019; De Marchis, Schmid, Bibbo, Bernabucci, & Conforto, 2013), but even in single-joint submaximal isometric tasks as demonstrated for the distribution of neural drive to the knee extensors (Hug et al., 2015). This demonstrates that the differences found in the Experiment 2 between UT and ST may be due to the individual neuromuscular characteristics prior to the study.

Concerning long-term trained individuals, more differences were found, revealing that some neural adaptations only occur at the long-term. We found generally lower activity of the agonist muscles, namely the VL and RF, for the same load percentage. Adaptations in torque-agonist relationship were observed after 16 weeks of squat training, and differed when the relationship was defined with absolute or relative values (Häkkinen & Komi, 1983). More precisely, absolute torque-agonist relationship showed a shift to the right, namely at higher force levels during unilateral and bilateral knee extensions, but when the torque was presented as a relative scale the relationship presented an higher EMG to the same relative

torque, with particular emphasis in the mid-zone of the relationship considering the 40 and 60% MVC. This difference may have emerged from EMG processing since the authors averaged the integrated EMG signals of VL, RF and VM without normalization. Although the maximum integrated EMG during MVC was not significantly changed, slight increases were observed in particular muscles and the fact they did not normalize the submaximal signals may have accounted for the reported results. Furthermore, 6 months of dynamic leg extensions have also resulted in a shift to the right of the absolute torque-agonist relationship, indicating that the activation of the same motor units resulted in greater torque production (Narici et al., 1996), and long-term resistance trained individuals have also presented the same shift (Balshaw et al., 2019). Additionally, concerning relative torque-agonist EMG, the nature of the relationship was generally linear for long-term trained while being curvilinear for untrained individuals, which means above 40% MVC the muscle activity increases at a greater rate with the increase in torque production (Amarantini & Bru, 2015). Overall, these results point to a greater neuromuscular efficiency, with lower agonist activity for the same mechanical output, or from other point of view a greater torque production for the same motor unit activation. Our study brings new insights into the current knowledge, because the general activity of VL and RF was different between UT and LT, as expected and confirmed by the group x intensity interaction, but the RF activity was similar between ST and LT with both groups revealing lower muscle activity for the same relative torque when comparing to UT. Without disregarding the above mentioned interindividual variability concerning RF, these results suggest that the role of biarticular muscles is of extreme relevance and can contribute for adapted neuromuscular output during the first weeks of training.

Contrary to our hypothesis, we did not find lower BF activity comparing the trained groups with the UT. Previous research found decreased antagonist activity compared to the same agonist activity after 4 weeks (Tillin et al., 2011) and 12 weeks of isometric knee extension training (Balshaw et al., 2019). When specifically training the evaluated task, it appears that the antagonist co-activation also presents a shift to the right. The dynamic and more ecologic squat program elicited a different continuous recruitment of the BF as knee extension antagonist but hip extension agonist, which may have contributed to the generally similar agonist-antagonist relationships. Additionally, the reported studies applied different processing methods with one study considering the agonist EMG corrected to muscle-

electrode distance and the antagonist EMG as an average between BF and semitendinosus (Balshaw et al., 2019) and the other using the agonist muscle normalized to Mmax and the antagonist muscle as the RMS/RMS at MVC (Tillin et al., 2011). Our study only evaluated BF which may be a poor representation of the antagonist activity (Santos et al., 2023), and the fact we used muscle activity at MVC to normalize the submaximal signals may lead to different results from the above mentioned studies. It is also interesting to note that, the general agonist and antagonist activity was significantly higher for UT when compared to LT at 80% MVC, which means that the high motor unit recruitment of the agonist muscles and the respective antagonist activity probably imply a greater co-contraction of the BF as a joint stability mechanism which leads to a clear need of increase the neural input to the agonist muscles and thus a less efficient activity to achieve the desired torque. The quadratic relationship characterizing torque-agonist or antagonist of the UT may also affect the general activity at high-torque contractions (Amarantini & Bru, 2015). On the other hand, only at 20% MVC it was observed a group x muscle interaction, which may imply that the neural mechanisms involved to control intermuscular coordination at low-torque production are different between individuals with different training status.

Intermuscular coherence

Following the results from the above section, we may interpret that training adaptations are specific to the role of the muscle during the task. Thus, the individual muscle recruitment involves the need of coordinated actions between muscles with different functional roles. The muscle coupling between pairs of muscles provides a measure of intermuscular coordination, and IMC distinguishes the signal input frequencies and correlates the power spectral densities of two muscles, allowing to infer about how the central nervous system may control different muscles (Grosse, Cassidy, & Brown, 2002) and how this control is modulated in different conditions, for example concerning training experience and age (Walker et al., 2019) or fatigue (Santos, Correia, Vaz & Pezarat-Correia, 2024a).

Short-term training of 6 weeks revealed exacerbated patterns of coherence in some specific bands of interest. For the agonist muscles, this was shown specially at the higher torque levels (> 60% MVC). The significant coherence peaks at 8-14 Hz as well as 15-25 Hz indicated oscillations at alpha and beta band, respectively. The alpha band has been linked to cortical

and subcortical activity as well as peripheral integration (Erimaki & Christakos, 2008; Klass, Lévénez, Enoka, & Duchateau, 2008; McAuley & Marsden, 2000). This implies the importance of alpha power in the integration between the somatosensory and motor cortices (Thies, Zrenner, Ziemann, & Bergmann, 2018). Additionally, and although being from multifactorial origin, the nervous system oscillations around 10 Hz are also linked to physiological tremor (McAuley & Marsden, 2000). In the evaluated submaximal tasks, it was asked to the participants to sustain a given torque level. Those tasks involve, on the one hand, voluntary contractions at submaximal intensities, and on the other hand, the need to maintain the same torque production along time, namely with the integration of peripheral feedback. This is compatible with the above-mentioned physiological causes that may elicit oscillations at alpha band. The integration of information from Ia afferents and subcortical centers will affect the excitability of corticospinal neurons in the motor cortex (McAuley & Marsden, 2000; Thies et al., 2018). Additionally, the significant coherence peaks at beta band may also be attributed to the corticospinal pathway (Baker, Olivier, & Lemon, 1997; Farmer et al., 1993; Kattla & Lowery, 2010; Mima & Hallett, 1999), although this band has also been linked to sensory information from Ia afferents and Renshaw cells as well as the communication between the motor cortex and other cortical and subcortical centers (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013; Ushiyama et al., 2011).

The peaks at 40-60 Hz band, the gamma band, are also associated to the corticospinal drive, namely during strong voluntary efforts (Brown, 2000; Brown, Salenius, Rothwell, & Hari, 1998; Mima, Simpkins, Oluwatimilehin, & Hallett, 1999). It is interesting that the coherence at gamma band increased after training between agonist muscles. This may reveal that 6 weeks of training induce neural adaptations in intermuscular coordination, with increased coherence indicating greater motor unit synchronization (De Luca & Erim, 2002; De Luca, Roy, & Erim, 1993; Farmer, 1998) originated from the input to shared corticospinal pathways to the muscles in strong contractions (Brown, 2000; Brown et al., 1998; Mima et al., 1999). Increased gamma band coherence was also observed after 14 weeks of strength training only at 70% MVC and not at 20% MVC, which is in line with our results (Walker et al., 2019). Firstly, we found lower IMC between VL and VM only at 20% MVC, which may imply that a reduction in shared corticospinal neurons to the monoarticular knee extensors provides a more efficient muscle recruitment during low torque levels. Secondly, we found increased

gamma oscillations between VL and VM at 60% MVC and between VL and RF at 80% MVC, which may imply a modulation of the agonist coordination during high torque contractions. In our previous work (Santos, Vaz, Gomes, Infante & Pezarat-Correia, 2024b) we found that 6 weeks of squat training led to an increased IMC between VL and RF at 15-25 Hz band in maximal isometric leg-press exercise. Although the task was maximal, as in the current study we asked the participants to maintain high torque submaximal efforts during 10s, the attentional focus may have shifted the frequencies of coherence toward the gamma band. Integrating somatosensory and visual information has revealed to increase corticomuscular oscillations towards the gamma band, especially in periodically modulated isometric force tasks (Omlor, Patino, Hepp-Reymond, & Kristeva, 2007) or during isotonic tasks (Gwin & Ferris, 2012). Additionally, the greater interaction between VL and RF at 80% MVC may rely on greater coordination between two knee extensors with distinct anatomical and functional roles. As described in the previous section, the action of RF during knee extension may be optimized with training regarding the regional activation involved in the knee extension (Watanabe, Vieira, Gallina, Kouzaki, & Moritani, 2021) and that may imply an adapted coordination with the vastii muscles with greater intermuscular motor unit synchronization. This may also be observed from the time x intensity interaction where the VL-RF coherence at gamma band increased linearly with intensity at W0, but after the 6 weeks of training increased less steeply until 60% MVC, only augmenting significantly at 80% MVC.

Long-term trained individuals revealed generally lower IMC coherence between the agonist muscles. Previous research has demonstrated that trained athletes present reduced lower limb corticomuscular coherence at beta band during submaximal contractions at 30% MVC than untrained individuals (Ushiyama et al., 2010). Also, lower coherence at beta band was also shown between RF and VM in resistance trained individuals during a maximal isometric knee extension (Charissou et al., 2016). On the contrary, in our previous work, we found greater IMC between VM and RF in resistance trained individuals (Santos et al., 2024c). The difference may emerge from the fact that in that study we evaluated a multi-joint leg press task, while here we focused only on knee extension. The greater IMC at beta band may be representative of greater corticospinal input to RF and VM, which imply a more efficient coordination between biarticular and monoarticular muscles during multi-joint tasks.

Namely, the RF is antagonist on the hip and agonist on the knee during leg-press, while being only agonist during knee extension contractions. This may have contributed to the apparent contradictory results. Furthermore, agonist IMC was significantly lower for LT at alpha and beta bands during 20% and 40% MVC, respectively, but also generally lower gamma oscillations, which shows the different need of synchronous control of agonist muscles during submaximal contractions for the chronically trained individuals.

It is also interesting to note that, at some specific bands and intensities, it seems that there is a trend to an increased IMC indicating greater motor unit synchronization between agonist muscles after short-term training and then the coherence appears to generally decrease with long-term training. Although we may look with caution to those results, especially considering the small sample size as well as some reliability measures between BSL and W0, those results were observed in various bands as well as various intensities and may be an important insight from this study. Nevertheless, those results are compatible with the Hebbian plasticity to training (Carson, 2006), since the initial increase in IMC following short-term training may imply that the corticospinal neurons responsible for coordinating the agonist muscles are firing together more frequently due to the increased training stimulus and that this leads to strengthened connections between them and enhanced synchronization. However, with long-term training the decreased IMC may imply, on the one hand, that the neural circuits involving subcortical and cortical structures and the integration of sensory information may become more efficient, playing an important role in the excitability/inhibition of the corticospinal neurons and thus leading to a reversion concerning their synchronous activation. On the other hand, the muscular adaptations, more pronounced at the long-term (Folland & Williams, 2007; Sale, 1988) may also influence the motor unit recruitment and firing rates as the muscle becomes more efficient.

Concerning agonist-antagonist IMC, the significant coherence peaks encompassing 8-14 Hz and 15-25 Hz indicated oscillations at alpha and beta band, and in addition a peak at 40-60 Hz were also observed. After short-term training agonist-antagonist IMC at beta and gamma bands increased at higher torque levels (> 60% MVC), which means an increased shared corticospinal input between agonist and antagonist muscles, possibly implying mechanisms regarding peripheral feedback (Farmer et al., 1993; Kilavik et al., 2013; Ushiyama et al.,

2011). The fact that we used submaximal contractions dependent on peripheral and visual feedback as already mentioned, may have resulted in greater synchronization and co-contraction to better control the elicited torque target. As we did not find differences in BF amplitude following this period of training, we may interpret that although the recruited motor units remain the same, the greater synchronization to the agonist muscle spikes may be a way to ensure stability of the knee joint. For example, badminton players presented higher tibialis anterior and gastrocnemius lateralis synchronization than untrained individuals in an isokinetic dorsiflexion which may have been a more effective control strategy of the ankle (Wang et al., 2019). On the other hand, in our previous work (Santos et al., 2024b) we reported that during a maximal isometric leg-press, although the IMC between tibialis anterior and gastrocnemius lateralis has decreased, the IMC between VL and BF or between RF and BF was not clearly modified by 6 weeks of squat training. The different neural strategies concerning the evaluated task, training mode and the muscle roles (even when addressing agonist-antagonist IMC, the role of pairs of muscles located on the thigh or on the shank are different in the control of the knee and ankle, respectively) may be considered when comparing the results of the studies (Santos et al., 2023).

Additionally, in the current study, LT have also presented lower IMC at > 40 Hz between agonist and antagonist muscles. This is in line with the IMC between agonist muscles, which augmented at short-term but diminished at the long-term training. Those transitional adjustments may be important until the central commands become more efficient regarding the task-specific demands (Ushiyama et al., 2010). In our previous work, although the IMC between VL and BF in a maximal isometric leg-press was reduced after 2 weeks of training, no differences were observed from pre- to post-training of six weeks (Santos et al., 2024b), which has been maintained with long-term training as revealed by the absence of differences between untrained and powerlifters/weightlifters (Santos et al., 2024c). As mentioned previously, the different task, with the leg-press implying a BF recruitment as agonist of hip extension, may have contributed to the absence of differences following training, while during single-joint knee extension the antagonistic behavior of BF may have been changed, namely with decreased number of shared corticospinal projections at a greater extent during strong contractions > 60% MVC. Since we did not find generally lower amplitude of BF or different agonist-antagonist relationships considering the amplitude analysis of EMG, it may

imply that a lower synchronized activation of corticospinal neurons allows a more efficient control of the knee joint. It is also interesting that different modulation of the higher frequencies of beta band IMC with torque level have been shown, which implies different neural adaptations in the control of antagonist muscle with training status. On its turn, when considering corticomuscular coherence, previous research has shown higher values for resistance trained when compared to endurance trained individuals, although both groups have presented significant coherence (Dal Maso, Longcamp, Cremoux, & Amarantini, 2017), which implies that neural input from the motor cortex modulates the intrinsic spinal circuits associated to reciprocal innervation (Nielsen, 2016). Additionally, coactivation of the antagonist muscles has been shown to be associated to subcortical circuits, namely involving the cerebellum and basal ganglia (Latash, 2018).

It is important to consider the reliability calculations that involved the experimental group as its own control. Previous research reported no differences between sessions in agonist and antagonist EMG during submaximal contractions (Tillin et al., 2011) and our data support these results with most variables concerning EMG normalized amplitude and the slopes of the established relationships presenting ICC > 0.75. However, caution should be taken because other variables presented moderate relative reliability which imply that absolute values of reliability measured by SEM should be considered when interpreting results, especially for RF and VM at > 60% MVC. Considering that the individuals who participated in this study did not present any experience in general strength training, this may also reflect at some extent that the muscle activity at higher loads may present between-session variability or even some learning effect (Santos et al., 2020). This may have been mitigated by the familiarization session, but the abundancy and redundancy of the musculoskeletal system may influence muscle recruitment and relative contributions of the synergist muscles (Hirashima & Oya, 2016). This may have also affected the IMC calculations, with some adjustments in EMG patterns between BSL and W0 resulting in some inter-day variability. Nevertheless, IMC calculated from EMG data recorded with bipolar electrodes has revealed to be reliable between VL and VM (Mohr, Schön, von Tscharner, & Nigg, 2018) and moderate to excellent relative reliability was observed in most variables of our study, which is in line with our previous work concerning maximal isometric force production (Santos et al., 2024b).

CONCLUSION

Two experiments were conducted to assess the chronology of training adaptations in intermuscular coordination during isometric submaximal contractions. Six weeks of training did not alter the amplitude of EMG signals of the agonist and antagonist muscles at any torque level, as well as the relationships between torque and muscle activity nor between muscles with different anatomical/functional roles. However, at the long-term, strength training leads to adaptations concerning agonist activity of VL and RF, with a less steep slope of torque-agonist relationship revealing that lower activity is needed to the same relative mechanical output. Concerning antagonist activity, we did not find generalized lower activity as it was expected. This result may be related to the training program only involving squats and thus implying the recruitment of BF as an agonist of hip extension. Regarding IMC analysis, six weeks of training led to a general increase at beta and gamma bands, with particular emphasis between RF and VL, which implies specific coupling between biarticular and monoarticular muscles, namely with increased shared corticospinal input. However, at the long-term it was observed a generally lower IMC, which suggest transitional adjustments in coordination during the initial weeks of training that will be reverted when the system becomes more efficient. This was also observed concerning agonist-antagonist IMC, indicating a greater motor unit synchronization following six weeks of training, which is decreased at the long-term, especially at high torque levels and concerning the gamma band implied in corticospinal connections during strong contractions. The described results suggest that agonist-agonist and agonist-antagonist coordination patterns are adapted with strength training, and that those mechanisms remain adapting overtime, providing new evidence that neural mechanisms are not limited to the first weeks of training and that intermuscular coordination has an important role during force production.

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Chapter 7

Chronology of adaptations to strength training: muscle coordination during load-velocity profiling

Santos, P.D.G., Vaz, J.R., Gomes, M., Fitas, A., Arrenega, C., Oliveira, J., & Pezarat-Correia, P. (2024). Chronology of adaptations to strength training: muscle coordination during load-velocity profiling [Unpublished manuscript]. Faculty of Human Kinetics, University of Lisbon.

ABSTRACT

Neural adaptations to strength training in complex tasks involve changes in the patterns of muscle activation. Namely, muscle synergy extraction has been used to assess changes in intermuscular coordination with training as well as differences between three groups with different training status (untrained, short-term and long-term trained). However, it is not fully understood how intermuscular coordination evolves at different training stages. Thus, two experiments were conducted to better understand i) the effects of six weeks of squat training in muscle synergies at different intensities used to assess the individual load-velocity profiles (LVP) of the squat, and ii) the long-term adaptations in coordination and in the LVP by comparing groups with different training status. Electromyography (EMG) of seven lower limb muscles was collected during squats at four loads (40-90% 1RM), which was used to extract muscle synergies. Six weeks of squat training led to increased dynamic strength (1RM) and modified LVP, namely with decreased relative theoretical maximal load and a less steeper slope. Concerning muscle synergies, two muscle synergies were used to characterize muscle activation during the squat. After the training period, differences were found only in the spatial component concerning the weighting of each muscle within the synergies as well as some shifts in some individual EMG patterns. Furthermore, when comparing the groups, the temporal component of the synergies presented differences with an anticipation of synergy #1 and a delay of synergy #2, with different muscle weightings namely concerning the muscles acting around the ankle. It was shown that muscle synergies are flexibly adapt with strength training and that adjustments in intermuscular coordination are progressive overtime.

Keywords: resistance-training, electromyography, muscle synergy, squat load-velocity profile, physical fitness expertise

INTRODUCTION

The load-velocity profile (LVP) is a practical tool for testing individual neuromuscular capacities and monitoring training adaptations. The LVP is based on the well-known inverse relationship between external load and concentric movement velocity. A quasi-linear relationship was reported between external force and leg-extension velocity for the leg-press exercise, with the segmental dynamics cancelling the hyperbolic relationship between muscle force and leg-extension velocity (Bobbert, 2012). However, given that neither the high-force/low-velocity nor the low-force/high-velocity regions are typically tested when establishing the individual LVP, this model is not exempt of limitations. For instance, double-hyperbolic relationships have been unraveled when considering high-forces above 90% (Alcazar, Csapo, Ara, & Alegre, 2019; Alcazar, Navarro-Cruz, et al., 2019). Nevertheless, a linear model is usually applied to multi-joint exercises, namely the back squat, with strong inverse linear relationships between movement velocity and external load (Conceição, Fernandes, Lewis, Gonzaléz-Badillo, & Jimenéz-Reyes, 2016; Fitas et al., 2024; Martínez-Cava, Morán-Navarro, Sánchez-Medina, González-Badillo, & Pallarés, 2019; Sánchez-Medina, Pallarés, Pérez, Morán-Navarro, & González-Badillo, 2017). The linear fitting of the LVP provides, at least, three distinct variables: 1) the theoretical maximal load (LD0), represented by intercept in the vertical axis and correlated with maximal voluntary contraction (Morales-Artacho et al., 2018), 2) the theoretical maximal velocity (V0), represented by the intercept at the horizontal axis, and 3) the slope of the linear fitting.

The LVP is highly sensitive to training interventions. For example, the mean concentric velocity associated with a predetermined set of relative loads exhibited a greater increase after 4 weeks of power vs. strength training (Pérez-Castilla & García-Ramos, 2020). The configuration of training sets also resulted in different adaptations after 5 weeks of strength training. In specific, exercise schemes with 16 sets of 2 repetitions were more effective for eliciting changes in the squat LVP compared to that seen with a more traditional approach involving 4 sets of 8 repetitions (Iglesias-Soler, Rial-Vázquez, et al., 2021; Rial-Vázquez et al., 2022). Despite this, there is compelling evidence that the magnitude of adaptations in specific regions of the LVP is primarily modulated by training load (Behm & Sale, 1993;

Cormie, McGuigan, & Newton, 2010). However, it remains largely unclear exactly how these adaptations emerge overtime.

Strength training optimizes the processes by which the central nervous system (CNS) recruits the muscles to regulate force and/or power output. Chronic adaptations to strength training may originate at any level of the neuromuscular system (i.e. from the cortex to the motor units) and have been shown to ensure a more efficient force production (Balshaw, Massey, Maden-Wilkinson, Lanza, & Folland, 2019; Del Vecchio et al., 2019; Kidgell, Bonanno, Frazer, Howatson, & Pearce, 2017; Lahouti, Lockyer, Wiseman, Power, & Button, 2019; Santos, Vaz, Correia, Neto, & Pezarat-Correia, 2023). Surface electromyography (EMG) has been used to characterize neuromuscular adaptations and to study the coordinated recruitment of muscles during complex motor tasks. For instance, by enabling the extraction of muscle synergies, EMG provides information about the timing of activation and the weighting of each muscle in each synergy during the completion of dynamic movements (Bizzi & Cheung, 2013; Hug, 2011). Muscle synergies have been explored during walking and running (Cappellini, Ivanenko, Poppele, & Lacquaniti, 2006), postural control tasks in response to unexpected external perturbations (Kim, Kim, Kim, & Yoon, 2018), pedaling (Hug, 2011; Hug, Turpin, Guével, & Dorel, 2010), rowing (Turpin, Guével, Durand, & Hug, 2011b), backward giant swing (Frère & Hug, 2012) or breaststroke swimming (Vaz et al., 2016). Strength training related tasks, such as the power clean (Santos et al., 2021) or the bench press (Kristiansen, Madeleine, Hansen, & Samani, 2015), have also been examined and there is preliminary evidence that experienced weightlifters and powerlifters employ neural strategies acquired after the repeated and chronic exposure to strength training. The adaptive plasticity of muscle synergies is further supported by past research showing that a five-week bench-press training regimen alters muscle coordination in previously untrained individuals (Kristiansen, Samani, Madeleine, & Hansen, 2016a). Similarly, four weeks of wobble board training were also shown to modify the modular organization during single-leg drop landing (Silva, Oliveira, Mrachacz-Kersting, & Kersting, 2018). Taken together, the available literature suggests that the components of muscle synergies can be modified by training.

Although neural adaptations to strength training may be particularly evident during the first weeks of intervention (Folland & Williams, 2007; Sale, 1988), it is still unknown how the adaptations in coordination arise during this early period and how do they continue to evolve during the later stages of training. Balshaw and colleagues (Balshaw et al., 2019) conducted a study comparing untrained with short-term and long-term trained individuals. Their data showed that while some adaptations, such as agonist activation during maximal contractions (when corrected to muscle-electrode distance), manifest themselves within 12 weeks of training, others, such as torque-agonist and torque-antagonist relationships, continue to adapt overtime. Thus, the chronological definition of strength training adaptations during the initial weeks, but also in the long-term, is useful to discriminate between chronic responses that plateau and others that continue to evolve over time. Ultimately, this allows introducing advanced training methods at specific time points of strength-training adaptation (Santos et al., 2023).

The present study compiles two experiments aimed at better understanding: (experiment #1) the effects of six weeks of back-squat training in coordination, and (experiment #2) the long-term adaptations in coordination. Experiment #1 was designed to determine the training effects in LVP, as well as the evolution of LD0 and V0 in untrained participants during the initial stages of strength training. It also sought to understand the adaptations in coordination by characterizing the individual EMG profiles and lower-limb muscle synergies at different external loads. Secondarily, it sought to evaluate the time course of these adaptations during the six weeks. Experiment #2 was designed to compare the LVP outputs between untrained with short-term and long-term trained individuals. In addition, it intended to discriminate short- and long-term adaptations in coordination by characterizing the individual EMG profiles and lower-limb muscle synergies obtained at different external loads. It was hypothesized that an attenuated slope of the relative LVP would accompany gains in maximal strength resulting from training. In addition, it was hypothesized that these changes would be accompanied by altered coordination at the level of muscle synergies extracted from the lower limb. Finally, it was hypothesized that individuals with longer training experience would manifest muscle coordinative strategies unattainable with only 6 weeks of strength training.

METHODS

Participants

Experiment 1

Eleven male participants were included in this experiment (age: 22.6 ± 3.1 years; height: 176.4 ± 7.9 cm; body mass: 70.5 ± 14.9 kg). All participants were healthy and without previous history of musculoskeletal injuries within the last 6 months. Although all participants were active Sports Sciences students, none of them had any strength training background. Written informed consent was obtained upon entry to the study. The study complied with the principles set forth in the Declaration of Helsinki and was approved by the Faculty's Ethics Committee (CEIFMH Nº: 24/2021).

Experiment 2

Thirty-one participants were included in this experiment. Eleven participants were untrained (UT: age: 26.2 ± 3.6 years; height: 173.0 ± 7.2 cm; body mass: 66.6 ± 8.2 kg) and nine were long-term trained (LT: age: 27.1 ± 6.0 years; height: 173.6 ± 6.4 cm; body mass: 81.8 ± 8.0 kg). Although all UT were active Sports Sciences students with no previous strength training background, while LT were powerlifters or weightlifters with at least two years of regular practice. The remaining 11 participants were the participants also assigned to Experiment 1. This group was originally similar to UT and trained for 6 weeks. At the conclusion of the training intervention, this group of participants was defined as short-term trained (ST). All participants were healthy males, without previous history of musculoskeletal injuries within the last 6 months. Due to EMG data collection issues, one UT participant and another LT participant were only accounted for LVP variables.

Data collection

Experiment 1

Experimental approach. Previously untrained participants were included in a high-bar back-squat training program to assess the effect of strength training in the ability of the neuromuscular system to generate powerful contractions with increasing submaximal loads

and to assess the time course of adaptation in intermuscular coordination. Each participant was requested to visit the laboratory in six occasions. The first session was used to familiarize the participants with the testing procedures, as well as with the back-squat exercise. In this session, the participants performed the squats at maximum concentric velocity with progressive load increments until the barbell reached a mean concentric velocity (MCV) < $0.7\ m.s^{-1}$ (Gomes, Fitas, Santos, Pezarat-Correia, & Mendonca, 2024). The remaining five testing sessions were similar between them and were used to obtain the individual LVP and the respective coordinative patterns. The first of these five sessions was scheduled for one-week post-familiarization and was used as baseline (BSL), after which the participants were instructed to maintain their regular physical activity. After another two weeks of maintaining their regular physical activity, the participants were tested once again. This session was defined as the beginning of the training period (W0). After W0, the participants started the training intervention and were evaluated every two weeks. Thus, the 3rd, 4th and 5th testing sessions were conducted after two (W2), four (W4) and six weeks of training (POS), respectively. The final testing session (6th week) corresponded to the conclusion of the training program. Each evaluation was conducted after at least 48h following the last training session.

Strength training. The training program had an absolute duration of six weeks and a frequency of three sessions per week (18 exercise sessions). The prescription consisted of five sets of ten back-squat repetitions with an interset rest period of two min. The exercise relative load was set at 75% of one-repetition maximum (1RM) and all participants were instructed to complete each repetition with an explosive concentric phase, following a controlled eccentric phase. Spotting was provided in the final repetitions of the last sets. Whenever spotting was required in two or more repetitions, the load for the subsequent set was reduced by 2.5 kg. The relative load was maintained during the training program, with absolute load progressions being performed every two weeks based on the back-squat 1RM (determined at each testing session).

EMG. All tests were accompanied by data EMG data collection. The EMG signals were recorded on seven muscles of the right side of the body: gluteus maximus (GM), vastus lateralis (VL), rectus femoris (RF), vastus medialis (VM), biceps femoris long head (BF),

lateral gastrocnemius (GL) and tibialis anterior (TA). These muscles were selected to assess the agonist muscles during the lower-limb triple extension and to assess agonist-antagonist pairs of each lower-limb joint. The electrodes were placed according to SENIAM recommendations (Surface EMG for Non-Invasive Assessment of Muscles). Before the placement of the electrodes, the skin was shaved and cleaned with alcohol to minimize skin impedance. Surface EMG was acquired using eight bipolar surface electrodes (EMG Delsys, Trigno™), fixed with specially designed adhesive interface, aligned with the muscle fibers (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000) and then additionally fixed with tape to avoid movement artefacts. EMG signals were preamplified, band-pass filtered between 20 and 450 Hz and digitized at 1000 Hz. Subsequently, the EMG signals were corrected for the 48-ms delay inherent to the Trigno EMG system.

Testing procedures. After the EMG electrodes placement, the participants completed a warm-up protocol consisting of 5 min of unloaded cycling (Monark Ergomedic 828 E cycle ergometer; Monark Exercise AB, Vansbro, Sweden), followed by 1 set of 10 callisthenic squats and 1 set of 6 back-squats with the barbell unloaded performed at maximal concentric velocity. Squatting position was set to shoulder width apart or slightly wider, with a high-bar position on the upper trapezius. A squat depth eliciting a knee angle of 80-90º was requested to the participants. The participants were asked to pause 1s at the bottom and from this position, the participants were instructed to complete the concentric phase of the lift as fast as possible until full extension of the knee and hip. Jumping was not allowed, although the heels could lift off from the floor. The participants were instructed to perform the eccentric phase in a controlled way (velocity between 0.45 and 0.65 $m.s^{-1}$). The 1RM of the high-bar back-squat was determined directly with the completion of a single maximal lift after progressive load increments (Gomes et al., 2024; Mendonca, Fitas, Santos, Gomes, & Pezarat-Correia, 2023).

The progressive loading protocol began with an empty barbell and subsequent set loads were based on the individual 1RM estimation from familiarization session. Until the barbell reached a mean concentric velocity (MCV) of 0.7 $m.s^{-1}$, increments of ~15% of the estimated 1RM were performed. After this, loading increments varied between 2.5 and 10 kg until 1RM was finally determined. For lighter (MCV > 1.15 $m.s^{-1}$), medium (0.7 > MCV >

1.15 $m.s^{-1}$), and heavier (MCV < 0.7 $m.s^{-1}$) loads, the number of attempts varied between 3 and 5, 2 and 3, and 1 and 2, respectively (Fitas et al., 2024; Gomes et al., 2024). MCV was taken from the start of the concentric phase of each lift to the instant corresponding to the maximum height of the barbell, with a previously validated Chronojump linear position transducer (Chronojump, Barcelona, Spain), which sampled the barbell's velocity at a frequency of 1000 Hz , coupled to the end of the barbell (Pérez-Castilla, Piepoli, Delgado-García, Garrido-Blanca, & García-Ramos, 2019). Additionally, to ensure that continuous raw data of the barbell displacement could be used to the phase definition of the EMG analysis, the barbell vertical trajectory was also monitored by a linear position transducer (Celesco, PT9510, Celesco, Canoa Park, USA). The interset rest period was 3 min for lighter as well as medium loads, and 4-5 min for heavier loads. The between-repetition rest period was 3-5 s, and only the best attempt for each load was recorded.

Experiment 2

Experimental approach. To assess the effect of short- vs. long-term strength training in intermuscular coordination during powerful contractions with increasing submaximal loads, UT participants were compared to ST (post-6 weeks of training) and to LT (post-training for at least 2 years). Each UT and LT participant visited the laboratory in two occasions. The first session was used to familiarize the participants with the testing tasks as well as with the back-squat exercise (in the case of UT). This session was similar to the familiarization session described in Experiment 1. The second session was used to obtain the individual LVPs and the respective coordinative patterns. The remaining procedures of data collection were similar to those presented for Experiment 1.

Data processing

Load-velocity profile. The individual LVP was obtained based on the linear relationship between MCV and relative load (Banyard, Nosaka, & Haff, 2017; Fitas et al., 2024; Thompson, Rogerson, Ruddock, Banyard, & Barnes, 2021). Slope, LD0 and V0 were calculated considering a multi-point approach of four back-squat loads and the respective MCV. The selection of these 4 points included loads between 40 and 90% of 1RM, and if

there were not 4 points within this range, the closest point (above 35 or below 95% of 1RM) was chosen. The linear fitting of this relationship allowed to calculate LD0 and V0, as the y-axis and x-axis intercepts, respectively, and the corresponding slope. As the present study intended to assess the impact of strength training on intermuscular coordination at each of the 4 points, we ensured that each data point could be included in one of 4 ranges of relative load: 1) first point corresponding to a light load (between 35 and 50%, with a midpoint of 42.5% of 1RM), 2) second point corresponding to a moderate-light load (between 50.1 and 65% with a midpoint of 57.5% of 1RM), third point corresponding to a moderate-heavy load (between 65.1 and 80% with a midpoint of 72.5% of 1RM) and 4) fourth point corresponding to a heavy load (between 80.1 and 95% with a midpoint of 87.5% of 1RM).

EMG pre-processing. Raw EMG signals were rectified and smoothed with a low-pass filter (12 Hz, 4th order Butterworth). Then, amplitude normalization was made to the average value of the 100 ms across the peak of the linear envelopes of each muscle during the 1RM. Finally, time normalization and interpolation to 200 points (100 points for the eccentric and 100 points for the concentric phases) was used to relativize each phase because the same relative time phases may be different for different individuals. The movement phases were based on the linear displacement of the barbell. Eccentric phase was defined from the moment at which the barbell started to descend until its lowest position, and concentric phase was defined from the lowest position of the barbell until the highest position after the explosive squat. Each phase corresponded to 100 data points.

Extraction of muscle synergies. Extraction of muscle synergies was computed through nonnegative matrix factorization, implementing the algorithm proposed by Lee and Seung (Lee & Seung, 1999). Matrix factorization minimizes the residual Frobenius norm between the initial matrix and its decomposition, given as:

$$E = WC + e$$

$$\min_{\substack{W\geq 0\\ C\geq 0}} ||E - WC||_{FRO}$$

where E is a p-by-n matrix (p = number of muscles; n = number of time points), W is a p-by-s (s = number of synergies), C is an s-by-n matrix and e is a p-by-n matrix. || ||FRO establishes the *Frobenius* norm and e is the residual error matrix. Therefore, the two multiplication

matrices in which the initial matrix is decomposed, represent two components: the muscle synergy vectors (W), expressing the relative weight of each muscle within each synergy and the synergy activation coefficient (C), expressing the relative activation time of the muscle synergies during the squat. The algorithm was repeated 100 times.

Muscle synergies were extracted at each of the four relative loads selected previously. At the light load, three repetitions were analyzed and therefore *E* consisted in a 7 column by 600 rows matrix. At the moderate-light and moderate-heavy loads, two repetitions were analyzed and therefore *E* consisted in a 7 column by 400 rows matrices. At the heavy load, one repetition was analyzed and therefore *E* consisted in a 7 column by 200 rows matrix. The number of selected muscle synergies was dependent on variance accounted for (VAF). Therefore, the number of muscle synergies was the smallest number defining 90% of VAF, considering that each synergy should represent at least 5% of VAF. The application of the NMF does not sort muscle synergies in the same order within and between participants, which required manual sorting of muscle synergies were.

Statistics

Experiment 1

Statistical analyses were made using jamovi software (version 2.3.28.0, Sydney, Australia). Normality was verified through the Shapiro-Wilk test. A repeated-measures ANOVA with four levels (W0, W2, W4 and POS time-points) was used to assess differences during the time course of the training program concerning LVP variables, VAF and muscle vectors. When data were not normally distributed, a Friedman test was used, and when sphericity was not assumed, a Greenhouse-Geisser correction was made. Tukey adjustments were used in *Post hoc* tests of ANOVA, and Durbin-Conover adjustments were used in *Post hocs* of Friedman test. These analyses were computed on all LVP variables, as well as in VAF and muscle vectors of the extracted synergies at each load.

The maximum cross-correlation function (r_{max}), indicating the waveform similarity, was used to assess differences in individual EMG patterns as well as in synergy activation coefficients. Simultaneously, the lag times at the maximum cross-correlation function were determined

using Matlab 2018a (Mathworks Inc., Natick, MA, USA) *xcorr* function for centered data (option "coeff"), which allowed to assess differences in timing of activation of muscles and synergies. The cross-correlation between W0 and the remaining moments of evaluation (W2, W4 and POS) was determined, representing the index of variability at each time point for each load. A unilateral t test, with 0 as reference value, was used to assess differences in the lag-time between moments. Additionally, repeated measures ANOVA with three levels was used to assess if there was a trend to an adjustment in muscle and synergy lags overtime.

A repeated measures t-test between BSL and W0 was used to ensure that 1RM, LVP variables, VAF and muscle vectors were not different. The relative reliability of the LVP variables, VAF and muscle vectors of the extracted synergies was computed at each load between the BSL and W0 time points. This was done by calculating two-way mixed-effects intraclass correlation coefficients (ICC(3,1)) (Koo & Li, 2016), with 95% confidence interval. ICC values were qualified as poor, <0.5; moderate, 0.5-0.75; high, 0.75-0.9; excellent, >0.9 (Koo & Li, 2016). Additionally, the standard error of measurement (SEM) was calculated as an absolute reliability measurement (Weir, 2005). To verify the magnitude of intra and interindividual variability of the mechanical variables, we calculated within- and between-subject co-variance (CV). A sample Student's t-test with the respective midpoint of the four relative loads as reference value was used to guarantee that the used loads were not different. Additionally, a repeated-measures ANOVA with four levels (W0, W2, W4 and POS time-points) was used to guarantee that each participant used similar relative loads across sessions. To verify the reliability of EMG profiles and activation coefficients we calculated the r_{max} and the corresponding lag times between BSL and W0. A sample Student's t-test with zero as reference value was used to evaluate the differences in the lag time. All statistical analyses were performed using a significance level of $p < 0.05$. Data were presented as mean ± standard deviation. Cohen' *d* was calculated as measure of effect size. Effect size was considered small, medium or large for Cohen' *d* of 0.2 – 0.5, 0.5 – 0.8 and > 0.8, respectively (Cohen, 2013).

Experiment 2

A one-way ANOVA with three levels (UT, ST and LT groups) was used to assess between group differences. When normality was not assumed, a Kruskal-Wallis test was used, and when Levene's homogeneity of variances was not assumed, a Welch correction was made. Tukey adjustments were used in *Post hoc* tests of ANOVA, and Dwass-Steel-Critchlow-Fligner adjustments were used in *Post hocs* of Kruskal-Wallis test. The previously described analysis was made concerning LVP variables as well as VAF and muscle vectors of the extracted synergies at each load.

A cross-correlation function was used to assess r_{max} and the corresponding lag times of EMG profiles and activation coefficients, as described in Experiment 1. The index of between group variability was assessed by averaging the r_{max}-values of all the between-group pairing, namely with 70 UT-LT pairs (10 UT x 7 LT), 110 UT-ST pairs (10 UT x 11 ST) and 77 ST-LT pairs (11 ST x 7 LT). The calculated indexes were used as indicators of the waveform consistency between groups. Additionally, a sample Student's t-test with 0 as reference value was used to assess differences in the lag-time between groups.

RESULTS

Experiment 1

Reliability. No differences were found between BSL and W0. All LVP variables reached high to excellent relative reliability between BSL and W0 (0.75 < ICC < 0.97). The SEM of the slope, 1RM, LD0 and V0 were 7.92 $kg.s^{-1}.m^{-1}$, 3.2 kg, 5.93% and 0.07 $m.s^{-1}$, respectively. The relative reliability of VAF of the attempted loads was moderate to high (0.72 < ICC < 0.86), with the corresponding SEM ranging from 0.008 to 0.025. Concerning muscle vectors, ICC values revealed that most of the 56 variables (7 muscle vectors x 2 extracted synergies x 4 loads) presented poor reliability (62.5% of the variables), although the remaining 37.5% of the variables presented moderate (26.8%) to high (10.7%) reliability. The cross-correlation analysis between BSL and W0 revealed that EMG profiles presented a r_{max} of 0.95 ± 0.04 (0.90 < r_{max} < 0.98) and that activation coefficients presented a r_{max} of 0.91 ± 0.09 (0.84 < r_{max} < 0.96). No differences in lag times were found for any EMG profile or synergy at any load.

Load-velocity profile. First, it is important to note that the four relative loads did not differ from the central point defined in the Methods section. Light, moderate-light, moderate-heavy and heavy loads corresponded to 43.3 ± 3.5%, 57.8 ± 3.4%, 73.0 ± 3.6% and 87.6 ± 2.7% of the RM, respectively, without significant differences from the midpoint. In addition, the ANOVA comparing the relative loads at each evaluation session did not present differences. Concerning the intra and interindividual variability of Slope, V0, LD0 and 1RM, we observed within-subjects CV of -4.97%, 2.14%, 3.25% and 1.85%, and between-subjects CV of 18.11%, 11.08%, 8.29% and 11.99%, respectively.

According to the ANOVA, all LVP variables changed significantly over time. In specific, training increased V0 (F = 7.02; p = 0.001; d = 1.18) and 1RM (F = 85.20; p < 0.001; d = 4.13), but decreased LD0 values (F = 5.77; p = 0.025; d = 1.08). Slope also changed significantly towards a less steep LVP (F = 7.64; p < 0.001; d = 1.24). Post hoc pairwise comparisons have shown that 1RM increased every two weeks during the six weeks of training (all p < 0.001). For slope, V0 and LD0, significant differences were only observed between W0 and all other time points. Figure 7.1 shows LVP at the four time points and Table 7.1 presents detailed information about LVP variables.

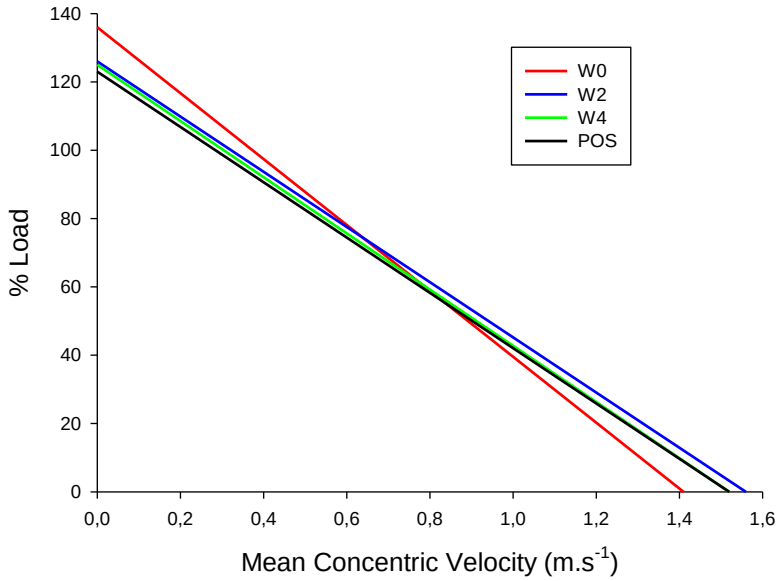

Figure 7.1. Load-velocity profile overtime. W0 – Training beginning moment; W2 – Week 2 of training; W4 – Week 4 of training; POS – Week 6 of training (end).

Table 7.1. Mechanical variables concerning dynamic strength and load-velocity profile of Experiment 1.

Variable	W0	W2	W4	POS
1RM (kg) *	105 ± 11.9	116 ± 14.3	125 ± 14.9	130 ± 16.3
LD0 (%) #	136 ± 9.0	126 ± 10.2	125 ± 6.8	123 ±7.6
V0 ($\boldsymbol{m.s^{-1}}$) §	1.41 ± 0.15	1.56 ± 0.12	1.52 ± 0.12	1.52 ± 0.10
Slope ($\boldsymbol{kg.s^{-1}.m^{-1}}$) §	-98.4 ± 16.1	-81.7 ± 11.9	-83.0 ± 9.4	-81.7 ± 8.6

LD0 – Theoretical maximal load; POS – Ending of training; 1RM – Repetition maximum; V0 – Theoretical maximal velocity; W0 – Training beginning moment; W2 – Week 2 of training; W4 – Week 4 of training. * $p < 0.05$ in overall repeated measures ANOVA and in all post hoc comparisons; # $p < 0.05$ in overall repeated measures ANOVA and in the post hoc comparisons involving W0; § $p < 0.05$ in overall repeated measures ANOVA and in the post hoc comparisons between W0 and W2 as well as between W0 and POS.

Muscle synergies. Using the VAF criteria to identify the number of muscle synergies, two synergies were enough to characterize muscle coordination during the back squat. The two extracted synergies accounted for the four evaluated loads between 93.6 to 95.1% of the VAF. Generally, synergy #1 was represented by the knee extensors and TA and synergy #2 was mainly defined by the activity of GL but also GM and BF. The single joint muscles of the quadriceps (VL and VM) were also represented in synergy #2, although with less weight than in synergy #1. Nevertheless, the activity of GM and BF was also distributed in synergy #1 and activity of TA was also distributed in synergy #2. Significant results of the ANOVA were observed in VAF of synergy #2 at the moderate-light load ($F = 3.59$; $p = 0.026$; $d = 0.89$) with a trend to decrease although without any significant post hoc comparison. Additionally, between W0 and POS there was a significant decrease of VAF of synergy #1 at the heavy loads ($p = 0.03$; $d = 0.76$).

Considering muscle vectors of synergy #1, the overall results of the ANOVA showed a trend for decreasing the weight of RF at light loads ($F = 7.37$; $p < 0.001$; $d = 1.28$ and an increasing the weight of TA at moderate-light loads ($\chi^2 = 10.80$; $p = 0.013$; $d = 0.89$) with training. The RF changes were particularly evident between W0 and POS ($p = 0.007$; $d = 1.03$), while post hoc comparisons of TA revealed only changes between W0 and W4 ($p < 0.001$; $d = 0.76$). Additionally, the muscle vector of TA in synergy #1 also presented a difference between W0 and W4 at heavy loads ($p = 0.037$; $d = 0.64$). Regarding muscle vectors of synergy #2, the overall results of the ANOVA did not show any significant effect of training, although a significant increase in GL muscle vector at heavy loads between W0 and POS was observed ($p = 0.044$; $d = 0.74$).

The indexes of similarity of activation coefficients between W0 and the remaining time points at the attempted loads for synergy #1 were 0.95 ± 0.03 and for synergy #2 0.88 ± 0.09. Regarding the EMG profiles, the similarity indexes across all loads were 0.94 ± 0.04 for GM, 0.97 ± 0.02 for VL, 0.96 ± 0.02 for RF, 0.97 ± 0.02 for VM, 0.94 ± 0.03 for BF, 0.92 ± 0.04 for GL and 0.91 ± 0.05 for TA. No differences in lag times were observed in activation coefficients in response to the training program. Activation coefficients as well as muscle vectors of the synergies at W0 and POS are depicted in Figure 7.2. Concerning the EMG profiles, significant shifts were observed between W0 and POS with a delay for VM at

moderate-light load (-0.23% ± 0.31; p = 0.037; d = 0.72) and an anticipated activation of GL at moderate-heavy load (1.20% ± 1.74; p = 0.045; d = 0.69) as well as an anticipated activation of GM at light (2.70% ± 1.91; p < 0.001; d = 1.41) and heavy loads (1.85% ± 2.55; p = 0.037; d = 0.73). Other shifts were observed between W0 and W4 for TA at light loads (1.27% ± 1.89; p = 0.049; d = 0.68), VL at moderate-light and heavy loads (0.55% ± 0.69; p = 0.026; d = 0.79 and 1.09% ± 1.62; p = 0.049; d = 0.67, respectively) and GM at light and heavy loads (2.75% ± 1.57; p < 0.001; d = 1.75 and 2.82% ± 3.27; p = 0.017; d = 0.86, respectively). Between W0 and W2 only one shift was observed for GM at moderate-heavy loads (1.67 ± 2.25%; p = 0.034; d = 0.74). All these shifts represented an anticipated profile of muscle activation. Additionally, an overall significant result of the ANOVA showed a trend for a continuous delay of RF profile at heavy loads (χ^2 = 7.20; p = 0.027; d = 0.64).

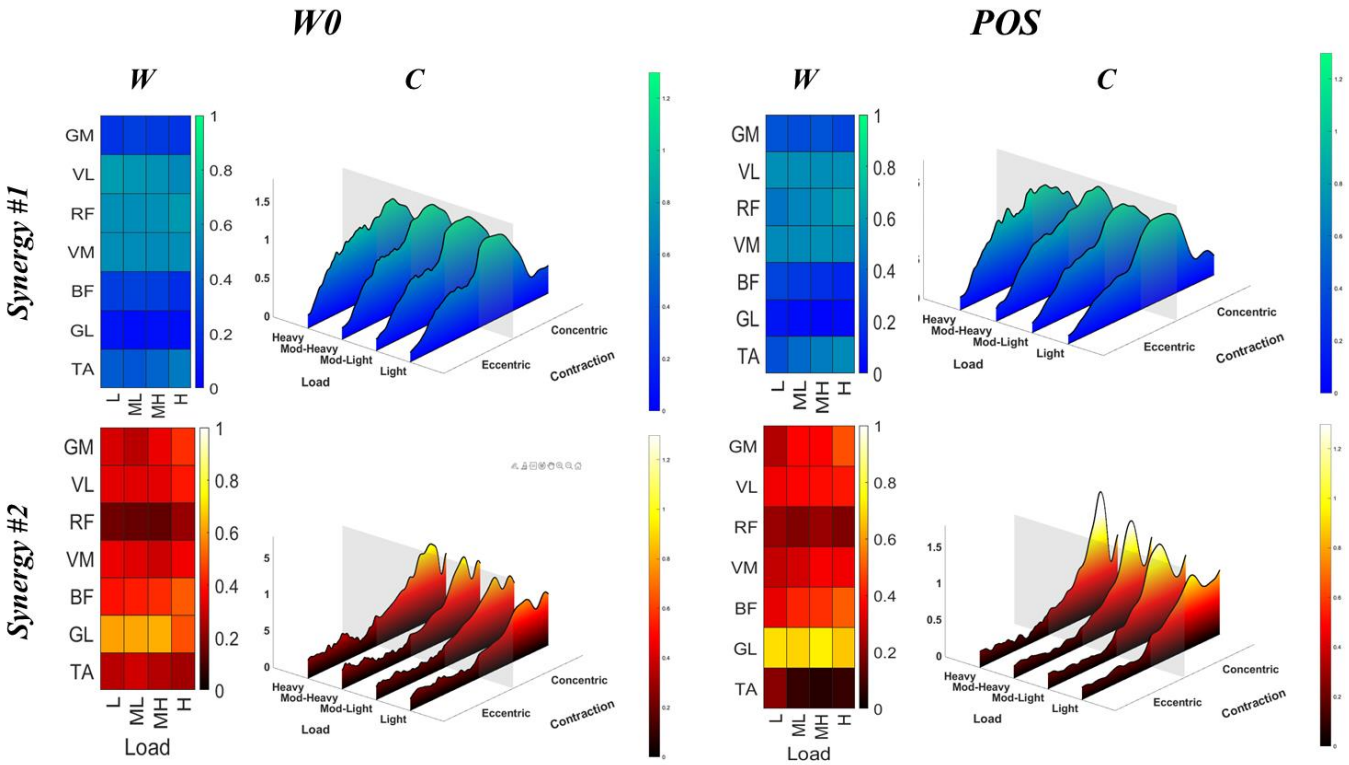

Figure 7.2. Muscle vectors (W) and activation coefficients (C) at all loads during pre-training (W0 – blue color) and post-training (POS – red color) evaluations. The heat maps represent the muscle weightings at each load with a color scale from 0 to 1, with lighter

colors indicating greater contribution within the synergy. Activation coefficients represent the activation of each synergy (vertical axis) during the eccentric and concentric phases of the squat (bottom right axis) at each load (bottom left axis). BF – Biceps Femoris; GL – Gastrocnemius Lateralis; GM – Gluteus Maximum; H – Heavy load; L – Light load; MH – Moderate-heavy load; ML – Moderate-light load; RF – Rectus Femoris; TA – Tibialis Anterior; VM – Vastus Medialis; VL – Vastus Lateralis.

Experiment 2

Load-velocity profile. Mechanical variables concerning the LVP established between mean concentric velocity and relative load were not different between groups. Absolute 1RM was different (F = 38.75; $p < 0.001$; $d = 2.64$), and post hoc comparisons showed significant differences at each group pairing ($p < 0.001$ for all comparisons; $1.77 < d < 4.43$). LVP variables of the three groups are detailed in Table 7.2.

Table 7.2. Mechanical variables concerning dynamic strength and load-velocity profile of Experiment 2.

Variable	UT	ST	LT
1RM (kg) *	100 ± 14.3	130 ± 16.3	176 ± 22.4
LD0 (%)	125 ± 18.3	123 ±7.6	134 ± 15.8
V0 ($\boldsymbol{m.s^{-1}}$)	1.60 ± 0.34	1.52 ± 0.10	1.40 ± 0.15
Slope ($\boldsymbol{kg.s^{-1}.m^{-1}}$)	-82.2 ± 23.9	-81.7 ± 8.6	-98.2 ± 22.6

LD0 – Theoretical maximal load; LT – Long-term trained group; 1RM – Repetition maximum; ST – Short-term trained group; UT – Untrained group; V0 – Theoretical maximal velocity. * $p < 0.05$ in overall between-group ANOVA and in all post hoc comparisons

Muscle synergies. The same two synergies used to characterize muscle coordination in Experiment 1 were extracted for group comparison. The average VAF across loads accounting two synergies was 0.95 ± 0.01 for UT, 0.96 ± 0.01 for ST and 0.96 ± 0.02 for LT. Significant differences between groups were only found for VAF of the two extracted synergies at light loads (F = 4.71; $p = 0.019$; $d = 0.89$), with post hoc comparisons showing higher VAF for LT than UT (0.96 ± 0.02 and 0.93 ± 0.02, respectively; $p = 0.014$; $d = 1.59$).

Regarding muscle vectors, between group differences were observed in the muscles acting around the ankle. For synergy #1, the ANOVA of GL weighting at light, moderate-light and moderate-heavy loads showed differences ($2.01 < F < 3.73$; $0.031 < p < 0.034$; $0.83 < d < 0.87$), greater for LT when compared to UT at light and moderate-light loads ($p = 0.038$; $d = 0.14$ and $p = 0.034$; $d = 1.61$, respectively), but not when compared to ST ($p > 0.05$). However, LT and ST GL vectors differed at moderate-heavy loads ($p = 0.043$; $d = 1.11$). Additionally, TA vector at light loads was different, namely with a trend for a lower value for LT than ST and UT ($F = 3.67$; $p = 0.04$; $d = 0.78$). For synergy #2, TA vector at light loads was different ($F = 5.35$; $p = 0.004$; $d = 1.42$), greater for LT than UT ($p = 0.003$; $d = 0.48$) but not than ST ($p > 0.05$).

Concerning activation coefficients, indexes of similarity between UT and LT were 0.92 ± 0.05 and 0.83 ± 0.08 for synergies #1 and #2, respectively. Between UT and ST indexes of similarity were 0.94 ± 0.04 and 0.89 ± 0.06 for synergies #1 and #2, respectively. Between ST and LT indexes of similarity were 0.91 ± 0.06 and 0.83 ± 0.08 for synergies #1 and #2, respectively. The corresponding lag times revealed a delay of synergy #1 at all loads in LT individuals when compared to UT ($-9.13 < lag < -4.89\%$; $p < 0.002$; $0.38 < d < 0.81$) and ST ($-8.05 < lag < -4.35\%$; $p < 0.013$; $0.32 < d < 0.58$) groups. ST have also shown a delay of synergy #1 when compared to UT at light and moderate-heavy loads (lag = -3,70%; $p = 0.001$; $d = 0.34$ and lag = -3,86%; $p < 0.001$; $d = 0.40$, respectively) although an anticipated activation of synergy #1 was observed at heavy loads (lag = 1.9%; $p = 0.028$; $d = 0.21$). Regarding synergy #2, it was observed an anticipation for LT when compared to UT at all loads ($5.20 < lag < 9.20\%$; $p < 0.001$; $0.46 < d < 0.71$) and to ST only at moderate-heavy and heavy loads (lag = 5.11%; $p = 0.001$; $d = 0.43$ and lag = 7.20%; $p < 0.001$; $d = 0.57$, respectively). ST have also presented anticipated synergy #2 when compared to UT at light, moderate-light and heavy loads ($1.65 < lag < 3.84\%$; $p < 0.009$; $0.26 < d < 0.63$). Figure 7.3 represents a graphical comparison between groups of the activation coefficients and muscle vectors averaged across all loads.

Regarding EMG profiles, when compared to UT, LT delayed GM (lag = -1.14%; $p = 0.048$; $d = 0.28$) and VM (lag = -1.42%; $p = 0.001$; $d = 0.43$) at light loads as well as TA across loads ($-10.09 < lag < -2.98\%$; $p < 0.036$; $0.26 < d < 0.72$), while anticipating GL at light,

moderate-light and heavy loads (3.65 < lag < 4.64%; $p < 0.02$; $0.29 < d < 0.52$). Concerning ST, the LT delayed GM (-3.87 < lag < -1.96%; $p < 0.005$; $0.39 < d < 0.66$) and TA (-6.93 < lag < -3.68%; $p = 0.018$; $0.28 < d < 0.40$) across all loads, while anticipating GL only at heavy loads (lag = 4.28%; $p = 0.001$; $d = 0.40$). When compared to UT, the ST presented an anticipated GL activation only at light and moderate-light loads (lag = 2.59%; $p < 0.001$; $d =$ 0.44 and 2.22%; $p < 0.001$; $d = 0.48$, respectively) and a delay of TA at light and moderate-heavy loads (lag = -3.66%; $p < 0.001$; $d = 0.29$ and -4,68%; $p < 0.001$; $d = 0.41$, respectively). Between UT and ST as well as between ST and LT, other significant shifts were observed, as it can be verified in Table 7.3.

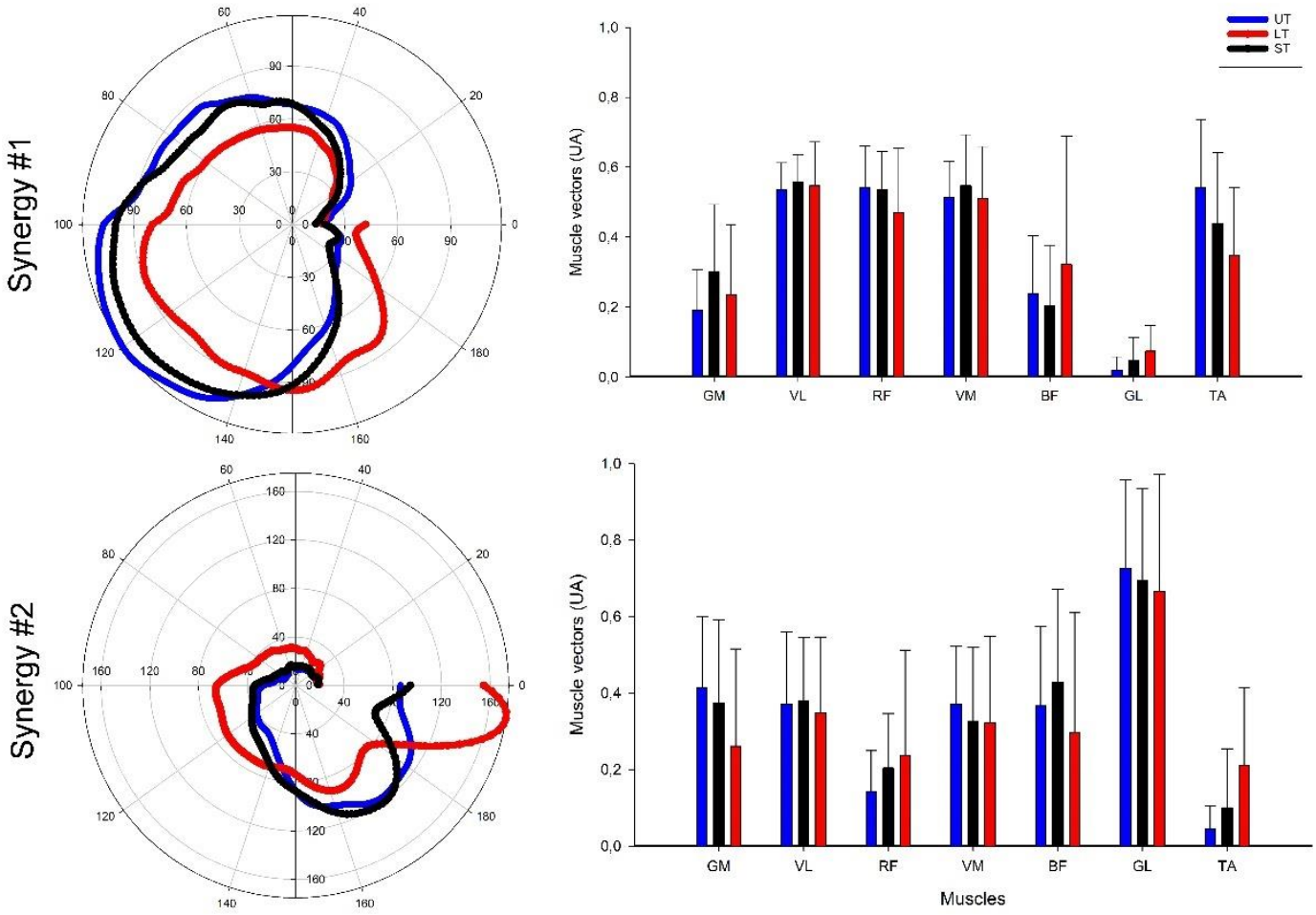

Figure 7.3. Averaged synergy activation coefficients and muscle vectors across loads. Left panel refers to synergy activation coefficients and right panel to muscle vectors. Upper panel refers to Synergy #1 and lower panel to Synergy #2. Upper hemisphere of the activation coefficient graphs refers to the eccentric phase of the squat, while the lower hemisphere corresponds to the concentric phase. Blue color concerns to UT, red color to LT and black color to ST groups. BF – Biceps Femoris; GL – Gastrocnemius Lateralis; GM – Gluteus Maximum; LT - Long-term trained group; RF – Rectus Femoris; ST - Short-term trained group; TA – Tibialis Anterior; UT – Untrained group; VM – Vastus Medialis; VL – Vastus Lateralis. * Significant between-group differences between the averaged muscle vectors.

Table 7.3. Intergroup similarity indexes (r_{max}) and lag times (%) of individual EMG profiles between untrained (UT), short-term trained (ST) and long-term trained (LT) groups. Bold values represent statistical differences from zero.

		UT x ST				**UT x LT**				**ST x LT**			
		% lag	***p***	***d***	**r_{max}**	**% lag**	***p***	***d***	**r_{max}**	**% lag**	***p***	***d***	**r_{max}**
Individual EMG Profiles													
GM	Light	2.14 ± 5.08	**<0.001**	0.42	0.93 ± 0.05	-1.14 ± 4.01	**0.048**	-0.28	0.92 ± 0.04	-3.87 ± 6.40	**<0.001**	-0.61	0.92 ± 0.04
	Mod-light	2.65 ± 4.54	**<0.001**	0.59	0.92 ± 0.04	-1.26 ± 8.08	0.274	-0.16	0.92 ± 0.04	-3.85 ± 5.84	**<0.001**	-0.66	0.91 ± 0.04
	Mod-heavy	2.37 ± 3.99	**<0.001**	0.59	0.92 ± 0.04	-0.63 ± 4.04	0.341	-0.14	0.91 ± 0.04	-2.58 ± 4.64	**<0.001**	-0.56	0.90 ± 0.04
	Heavy	2.55 ± 4.96	**<0.001**	0.52	0.91 ± 0.05	0.53 ± 2.53	0.141	0.21	0.91 ± 0.04	-1.96 ± 4.98	**0.005**	-0.39	0.90 ± 0.05
VL	Light	0.69 ± 4.37	0.104	0.16	0.96 ± 0.02	-0.81 ± 4.03	0.098	-0.20	0.96 ± 0.02	-1.80 ± 4.21	**<0.001**	-0.43	0.96 ± 0.02
	Mod-light	0.38 ± 5.04	0.435	0.08	0.96 ± 0.02	-0.81 ± 3.68	0.068	-0.22	0.96 ± 0.02	-1.40 ± 3.40	**0.001**	-0.41	0.96 ± 0.02
	Mod-heavy	-0.93 ± 4.52	**0.034**	-0.21	0.95 ± 0.02	-0.62 ± 3.58	0.151	-0.17	0.96 ± 0.02	-0.10 ± 2.76	0.742	-0.04	0.96 ± 0.02
	Heavy	0.95 ± 4.46	**0.029**	0.21	0.95 ± 0.02	0.78 ± 3.91	0.100	0.20	0.96 ± 0.01	-0.10 ± 3.31	0.784	-0.03	0.96 ± 0.02
RF	Light	0.19 ± 4.70	0.671	0.04	0.94 ± 0.03	0.00 ± 4.93	1.000	0.00	0.94 ± 0.03	-0.23 ± 4.26	0.641	-0.05	0.94 ± 0.03
	Mod-light	0.73 ± 5.23	0.149	0.14	0.93 ± 0.04	0.48 ± 470	0.400	0.10	0.94 ± 0.03	-0.70 ± 4.11	0.137	-0.17	0.94 ± 0.03
	Mod-heavy	-7.20 ±15.22	**<0.001**	-0.47	0.94 ± 0.03	-0.88 ± 6.57	0.266	-0.13	0.93 ± 0.03	2.04 ± 6.51	**0.008**	0.31	0.92 ± 0.04
	Heavy	0.15 ± 8.53	0.85	0.02	0.93 ± 0.03	2.40 ± 10.53	0.061	0.23	0.91 ± 0.05	1.62 ± 4.60	**0.003**	0.35	0.92 ± 0.06
VM	Light	1.88 ± 6.72	**0.004**	0.28	0.95 ± 0.03	-1.42 ± 3.31	**0.001**	-0.43	0.95 ± 0.02	-2.27 5.34	**<0.001**	-0.42	0.95 ± 0.02
	Mod-light	1.58 ± 7.05	**0.022**	0.22	0.94 ± 0.03	-0.28 ± 4.84	0.631	-0.06	0.96 ± 0.02	-1.82 ± 6.51	**0.016**	-0.28	0.95 ± 0.03
	Mod-heavy	1.15 ± 6.11	0.053	0.19	0.95 ± 0.02	0.36 ± 5.79	0.607	0.06	0.94 ± 0.06	-0.38 ± 6.92	0.634	-0.05	0.93 ± 0.06
	Heavy	1.83 ± 4.89	**<0.001**	0.38	0.95 ± 0.02	0.73 ± 4.34	0.165	0.17	0.95 ± 0.02	-1.01 ± 4.62	0.058	-0.22	0.95 ± 0.02
BF	Light	-4.27 ±16.74	**0.009**	-0.26	0.88 ± 0.10	-2.83 ±10.55	0.062	-0.27	0.85 ± 0.09	-4.52 ± 9.01	<0.001	-0.50	0.90 ± 0.04
	Mod-light	-7.95 ±22.27	**<0.001**	-0.36	0.89 ± 0.07	-0.91 ±11.38	0.572	-0.08	0.83 ± 0.07	-3.81 ± 9.72	0.002	-0.39	0.88 ± 0.05
	Mod-heavy	-2.27 ±16.96	0.165	-0.13	0.89 ± 0.05	1.68 ± 8.35	0.125	0.20	0.86 ± 0.05	-0.92 ± 6.21	0.231	-0.15	0.91 ± 0.03
	Heavy	1.05 ± 6.38	0.089	0.17	0.86 ± 0.06	0.67 ± 7.63	0.501	0.09	0.83 ± 0.07	0.70 ± 5.34	0.287	0.13	0.89 ± 0.05
GL	Light	2.59 ± 5.83	**<0.001**	0.44	0.89 ± 0.06	3.65 ± 10.21	**0.004**	0.36	0.80 ± 0.07	-1.02 ±10.18	0.381	-0.10	0.82 ± 0.07
	Mod-light	2.22 ± 4.59	**<0.001**	0.48	0.89 ± 0.04	4.64 ± 8.97	**<0.001**	0.52	0.86 ± 0.06	2.06 ± 9.97	0.074	0.21	0.85 ± 0.07
	Mod-heavy	0.08 ± 2.93	0.0783	0.03	0.91 ± 0.04	1.49 ± 10.85	0.254	0.14	0.80 ± 0.09	0.26 ± 9.27	0.807	0.03	0.81 ± 0.08
	Heavy	-1.18 ±10.19	0.229	-0.12	0.84 ± 0.06	4.31 ± 15.11	**0.020**	0.29	0.76 ± 0.11	4.28 ± 10.61	**0.001**	0.40	0.79 ± 0.09
TA	Light	-3.66 ±12.48	**<0.001**	-0.29	0.88 ± 0.05	-6.96 ±10.98	**<0.001**	-0.63	0.87 ± 0.08	-3.68 ±12.86	**0.014**	-0.29	0.85 ± 0.08
	Mod-light	-2.14 ±12.39	0.074	-0.17	0.88 ± 0.06	-6.39 ±14.64	**0.001**	-0.44	0.85 ± 0.09	-4.49 ±16.23	**0.018**	-0.28	0.83 ± 0.10
	Mod-heavy	-4.68 ±11.49	**<0.001**	-0.41	0.89 ± 0.06	-10.09±13.97	**<0.001**	-0.72	0.84 ± 0.08	-6.93 ±17.21	**0.001**	-0.40	0.85 ± 0.08
	Heavy	0.42 ± 10.61	0.677	0.04	0.88 ± 0.05	-2.98 ±11.66	**0.036**	-0.26	0.86 ± 0.08	-4.64 ±13.86	**0.004**	-0.34	0.86 ± 0.08

BF – Biceps Femoris; GL – Gastrocnemius Lateralis; GM – Gluteus Maximum; RF – Rectus Femoris; TA – Tibialis Anterior; VM – Vastus Medialis; VL – Vastus Lateralis

DISCUSSION

The present study aimed to address the chronology of training adaptations in LVP, as well as in muscle coordination at the evaluated loads. LVP adapted over the initial 6 weeks of training with increased dynamic strength being accompanied by changes in LVP variables. The sensitivity of the LVP to individual adaptations coupled with the absence of differences between groups with different training background, suggests that the LVP may be suitable to detect changes in specific interventions. Two muscle synergies were extracted to characterize lower-limb coordination during the back squat, with a general maintenance of the global organization of muscle recruitment. Differences concerning the timing of activation of muscle synergies were not observed after 6 weeks of training, although significant shifts in some of the analyzed muscles were observed. Furthermore, the LT individuals presented a delay of synergy #1 compared to UT and ST, and an anticipation of synergy #2 compared to both groups. Between group differences were also observed for ST and UT, with specific shifts concerning the evaluated loads. The shapes of muscle synergies were generally similar between groups. Regarding muscle vectors, training led to adaptations in the weight of specific muscles within the synergies, and expertise influenced the weights of muscles acting around the ankle.

First, it is important to consider the reliability analyses that involved the experimental group as its own control. Concerning LVP variables, our study revealed high to excellent reliability between BSL and W0, although caution should be taken considering V0 because when calculating 95% confidence intervals (1.96 x SEM), the change from W0 to POS is within this range (Weir, 2005). Previous research evaluating reliability of linearly determined LVP in bench press and squat (Iglesias-Soler et al., 2019) observed that MCV at different loads ranging from 20 to 90% RM is reliable in the squat (Banyard, Nosaka, Vernon, & Haff, 2018), although V0 may not be reliable (Gomes et al., 2024). Furthermore, a single session with absolute incremental loading appears to be valid to determine LVP (Gomes et al., 2024). Concerning EMG data, the extracted muscle synergies were reliable across BSL and W0. The robustness of muscle synergies across days was already discussed in previous studies concerning daily activities (Taborri, Palermo, Del Prete, & Rossi, 2018), but also concerning strength-training tasks as the bench press (Kristiansen, Samani, Madeleine, & Hansen,

2016b) or the power clean (Santos et al., 2020). Between-day relative reliability of VAF was moderate to high, although absolute reliability measured by SEM was 0.008 to 0.025 of scatter around the actual score, which represents a low dispersion. Activation coefficients were also similar, with high r_{max} values revealing similar coefficient shapes. Moreover, no lags were found between moments. On the other hand, muscle vectors presented greater variability than activation coefficients, which had already been shown in the previous studies assessing muscle synergy's reliability (Kristiansen et al., 2016b; Santos et al., 2020). This reflects variations in muscle weight within each synergy across sessions. Muscle vectors may be greatly affected by slight deviations in electrode placement and a slight learning effect may be observed from the first to the second session, in which muscle recruitment may be modulated in response to abundancy and redundancy of the musculoskeletal system (Hirashima & Oya, 2016; Latash, Scholz, & Schöner, 2007). Furthermore, Santos and colleagues (2020) have reported that strength training background affects the stabilization of muscle vectors across days in new motor tasks, suggesting that adaptations in coordination may result from previously existing muscle synergies that are flexibly exploited and adjusted during the acquisition of new motor skills (Carson, 2006). The fact that the individuals who participated in this study were absolutely unexperienced in strength tasks may have led to a greater variability in muscle vectors.

Load-velocity profile

Previously untrained individuals demonstrated adaptations across all variables of LVP. Maximum dynamic strength increased every 2 weeks. Maximum dynamic strength has been shown to be increased after single-joint dynamic strength training following 2 weeks of wrist flexion (Mason et al., 2020) or 3 weeks of elbow flexion training (Mason et al., 2017). Additionally, multi-joint strength training focusing on the back squat induced an increase in 1RM accompanied by decreased intracortical inhibition after 4 weeks (Weier, Pearce, & Kidgell, 2012), as well as altered activity of squat synergist muscles after 6 weeks over specific repetition conditions (Nicholson, Ispoglou, & Bissas, 2016). Furthermore, 6 weeks of knee extension training was effective to increase 1RM with low (30%RM) or high loads (80%RM), although the high-loads provided a strength increase immediately after 3 weeks and a greater magnitude increase following 6 weeks (Jenkins et al., 2017).

Considering the correlation between isometric strength and LD0 (Morales-Artacho et al., 2018), it would be reasonable that LD0 would also increase. However, we observed a reduction in LD0. This is due to the use of relative loads instead of absolute loads in this study, with the increased 1RM contributing to generally lower relative intensities even with increased absolute loads. This decreased relative LD0 was accompanied by an increase in V0 and a consequent less steep slope. Since LD0 is the hypothetical maximum isometric strength, it can be hypothesized that lower LD0 values mean a greater capacity to reach near maximum voluntary output dynamically. Previously trained individuals have shown to present greater voluntary activation during force production (Grosprêtre, Gimenez, & Martin, 2018; Lattier, Millet, Maffiuletti, Babault, & Lepers, 2003) and strength training has revealed to increase voluntary activation, especially when high-loads are used (Jenkins et al., 2017). Furthermore, the ratio between maximal dynamic and isometric force measured by the dynamic strength index has shown to increase after ballistic or maximal strength training of the upper limb (Young, Haff, Newton, Gabbett, & Sheppard, 2015), which may be justified by a greater capacity to dynamically recruit the agonist muscles. However, contradictory results have been found for the lower limb, with strength training decreasing this index as a result of greater maximal strength but not ballistic strength values (Comfort et al., 2018). These results may be attributed to the applied training program that used high-loads and thus did not impact the unloaded countermovement jump used to calculate the index. In addition, the dynamic exercises used to calculate upper and lower limb dynamic strength index represent different regions of the intensity spectrum, namely ballistic bench press at 45% RM and unloaded countermovement, respectively. Nevertheless, the squat training applied in the present study resulted in greater absolute dynamic strength and a decreased hypothetical relative isometric strength, which is consistent with a greater voluntary capacity of dynamic force production.

On the other hand, greater V0 was obtained, which means that individuals present greater maximal hypothetical unloaded velocity following strength training. Similar loading dynamics in leg press training led to increased myosin heavy chain type IIa and decreased myosin heavy chain type IIx (Izquierdo et al., 2011). Although it was demonstrated that when previously untrained individuals perform a strength training program the conversion from myosin heavy chain IIX to IIa may result in unaltered maximal unloaded velocity as well as

rate of force development (Andersen et al., 2005), there is evidence supporting that high-load strength training induces increased velocity or power output at low loads as well as in other unloaded tasks as jumps or sprints (Abade et al., 2021; Dorrell, Moore, & Gee, 2020; Moss, Refsnes, Abildgaard, Nicolaysen, & Jensen, 1997). Additionally, different loading mechanics have been shown to modify the LVP specifically. Power training at 40%RM increased, to a greater extent, the mean velocity associated with all %RM vs. heavy-strength training (Pérez-Castilla & García-Ramos, 2020). Cluster sets have also shown to impact differently the LVP compared to that seen with traditional back squat strength training, although similar results were attained in the bench press. While traditional strength training increased absolute theoretical maximal force during the back squat, cluster sets increased V0 as well as the slope of the LVP (Rial-Vázquez et al., 2022). Similar results were observed regarding LVP, i.e., when relative loads were used in the linear fitting (Iglesias-Soler, Rial-Vázquez, et al., 2021). Our results are closer to the results obtained after cluster organization of strength training, although we used a traditional loading prescription. The differences that we obtained with traditional strength training in LD0, V0 and slope may rely on the strength-training inexperience of the participants included this study, contrary to the previous referred studies that used individuals with at least 3 months of strength training experience (Iglesias-Soler, Rial-Vázquez, et al., 2021; Rial-Vázquez et al., 2022). It has been shown that different training status leads to different adaptations subsequent to distinct strength training modalities (James et al., 2018), and it was suggested that weak individuals may benefit more with strength training than power training (Cormie et al., 2010). Additionally, cluster sets increase the number of repetitions at optimal velocity or power output (García-Ramos et al., 2016; Oliver et al., 2016; Rial-Vázquez et al., 2022). It is important to note that we used a percentage-based method (PBT) of loading prescription and not a velocity-based method (VBT). Recent reviews have shown superiority of VBT approaches when compared to PBT in strength, jump or sprint gains (Held, Speer, Rappelt, Wicker, & Donath, 2022; Włodarczyk, Adamus, Zieliński, & Kantanista, 2021), although other reviews concluded that there is no clear evidence demonstrating more effective strength or power adaptations following VBT (Liao et al., 2021; Orange et al., 2022). In this regard, the fact that we adopted a traditional strength training program in untrained individuals and not one that allowed to maintain velocity and power near maximum over all session, may have led to different

adaptations, although we cannot speculate that a VBT or cluster set prescription would be more effective in modifying LVP.

When comparing UT with ST and LT, it was observed that group differences were limited to 1RM. LT individuals had greater dynamic strength than ST and UT, and ST had greater strength than UT. This is not surprising since, as it was demonstrated in Experiment 1 and discussed above, dynamic strength training leads to increased dynamic strength values. However, the LVP parameters were not different between groups. This shows that LVP is a sensitive tool to evaluate training adaptations to specific training programs and that it should be used based on individual monitoring rather than characterizing different groups, possibly depending on individual characteristics. Previous research has shown that the LVP characteristics present great interindividual variability (Iglesias-Soler, Mayo, Rial-Vázquez, & Haff, 2021; Thompson et al., 2021) which was corroborated by the within- and between-subjects variability analysis demonstrating greater interindividual variability for all variables. Also, when individualized LVP is considered to monitor training the transfer of adaptations to jumping performance has greater magnitude than when using group-based LVP (Dorrell et al., 2020). Thus, the absence of differences in the LVP parameters dictates that individualized LVP is useful to monitor training adaptations to specific training stimulus, and that the non-uniformity of the training specificity in individuals of different groups and the subject-specificity of the LVP variables, does not ensure that the between-group comparison will provide practically meaningful results.

Muscle synergies

Two muscle synergies were extracted to characterize the back-squat exercise. Previously studied tasks such as the swimming breaststroke (Vaz et al., 2016), rowing (Turpin et al., 2011b), backward giant swing (Frère & Hug, 2012) or power clean (Santos et al., 2021) have been characterized by the extraction of three muscle synergies. In addition, analysis of bench press resulted in only two synergies accomplishing VAF criteria (Kristiansen et al., 2015), as well as in the back-squat as shown in the present study. This may rely on the lower complexity of the tasks when compared to those previously enumerated, depending on the available degrees of freedom (Frère & Hug, 2012). However, the squat has been previously studied regarding the extraction of muscle synergies and three muscle synergies were

identified by Smale and colleagues (Smale, Shourijeh, & Benoit, 2016). This difference likely relies on the methods concerning muscle synergy analysis. Although both studies used valid methods, four different methodological approaches were considered. First, the number of selected muscles was different. We selected seven lower-limb muscles, while the mentioned study selected 12 lower-limb muscles. It is well known that the number of selected muscles affects the number of extracted muscle synergies and that more muscles will lead to a greater matrix reconstruction (Brambilla & Scano, 2022; Steele, Tresch, & Perreault, 2013). The lower number of muscles monitored in our study led to two synergies extracted instead of three as reported by Smale and colleagues. Second, the filtering technique may influence the number of extracted synergies, namely concerning the degree of smoothing of the linear envelope (Hug, Turpin, Dorel, & Guével, 2012). Third, the amplitude normalization was different, with our study using the 1RM repetition as the task eliciting the maximum of each muscle because it was beyond our aim to infer about the degree of activation. Conversely, Smale and colleagues used an isometric MVC to each muscle. The use of non-normalized, normalized to the maximum voluntary contraction or normalized to the evaluated dynamic task may impact the number of extracted synergies (Turpin, Uriac, & Dalleau, 2021). Fourth, although both studies used nonnegative matrix factorization for extraction of muscle synergies, Smale and colleagues concatenated the original EMG data, limiting the signal variability to the coefficients and minimizing the subjective error associated to manual sorting of muscle synergies (Shourijeh, Flaxman, & Benoit, 2016), although small influence has been detected between both approaches (Oliveira, Gizzi, Farina, & Kersting, 2014). In line with this, similar structure of synergies may be seen between both studies. We observed a greater contribution of the knee extensors and the TA during synergy #1, mainly active during the eccentric phase and the beginning of the concentric phase. Smale and colleagues reported increased vastii weight in synergy #1 (beginning of concentric phase) and RF and TA in synergy #2 (eccentric phase), whose differences may be interpreted concerning the enumerated methodological differences between studies that led to a merged extraction of these synergies in our study. Additionally, synergy #2 in our study reflects mainly the contribution of GL, but also from GM and BF during the end of the concentric phase, which may be associated to synergy #3 of Smale and colleagues (2016).

Other study, comparing the back-squat muscle synergies at various external loads has also found different synergies, with VAF criteria being accomplished with 7 synergies (Kenville, Clauß, & Maudrich, 2024). Although this study has monitored similar muscles to our study, switching GL by medial gastrocnemius and not collecting GM, they monitored muscles from both limbs, which resulted in a greater number of synergies. The sequence of recruitment of muscles during the identified synergies was also similar. The same study also reported no differences between extracted muscle synergies at 50, 62.5 and 75% of 3RM, which reflects the CNS consistency in recruiting spatiotemporal instructions to achieve a specific movement independently from the external load (Kenville et al., 2024). That data corroborate previous research showing the robustness of muscle synergies across different loading conditions. Namely, global structure of synergies was also consistent during pedaling across different mechanical constraints, with slight temporal adjustments (Hug, Turpin, Couturier, & Dorel, 2011). Additionally, different power outputs elicited robust organization of muscle synergies during rowing, with changes in the activity degree contributing for different mechanical demands (Turpin, Guével, Durand, & Hug, 2011a).

Generally, synergies were robust regarding adaptations to the training program applied in Experiment 1 as well as between groups with different level of expertise as seen in Experiment 2. Differences from W0 to POS at heavy loads were observed in VAF of synergy #1, concomitant with increased muscle weighting of GL in synergy #2. Training may have led to an adaptive process that increased the contribution of GL during synergy #2, mainly active during the end of the concentric phase, and thus increasing the activation during plantar flexion, which may have accounted for the difference in variance overtime. Considering the muscles acting around the ankle, TA weighting has also suffered some changes in synergy #1 during the training program. Additionally, the LT individuals also showed greater incorporation of GL in synergy #1 when compared to the UT and ST groups at all loads, except for the heavy loads, which may have accounted for the difference in variance between UT and LT at light loads. As synergy #1 refers to eccentric and beginning of concentric phase, this may suggest that greater GL weight means a greater pre-tension of the muscle sarcomeres and an increased joint stiffness, anticipating the powerful contraction of the plantar flexors. It has been proposed that a preceding eccentric action leads to a residual force enhancement during isometric actions. It is likely that the mechanisms causing this

phenomenon, namely titin elasticity (de Campos, Orssatto, Trajano, Herzog, & Fontana, 2022; Fukutani & Herzog, 2019) may be present when the eccentric action precedes a concentric action, and that training may influence titin isoforms as well as the expression of titin-linked putative mechanosensing proteins and consequently stiffness properties (Fry et al., 2003; Wette et al., 2021). Additionally, although the force enhancement during the concentric phase due to stretch-shortening cycle depends not only on the sarcomere pre-tension but also on reflex mechanisms and tendon elasticity (Finni, Ikegawa, & Komi, 2001; Trimble, Kukulka, & Thomas, 2000), and that stretch-shortening eccentric-concentric actions lead to greater velocity and power output in strength exercises (Pérez-Castilla, Comfort, McMahon, Pestaña-Melero, & García-Ramos, 2020), in our study the controlled eccentric phase involved different contraction dynamics. Thus, we may presume that greater activation led to greater force level reached before the concentric phase and mechanisms possibly related with sarcomere structure may be on the origin of plantarflexion force enhancement on the long-term. Additionally, adaptations in GL weight within the synergy may rely on an optimized action of the gastrocnemius as biarticular muscles antagonists of knee extension and main agonists of plantarflexion. A proper maintenance of muscle length to an adequate force production condition regarding force-length relationship was proposed by Cleland (1867). Besides, new insights into the biarticular muscles show that specific regional fiber activation may modulate its function (Watanabe, Vieira, Gallina, Kouzaki, & Moritani, 2021). Nevertheless, 6 weeks of training do not seem enough to achieve different weightings. It is also interesting to note that weighting of TA for LT participants was different at light loads, with decreased weighting in synergy #1 when compared to UT and ST and increased weighting in synergy #2 only when compared to UT which may ensure greater balance at the ending of the movement. This suggests that long-term training led to a greater coordination between agonist and antagonist muscles promoting a greater stabilization around the ankle that allow a greater force output of the agonist muscles and a more efficient kinetic transmission to the ground. Furthermore, 6 weeks may lead to some extent of these coordination adaptations, although it seems likely that they continue evolving overtime.

It is also notable the decreased contribution of RF in synergy #1 at light loads after the training program. In our previous work, RF coordination with the single-joint knee extensors showed to be modified by training, and it was also observed a decreased rate of activation

during an isometric maximal leg press. The biarticular role of RF may have contributed to these results, optimizing the force transmission from the hip to the knee (Santos et al., 2024). The fact that RF presents less contribution in synergy #1 after training shows that its relative activation is reduced during eccentric and beginning of concentric phase, which probably will allow to reduce antagonist force in the hip to a more efficient hip extension and consequent force transmission to the distal joints during fast movements. Furthermore, a different mechanism is suggested for RF motor control when compared to the monoarticular portions of quadriceps. Lower intermuscular coherence at gamma band, investigating motor unit synchronization between different muscles and the influence of the corticospinal pathway (Conway et al., 1995; Grosse, Cassidy, & Brown, 2002), were observed during squats between RF and VL or VM when compared to intermuscular coherence between VL and VM, which may suggest decreased common corticospinal input between monoarticular and biarticular muscles and thus a more independent central input (Maudrich et al., 2022).

The previous enumerated training adaptations are in line with past research showing that muscle synergies may be modulated by training. For example, different neural coordination strategies were reported in response to unexpected external perturbations by elite hockey players (Kim et al., 2018) or during a smash shot by elite badminton players (Matsunaga & Kaneoka, 2018). Also, weightlifters have shown different composition of the extracted synergies compared to untrained individuals (Santos et al., 2021) while other study demonstrated different synergies only at heavy loads (90% RM) with greater plantar flexor contribution in the synergy related to double-knee bend (Hakariya, Kibushi, & Okada, 2023). The absence of differences at lighter loads in the study of Hakariya and colleagues (2023), compared to the study of Santos and colleagues (2021), may rely on the training background of the inexperienced group. While Santos and colleagues (2021) evaluated fully inexperienced individuals in response to the power clean, Hakariya and colleagues (2023) evaluated individuals with 1 year of training background, which means that they already had some extent of adaptations leading to similar patterns to the highly experienced weightlifters. Regarding longitudinal studies, 4 weeks of sensorimotor training led to different coordination patterns at the ankle during landing (Silva et al., 2018) and 5 weeks of bench press training has also led to changes in synergy components (Kristiansen et al., 2016a) which corroborated the differences observed between powerlifters and untrained individuals (Kristiansen et al.,

2015). Nevertheless, we should account that previously untrained individuals may explore the solutions provided by the musculoskeletal redundancy of motor behaviors (Latash et al., 2007) to achieve coordination strategies adapted to individual anthropometrics and muscle characteristics as size and architecture (Kristiansen et al., 2015), and that this may be reflected by changes in muscle vectors during initial weeks of training.

The temporal components of muscle synergies were not modified by training. However, occasional shifts were observed in some muscles. Most of these shifts may arise from the inherent variability of movement, and the resultant effect sizes were not large, with exception of the GM pattern of activation at light and heavy loads, namely after 4 weeks of training that was subsequently maintained until the 6th week. The EMG profile of GM was anticipated, which may have been a more efficient way to increase force of hip extension during the beginning of concentric phase as well as to stabilize knee and pelvis due to its attachment at the iliotibial band (Schoenfeld, 2010). As it was discussed previously, the lower weight of RF during synergy #1 may lead to greater capacity to activate GM earlier in the transition between the eccentric and concentric phases. It is thus plausible that during different mechanical demands, the patterns of contraction may present load-specific adaptations. When determining the LVP, usually loads between 40 to 90% RM are used, and a quasi-linear relationship may be suitable to describe velocity at each load (Bobbert, 2012). However, a double hyperbolic fitting has been suggested providing specific kinetic outputs at high-force/low-velocity and low-force/high-velocity regions (Alcazar, Csapo, et al., 2019). Considering the lightest loads, studies that determined force-velocity relationship at low forces (< 40% maximum voluntary contraction) showed that although the linear pattern at moderate forces is maintained, the pattern at low-force/high-velocity region is deviated upwards becoming curvilinear, which may be due to a regulatory function of the myosin thick filaments allowing that the binding to actin is only matched depending on external mechanical conditions (Alcazar, Csapo, et al., 2019; Irving, 2017). For example, it was shown that near maximal force, there is a second hyperbola regarding force-velocity relationship (Alcazar, Csapo, et al., 2019), probably caused by velocity-specific cross-bridge kinetics (Piazzesi et al., 2007). The fact that GM presented different patterns of activation at the light loads (~40%RM) and heavy loads (~90%RM) may rely on adaptations in the hip extension moment-velocity relationship influencing these specific regions of the LVP.

Although the activation coefficients remained similar during the 6-week period, between-group differences were found. Synergy #1 presented high values of similarity between the three levels of training experience, which means that the synergy shape was consistent between groups. Since this synergy refers to muscle coordination during lowering and initial rising of the squat, although our data cannot ensure this, it may be possible that, even the UT persons, are used to similar patterns during daily activities and that this synergy may be a shared neural pattern between different behaviors (d'Avella & Bizzi, 2005). Further research is needed to explore the transferability of daily used muscle synergies to specific strength-related tasks. However, the same synergy revealed to be delayed in the LT individuals compared to UT and ST. A delay of muscle synergies in trained individuals compared with individuals with less or without experience was also observed in breaststroke swimming (Vaz et al., 2016) and the power clean (Santos et al., 2021). The differences may be explained by the sum of small changes in individual EMG profiles of muscles contributing to this synergy. The pattern of activation of the TA was also delayed by the LT compared to UT and ST, which may rely on specific strategies of ankle stabilization during synergy #1, but also on the coordination between the mono and biarticular knee extensors. Regarding synergy #2, lower values of similarity were found namely between the LT and the other two groups. This may suggest that long-term training leads to specific adaptations in this muscle synergy. Previous research has reported greater intragroup variability concerning a specific muscle synergy in experienced individuals (Kristiansen et al., 2015; Santos et al., 2021; Turpin et al., 2011b), which may result from individualized adaptations that better fit individual characteristics. Although we do not present results concerning interindividual variability within groups, the lower r_{max} of the LT may be related to a more variable performance between individuals. Nevertheless, it is interesting that synergy #2 was generally anticipated by the LT, with a concomitant anticipation of GL which is the primary contributor for this synergy. Synergy #2 was anticipated by LT when comparing to UT at all loads, but only at heavy loads when compared to ST. Additionally, the ST anticipated this synergy at all loads with exception of moderate-light loads when comparing to UT. This means, that the timing of activation of synergy #2 adapts overtime, with the timings of activation at light and moderate-light loads of the ST being already similar to the LT but not at moderate-heavy and heavy loads. Thus, the recruitment of synergy #2 is modulated at lighter loads in the first six

weeks of training, but modulation at heavier loads may require longer training periods, although the different training backgrounds of the group-comparison do not allow to clearly conclude this. Also, the composition of this synergy relies mainly on GL activity, whose individual pattern presented a similar time adjustment.

Some specific aspects concerning the limitations in the extraction of muscle synergies as well as possible issues concerning the reliability measures of muscle synergy variables and load-velocity profiling have been addressed throughout the study. In addition, it is important to consider the small sample size, and the corresponding statistical power did not allow to perform any statistical approach that could explain how the intermuscular coordination affected the LVP. Since the between-group comparison showed differences regarding muscle synergy components in the absence of differences in the LVP, and the training intervention showed only slight differences in muscle weightings within the synergies while modifying the LVP, we could possibly interpret that although intermuscular coordination adapts overtime, it does not effectively contribute to mechanical changes regarding squat LVP. However, we cannot clearly associate the changes in muscle synergies to adaptations in LVP, and from our study we cannot simply exclude the influence of intermuscular coordination in training adaptations during complex tasks. Thus, future research should address this question, observing the general evolution of muscle synergies throughout a longer training period with a greater sample size that may allow to perform statistical approaches that explain the real influence of intermuscular coordination in specific mechanical variables. Additionally, the monitoring of abdominal and lower back muscles would be useful to a better understanding of the coordination between trunk and lower limb.

CONCLUSION

Two experiments were conducted to better understand training adaptations in intermuscular coordination. Six weeks of strength training led to changes in LVP. Previously untrained individuals decreased LD0 presenting a trend for an increased V0, which resulted in a less steep fitting of the relationship between movement velocity and relative external load. Additionally, 1RM has increased significantly every two weeks. Although differences in 1RM were also found between groups with different levels of training experience, there were no differences in LVP variables, which suggests that LVP accounts for individual differences in response to specific training programs while not being necessarily different between groups. Two muscle synergies were enough to characterize coordination patterns during squat. Synergy #1 was composed mainly by the knee extensors and TA during the eccentric phase and beginning of the concentric phase, while synergy #2 reflected the contribution of GL during the end of the concentric phase. BF and GM were distributed by both synergies, although with greater weightings in synergy #2. The synergies were generally stable, although specific changes in their components were observed after training and between the analyzed groups. The significant differences in muscle vectors concerned mainly the distribution of the muscles acting around the ankle (GL and TA) in the two extracted synergies, and these adaptations has shown to be continued until later stages of training adaptations. Furthermore, although the temporal component of synergies was not modified by 6 weeks of training, some shifts were found in individual EMG profiles, namely with an anticipated pattern of GM at light and heavy loads. Between groups, muscle synergies presented similar patterns although the index of similarity between LT and the other groups was lower for synergy #2, with a delay of synergy #1 and an anticipation of synergy #2. It was shown that the time adjustments are progressive overtime, with the anticipation at lighter loads being achieved during the first six weeks of training while the adjustments at heavy loads possibly needing longer interventions to significantly change. These adjustments were caused by a similar pattern of adaptations in GL. This study brings new insights into the strength training adaptations in intermuscular coordination at short- and long-term training stages. Future research should focus on developing the current knowledge concerning muscle synergies adaptations after squat training.

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Chapter 8

General Discussion

THESIS OVERVIEW

The current Doctoral thesis compiled six studies. The purpose of the thesis arises from the well-known chronology of neuromuscular adaptations to strength training, namely with the initial strength gains not being accompanied by muscle adaptations. Thus, it is suggested that neural adaptations play an important role in strength gains during early stages, while muscular adaptations are preponderant during later stages of strength training as it was vastly recommended by seminal studies (Folland & Williams, 2007; Moritani & deVries, 1979; Sale, 1988). Nevertheless, this view may be limited because recent studies have found that the muscle may present adaptations sooner than those studies suggested, namely concerning architectural parameters (Seynnes, De Boer, & Narici, 2007) while the neural mechanisms may remain adapting with long-term training possibly preventing stagnation in strength development (Balshaw, Massey, Maden-Wilkinson, Lanza, & Folland, 2019; Pearcey, Alizedah, Power, & Button, 2021; Škarabot, Brownstein, Casolo, Del Vecchio, & Ansdell, 2021). One important contribution to a better performance during strength exercises are the intermuscular coordination mechanisms. Recently, research around this topic has contributed to the development of the methodological procedures when assessing coordination and those approaches have revealed to be sensitive to a comprehensive understanding of training adaptations. Namely, the analysis of individual EMG profiles, the extraction of muscle synergies and the calculation of intermuscular coherence have provided important insights into the study of coordination. However, the use of those processing methods when monitoring strength training programs are scarce (Kristiansen, Samani, Madeleine, & Hansen, 2016; Walker et al., 2019) and the relevance of intermuscular coordination during the time course of training adaptations is not fully understood. Thus, this thesis intended to provide new evidence concerning the intermuscular adaptations to strength training overtime.

The six studies, previously presented in this document, allowed to better understand the intermuscular coordination adaptations to strength training and what are the timings of manifestation overtime. First, a systematic review evaluating 20 cross-sectional studies comparing electromyographic outcomes of resistance trained and untrained individuals was conducted to organize the current knowledge about long-term neural adaptations to strength training (Santos, Vaz, Correia, Neto, & Pezarat-Correia, 2023). This review defined the long-term neural characteristics of resistance trained individuals regarding agonist, antagonist and

synergist muscle activation. The elucidation about the neurophysiological long-term adaptations, namely concerning intermuscular coordination, clarifies how it influences the mechanical output and how those mechanisms may remain being modulated at later training stages. The second study was also a systematic review evaluating 13 articles, in this case concerning the acute adaptations in intermuscular coordination to training (Santos, Correia, Vaz & Pezarat-Correia, 2024a). The study of intermuscular coordination during or after fatiguing protocols has been done through the calculation of IMC. This approach allows to infer about the neural origin of intermuscular coupling concerning the correlation between the power spectral densities of two EMG signals, and has demonstrated to be particularly sensitive when assessing the effects of fatigue. Thus, this review organized the current knowledge about the acute responses concerning the shared central input between muscles with different anatomical and functional roles during different strength-related tasks.

Following the two systematic reviews, a first experimental study was conducted. This study aimed to follow the rationale established by the systematic reviews, comparing the neural strategies of agonist activation and intermuscular coordination between powerlifters/weightlifters and untrained individuals before and after a strength training session (Santos et al., 2024e). The use of 5 x 10 repetitions with 75% RM of back-squat allowed to induce fatigue with a multi-joint complex task, and it was assessed its impact in a maximal isometric lower limb triple extension in a leg press machine. The assessment of the effects of the training protocol on maximal and rapid force were accompanied by measurements of surface EMG that allowed to determine the rate of activation of the knee extensor agonist muscles, and the coordination between pairs of muscles with distinct functional roles. Additionally, the different training effects between the two described populations suggest that long-term training induces specific neural strategies and that acute training responses depends on training background.

After, we conducted three longitudinal studies where previously untrained individuals started a strength training program 3x/week with the load dynamics described above. The training program lasted 6 weeks and intended to induce short-term adaptations in the engaged individuals. As we have already studied the acute effects of training, as well as compared the intermuscular coordination characteristics of long-term trained to untrained individuals

during isometric maximal force production, we assessed if a short-term training program could lead to those differences or if they only manifest at the long-term (Santos, Vaz, Gomes, Infante & Pezarat-Correia, 2024b). At the same time, the individuals were evaluated in tasks regarding isometric submaximal force production as well as dynamic strength. Thus, the individuals were evaluated during isometric submaximal knee extensions at different intensities from 20 to 80% MVC, as well as dynamic explosive squats with different loads at the maximal intended velocity. This allowed to better understand short-term training adaptations regarding, on the one hand, torque-EMG relationships and IMC during submaximal force production (Santos et al., 2024d), and on the other hand, lower limb individual EMG profiles and muscle synergies during the load-velocity profile of the back squat (Santos et al., 2024c). Each of these studies provided two distinct but integrated experiments, with the first one evaluating the short-term training adaptations as described, but also a second experiment comparing the short-term trained individuals to long-term trained and untrained ones. This experimental design, adapted from Balshaw and colleagues (Balshaw et al., 2019) allowed to define the chronology of strength training adaptations in intermuscular coordination.

The more relevant outcomes of each study will be discussed below, intending to clearly define what is known about intermuscular coordination concerning acute, short-term and long-term adaptations to strength training.

MAIN FINDINGS

Acute adaptations to fatigue

When studying the acute responses to strength training, we should consider that they are different regarding training status, and different training methods may be more adjusted to one population than the other (Counts et al., 2017; Krzysztofik, Wilk, Wojdała, & Gołaś, 2019). While the use of traditional sets led to similar acute response in what concerns to EMG activity, the use of advanced methods, namely forced repetitions, promoted different levels of acute fatigue (Ahtiainen & Häkkinen, 2009). Within each set the EMG activity increased as well as the blood lactate concentrations, which could be interpreted as the fatigue being of peripheral rather than neural origin. However, during the forced repetitions EMG amplitude decreased in last repetitions for the LT, which could represent neural fatigue, suggesting that UT cannot activate the same amount of motor units not reaching fatigue at the neural level (Ahtiainen & Häkkinen, 2009). In according with these results, increased EMG activation during fatigue protocols have been found (Viitasalo & Komi, 1977) and LT also demonstrated to have the ability to achieve their maximum neural output during squats until failure, while UT do not (Pick & Becque, 2000). However, both LT and UT individuals presented neural fatigue in the plantar flexors determined by the percentage of voluntary activation while only UT participants decreased the central activation ratio, representing the amplitude of evoked force produced by the inactive fibers of the muscle with the voluntary activation of all muscles involved in the action (Hartman, Ryan, Cramer, & Bemben, 2011). Nevertheless, the type of contraction has different implications in the acute neural adaptations to fatigue, and for instance, different EMG activity was observed during the concentric and eccentric portions of the exercise (Ebenbichler et al., 2017), while other studies did not find differences (Beck, Kasishke Ii, Stock, & DeFreitas, 2012; Ye, Beck, Defreitas, & Wages, 2014; Ye, Beck, & Wages, 2015). Training status did not influence the neural response to eccentric training and both groups decreased EMG activity, maybe representing the lower ability to recruit higher-threshold motor units (Ye et al., 2015). One session of eccentric training also appeared to induce a greater capacity to recruit motor units, increasing the agonist activation in UT after 10 days (Kawczyński, 2019), but rapid force production was affected by one session of eccentric training only returning to baseline after 168h which was

accompanied with decreased rate of EMG rise (Farup, Rahbek, Bjerre, de Paoli, & Vissing, 2016). Also, three weeks of eccentric training of wrist flexor muscles showed to produce more contralateral effects to the untrained limb while modulating corticospinal excitability and inhibition, which imply specific neural adaptation to eccentric training (Kidgell et al., 2015).

The CNS strategies to overcome the effects of fatigue include acute adaptations in intermuscular coordination. Namely, concerning protocols with low intensity contractions, which are associated to substantial central fatigue (Burnley, Vanhatalo, & Jones, 2012; Yoon, Schlinder Delap, Griffith, & Hunter, 2007), it was previously shown that there is an alternating pattern of activity between synergist muscles (Tamaki et al., 1998) although it depends on individuals characteristics (McLean & Goudy, 2004) and that the relative activity of accessory muscles is modified during fatiguing protocols depending on the need of postural adjustments (Rudroff, Barry, Stone, Barry, & Enoka, 2007). Also, when considering global coordination, after a fatiguing rowing task, the extraction of muscle synergies has revealed that modular organization of coordination is not affected by fatigue, but rather depends on increased muscle activity of specific muscles (Turpin, Guével, Durand, & Hug, 2011a) although slight differences in specific modules were observed after a running protocol (Matsunaga, Imai, & Kaneoka, 2017). Nevertheless, the use of muscle synergy analysis may provide important insights into the study of coordination and how the CNS controls the neuromusculoskeletal system redundancy, but when studying fatigue because of the methodological steps of the extraction, as the filtering techniques or the VAF criteria, useful information may be lost. However, when combining muscle synergy extraction to frequency analysis, a more effective description of the effects of fatigue may be achieved. Namely, the effect of fatigue in muscle synergies during strength-related tasks was assessed considering one-legged and two-legged squat. Three synergies were extracted for two-legged squat, while four synergies were extracted for single-legged squat. Two-legged squats did not suffer significant differences with fatigue, whereas in single-legged squat one synergy with general coactivation became a predominantly knee extensor synergy after fatigue. Those results were complemented by a continuous wavelet transform that allowed to better identify neural adaptations to fatigue in the two squatting variations (Smale, Shourijeh, & Benoit, 2016).

Thus, the analysis of the spectral properties of EMG signals and the use of IMC calculations provides a sensitive tool to assess the respective mechanisms of fatigue.

As mentioned during this document, IMC regards to motor unit synchronization in different muscles and provides information about how the central mechanisms interact to produce movement or joint torques when referring to isometric contractions (Farina, Merletti, & Enoka, 2014; Grosse, Cassidy, & Brown, 2002). The systematic review reported in Chapter 3 of this document allowed to better understand the acute effects of fatiguing contractions on the underlying mechanisms inferred by IMC analysis. It was demonstrated that across studies different responses are observed in the different frequency bands. Delta band (0-5 Hz) representing the common drive to muscles (De Luca & Erim, 1994; De Luca, LeFever, McCue, & Xenakis, 1982), and the synchronous modulation of motor unit firing rates (Lowery, Myers, & Erim, 2007) was generally increased in all studies (Danna-Dos Santos et al., 2010; Rossato et al., 2022; Semmler, Ebert, & Amarasena, 2013) although it depends on the fatiguing task as well as the task where IMC is evaluated (Watanabe, Saito, Ishida, Tanabe, & Nojima, 2018). Alpha band (5-15 Hz) has been linked to cortical and subcortical activity as well as peripheral integration (Erimaki & Christakos, 2008; Klass, Lévénez, Enoka, & Duchateau, 2008; McAuley & Marsden, 2000), being also associated with physiological tremor (McAuley & Marsden, 2000). Generally, fatigue has also led to greater IMC at this band concerning unilateral and bilateral IMC of the agonist muscles (Boonstra, Daffertshofer, van As, van der Vlugt, & Beek, 2007; Boonstra et al., 2008) and between an agonist-antagonist pair (Wang et al., 2015), although unchanged coherence was observed in other studies especially when the evaluated tasks or fatiguing protocols were not merely isometric (Chang et al., 2012; Watanabe et al., 2018). Beta band (15-35 Hz), associated to the corticospinal tract (Baker, Olivier, & Lemon, 1997; Farmer, Bremner, Halliday, Rosenberg, & Stephens, 1993; Kattla & Lowery, 2010; Mima & Hallett, 1999) but also to oscillations within the sensorimotor cortex and integration of sensory information (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013; Ushiyama et al., 2011) present mixed results, with some studies presenting increased IMC (Chang et al., 2012; Danna-Dos Santos et al., 2010; Wang et al., 2011) and other reporting unaltered or decreased IMC at some specific tasks (Charissou, Vigouroux, Berton, & Amarantini, 2016; Dos Santos et al., 2020; Kattla & Lowery, 2010; Semmler et al., 2013), depending not only on the task but also on age, training

status or the analyzed muscles. Additionally, IMC at beta band between a pair of agonist-antagonist muscles revealed to increase in the only evaluated study which suggests a closely related organization of corticospinal connections between antagonistic muscles (Wang et al., 2015). Finally, the gamma band, also associated to the corticospinal pathway during strong or dynamic tasks and to attentional focus (Conway et al., 1995; Mima & Hallett, 1999), was generally maintained after fatigue, which relies on the generally low level of elicited torque during the evaluated tasks.

Only one of the above-mentioned studies reported fatigue effects in a maximal task (Charissou et al., 2016). These authors reported that IMC at beta band between knee extensor agonist muscles remain stable in previously trained individuals while decreasing in untrained ones. The fatigue protocol used in this study encompassed repetitions of 10 submaximal isometric knee extensions at 40% MVC. In the study presented in Chapter 4, we evaluated IMC at various frequency bands as well as between different lower limb muscles during a maximal isometric leg-press using a fatiguing protocol of 5 x 10 repetitions with 75% RM of dynamic back squats. We observed a generally increased coherence at higher frequencies (>60 Hz) which may rely on one hand in the maximal evaluated task and on the other hand the dynamic fatiguing protocol with high loads. This is compatible with the idea that the efferent drive during strong isometric voluntary contractions or dynamic effort may shift the IMC towards higher frequencies in the gamma band (Brown, 2000; Brown, Salenius, Rothwell, & Hari, 1998; Gwin & Ferris, 2012; Mima, Simpkins, Oluwatimilehin, & Hallett, 1999), increasing motor unit synchronization to compensate possible drops in discharge rate (Aoki, Uchida, & Inoue, 2005; Hwang, Lin, Huang, & Chen, 2020). However not all studies have found increased gamma band IMC after fatigue, and dynamic knee extensions with 20 or 70% RM led to maintained or decreased IMC at gamma band, respectively (Castronovo, De Marchis, Schmid, Conforto, & Severini, 2018). Nevertheless, it is important when analyzing studies regarding IMC calculations that the data processing involves numerous steps and that different methodological approaches may lead to different results. Also, as already mentioned, the tasks performed by the individuals as well as the selected muscles are determinant to the final output. For example, the fact that in Chapter 4 we used a multi-joint exercise was determinant to the results obtained regarding IMC between the monoarticular portions of quadriceps with increased alpha and beta oscillations, while the bi-articular

portion, the RF, did not present different interactions with those muscles after fatigue, but differed concerning the rate of EMG activation. Furthermore, the RF presented an increased rate of activation in resistance-trained individuals while decreasing in untrained individuals, which indicates the different acute adaptability of individuals with different training status and the specific role of bi-articular muscles. In addition, the IMC between synergist muscles acting on different lower limb joints as well as between agonist-antagonist pairs has also been increased in beta and/or gamma band for both groups, implying an adapted global coordination following fatigue.

Short-term adaptations

Research about the neuromuscular adaptations to strength training requires complex methodological approaches concerning data collection and involves that participants are accompanied along time. This makes, on the one hand, that the general samples used in studies with this aim are usually small including previously untrained or recreationally active individuals, because the inclusion of athletes is not feasible, and on the other hand, that the training periods are limited to few weeks (generally less than 12 weeks). Previously, short- and medium-term training were defined as ≤ 6 weeks and 7-23 weeks, respectively, while long-term training was defined as ≥ 23 weeks (Ashton et al., 2020). Additionally, it was proposed that 1 year of continuous training should be required to induce chronic strength training adaptations, and that neural adaptations are continuously contributing to strength gains even at the long-term (Pearcey et al., 2021), with intermuscular coordination and the underlying mechanisms presenting a determinant role (Aagaard, Bojsen-Møller, & Lundbye-Jensen, 2020), although there is a general lack of knowledge concerning this topic.

Previous research has found decreased antagonist activity following 2 weeks of high-load wrist flexor training accompanying the increased corticospinal excitability and reduced short-interval intracortical inhibition (Mason et al., 2020). Additionally, corticospinal excitability increased while corticospinal inhibition decreased after 3 weeks of high-load elbow flexion training in the agonist elbow flexor muscles but also in the synergist wrist flexor muscles, suggesting changes in more than one site of motor cortex and along the corticospinal pathway (Mason et al., 2017). In other study, maximal isometric knee extension training led to

decreased co-activation after only 1 week of training, remaining decreased at the end of an 8-week program (Carolan & Cafarelli, 1992). Concerning eccentric training, reduced antagonist co-contraction was also observed after continued 20-day intense isokinetic eccentric training of the elbow flexors (training each 2nd day), improving coordination between agonist and antagonist even with decreased strength in result of the inflicted muscle damage of the agonist muscles (Krentz & Farthing, 2010). However, isoinertial eccentric training of the plantar flexors (4 times per week) led to increased concentric and eccentric strength which seems to be related with decreased antagonist activity (Pensini, Martin, & Maffiuletti, 2002). Additionally, 6 weeks of eccentric hamstring training with Nordic hamstring exercise resulted in decreased co-activation of the antagonist muscles (Delahunt, McGroarty, De Vito, & Ditroilo, 2016), although this result may not be generalized, for example when considering isokinetic training or other muscles as the elbow flexors (Colson, Pousson, Martin, & Van Hoecke, 1999). Also, isokinetic and isoload eccentric training appeared to be ineffective in decreasing antagonist activity even after 9 weeks (Guilhem, Cornu, Maffiuletti, & Guével, 2013). It was also demonstrated that when exercises against external loads are performed with intentional maximal co-contraction of the antagonist muscles, no changes in antagonist activity are observed (Driss et al., 2014; Maeo, Yoshitake, Takai, Fukunaga, & Kanehisa, 2014) and small effects were observed when the agonist contraction was preceded by an antagonist contraction (Cardoso et al., 2015).

Concerning the specificity of training, elbow flexor training with low loads at maximal angular velocity has also induced a reduction in antagonist activity only at the maximal evaluated velocities (300°/s), which suggests a velocity-specificity of the movement (Pousson, Amiridis, Cometti, & Van Hoecke, 1999), although no differences were found during slow and fast concentric and eccentric contractions after 3 months of strength training (Andersen, Andersen, Magnusson, & Aagaard, 2005). Also, different training modalities led to different co-contraction adaptations following 12 weeks of training, with traditional strength training increasing co-activation during jumping while specific training including Olympic weightlifting movements has maintained co-contraction resulting in greater improvements in jumping performance (Arabatzi & Kellis, 2012). Also, ten weeks of deadlift training resulted in decreased co-contraction during isometric knee extension (Stock & Thompson, 2014). However, increased antagonist activity of BF during side-step cutting

exercise as well as decreased activity of gastrocnemius muscles during pre-activation phase were observed after 10 weeks of strength training (Jeong, Choi, Song, & Shin, 2020). The training task and dynamics, and the evaluated task are determinant to the changes in antagonist activity as well as the muscle group, type and velocity of muscle contraction, intensity and joint angle.

Regarding the synergistic behavior of muscles, isoinertial training led to a greater magnitude increase in isoinertial rather than isometric strength, which was also observed concerning agonist activity, although modified activity of the stabilizer muscles was observed across tasks (Buckthorpe, Erskine, Fletcher, & Folland, 2015). Eight weeks of strength training with unconstrained-path chest press machine have also led to an adaptation concerning the stabilizers activity while training with constrained-path chest press machines did not lead to changes in stabilizers activity (Cacchio et al., 2008). Suspended push-up training has also increased muscle activity not only of the agonist muscles but also of the trunk stabilizers, namely the rectus abdominis, external and internal obliquus, resulting in increased muscle thickness of the rectus abdominis and external obliquus (Kohiruimaki, Maeo, & Kanehisa, 2019). Additionally, unstable push-up training has also led to decreased co-contraction and lower fatigue indexes of agonist and synergist muscles than stable push-up training (Lima, Li, Low, Herat, & Behm, 2018). Also, 8 weeks of strength training using functional exercises as leg press with high loads induced neural adaptations to the plantar flexors during single-joint tasks (Fimland, Helgerud, Gruber, Leivseth, & Hoff, 2009), although multi-joint leg-press did not change the knee extensor activation (Stien, Pedersen, Ravnøy, Andersen, & Saeterbakken, 2020) and that knee extensions elicit greater synaptic input than leg press (Boccia, Martinez-Valdes, Negro, Rainoldi, & Falla, 2019). Furthermore, squat training using different repetition mechanics (strength, hypertrophy or cluster regimens) induced similar increment in knee extensor and hip extensor muscles activity during a maximal bilateral isometric test (Nicholson, Ispoglou, & Bissas, 2016).

As already mentioned during this document, few studies evaluated the global coordination and the central mechanisms of motor control that allow the possibility of a wide variety of complex movements. The assessment of muscle synergies and intermuscular coherence allowed to bring new insights into this topic. Previously, muscle synergies were found to

remain similar following a bench press training program of 5 weeks, although the contribution of the analyzed muscles changed after training modifying the muscle vectors during the concentric phase which tend to present less variability among highly trained powerlifters (Kristiansen et al., 2016). In turn, 4 weeks of wobble board sensorimotor training modified the modular organization of movement during the early phase of landing, dividing one muscle synergy encompassing the plantar flexors and evertors and reducing the activity of secondary muscles (Silva, Oliveira, Mrachacz-Kersting, & Kersting, 2018). Concerning IMC analysis, one study has previously found that strength training of 14 weeks increased gamma oscillations during high intensity contractions (70% MVC) between synergist muscles, which suggests that the central control of muscle coupling may be adapted with training (Walker et al., 2019).

The articles presented in Chapters 5 to 7 provided a better understanding of the adaptation in the mechanisms implied in changes of intermuscular coordination. During maximal multi-joint contractions assessed with an isometric leg-press exercise, we found that the role of biarticular muscles is crucial when developing force production characteristics following short-term training of 6 weeks. Namely, we found that although the RF muscle has decreased its rate of activation, measured by RER, the coherence at beta band between RF and the VL increased. Although previous studies have found increased RER following training (Aagaard, Simonsen, Andersen, Magnusson, & Dyhre-Poulsen, 2002; Del Balso & Cafarelli, 2007; Jenkins et al., 2016), the result of our study may be related with the generally decreased activity of RF during closed-chain multi-joint task (Boccia et al., 2019; Ema, Sakaguchi, Akagi, & Kawakami, 2016). Nevertheless, the lower activation may allow to decrease the opposite action of RF during hip extension, and the greater IMC at beta band may imply a greater common corticospinal drive to the muscles allowing a more effective motor control of the knee during maximal force production. Also, between synergist muscles acting at different joints, namely VL and GL, IMC at beta band was decreased after the training period which may be related to the role of GL as ankle stabilizer (Schoenfeld, 2010), supporting the idea of the synergistic recruitment of muscles (Aumann & Prut, 2015; Bizzi & Cheung, 2013). Furthermore, agonist-antagonist coupling was changed regarding GL and TA showing generally decreased IMC, which may also be related to the control of the ankle. Additionally, the agonist-antagonist pairs concerning the muscles acting around the knee showed

transitional adjustments during the training period which result in specific neural strategies until the system becomes more efficient with task-specific optimization of central commands achieved with long-term training (Ushiyama, Takahashi, & Ushiba, 2010). Overall, the discussed neural adaptations resulted in greater maximal force output as well as peak rate of force development.

Concerning submaximal isometric force production during knee extensions, we corroborated previous research reporting that short-term training is not sufficient to induce changes in torque-agonist relationships (Balshaw et al., 2019; Häkkinen & Komi, 1983; Tillin, Pain, & Folland, 2011), although it may depend on interindividual variability (Rabita, Pérot, & Lensel-Corbeil, 2000). However, we did not find differences in torque-antagonist or agonist-antagonist relationships following 6 weeks of training, which is contrary to previous studies reporting a shift to the right representing lower antagonist activity during submaximal contractions (Balshaw et al., 2019; Tillin et al., 2011), although those differences may emerge from different methodological approaches. This was accompanied by different coupling between agonist muscles after the 6 weeks of training concerning alpha and low-beta bands, which may rely on increased corticospinal input also modulated by other cortical and subcortical mechanisms as well as peripheral integration (Baker et al., 1997; Erimaki & Christakos, 2008; Klass et al., 2008; McAuley & Marsden, 2000; Mima & Hallett, 1999). Additionally, IMC at gamma band was also increased, namely during intensities above 60% MVC, which is in line with previous research (Walker et al., 2019) and is associated to the corticospinal drive and attentional focus during strong or dynamic efforts (Brown, 2000; Brown et al., 1998; Mima et al., 1999). In Chapter 5 we found greater IMC between the same muscles but in the beta band following the training period, which may also rely on corticospinal connectivity without the component of visual and peripheral feedback. Also, agonist-antagonist coupling increased at alpha and beta bands during higher torque levels (> 60% MVC) which supports common corticospinal control of antagonist muscles, with greater motor unit synchronization even in the absence of changes in amplitude, and a better integration of peripheral and visual feedback.

The previously discussed results regard to isometric tasks. The evaluation of squat load-velocity profile (LVP) and the respective extraction of muscle synergies at four intensities

were representative of the adaptations in specific coordination patterns when performing the trained task. The squat RM increased after 6 weeks of squat training and squat LVP was modified, decreasing LD0 and attenuating the slope with a trend to an increased V0. Although we could expect that maximal theoretical strength would increase, the fact that RM increased, and we used relative loads contributed to this result, which may also imply a greater capacity to concentrically reach near maximum voluntary output. Additionally, the maximal theoretical velocity increased, meaning that traditional repetition dynamics modify the LVP of previously untrained individuals. At the same time, although muscle synergies have remained robust, some changes were observed in spatial distribution of muscles within the two extracted synergies as well as in individual EMG profiles. Namely, the weighting of GL was changed across synergies during heavy loads as well as the weighting of RF during light loads, corroborating previous findings regarding the modification of synergy components following training (Kristiansen et al., 2016; Silva et al., 2018). In addition, although the temporal component of synergies remained unchanged, the pattern of GM activation was anticipated during light and heavy loads, and overall, this may be a global short-term adaptation to a more effective motor control, with the coordination between mono- and bi-articular muscles being determinant during strength training adaptations (Watanabe, Vieira, Gallina, Kouzaki, & Moritani, 2021).

Long-term adaptations

As previously stated, the long-term adaptations to strength training are not easily assessed because of the need of training monitoring and evaluation over at least 1 year. Also, the inclusion of trained individuals in scientific studies are not always feasible concerning the specific periodization and rigorous training prescription that are not always adaptable to a research program. Thus, the long-term adaptations to strength training are usually provided by studies comparing untrained with highly trained individuals, such as powerlifters or weightlifters.

In Chapter 2 of this Thesis, it was presented the current state of art concerning training differences between untrained and experienced resistance trained individuals in EMG outcomes in agonist, synergist and antagonist muscles. Maximal force production was

generally accompanied by increased agonist activity (Balshaw et al., 2019; Grosprêtre, Gimenez, & Martin, 2018; Škarabot, Balshaw, et al., 2021), although other studies did not report differences (Ahtiainen & Häkkinen, 2009; Lattier, Millet, Maffiuletti, Babault, & Lepers, 2003; Wang et al., 2019). The assessment of maximal neural output exclusively through EMG analysis during maximal voluntary contractions may not be the best option, and the inclusion of peripheral nerve stimulation that allows to normalize EMG to Mmax may be considered when possible (Škarabot, Balshaw, et al., 2021). Also, the highly trained individuals appear to have a greater rate of activation during rapid contractions resulting in increased mechanical output, namely concerning RFD during the initial 50ms after the onset of contraction (Orssatto, Wiest, Moura, Collins, & Diefenthaeler, 2020; Tillin, Jimenez-Reyes, Pain, & Folland, 2010). The greater capacity of agonist activation during strength-related tasks relies on the plasticity of nervous system, namely concerning spinal mechanisms regarding the recruitment of the alpha motoneurons and influenced by the reticulospinal pathway, as well as the intracortical circuitry (Pearcey et al., 2021).

The agonist recruitment during submaximal tasks is generally changed only with long-term training. As discussed in the previous section concerning short-term adaptations, torque-agonist relationship appears to be modified only after prolonged training. Studies with training periods above 16 weeks have found that this relationship is shifted to the right (Häkkinen & Komi, 1983; Narici et al., 1996), increasing the neuromuscular efficiency, and that is also observed in long-term trained individuals (Amarantini & Bru, 2015; Balshaw et al., 2019; Pearcey, Power, & Button, 2014). In study of Chapter 6, this was also corroborated, with the long-term trained individuals presenting lower EMG amplitude for each relative intensity, namely concerning VL and RF. Furthermore, we found that the activity of RF was lower in short-term and long-term trained individuals when compared to the untrained group, which shows that although the vastii muscles may only contribute to the differences following long-term training, the RF as a bi-articular muscle may improve its function during submaximal force production. Nevertheless, we should not discard the inherent interindividual variability (Amarantini & Bru, 2015; Rabita et al., 2000) an the fact that significant differences were not found after 6 weeks of training. Long-term trained individuals have also presented generally lower IMC between agonist muscles during submaximal contractions in our study, which is in line with lower corticomuscular coherence

at beta band of trained athletes (Ushiyama et al., 2010). It is also interesting that the short-term training increased IMC, reflecting greater motor unit synchronization between muscles, but at long-term training the IMC decreased, which may be seen as temporary adjustments improving motor control until fully developed mechanisms from cortex to motor unit influenced by long-term muscular adaptations. However, when considering maximal isometric multi-joint contractions, we observed greater beta band for the long-term trained individuals between VM and RF, although research concerning single-joint knee extensions have found contrary results, i.e., greater IMC for the untrained individuals (Charissou et al., 2016). The different tasks involve different agonist recruitment (Boccia et al., 2019; Ema et al., 2016), and the different methodological approaches for the calculation of IMC has also impacted the results.

The adaptations concerning the control of antagonist muscles are not fully understood. Generally, after strength training programs, antagonist activity decreases (Krentz & Farthing, 2010; Mason et al., 2020; Pensini et al., 2002; Tillin et al., 2011), although other studies do not report differences (Aagaard, 2002; Andersen, Andersen, Magnusson, Suetta, et al., 2005; Remaud, Cornu, & Guével, 2010; Seynnes et al., 2007). Also, generally long-term trained individuals present lower antagonist activity (Amarantini & Bru, 2015; Grosprêtre et al., 2018; Pearcey et al., 2014; Wang et al., 2019). As discussed along this document, the disparity of results may depend on several methodological and physiological factors, as the evaluated tasks, training programs, muscle group, type and velocity of muscle contraction, intensity and joint angle, as well as the processing methods of EMG (Santos et al., 2023). Nevertheless, it was suggested that it may be only significant in submaximal contraction (Balshaw et al., 2019) and that differences in torque-antagonist and agonist-antagonist relationships may be observed after short-term training (Balshaw et al., 2019; Tillin et al., 2011), although they continue to evolve overtime (Amarantini & Bru, 2015; Balshaw et al., 2019). We did not corroborate these results regarding the amplitude analysis. However, when assessing the muscle coupling between agonist-antagonist pairs it was observed that LT present lower IMC at gamma band during submaximal contractions, namely above 60% MVC, implying that corticospinal connections between antagonist muscles in tasks involving peripheral and visual feedback are reduced at long-term training, allowing a more efficient control even in the absence of differences in EMG amplitude. The modulation of antagonist

control during submaximal tasks was previously shown (Dal Maso, Longcamp, Cremoux, & Amarantini, 2017). Concerning maximal isometric multi-joint contractions, we did not find significant differences between groups between the knee extensors and BF, which may be related to the different tasks as mentioned before. Furthermore, no differences regarding agonist-antagonist pairing between muscles acting around the ankle were observed in our study, despite previous research has shown that badminton players present greater GL-TA IMC at beta band during isokinetic dorsiflexion contraction (Wang et al., 2019).

Calculation of IMC has also been associated to muscle synergy extraction (De Marchis, Severini, Castronovo, Schmid, & Conforto, 2015) and beta oscillations within the central nervous system have been linked to muscle synergies (Aumann & Prut, 2015). Muscle synergies have been studied concerning the effect of expertise in a large variety of tasks as rowing (Turpin, Guével, Durand, & Hug, 2011b), breaststroke swimming (Vaz et al., 2016), backward giant swings (Frère & Hug, 2012), badminton smash shots (Matsunaga & Kaneoka, 2018) or postural adjustments during platform perturbations (Kim, Kim, Kim, & Yoon, 2018). Regarding strength training, the expertise effect was assessed concerning the bench press (Kristiansen, Madeleine, Hansen, & Samani, 2015) and the power clean (Hakariya, Kibushi, & Okada, 2023; Santos et al., 2021). In the study of Chapter 7, although the absence of between group differences in LVP demonstrating that it is a sensitive tool to assess training adaptation when it is based on individual rather than group profiles, some specific differences in intermuscular were observed during dynamic squats. Namely, the long-term trained presented some specific spatial distribution of muscle recruitment suggesting plantar flexor pre-tension anticipating the concentric phase and modulated TA activity, which may imply a more effective ankle stabilization that allow that the muscles acting on the hip and knee may exert greater torque levels leading to an improved kinetic transmission to the ground. Additionally, concerning the temporal component of muscle synergies, synergy #1 (eccentric and beginning of concentric phase) presented higher indexes of similarity and was delayed for long-term trained individuals which has been previously observed concerning other tasks (Santos et al., 2021; Vaz et al., 2016). This was justified by a delay of individual EMG profiles. Additionally, synergy #2 (concentric phase) presented lower between-group similarity indexes, suggesting a more effective neural strategy with long-term training and an individualized adaptation (Kristiansen et al., 2015; Santos et al.,

2021; Turpin et al., 2011b). This synergy was anticipated with a parallel anticipation of the GL activation by the long-term trained, but only at heavy loads the difference was significant between short- and long-term trained individuals, which means that the very precise timings of activation remain adapting overtime.

CONCLUSION

Strength training adaptations are not limited to the first months of regular practice but remain evolving overtime. Current research suggests that the model presented by Sale (Sale, 1988) assigning the neural adaptations to the first weeks of training and the continuous gains of strength following those weeks being assigned to muscular adaptations, is simplistic. We must consider that muscular adaptations are also present during the first weeks of training and that neural mechanisms remain adapting overtime. Thus, the Sale's based model adjusted by Pearcey and colleagues (Pearcey et al., 2021) accounts the current knowledge concerning the chronology of neuromuscular adaptations to training. The plasticity of the nervous system has been studied and the sites of adaptations have been characterized, and although future research should focus on integrating multilevel recording techniques (as stimulation techniques, high-density EMG, electroencephalography, neuroimaging techniques or auditory startle stimuli), the alpha motoneuron, supraspinal circuitries and reticular formation appear to present the greatest plasticity in the nervous system (Aagaard et al., 2020; Pearcey et al., 2021; Škarabot, Brownstein, et al., 2021). However, intermuscular coordination, especially during complex tasks, remains a topic with insufficient research but with strong potential to a better understanding of the neural adaptations to strength training.

This Thesis investigated the adaptations in intermuscular coordination to acute training sessions (i.e. the effects of fatigue), to short-term training of 6 weeks and to long-term training assessed by the comparison between powerlifters/weightlifters and untrained individuals. First, we observed that muscle coupling considering pairs of agonist, synergist or antagonist muscles are affected with acute fatiguing training sessions and that the type adaptations depend on several factors as the evaluated task, fatigue protocol, collected muscles or the type of contraction. Nevertheless, although we did not find between group differences in the acute intermuscular coordination adaptations, we observed a greater impact of training in the trained than the untrained individuals as well as a different RF activation after fatigue. We should consider that untrained and highly trained individuals present different muscle recruitment during strength training sessions, and therefore further research with advanced training methods may address the impact of training status in muscle coupling. Second, the inclusion of untrained individuals in a short-term training program of 6 weeks

allowed to better understand how may changes in intermuscular coordination lead to improved mechanical output. Namely, different coupling between agonist, synergist and antagonist muscles as well as modified agonist activation during maximal isometric force production led to increased maximal and rapid force. Additionally, different coupling between agonist and/or antagonist muscles during submaximal isometric contractions was also observed, although torque-EMG relationships of muscles with different anatomical and functional roles remained unchanged. Also, squat load-velocity profile was adapted with 6 weeks of training, which was accompanied by differences in muscle coordination assessed by muscle synergy extraction, namely regarding muscle weightings within the synergies. Third, the comparison between untrained, short-term trained and long-term trained individuals allowed to better understand the chronic adaptations to training. During maximal isometric contractions, long-term training led to an increased maximal and rapid force production, namely at some specific time intervals. This was accompanied by differences in agonist activation as well as differences in coupling between agonist, synergist and antagonist muscles. Furthermore, during submaximal isometric contractions, long-term training led to increased neuromuscular efficiency and a simultaneous adaptation in coupling between agonist and/or antagonist muscles. No differences were observed between groups with different training status in LVP, and this relies on the suggestion that this evaluation methodology should be applied individually to assess adaptations to specific training programs. However, different patterns of coordination during dynamic squats concerning the spatial distribution of muscles within the synergies but also the temporal activation of the synergies were observed which corroborated the continuously adapting intermuscular coordination patterns overtime.

The chronology of adaptations to training, namely in intermuscular coordination, should be understood in a practical context. The comprehension on what underlying mechanisms concerning intermuscular coordination adaptations may evolve in an initial training stage but also at later training stages when individuals have several months or years of continued practice, may allow to better direct the training prescription to promote specific neuromuscular responses concerning agonist, synergist and antagonist muscles. This may consider the specific sports modalities, allowing a more effective training strategy that promotes adaptations overtime and opposes to stagnation in strength gains.

LIMITATIONS AND FUTURE RESEARCH

As indicated in the respective Chapters of this Thesis the limitations of each study were already addressed. Thus, this section will generally describe some methodological issues, suggesting possible research lines that may provide new insights into the results reported in this document.

The great limitation of the experimental studies was that a small sample size was used, and although reliability measures were provided at each study, it would be reasonable to include more individuals to further investigate the adaptations in intermuscular coordination to strength training. Thus, the inclusion of healthy untrained males in the longitudinal studies means that our results may not be extrapolated to other populations, and the comparison between groups with different training background would benefit from a greater sample size that would increase statistical power of the results. Additionally, and as discussed previously, the methodological issues, namely concerning data processing of EMG signals in IMC calculations and muscle synergy extraction should be interpreted with caution when comparing to other studies, since there is a vast disparity of approaches.

Although the articles included in the present Thesis provided a better understanding of the intermuscular adaptations to strength training, novel research is needed to clarify the implied neurophysiological mechanisms to a better coordination. Regarding the effects of fatiguing protocols in intermuscular coordination, it would be helpful to understand how does intermuscular coherence between agonist pairs as well as agonist-antagonist pairs of muscles relate to acute adaptations in force fluctuations concerning different joints, and what are the responses concerning intermuscular coherence of individuals with different training background during different strength training fatiguing protocols, with different repetition mechanics (for example, traditional method vs forced repetition method vs 3/7 method). Concerning short-term adaptations, better understanding on how the neuromuscular system adapts during sustained submaximal tasks is needed. Although we provided short-term adaptations in intermuscular coherence at different contraction intensities, the evaluation of intramuscular coordination variables (for example, motor unit recruitment thresholds or firing frequency, measured by high-density EMG) in synergistic muscles with different anatomical and functional characteristics as the VL or the RF, would add important insights

into the mechanisms of motor control, namely in the specific differences between mono- and bi-articular muscles. Furthermore, this would help to understand how the adaptations in neural mechanisms may modify torque complexity with training. Still concerning short-term adaptations to strength training, it would provide important knowledge study designs that allowed 1) to compare differences in intermuscular coordination adaptations with different training methods (for example, hypertrophic vs power training) in tasks as the bench press or squat as well as the corresponding changes in the kinetics of the exercises, 2) to understand the adaptations concerning more complex movements as the Olympic weightlifting derivatives, namely regarding muscle synergy extraction from muscles of the upper and lower limbs and trunk, or 3) to assess the training transfer of coordination from the trained task to an untrained task (for example, how may squat training induce changes in coordination of a different exercise involving lower limb triple extension, such as the deadlift). Finally, regarding long-term training it will always be difficult to assess the real changes overtime because it would be needed a follow-up of several years. Nevertheless, the follow-up of trained individuals, for example weightlifters or powerlifters of national level, during specific training mesocycles would enable to understand if the intermuscular coordination mechanisms remain adapting at the long-term and if they may possibly be responsible for the slight strength gains during tapering.

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