

Cortico-muscular Coherence in Sensorimotor Synchronisation

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Statement of Authentication

The work presented in this thesis is, to the best of my knowledge and belief, original except as acknowledged in the text. I hereby declare that I have not submitted this material, either in full or in part, for a degree at this or any other institution.

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Declaration

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Abstract

This thesis sets out to investigate the neuro-muscular control mechanisms underlying the ubiquitous phenomenon of sensorimotor synchronisation (SMS). SMS is the coordination of movement to external rhythms, and is commonly observed in everyday life. A large body of research addresses the processes underlying SMS at the levels of behaviour and brain. Comparatively, little is known about the coupling between neural and behavioural processes, i.e. neuro-muscular processes. Here, the neuro-muscular processes underlying SMS were investigated in the form of cortico-muscular coherence measured based on Electroencephalography (EEG) and Electromyography (EMG) recorded in human healthy participants. These neuro-muscular processes were investigated at three levels of engagement: passive listening and observation of rhythms in the environment, imagined SMS, and executed SMS, which resulted in the testing of three hypotheses: (i) Rhythms in the environment, such as music, spontaneously modulate cortico-muscular coupling, (ii) Movement intention modulates cortico-muscular coupling, and (iii) Cortico-muscular coupling is dynamically modulated during SMS time-locked to the stimulus rhythm.

These three hypotheses were tested through two studies that used Electroencephalography (EEG) and Electromyography (EMG) recordings to measure Cortico-muscular coherence (CMC). First, CMC was tested during passive music listening, to test whether temporal and spectral properties of music stimuli known to induce groove, i.e., the subjective experience of wanting to move, can spontaneously modulate the overall strength of the communication between the brain and the muscles. Second, imagined and executed movement synchronisation was used to investigate the role of movement intention and dynamics on CMC.

The two studies indicate that both top-down, and somatosensory and/or proprioceptive processes modulate CMC during SMS tasks. Although CMC dynamics might be linked to movement dynamics, no direct correlation between movement performance and CMC was found. Furthermore, purely passive auditory or visual rhythmic stimulation did not affect CMC. Together, these findings thus indicate that movement intention and active engagement with rhythms in the environment might be critical in modulating CMC. Further investigations of the mechanisms and function of CMC are necessary, as they could have important implications for clinical and elderly populations, as well as athletes, where optimisation of motor control is necessary to compensate for impaired movement or to achieve elite performance.

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List of Abbreviations

CMC	Cortico-muscular Coherence
EEG	Electroencephalography
EMG	Electromyography
FDI	First Dorsal Interosseous
FDS	Flexor Digitorum Superficialis
fMRI	Functional Magnetic Resonance Imaging
MEG	Magnetoencephalography
PET	Positron Emission Topography
PFC	Pre-frontal Cortex
PMC	Pre-motor Cortex
SMA	Supplementary Motor Areas
SMS	Sensorimotor Synchronisation

Chapter 1: General introduction

An intriguing question about motor control in daily life is how people effectively time their actions with continuously changing environments. For example, when we are dancing to music, hitting a tennis ball with a racquet, or coordinating our actions with other people, we carry out sequential movements that need to be temporally aligned with input from different sensory modalities. The task of coordinating movement with respect to such external events is commonly referred to as sensorimotor synchronisation (SMS) (Repp 2005; Repp and Su, 2013). Broadly speaking, SMS is the temporal coordination of an action with a sequence of external events, i.e., an external rhythm (Repp, 2005). It requires the precise coordination of perceptual, motor, and cognitive processes.

SMS is a fundamental human skill that is the basis of numerous forms of everyday activities, which can occur rather spontaneously as in clapping crowds (Néda et al., 2000) or side-by-side walking (van Ulzen et al., 2008), or be the explicit goal to achieve artistic or athletic perfection, as in musical ensembles (Keller and Appel, 2010) or rowing crews (Wing and Woodburn, 1995). Due to their training, musicians are particularly good at synchronising their movements to auditory external rhythms. In lab settings SMS is often measured using a tapping paradigm where participants tap their finger in time with a metronome (or other rhythm). Musicians are known to tap closer to the beat in a more consistent way and maintain accurate synchronisation with faster metronomes (Repp, 2005; Repp and Su, 2013).

On the other hand, individuals with movement pathologies such as Parkinson's, Huntington's and stroke patients have difficulties with SMS (Schaefer, 2014). Difficulties with SMS are not only related to impaired movement performance. They have also been found in relation to, for example, reading difficulties and dyslexia (Corriveau and Goswami,

2009; Wolff, 2002). Similarly, social pathologies such as Schizophrenia and Autism have been linked to decreased SMS performance and interpersonal synchronisation (e.g., Kupper et al., 2010; Marsh et al., 2013; Varlet et al., 2012b). Based on those findings, synchronising with rhythmic cues has successfully been implemented in rehabilitation programs (Rolka and Silverman, 2015; Schaefer, 2014; Yoo and Kim, 2018). Functional SMS skills and their underlying mechanisms are thus highly relevant for everyday interactions.

Successful SMS requires both rhythmic perception and action, as well as some form of coupling between them, supported by shared neural substrates in which the motor system has been suggested to play a central role (Phillips-Silver et al., 2010; van der steen and Keller, 2013).

A widespread network of brain areas is involved in sensorimotor synchronisation, but predominantly motor areas, as shown in Figure 1. This figure depicts the feedback and feedforward interactions that occur during SMS, auditory-motor synchronisation more specifically. The sound is processed by auditory circuitry, which in turn is used in pre-motor areas for motor planning and to adjust motor commands generated in the motor cortex to achieve synchrony between the motor output and sound. Output signals from premotor areas, in turn, are believed to modulate responses within the auditory cortex, even in the absence of sound. Conversely, motor representations or simulations are thought to be active when hearing sound, even in the absence of movement. The motor areas thus also play a significant role in (auditory) perception, likely due to their role in timing mechanisms. There is therefore a tight linkage between sensory and motor mechanisms (Zatorre et al., 2007).

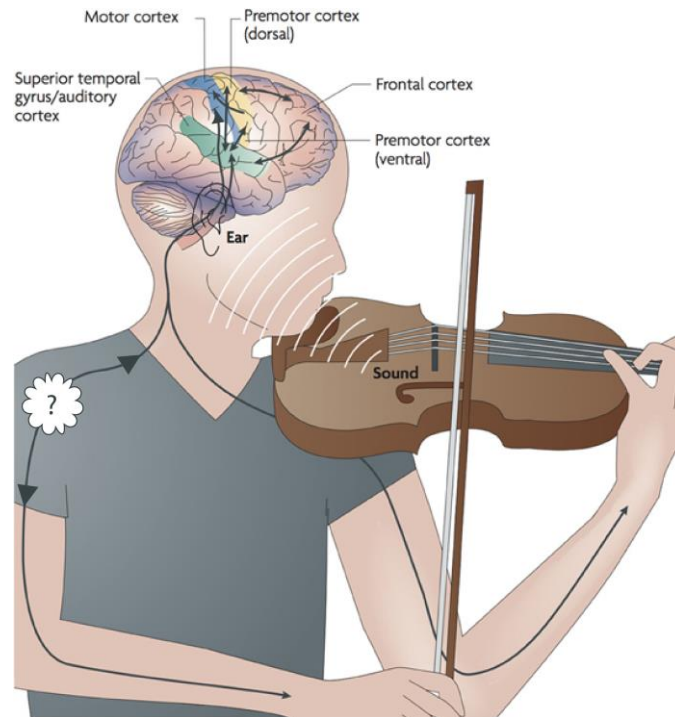


Figure 1. Auditor-motor interactions in SMS. Adapted from Zatorre, R. J., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music: Auditory-motor interactions in music perception and production. *Nature Reviews Neuroscience*, 8(7), 547–558. <https://doi.org/10.1038/nrn2152>.

These motor areas also show particularly strong functional auditory-motor connections in humans that are unseen in other species and allow for quick communications between the auditory cortex and motor regions, which can be improved by training as shown in highly skilled musicians (Chen et al., 2008b, Rosenkranz et al., 2007, Zatorre et al., 2007). Highly efficient perception-action coupling is often cited as an explanation for musicians' superior synchronisation skills.

Motor areas are not only active when performing synchronised movement, but also when movement is imagined (Farah, 1984; Lotze et al., 2006; Munzert et al., 2009), and

while an external rhythm is being perceived, even in the absence of any movement intention (Bengtsson, 2009; Chen et al., 2008a; Grahn and Brett 2007). Motor activity during rhythm perception thus indicates a key role for the motor system in sensory perception.

The importance of the motor system in the perception of rhythms is thought to be related to its timing function (Coull, 2015; Merchant and Yarrow, 2016). It is assumed that the motor system functions as a central timekeeper based on motor simulations (Patel and Iversen, 2014). The external events composing the rhythmic stimulus are tracked and anticipated by repeated movement-like processes in the motor system that are coordinated through rapid bidirectional communication with the auditory cortex (Arnal, 2012; Iversen, 2009; Morillon and Baillet, 2017; Patel and Iversen, 2014; Ross et al., 2016).

The brain tracks environmental rhythms with specific involvement of the motor system (Doelling and Poeppel, 2015; Fujioka et al., 2012, 2015; Lenc et al., 2018, 2020; Nozaradan et al., 2011, 2012; Nozaradan, 2014; Praamstra, et al., 2006; Saleh et al., 2010). This tracking generates predictions about upcoming events, which help detection and processing of those sensory events, both in sensory and motor areas (Henry and Obleser, 2012; Lakatos et al., 2005; Steriade, et al., 1993; VanRullen et al., 2011; te Woerd et al., 2018; Zoefel et al., 2018). The tracking of rhythms and their predictions are relevant to SMS performance (Bouvet et al., 2020; Lenc et al., 2020; Nozaradan et al., 2016), and can be modulated by cognitive processes such as attention and imagery (Fujioka et al., 2014).

As the importance and the functional role of the cortical motor system in both rhythm perception and production is becoming more understood, questions about the underlying neuromuscular processes remain unanswered. Specifically, the main gap this thesis aims to fill is understanding how external rhythms modulate activity along the cortico-muscular pathway, and thus, intrinsic behavioural motor functioning. Cortico-muscular activity is

important because movement can be facilitated along the cortico-muscular pathway when listening to music with a strong sense of beat, i.e. a perceived regular periodicity, and movement seems to be facilitated on the beat compared to off the beat (Cameron et al., 2012; Stupacher et al., 2013). Such findings suggest that the processing of rhythm by the brain's motor system can extend directly to the muscles, providing a mechanism by which rhythm might influence movement (Cameron and Grahn, 2014).

In this thesis, the links between the brain and the muscles underlying SMS was investigated by measuring cortico-muscular coherence (CMC). CMC is a measure that quantifies the degree of synchronisation between cortical and muscular activities, which has been shown to play a critical role in movement production and control (Halliday et al., 1995). CMC can be used to assess the communication between cortical regions and muscles, by combining Electroencephalography (EEG) or Magnetoencephalography (MEG) with Electromyography (EMG) (Fries, 2005). CMC has been shown to be relevant for understanding optimal motor control, as it is impaired post-stroke and in other motor deficits (e.g., Larsen et al., 2017; von Carlowitz-Ghori et al., 2014). It has also been related to movement performance accuracy (Kristeva-Feige et al., 2002; Kristeva et al., 2007; Witte et al., 2007), suggesting that CMC captures functional activity along the cortico-muscular pathway.

Moreover, CMC is sensitive to rhythms in the environment (Piitulainen et al., 2015; Safri et al., 2006; 2007; Varlet et al., 2020b), such as observing someone else's actions (Hari et al., 2014), making this measure of cortico-muscular communication suitable to better understand sensorimotor synchronisation. CMC thus provides a novel insight to understand the extent of neuro-muscular modulation in response to environmental rhythms during sensorimotor synchronisation.

The aim of the current thesis is to use CMC to study the modulation of communication between the brain and muscles during SMS, see Figure 1. CMC will capture the activity along the cortico-muscular pathway at varying levels of engagement of the motor system by testing music listening and imagined SMS (without movement execution), in addition to actual SMS. Music listening, imagined SMS, and actual SMS all engage the motor system and are expected to involve the same mechanism of timekeeping through action simulation. Yet, they provide different levels of movement intention and thus different processes and/or levels of cortico-muscular activity. The main question is: “how does the motor activity and the previously shown movement facilitation induced by external rhythms extend to modulations at the level of the cortico-muscular coupling?”, as depicted in Figure 1. Specifically, does music listening, imagined SMS, or executed SMS modulate cortico-muscular coupling?

The main hypotheses that will be tested are:

- (i) Rhythms in the environment, such as music, spontaneously modulate cortico-muscular coupling.
- (ii) Movement intention modulates cortico-muscular coupling, i.e., rhythmic movement as well as motor imagery in time with a metronome.
- (iii) Cortico-muscular coupling is dynamically modulated during sensorimotor synchronisation time-locked to the stimulus rhythm.

These hypotheses are tested in this thesis across two studies that use EEG and EMG recordings to measure CMC. First, CMC is tested during passive music listening, which can encourage movement even in the absence of the intention to move, to test if musical rhythm can modulate the overall communication between the brain and muscles. Then, to investigate

the role of movement intention and dynamics in CMC, imagined and executed movement synchronisation is used to test whether CMC is dynamically modulated in response to presented rhythms, imagined SMS or executed SMS.

Ultimately, the outcome of these studies will further the understanding of (rhythmic) motor control, which will especially benefit clinical populations exhibiting motor impairments by informing new perspectives for motor training and rehabilitation including rhythmic stimulation.

Chapter 2: Background

2.1 Sensorimotor synchronisation: a ubiquitous phenomenon

Sensorimotor synchronisation can readily be observed in everyday activities, as people commonly move along or in synchrony with the environmental rhythms they encounter (Lesaffre et al., 2008). For example, when listening to music, people have a tendency to tap their hands or feet along and when walking side-by-side, people tend to synchronise their strides together (van Ulzen et al., 2008). This can happen intentionally or spontaneously without any instruction or intention to do so (Schmidt and Richardson, 2008; van Ulzen et al., 2008).

SMS is particularly ubiquitous with musical rhythms. People tend to synchronise to a regular beat or pulse of rhythmic music. A beat is a perceived regularity or periodicity extracted from musical rhythmic patterns (London, 2004; Large, 2008). Phenomenologically, beat (or pulse) can be considered a percept; a response to patterns of timing and stress in the acoustic rhythm (Large, 2008), which generates a strong temporal expectation of subsequent beats (Nombela et al., 2013). The recurring grouping of beats or pulses is referred to as meter, such as the march (1/2) or waltz (3/4) pattern (Levitin et al., 2017). Different researchers use somewhat different descriptions and terminology for creating metric and non-metric sequences, but the underlying idea is similar: simple metric rhythms induce clear beat perception, complex metric rhythms less so and non-metric rhythms not at all.

Interestingly, humans do not need special training to perceive rhythms and produce coordinated movement to the beat in musical rhythms; rather it appears to be a robust, ubiquitous and intuitive behaviour (Merchant et al., 2015). Although rhythmic entrainment is a complex phenomenon that depends on a dynamic interaction between the auditory and

motor systems in the brain (Merchant and Honing, 2014; Zatorre et al., 2007), it emerges very early in development without formal training (Philips-Silver and Trainor, 2005). Indeed, even very young infants show preference for culturally specific metrical structure (Soley and Hannon, 2010), and infants show bias to interpret the meter of the auditory rhythm in a manner consistent with how they were moved to it (Phillips-Silver and Trainor, 2007).

This intuitive synchronisation ability extends to a wide variety of rhythms and tempi. Although studies of SMS have generally used isochronous sequences, humans can spontaneously or intentionally entrain to non-isochronous sequences as well, especially if the sequences induce beat perception (Patel et al., 2005; Fitch and Rosenfeld, 2007; Repp et al., 2008). For appropriate synchronisation, rhythms should fall within the synchronisation limits, which lie between .5 and 5 Hz for finger tapping, with most optimal SMS performance occurring in the 2 Hz range, i.e. 500-600 ms inter-onset intervals (IOI) or 100-120 bpm (Fraisse, 1982; Levitin et al., 2017; Repp, 2005; van Noorden and Moelants, 1999). Synchronisation is also not limited to the auditory modality. People have demonstrated SMS with visual, auditory and tactile rhythms (e.g., Iversen and Patel, 2015; Ammirante et al., 2016), but for sequences made up of discrete events (such as often found in music) an auditory dominance is commonly reported due to higher temporal resolution (Chen et al., 2002; Dunlap, 1910; Loras, 2012; Sugano et al., 2012).

2.2 Relevance of SMS

2.2.1 Expertise in SMS

Humans can perceive and produce simple (musical) rhythms without training. However, SMS improves with training, as highly trained musicians possess a particular expertise in SMS and children are usually more variable in movement synchronisation than

adults (Repp and Su, 2013). Van Noorden and Moelants (1999) found that young (i.e., 3 years old) children have a narrow synchronisation band around 2 Hz and do not adapt to tempi outside this range of movement production, and that the range for adaptation broadens with age, especially between the ages of 3 and 7.

Musicians perform complex rhythms with each other on a regular basis and, due to their extensive training in perceiving and producing complex rhythms, musicians outperform non-musicians on SMS tasks (Drake et al., 2000; Repp, 2010; Repp and Doggett, 2007). Musicians demonstrate lower variability when producing isochronous rhythms, they tap closer to the sound onsets, i.e. produce smaller asynchronies (Aschersleben, 2002), and their asynchronies are more consistent compared to non-musicians (Repp and Doggett, 2007). Within the population of musicians, percussionists have even more specific timing related expertise and outperform other musicians, i.e. they show the least variability in timing (Repp and Su, 2013).

Dancers also receive significant training in perceiving and producing rhythms, specifically coordinating body movement to external rhythms. Unlike in music, studies in dance often examine rhythm processing from a visual perspective (Calvo-Merino et al., 2010; Lee et al., 2015; Stevens et al., 2010), and SMS is studied using whole-body movements (Miura et al., 2011, 2013a, 2013b). Dancers are better at synchronising with auditory and visual rhythms than non-dancers, particularly if the task involves whole-body synchronisation (Karpati et al., 2016; Miura et al., 2011, 2013a, 2013b, 2016; Washburn et al., 2014). They usually produce less variable movement and move closer in time to the stimulus events (Miura et al., 2011, 2013a, 2013b).

Musicians and dancers possess specific rhythmic coordination skills, but athletes also have an advantage in motor coordination (e.g., Boichuk et al., 2017; Pion et al., 2014, 2015),

as their sport performance requires highly accurate timing of movement, although not always rhythmic (Janzen et al., 2014). A study comparing athletes, musicians, and controls showed that athletes outperform controls and musicians on some sensorimotor tasks (i.e., circle drawing) but not on the traditional tapping task (Janzen et al., 2014). This suggests that expertise leads to enhanced timing precision in domain-related timing tasks and reinforces timing skill.

2.2.2 Motor disorders and SMS

Timing mechanisms, which are well trained in the SMS experts mentioned previously, are necessary for coordinating precise and structured movements such as walking, but also for handwriting, typing, and talking (Knoblich et al., 2002; Nombela et al., 2013; Richardson et al., 2007; Salthouse, 1984). In pathological conditions, faulty timing processes can lead to impaired motor performance, such as in Parkinson's disease. In these conditions, musical rhythm can be used to influence the motor system (Cameron and Grahn, 2014; Nombela et al., 2013). The temporal sensitivity of the auditory system combined with the strong temporal characteristics of music (rhythm) can provide a regular temporal input to the motor system that might help to improve SMS performance in these patients (Nombela et al., 2013).

Individuals with movement pathologies such as Parkinson's disease and stroke suffer from such impaired motor timing and have indeed benefitted from rhythmic auditory cueing and musical interventions to improve their movement (Devlin et al., 2019; Nombela et al., 2013; Schaefer, 2014). The main movement problems associated with Parkinson's disease are tremor, rigidity, bradykinesia and postural instability, leading to problems with gait and balance (Davie, 2008). The positive effects of rhythmic cueing are relatively well established for this population (Arias and Cudeiro, 2008; del Olmo and Cudeiro, 2005; Hove & Keller,

2015; Lim et al., 2005; Rochester et al., 2009; Satoh and Kuzuhara, 2008; Thaut and Abiru, 2010). Auditory rhythms provide timing cues that improve the temporal structure of gait, i.e. speed, cadence and stride length, in Parkinson's disease (Thaut et al., 1996). Such cueing effects can be maximised by using auditory stimulus sequences that incorporate groove, bass-frequency, and are adaptive to the patients' gait (GABA principle, Hove & Keller, 2015). Rhythmic interventions might also help to find alternative neural pathways, to compensate for impaired basal ganglia function (Devlin et al., 2019).

After a stroke, a significant proportion of patients suffer from residual motor impairment, usually lateralised, depending on the side of the stroke (Dimyan and Cohen, 2011). Gait coordination after stroke has been shown to improve with auditory pacing during treadmill walking, especially when every footfall is cued (Roerdink et al., 2009). Furthermore, improvement in spatiotemporal control has been reported when cueing movement with the affected arm in stroke patients (Thaut et al., 2002).

In addition to motor pathologies, reading difficulties and dyslexia have been related to decreased synchronisation abilities (Corriveau and Goswami, 2009; Wolff, 2002). Musical (rhythm-based) interventions have shown to be particularly useful for dyslexia, because auditory and rhythmic processing is shared between literacy and music skills (Anvari et al., 2002; Grube et al., 2013). It is particularly beneficial for those with difficulty connecting sounds to symbols, sometimes called "auditory" dyslexia, because the challenge is specific to how the person processes the sounds of language (Rolka and Silverman, 2015). Additionally, music is a multisensory activity, which has been found to be an effective mode of learning for those with dyslexia (Oglethorpe, 2002; See Rolka and Silverman, 2015, for a review).

Similarly, social pathologies such as Schizophrenia and Autism Spectrum Disorder (ASD) have been linked to decreased SMS performance and interpersonal synchronisation

(e.g., Kupper et al., 2010; Marsh et al., 2013; Varlet et al., 2012b). Even though individuals with social pathologies such as ASD and Schizophrenia struggle with social interaction, motor development plays a large role in these disorders too, as cognitive and motor abilities are strongly linked in learning a social behaviour. Specifically, in children with ASD motor development is related to social skills development (Knoblich and Sebanz, 2008; Koehne, et al., 2016) and adults with Schizophrenia show motor impairments early in their motor development (Burton et al., 2016; Fish and Hagin, 1973; Jones et al., 1994; Murray et al., 2006; Walker et al., 1994).

Schizophrenia is considered a neurodevelopmental disorder (Catts et al., 2013; Feinberg, 1982; Lewis and Levitt, 2002; Murray and Lewis, 1987; Weinberger, 1987), and comes with various motor impairments, even prior to the onset of the disorder (Cannon et al., 2002; Pappa and Dazzan, 2009; Walther and Strik, 2012). Children with Schizophrenia also commonly show motor developmental delays and impaired motor skills, which are categorised as a clinically relevant early marker of the disorder (Burton et al., 2016; Jones et al., 1994; Murray et al., 2006). Moreover, the movement of schizophrenic individuals in interactions with peers show several abnormalities (Brune et al., 2008; Kupper et al., 2010), as well as decreased interpersonal synchronisation skills compared to those without the disorder (Varlet et al., 2012b).

Children with ASD are known to show motor dysfunction, including poor coordination of the upper or lower extremities and impaired performance of movement sequences (Bhat et al., 2011). Moreover, children with ASD have difficulty engaging in social-motor behaviours as they struggle to imitate observed behaviours (Casartelli et al., 2016; Vanvuchelen, et al., 2007) and struggle to maintain synchronous movement with others (Marsh et al., 2013; Pierno et al., 2006), which is known to relate to empathic ability (Behrends et al., 2012) and perceived feelings of connectedness among involved partners

(Lakens, 2010; Valdesolo et al., 2010). Therefore, social skills have been shown to improve along-side synchronisation performance on a simple tapping task using rhythm-mediated music therapy interventions (Yoo and Kim, 2018).

2.2.3 Improving elite movement performance with rhythm

As mentioned for rehabilitation, rhythmic auditory cues can be useful to aid with the temporal characteristics of a complex movement or sequence (MacPherson et al., 2009). The improvement of motor performance is, however, not restricted to rehabilitation settings (Karageorghis et al., 2009). Synchronising with rhythms has been implemented more generally to optimise physical and sport performances (e.g., Bacon et al., 2012; Bishop, 2010; Karageorghis et al., 2009; Roerdink et al., 2015; Simpson and Karageorghis, 2006; Terry et al., 2012).

There are some famous examples of elite athletes using pacing to improve their physical performance. As early as 1911, Ayres (1911) observed that competitors in a 6-day cycle race travelled 8.5% faster when a military band was playing. Ethiopian runner Haile Gebrselassie often requested the pop song “scat-man” and broke some world records synchronising his strides to the song (Bood et al., 2013; Damm et al., 2020; Simpson and Karageorghis, 2006). Jens Voigt carefully chose his music, both to motivate him and to pace his distance for the world hour record in track cycling, as there are no devices allowed that give feedback on elapsed time and/or travelled distance (Voigt and Startt, 2016).

Empirical studies have shown increased endurance when synchronising walking to music (Karageorghis et al., 2009) and decreased metabolic cost in synchronised cycling compared to non-synchronised cycling (Bacon et al., 2012). Furthermore, a recent meta-analysis showed significant positive effects of music listening on motor performance

(Karageorghis et al., 2020). It has been proposed that the physiological mechanisms that underlie the ergogenic effects of synchronous music are related to a reduction in the metabolic cost of exercise by promoting greater neuromuscular or metabolic efficiency (Smoll and Schultz, 1978; Szmedra and Bacharach, 1998).

The effect of auditory pacing extends beyond observable performance and movement dynamics to muscular activity as measured by EMG. Greater neuromuscular efficiency seems to be supported by less EMG variability during tapping and reaching movements to rhythms compared to silence (Safranek et al., 1982; Yoles-Frenkel et al., 2016). Rhythmic elbow flexion and extension was also found more economical due to less co-contraction of the biceps and triceps, when auditory pacing was added compared to silence (Thaut et al., 1991). An external rhythm can thus elicit changes in onset, duration, and variability of muscular activity in both simple and more complex movements, demonstrating auditory entrainment to an isochronous sequence at the level of the neuromuscular machinery (Damm et al., 2020).

2.3 Origin of SMS

Presumably, SMS developed due to evolutionary pressure, because the capacity to adapt and systematically respond to ecological rhythms provides evolutionary advantages (Phillips-Silver et al., 2010). Our everyday environment is filled with rhythmic information, from synchronised footsteps or music, to daylight levels and tides, weather changes, circadian rhythms, and even predator-prey dynamics (Bacaer, 2011; Lotka, 1925; Phillips-Silver, 2010; Volterra, 1926). Organisms synchronise their own biological rhythms to these and other rhythmic processes (Kreitzman and Foster, 2011).

By its nature, rhythmic movement generates rhythmic sensory cues. For example, locomotion generates rhythmic multisensory cues (i.e., auditory, visual, tactile and

vestibular), simply as a result of movement in space and time. As summarised by Phillips-Silver (2010), rhythmic information is provided when any land animal moves its limbs, when a bird flaps its wings, or when a bacterium rotates its flagella.

Those rhythmic cues generated by the rhythmic movements of surrounding organisms can be highly relevant to survival and reproduction, for example, to seek out moving prey or to avoid moving predators (Phillips-Silver et al., 2010). For reproduction, it may also be beneficial for an organism to produce rhythmic cues that could be detected by peers (e.g., crickets, fireflies, frogs, and katydids) (Greenfield, 1994a, 1994b; Merker, 2000). However, the production of rhythmic cues could also serve to find one another when gathering or social proximity is beneficial for purposes other than mating, like evading predators, or other mutually beneficial behaviours (Allee et al., 1949). These evolutionary advantages of detecting and responding to rhythmic sensory information in predator-prey interactions may thus have contributed to the development of sensorimotor synchronisation (Clayton et al., 2004; Kelley and Magurran, 2006; Phillips-Silver et al., 2010). The origin of SMS is thus thought to relate to selection pressures in favour of the capacity to recognise and process others' endogenous rhythms such as locomotion, respiration, and feeding (Merker, 2000; Merker et al., 2009; Phillips-Silver et al., 2010; Potts et al., 2005).

For humans, music and dance are some of the most universally enjoyed forms of SMS (Brown and Jordania, 2013). Every culture has some form of music with a beat, a perceived periodic pulse that dancers use to guide their movements and performers use to coordinate their actions (Brown and Jordania, 2013; Nettl, 2000; Patel, 2014). Darwin believed that our capacity for music had deep evolutionary roots and argued that “The perception, if not the enjoyment, of musical cadences and of rhythm is probably common to all animals, and no doubt depends on the common physiological nature of their nervous systems” (Darwin, 1871, p. 333).

Indeed, connections between the auditory and motor systems have been described along the phylogenetic scale from fishes to mammals (Mirjany et al., 2011). These auditory-motor connections developed over the evolution of species are used to explain the ‘auditory startle reflex’ (Lee et al., 1996) – a very rapid behavioural response to sudden sounds. This might explain the particular affinity for auditory-motor synchronisation over other modalities, i.e., short response times and high temporal resolution (e.g., Carney, 1999; Patel et al., 2005).

However, humans do have a particular advantage in audio-motor synchronisation unlike other species. Fitch (2012) called this “the paradox of rhythm”. Periodicity and entrainment seem to be among the most basic features of living things, yet the human ability to entrain motor output to auditory stimuli appears to be very rare (Fitch, 2012). The complexity of human synchronisation abilities lies in the flexibility to adapt and adjust their movement to a wide range of tempi, complex musical structures, and changing tempi (Large and Jones, 1999; Merchant and Honing, 2014). Our complex rhythmic entrainment capabilities are thought to have evolved gradually across primates. This theoretical view has been recently formalised into the gradual audio-motor hypothesis (Merchant and Honing, 2014). This hypothesis is supported by data from several primate species. Furthermore, Merchant and Honing (2014) have argued that the complex entrainment abilities of humans based on relative or beat-based timing, i.e. the perception of regular intervals, is particular to humans and monkeys, whereas an absolute or duration-based timing mechanism, i.e. perceiving a single discrete interval, is considered to be present across the entire primate order (Merchant et al., 2003; Merchant and Honing, 2014; Mendez et al., 2011).

2.4 Mechanisms of control of SMS

2.4.1 Behavioural

The modelling of synchronisation performance has been dominated by two main approaches. The first is the information processing approach (Repp et al., 2005). Information processing models are based on the assumption that cognitive control processes govern the production of synchronised movement responses represented as a discrete time series. These models commonly use forms of error correction and interval extraction to explain synchronisation behaviour (Vorberg and Wing, 1996; Wing and Kristofferson, 1973). Studies following this approach usually extract the temporal asynchronies between the stimulus and movement response in milliseconds and the variability of those asynchronies to measure synchronisation accuracy and stability, respectively.

The dynamical systems approach, on the other hand, follows the rationale that synchronised movement is emergent and a result of a dynamic coupling between two oscillators, i.e. the environmental rhythm and the movement effector (e.g., Schöner and Kelso, 1988; Fink et al., 2000; Torre and Balasubramaniam, 2009). Where the information processing approach mostly deals with discrete time series, the dynamical systems approach is concerned primarily with continuous movement, represented as a trajectory in phase space. Therefore, these dynamical systems studies commonly measure synchronisation as the relative phase angle or frequency ratios between those oscillators.

Although their methodology may differ, both approaches study the same phenomenon and their theories are not mutually exclusive. As proposed by Repp (2005), it is very well possible that each approach is suited to explain some aspects of SMS. An effort should be made to conjoin the results of both approaches to gain more insight in the effect of rhythms on movement.

In the following sections the control processes according to the two approaches, i.e. Information Processing and Dynamical Systems Theory, are elaborated further.

2.4.1.1 Information processing

Traditionally, the earliest models that are still prominent and relevant in the SMS literature have taken an information processing approach. In general, this approach compares the human brain to a computer or basic processor (Simon and Newell, 1964). This approach suggests that humans will process information sequentially as computers would do: "receives input, processes the information, and delivers an output". Following this analogy, the information processing approach describes SMS to rely on timekeeper mechanisms that receive input from the auditory sensors (the external pacer) and extract a discrete time-interval between events to guide movement production in time with those intervals.

2.4.1.1.1 Timekeepers

Timekeepers are at the core of the information processing approach to SMS. Timekeepers assume an explicit generation of discrete time intervals, i.e. it is a computational process that extracts the time-interval between two stimulus events and keeps track of the period that way.

One of the earliest models on time-keeping, the Wing-Kristofferson model, describes rhythmic movement (at a certain frequency) as a process that involves a central timekeeper, or clock, that controls the timing intervals and the peripheral motor system that implements the signals from the timekeeper (Wing and Kristofferson, 1973). In this approach, time is represented centrally, independent of the peripheral motor system. For SMS, however, more elaborate processes would need to be modelled, as it requires feedback on the movement's relation to the stimulus, allowing for adjustments of errors.

2.4.1.1.2 Error correction

In addition to a central timekeeper, error correction is essential to maintain accurate SMS, due to the inherent variability of body movements (Fitts, 1954; Woodworth, 1899). Two sources of variability are generally stated: timekeeper variance (the precision of the timekeeper) and motor implementation variance (motor variance for short). Together, these two sources add up to the total timing variance of the produced rhythmic movement (Wing and Kristoffersen, 1973). Without error correction, the variance inherent to any motor activity would accumulate from tap to tap, and ultimately drift towards large asynchronies (Hary and Moore, 1987; Repp et al., 2005; Voillaume, 1971; Vorberg and Wing, 1996).

After an extensive review, Repp (2005) shows that error correction involves at least two distinct processes: period correction and phase correction. Repp (2005) proposed that phase-related corrections rely on unconscious processes involved with controlling action – based on the perception of asynchronies (Schulze, 1992) – and period corrections involve conscious processes related to perception and planning – based on the perception of the difference between the internal timekeeper and the sequence IOI duration (Mates, 1994a, 1994b).

To maintain synchrony with an isochronous stimulus sequence, all that is required is a process of phase correction which modifies the intervals generated by an internal timekeeper without changing the underlying timekeeper period (Pressing, 1998, 1999; Semjen et al., 1998; Vorberg and Wing, 1996). However, when the IOIs of the external rhythm fluctuate, an additional process of period correction may be required to maintain accurate SMS (Mates, 1994a; Thaut et al., 1998).

2.4.1.2 Dynamical systems

Dynamical systems' explanations of SMS originate from a large field of mathematics that models how systems change qualitatively and self-organise over long time periods. For example, these models have been successful at describing predator-prey interactions (Bacaër, 2011), synchronously flashing fireflies (Buck and Buck, 1966), or audience applause (Néda et al., 2000). Because dynamical systems are self-organising, order emerges due to the physical restrictions of the system and the interactions between the systems' components rather than a controlling force (Haken, 2013; Haken et al., 1985; Kelso, 1995; Schöner and Kelso, 1988). In the case of movement timing, periodicity is not the goal, but the product of cells, bones, and muscles organising in an oscillatory manner (Colley, 2019; Kelso, 1995). Therefore, synchronous timing is described as emergent in the dynamical systems approach (Delignières et al., 2011; Repp and Steinman, 2010; Zelaznik et al., 2002), as it is considered to be a mere by-product of more fundamental processes that are, according to dynamical systems approaches, not a product of cognitive control (Treffner and Turvey, 1993). Similarly, limitations in synchronisation accuracy and stability are considered to be caused by physical limitations within the system, such as weak neuromuscular coupling.

2.4.1.2.1 Entrainment and Synchronisation

Entrainment is a broadly used term that refers to the process of alignment between systems. More specifically, entrainment is the spontaneous synchronisation, without driving forces, of periodic behaviour between two or more systems (Schöner and Kelso, 1988). The spontaneous alignment of movements to environmental rhythms is a form of entrainment. In the context of human behaviour and physiology, entrainment refers to the adaptive function by which we voluntarily or involuntarily synchronise our brains and bodies to the

environment (Ross and Balasubramaniam, 2014). Synchronisation occurs when two or more oscillators adjust their rhythms as a function of their interaction. In order for two periodic behaviours to become synchronised, the dynamical systems producing the behaviour must be coupled in some way. In Huygens' famous example of synchronising clocks hanging from common support, the coupling is mechanical. In sensorimotor synchronisation, systems are perceptually coupled (Beer, 1995; Wilson et al., 2005). When the frequency of stimulation provided by an external rhythm is fixed, like in SMS, the coupling is unidirectional. Hence, external rhythms like acoustic or visual metronomes, or music can be considered as forcing oscillators. Coupling strength between an external rhythm and movement effectors is then measured as the ability to keep in time with the external rhythm.

2.4.1.2.2 Preferred movement frequency

Synchronisation depends on two factors: coupling strength and frequency detuning. Coupling strength is the strength of interaction between the two oscillators and it is not always clear how to measure it quantitatively (Pikovsky et al., 2003). Frequency detuning refers to the distance between the preferred frequency of the two oscillators (Hanson, 1978). The preferred frequency of an oscillator, also called eigen frequency, is the natural frequency of the system measured when isolated, determined by its internal properties, with the ability to be restored after perturbation (Damm et al., 2019). When the two oscillators are within the so-called synchronisation region, the frequency of each oscillator is entrained towards a shared equal frequency. When the difference between two oscillators' preferred frequencies is too large, spontaneous synchronisation might not occur (Amazeen et al., 1995; Lopresti-Goodman et al., 2008; Schmidt et al., 1993). Even intentional synchronisation performance breaks down when reaching the maximum frequencies of the movement effector (Repp, 2003), as per their biomechanical limitations. This explains why tempo is one of the

fundamental factors affecting SMS performance, with the best SMS performance occurring around the preferred movement frequency (Moelants, 2002; Repp, 2005). When trying to synchronise with rhythms outside the synchronisation region of approximately 0.5-5 Hz, stimuli and movements start to drift apart (Repp, 2005).

2.4.2 Neural mechanisms

2.4.2.1 Brain areas and networks in SMS

Many brain areas are involved in SMS. Firstly, the sensory cortex related to the rhythm's modality, i.e. the auditory cortex for audio-motor synchronisation, is activated. Further, a widespread network of predominantly motor areas is involved in SMS: pre-motor cortex (PMC), supplementary motor areas (SMA), pre-SMA, cerebellum, and basal ganglia (Dhamala et al., 2003; Kung et al., 2013; Lewis et al., 2004; Petacchi et al., 2005; Rao et al., 1997; Schubotz et al., 2000, for a meta-analyses, see Chauvigné et al., 2014, and Merchant et al., 2015). Even without producing rhythmic movement, the motor system is actively involved in the perception of rhythms. A growing number of neuro-imaging studies show similar brain activity when *listening* to rhythms as when *producing* rhythms (e.g., Särkämö et al., 2016), including PMC, SMA, and the basal ganglia (Bengtsson et al., 2009; Chauvigné et al., 2014; Chen et al., 2008a; Chen et al., 2006; Grahn, 2009; Grahn and Brett, 2007; Grahn and Rowe, 2009; Kornysheva et al., 2010; Kung et al., 2013; Merchant et al., 2015; Schubotz et al., 2000).

When listening and synchronising to more complex rhythms, there is also evidence for a role of working memory in SMS in addition to the motor system (Bengtsson et al., 2009, Halpern and Zatorre, 1999; Koch et al., 2009; Stephan et al., 2002; Zatorre et al., 1996). The engagement of short-term memory processes by the pre-frontal cortex (PFC) is a function of

the complexity of the rhythmic stimulus, as revealed by the comparison of brain activation while listening to isochronous sequences vs. metrical or non-metrical sequences (Bengtsson et al., 2009). When tapping in synchrony with more complex and less metrically structured auditory rhythms, greater activation in the PFC of musicians was interpreted as reflecting greater contribution of working memory in the analysis of complex temporal structure (Chen et al., 2008b). Activity of the PFC is stronger in trained musicians, explaining their superior synchronisation performance, compared to untrained individuals (Chen et al., 2009).

SMA seems to play a vital role here between working memory and rhythm production, as the pre-SMA receives input from working-memory structures which define the temporal relations of events. On the other hand, the SMA- proper is close to the descending pathways and is assigned an implementation role (Kotz and Schwartz, 2011).

In sum, a widespread motor network is involved in both active synchronisation to rhythms as well as listening to rhythms without moving to them, showing that the motor system is involved in beat perception and the tracking of environmental rhythms.

2.4.2.2 Neural entrainment

Environmental rhythms entrain movement, but also affect ongoing neural oscillations (i.e. neural entrainment). Using EEG and MEG methods, periodic stimuli have been shown to modulate oscillatory brain activity (Snyder and Large, 2005). This is known as neural entrainment. Neural entrainment is a proposed mechanism for neural underpinnings of SMS, particularly spontaneous motor entrainment.

Neural entrainment suggests that groups of neurons entrain to the stimulus frequency by amplitude modulations and adjust their phase to align with the phase of the stimulus frequency. This is also described as Neural Resonance Theory (Escoffier et al., 2015; Large

and Snyder, 2009; Tierney and Kraus, 2014; Zhou et al., 2016). Models based on neural entrainment fit within the dynamical systems approach, as the neural resonance theory holds that listeners experience dynamical temporal patterns and asserts that some neural oscillations in distributed cortical and subcortical areas entrain to the rhythms of auditory sequences (Large, 2008).

The benefit of neural entrainment is optimised processing of rhythmic sensory information (Henry and Obleser, 2012). The amplitude of cortical neuronal oscillations can phase-lock to periodicities of an external sensory rhythm through attentional selection (Lakatos et al., 2008), such that the high excitability phases of the neural oscillation align with the periodic occurrence of the events to allow for optimal processing (Schroeder and Lakatos, 2009).

Stimulus-induced rhythmic modulations of brain activity can be measured using EEG and frequency tagging (see Nozaradan (2014) for a review). In frequency tagging, the stimulus frequency determines the frequency content in the neural data (EEG or MEG) (Nozaradan et al., 2018). The response spectrum presents narrow-band peaks at frequencies that are directly related to the stimulus frequency and that can be modulated, or even generated, by high-level perceptual or cognitive processes (Rossion, 2014).

When frequency tagging was applied to musical excerpts, neural activity elicited peaks at frequencies related to the perceived beat and meter frequencies— the perceived periodicities induced by, but not necessarily present within, the sound input (Lenc et al., 2018, 2020; Nozaradan et al., 2012). The neural activity elicited at beat and meter related frequencies, does not only relate to the perception of rhythms, but it also has relevance for the production of synchronised movement (Bouvet et al., 2020). The strength of beat and meter related frequency responses was positively correlated with synchronisation accuracy on a

tapping task (Nozaradan et al., 2016). This suggests that the neural response captured by this approach is related to the capacity to extract relevant temporal information from an auditory sequence with which to synchronise movements.

Neural entrainment during perception also extends to the motor system. Stimulus-locked amplitude modulations have been frequently reported for cortical activity around 20 Hz in response to periodic rhythms (e.g., Fujioka et al., 2009, 2010, 2014; Zion-Golumbic et al., 2012). Beta (~ 20 Hz) activity is the default oscillatory activity within the motor system (Murthy and Fetz, 1992; Niso et al., 2016), which is associated with sustained movement production (see Engel and Fries, 2010 for a review) and seems to be mainly generated in the pre-motor cortex (Hari, 2002; Jasper and Penfield, 1949; Salmelin and Hari, 1994).

This effect also extends from the main periodicity of the stimulus to the metrical structure of the stimulus. The metrical structure is represented in brain oscillations, i.e. the downbeats elicit a larger response than the other beats (Bouvet et al., 2020; Fujioka et al., 2010; Potter et al., 2009; Schaefer et al., 2011). Such oscillatory activities represent endogenous entrainment to the pulse or beat at different metrical levels of a rhythm (Large and Snyder, 2009) and have been proposed to play a role in spontaneous motor entrainment.

It is now established that the motor system is active during tasks of beat and rhythm perception without movement and that the dynamics of the motor system entrain to external rhythms in the environment. So what exactly is the function of the motor system in rhythm perception and production?

2.4.2.3 Role of motor system in SMS

The observation of shared neural activity between performing movement and listening to rhythms has led to a variety of audio-motor theories on the function of the motor system in rhythm processing, ranging from simple co-activation to a necessary predictive role.

Although audio-motor activity has been considered as mere co-action, i.e. the activity in the motor system observed when listening to auditory rhythms has been suggested to be merely a by-product of inhibited movement, it is generally agreed upon that the motor system plays a vital function in timing processes (Merchant and Yarrow, 2016).

Common-coding Theories. Domain-general frameworks have been developed, such as ideomotor theories and common-coding (Shin et al., 2010). Common-coding approaches consider perception and action to share common representations (Prinz, 1997). According to the common-coding framework, actions are coded as the predicted sensory effects of those actions (also known as action effects) (Ross et al., 2016). Viewing another person's movement activates these action-perception representations, allowing for prediction of the perceptual output of those actions. Common-coding theories are supported by studies showing shared neural substrates for perceived and performed movement (Prinz, 1997).

The discovery of mirror neurons (Di Pellegrino et al., 1992) directly supported common-coding theories and led to the emergence of mirror-neuron theories (Cook et al., 2014; Galesse and Sinagaglia, 2011). Mirror neurons have been argued to play an important role in generating inverse and forward internal models (Miall, 2003). Mirror neurons are most commonly known to be activated during visual observation, but have also been shown active when hearing an action without seeing the action (Kohler et al., 2002). Mirror neuron theories suggest that mirror neurons “mirror” the action that created the sound in the motor system. However, mirror neurons are commonly associated with the ventral premotor area (Ferrari et

al., 2003, 2005) and do not seem to be related to the dorsal premotor areas associated with beat/rhythm perception (Chen et al., 2008).

Motor Simulation Theories. Both common-coding and mirror-neuron theories reference some form of sensory prediction and simulation, but these are more passive “shadowing” or “mirroring” accounts of the motor system’s role. Recent evidence, however, has been in favour of active motor simulation theories of auditory-motor interactions (Cannon and Patel, 2021). Generally, motor simulation theories suggest that the motor system’s simulations play an active role in perception. The motor system is proposed to keep track of timing through motor simulations. Such simulations result in temporal predictions of upcoming events, which in turn aid the processing of the predicted events (Patel et al., 2014). More specifically, the motor system has been argued to be involved in generating temporal predictions via unconscious action simulation to predict when future (auditory) events will occur (Arnal, 2012; Cannon and Patel, 2021; Patel and Iversen, 2014; Keller et al., 2007; Pecenka et al., 2013; Ross et al., 2016; Schubotz, 2007). This is supported by work showing that temporal predictions in the context of regular auditory stimuli are driven by motor signals to the auditory cortex (Morillon and Baillet, 2017) and improved temporal perception when motor actions are performed in time with rhythmic stimuli, i.e. movement shapes perception (Manning and Schutz, 2013; Phillips-Silver and Trainor, 2005, 2007). In the context of beat perception, the efferent signals of these covert actions may act as an internal representation of the beat, or ‘pacing signal’, informing beat-based expectations and in turn facilitating movement to a beat (Kotz et al., 2016).

Action Simulation for Auditory Perception. One of the most popular motor simulation theories in the auditory domain is known as the Action Simulation for Auditory Perception (ASAP) hypothesis (Patel and Iversen, 2014). The ASAP hypothesis states that simulated actions in motor planning regions provide temporal predictions about external stimulus times

that influence activity in auditory regions (Arnal, 2012; Iversen, 2009; Morillon and Baillet, 2017; Patel and Iversen, 2014; Ross et al., 2016). The ASAP hypothesis assumes that the beat perceived with a rhythmic auditory stimulus is tracked and anticipated by repeated movement-like processes in the motor system that are coordinated through rapid bidirectional communication with the auditory cortex.

Recently, predictive coding approaches have gained interest (e.g., Vuust et al., 2018). In line with motor simulation theories, predictive coding theory also supports top-down predictions (Friston, 2005). Even more so, top-down predictions are inherent to any perception in this approach (Friston, 2005). In the predictive coding framework, information flow is driven by top-down sensory predictions about sensory effects (including proprioception), and the only conveyed bottom-up information is in the form of prediction errors (Clark, 2015). Predictive coding is a model that aims to reduce the prediction error between sensory input and top-down predictions of such sensory input. In predictive models such as predictive coding, primary information processing operates on predictions of sensory consequences, but in simulation-based models such as ASAP, top-down (anticipatory) and bottom-up (reactive) processes work in parallel, continuously influencing each other (Ross et al., 2016).

The idea of active motor involvement in auditory perception is not new (Bolton, 1894) and motor processes affecting sensory perception more generally has been described as active sensing (Schroeder et al., 2010). However, recent studies have found convincing support for top-down motor influences on sensory states in the form of sensory gain during movement (Morillon and Baillet, 2017; Niell and Stryker, 2010; Nozaradan et al., 2016; Wekselblatt and Niell, 2015) as well as temporal predictions encoded in sensorimotor delta and beta oscillations (Morillon and Baillet, 2017).

2.4.2.4 Timekeeping & temporal predictions

Many empirical studies have concluded that beat perception is anticipatory in nature (Miyake, 1902; Repp, 2005; Woodrow, 1932) and the motor system's involvement in beat perception is thus argued to be based on anticipatory timing processes. As discussed in motor simulation theories, rather than the passive tracking of timing, the motor system is thought to be the key generator of temporal predictions that influence auditory cognition (e.g., Morillon and Baillet 2017, Rimmele et al., 2018).

Temporal predictions. Sensory neural entrainment is the generally accepted mechanism of temporal prediction underlying the dynamic attending theory (Jones, 1976). The dynamic attending theory proposed that attention is directed in time through the entrainment of neuronal oscillations to periodic stimulation (Large and Jones 1999). In turn this attentional and neural entrainment optimises processing of those sensory periodic stimuli by aligning the high excitability phase of neural oscillations with the occurrence of (auditory) sensory events (Haegens and Zion-Golumbic, 2018).

The dynamic attending theory – and more generally oscillatory entrainment theories – provide an efficient neural mechanism to serve periodic temporal predictions (Rimmele et al., 2018). However, studies on aperiodic (yet predictable) patterns, as can be found in speech and music, have resulted in findings that do not align with oscillatory entrainment theories (e.g., Barczak et al., 2018; Breska and Deouel, 2017). These entrainment theories cannot account for the capacity of the brain to generate – and benefit from – temporal predictions inferred from aperiodic patterns.

Thus, a more recent view - building on the predictive coding approach of motor simulation and active sensing theories - has taken a new “processing constraint” approach (i.e., proactive sensing, Rimmele et al., 2018). Optimal stimulus processing occurs at the high excitability phase of neural oscillations (e.g., Henry and Obleser, 2012). Rather than a

mechanism of temporal prediction, neural oscillations constitutes an inherent processing constraint, i.e. stimulus processing is discrete and has a limited time-window (Rimmele et al., 2018; vanRullen, 2016). Stimulus processing then requires top-down influence, i.e. phase resetting of the ongoing neural oscillations, to process sensory information appropriately. Rather than proposing distinct mechanisms for periodic and aperiodic sequences, Rimmele et al. (2018) proposed neural entrainment to be only one manifestation of a common temporal prediction mechanism in which bottom-up entrainment and top-down phase resets co-occur synchronously.

Rimmele et al. (2018) furthermore proposed the motor system to be the generator of a flexible temporal predictive signal, although other structures might be involved as well (Aly and Turk-Browne, 2018; Barczak et al., 2018). This is not surprising due to the previously mentioned specific timing abilities of the motor system (Coull et al., 2011).

There is thus clearly suggestive evidence of action simulation to track and predict temporal regularities. Motor theories of perception, such as predictive coding and the ASAP hypothesis, propose that motor simulation is likely inherent to auditory beat-based timing (Ross et al., 2016). Interestingly, motor simulations can be explicitly manipulated during motor imagery, as discussed in the next section.

2.4.2.5 Imagining

Mental imagery is a multimodal mental construct that consists of either recalling previously perceived images or feelings, or envisaging forthcoming events (Guillot and Debarnotet al., 2019). Within this construct, “motor imagery” refers to the mental representation of an action without engaging in its actual execution (Guillot et al., 2012). Motor imagery involves an integrated simulation of covert physical movement, and may be

defined as a dynamic mental state during which the representation of a certain motor action is recounted in working memory without any overt motor output (Collet and Guillot, 2010; Decety and Grezes, 1999).

Motor imagery is very relevant to movement execution. A large body of work indicates that motor imagery is a valuable and cost-effective technique to improve motor performance and to enhance motor recovery (see reviews by Driskell et al., 1994; de Vries and Mulder, 2007; Guillot and Collet, 2008; Munzert et al., 2009). These benefits are explained by the fact that neural substrates and processes underlying motor imagery overlap with those underlying motor execution.

Movement-related areas of the brain (e.g., the ventral and dorsal parts of the PMC, as well as the SMA) and subcortical areas including the cerebellum and the basal ganglia, previously described in both rhythm perception and production, are also active during motor imagery of both simple and complex movements (e.g., Guillot et al., 2008; Lotze and Halsband, 2006; Munzert et al., 2009). In SMS in particular, overlapping neural substrates, which are similar to those reported in rhythm perception tasks, were found in covert (imagined) and overt tapping, albeit with lower activation while imagining than executing tapping (Miller et al., 2010; Osman et al., 2006; Oullier et al., 2005; Stavrinou et al., 2007).

Motor imagery includes motor commands for muscle contractions, which are blocked at some level of the motor system by inhibitory mechanisms (Guillot et al., 2012). The main difference between motor execution and motor imagery is thus the inhibition of the motor command, which explains the large overlap in active neural substrates between them.

The dynamics of motor activity also show clear similarities between motor imagery and execution. The EEG beta power desynchronisation prior to movement reported in previous studies (Doyle et al., 2005) is also observed during motor imagery (McFarland et al.,

2000; Nakagawa et al., 2011). These changes in beta power are usually considered to reflect increased activity in the sensorimotor cortex related to movement preparation (Kilner et al., 2005; Seki and Fetz, 2012; Wheaton et al., 2008).

Motor imagery, although it does not result in movement, has also been shown to affect cortico-muscular interaction. Subliminal muscular activity during motor imagery has been reported in many experimental studies (e.g., Decety et al., 1993; Lotze et al., 1999; Mulder et al., 2005; Yue and Cole, 1992). Gandevia et al. (1997) further demonstrated that in addition to activating the motoneurons, the skeleto-motor discharge was accompanied by afferent muscle spindle activity when the covert contraction was sufficiently strong. Such subliminal activity once again supports the idea that the motor command is actually prepared, and then blocked by inhibitory processes, during motor imagery.

Furthermore, TMS studies have provided converging evidence that motor imagery increases the cortico-motor excitability (Stinear, 2010). Excitability changes within motor cortical areas during motor imagery, including reduced intra-cortical inhibition, are comparable to those observed during motor preparation and execution (Abbruzzese et al., 1999; Kumru et al., 2008). This phenomenon is thought to mirror equivalent motor activity at the cortical level during both motor imagery and execution, as it appears that the corticospinal facilitation is highly specific to the motor task (Kasai et al., 1997; Stinear and Byblow, 2003, 2004, see Guillot et al., 2012 for a review). In addition, motor imagery has shown an increase of spinal excitability (Rossini et al., 1999), showing both spinal and spindle activation in task-relevant effectors (Bonnet et al., 1997; Gandevia et al., 1997; Hale et al., 2003).

Whilst motor imagery improves cortical facilitation and reduces intracortical inhibition, it does so in lower amplitude compared to motor execution to keep corticospinal

facilitation below the motor threshold for activating the alpha motor neurons pool during motor imagery (Clark et al., 2004; Leonard and Tremblay, 2007; Stinear, 2010).

All these corticospinal modulations during motor imagery that are highly similar to motor execution support the view that motor imagery gives us conscious access to motor planning and preparation processes (Jeannerod, 1994,1995). As previously mentioned, motor preparation processes in the SMA are linked to the proposed temporal prediction and time-keeping mechanisms. Since action simulation is considered to be a core part of proposed timekeeping mechanisms, imagined movement would provide conscious access to these action simulations and show motor activity at a level below motor thresholds, but supposedly above the level of motor activity elicited during “passive” perception.

2.5 Cortico-muscular Coherence

As described in the previous sections, major advancements have been made in uncovering neural mechanisms involved in SMS. However, brain activity, i.e. cortical and sub-cortical activity, alone do not provide the full picture of motor control. To gain insight into the motor control of rhythmic movement, cortico-muscular interaction along the corticospinal tract also needs to be explored.

There are some indications from Transcranial Magnetic Stimulation (TMS) studies that the effect of sensory rhythms extends beyond cortical activity to cortico-muscular interaction. TMS is used to indicate facilitation or inhibition of movement under certain conditions, as the motor excitability increases or decreases, measured by motor evoked potentials (MEPs) (Reis et al., 2008). TMS investigations have shown modulations of the cortico-muscular pathways in response to music. The motor cortical excitability is increased for high groove music and movement is facilitated on-the-beat compared to off-the-beat

(Stupacher et al., 2013). TMS measures the “readiness to move” as the amplitude of the MEPs to cranial stimulation, therefore this is a one-directional (top-down) measure that does not take into account somatosensory/proprioceptive feedback and the bidirectional coupling involved in motor control. The direct coupling between cortical and muscular activity, i.e. the activity from the cortico-spinal pathway, however, can be studied using cortico-muscular coherence (CMC).

2.5.1 What is CMC?

The coupling between cortical and muscular activity can be assessed with cortico-muscular coherence (CMC). This is done by calculating the cross-spectral coherence between the cortical and muscular signals (Halliday et al., 1995). Coherence is a linear temporal measure of how similar two signals are in the frequency domain, i.e. it is an extension of the Pearson correlation coefficient in the frequency domain and it is calculated by normalising the cross-spectra by the auto spectra (Mima and Hallett, 1999).

CMC is organised topographically; it usually peaks over primary motor regions contralateral to the active limb. Similar to cortical beta-oscillations associated with motor control, CMC has also been found mainly around the 20 Hz frequency and is associated with (pre)motor activity (Bourguignon et al., 2017; Brown et al., 1998; Chakarov et al., 2009; Conway et al., 1995; Halliday et al., 1998; Hari and Salenius, 1999; Salenius et al., 1997; for reviews see Bourguignon et al., 2019; Mima and Hallett, 1999).

2.5.2 Mechanisms driving CMC: top-down vs. bottom-up

Many studies have advocated for a top-down regulated mechanism of CMC driven by cortico-spinal efference (Brown et al., 1998; Gross et al., 2000; Murayama et al., 2001; Salenius et al., 1997). This top-down view is supported by the lead of efferent (top-down) signals ahead of afferent (bottom-up) signals in delay estimation, which is consistent with physiological conductance times (Gross et al., 2000; Petersen et al., 2012; Salenius et al., 1997). Although the efferent contribution was clearly dominant, directionality analyses using granger-causality also demonstrated that both efferent and afferent signals contribute to CMC, showing a similar delay of 25–30 ms in both directions for hand muscles (Petersen et al., 2012; Witham et al., 2011).

More specifically, afferent-dominant CMC was located slightly more posterior towards the primary (somato)sensory cortex than efferent-dominant CMC located on the primary motor cortex. In addition to the directionality analyses, evidence for bottom-up contributions to CMC, such as median nerve stimulation, indicated a more bidirectional view of CMC (Fisher et al., 2002; Riddle and Baker, 2005). These bottom-up contributions highlight the importance of a closed sensorimotor loop in generating CMC (Kilner et al., 2004). Therefore, CMC has also been described as a bidirectional coupling mechanism that constantly monitors the motor state and recalibrates when necessary (Androulidakis et al., 2007, 2006; Baker, 2007; Gilbertson et al., 2005; Witham et al., 2011).

Yet, in a recent review, Bourguignon et al. (2019) reinforces a passive top-down view of CMC and stated that CMC would rather reflect modulation of the motor command by the ~20-Hz mu rhythm. That is, the ~20-Hz mu rhythm causes rhythmic changes in neuronal excitability of the primary motor cortex, leading to synchronous discharge of these neurons. Therefore, at the population level, the motor command tends to structure according to the mu rhythm, inducing similar oscillations in EMG or contraction force (Bourguignon et al., 2019).

In sum, it has become clear that both afferent and efferent factors can modulate CMC magnitude. Moreover, there seems to be inter-individual variability in the relative level of afferent and efferent contributions to the coupling (Riddle and Baker, 2005; Witham et al., 2011). Therefore, it might also be useful to look at the functional role of CMC in motor control, as its physiological investigations show seemingly conflicting results that might be consolidated by its functional implications.

2.5.3 Functional role of CMC in motor control

CMC measures have been related to measures of functional motor control, supporting the view that CMC is a measure of functional coupling between the cortical and muscular system. For increased motor control and precision, higher levels of CMC have been observed (Kristeva et al., 2007, Witte et al., 2007). On the other hand, when cortico-muscular function is impaired, in post-stroke patients for example, decreased levels of CMC have been reported (von Carlowitz-Ghori et al., 2014; Braun et al., 2007; Fang et al., 2009; Larsen et al., 2017; Mima et al., 2001; Rossiter et al., 2013). Similarly, age related decreases in motor performance were found to be related to decreases in CMC in static contractions (Bayram et al., 2015, Graziadio et al., 2010; Johnson and Shinohara, 2012; Kamp et al., 2013) and dynamical movements (Yoshida et al., 2017b). This implies that factors that affect CMC influence motor control and vice versa.

Due to its increase with higher motor precision (Kristeva et al., 2007, Witte et al., 2007), CMC was hypothesised to reflect a stabilising mechanism meant to increase motor precision, i.e., reduce the error signal in a task involving a static target. Beta CMC has been proposed to be a mechanism for maintaining stable motor output, similar to the 20 Hz cortical beta activity, that is considered to “signal the status quo” in motor control (de Vries, 2012). This view was supported by evidence of the abolishment of CMC during movement (Kilner et al., 2000, 2003).

However, the function of CMC is more complicated than that, as several findings contradict a causal link between motor control or precision and beta CMC. In post-stroke patients, CMC magnitude has not been found to relate to the extent of impairment of motor function (Rossiter et al., 2013). Instead, after recovery of hand function, primary motor cortex activity has been found to compensate for the loss of efficient cortico-muscular

communication, demonstrating that CMC magnitude does not necessarily relate to motor function (Larsen et al., 2017). Furthermore, approximately 10-20% of the general population does not show significant CMC during upper limb motor tasks, without showing signs of loss of motor function (Yang et al., 2017). In addition, large inter-individual differences in CMC magnitude and frequency exist in healthy populations (e.g., Mendez-Balbuena et al., 2012). Findings like these have challenged the existence of a direct relation between CMC magnitude and motor function.

Results that flowed from the motor output stabilisation interpretation were also contradictory. One might expect higher CMC when higher motor precision (more stable motor output) is achieved, in line with the first finding of Kristeva et al. (2007) that indicated higher precision associated with higher CMC. Yang et al. (2009) reported the same effect in the opposite direction, i.e. lower precision and decreased CMC in severe fatigue compared to minimal fatigue. One might also expect the opposite, i.e. increased CMC when motor output is less stable, because more corrective processes would be engaged. Ushiyama et al. (2011) reported such results: lower precision but higher CMC in post-fatigue compared to pre-fatigue conditions. More recently, Ushiyama et al. (2017) also linked increased force fluctuation, i.e. lower precision, to increased CMC magnitude, reinforcing the idea of CMC as a stabilising mechanism engaged in corrective control.

In line with Ushiyama (2011), Divekar and John (2013) also found an inverse relationship between CMC and precision in an inter-muscle study, but provided a different view on the relationship between CMC and motor function. In all the previously mentioned studies – where it was possible to determine task difficulty – the more difficult task was associated with higher CMC levels. In their case, wrist flexion was compared to wrist extension, which is inherently less steady, and found higher CMC for wrist extension. The

authors thus proposed that CMC was related to the level of motor control as a function of the perceived difficulty and effort put into the task, rather than a correlate of motor performance.

Divekar and John (2013) suggested that in the context of maintaining high precision, performing a perceptually more difficult task, would possibly induce an increase in the relative engagement of precision enhancing mechanisms as a compensatory measure. Such mechanisms may involve an increase in the relative involvement of the direct corticospinal tract to facilitate finer motor control. Corticospinal involvement may also increase the gain of somatosensory afferents via the peripheral tracts to facilitate stronger feedback of muscle tension (i.e. afference from Golgi Tendon Organs) and muscle length variation (i.e. afference from muscle spindles), ultimately resulting in increased CMC magnitude.

Whereas Divekar and John (2013) explained intra-individual differences as a function of effort and/or perceived task difficulty, Mendez-Balbuena et al. (2012) found that inter-individual differences in CMC magnitude can be explained by differences in cortical motor efficiency. They defined cortical motor efficiency as cortical activation, i.e. the task-related desynchronisation, required for the same level of performance. Participants with lower cortical motor efficiency need stronger cortical activation for the same performance level as the participants with higher motor efficiency. Participants with lower motor efficiency did not display CMC at the start of the experiment, but did at the end, after motor adaptation occurred. This is in line with compensatory primary motor cortex activity in healthy aging (Kamp et al., 2013) and post-stroke (Rehme et al., 2012). This could also explain the trainability of CMC as an increase in cortical motor efficiency, or compensatory primary motor cortex activity.

2.5.4 Role of somatosensory feedback in CMC

Divekar and John's (2013) account of the relationship between CMC and motor control is particularly enticing, because it takes into consideration the importance of somatosensory feedback. The integration of somatosensory feedback is not only extremely relevant for motor control, but is also of particular interest in SMS. During SMS the time difference between the produced movement and perceived stimulus events, i.e. asynchrony, needs to be constantly monitored to make corrections for deviations from the target stimulus event.

Somatosensory stimuli have been shown to produce increases in beta band power (i.e., event-related synchronisation) in the contralateral sensorimotor cortex (Neuper and Pfurtscheller 2001; Salmelin and Hari 1994; Svoboda et al. 2004), and CMC has been suggested to be dependent on beta band power (Bourguignon et al., 2019; Salenius, 1997). Thus, the integration of somatosensory input with motor output has been proposed as a mechanism that modulates CMC magnitude (Kasuga et al., 2018; Kristeva et al., 2007). More specifically, CMC has been suggested to have a function related to modulation of feedback gain. Kasuga et al. (2018) found that CMC decreased during the adaptation period of motor learning, which was associated with decreased long latency reflexes. This study also provides an explanation for some of the results found in studies on the 'trainability' of CMC, as discussed in section 2.5.6.

2.5.5 Sensory effects on CMC

Sensory rhythms can affect motor control, i.e. movement dynamics (Ross and Balasubramaniam, 2014) and cortical dynamics (Fujioka et al., 2012, 2015; Nozaradan et al., 2011). Recently, studies have extended this to show that the magnitude of CMC can be

modulated by sensory stimuli. Sensory distractors, both auditory and visual, dynamically affect CMC (Piitulainen et al., 2015). Visual stimulation increases the peak value of CMC in the beta-band compared to no stimulation (Safri et al., 2007, 2006), and CMC increases within the first second after action observation (Hari et al., 2014). Moreover, audio-visual rhythmic stimulation at 2 Hz, i.e. humans' preferred movement frequency, has shown to influence beta band CMC (Varlet et al., 2020b).

Most of these studies do not test the effect of sensory *rhythms*. Varlet et al. (2020b) is the only study that directly measured the effect of isochronous sensory rhythms, i.e. auditory, visual, and audio-visual metronomes, on beta CMC. The other studies did not present sensory stimuli in rhythmic sequences. Safri et al. (2006) presented visual stimuli that needed to be ignored while maintaining a steady isometric contraction. Increased beta CMC was observed when the visual stimuli were presented compared to no stimulation (Safri et al., 2006). Similarly, Piitulainen et al. (2015) used auditory and visual distractors that were brief 100 ms presentations of 1kHz tones and checkerboard patterns, while the main task was to maintain a steady isometric pinch grip. In line with their distractive function, the effect on (beta) CMC was explained as a startle, i.e. motor response, derived from 'startle-like' EMG activity. Hari et al. (2014) found a similar reactive increase in CMC when observing other people's movement, suggesting that movement facilitation took place but was inhibited by sensorimotor activity. Safri et al. (2007) found an increase in beta CMC while passively observing the visual stimuli compared to no stimulation or counting the visual stimuli. This was explained within the same distractor paradigm as an effect of enhanced effort to maintain the motor task with concurrent visual stimuli, which aligns with Divekar and John's (2013) theory of perceived difficulty of the motor task.

2.5.6 Effects of attention

Divekar and John's (2013) account of the relationship between CMC and motor control also imply an effect of attention on CMC, as motor tasks requiring more effort might also require more attention. Attention has indeed been shown to affect CMC (Kristeva-Feige et al., 2002; Safri et al., 2006). That is, divided attention such as a double task – both motor and cognitive – decreased CMC magnitude (Johnson et al., 2011; Johnson and Shinohara, 2019), and increased attention increased CMC magnitude (Safri et al., 2006) and task performance (Kristeva et al., 2002). This is in line with the evidence for the influence of attention on motor unit activity and brain excitability (Murthy and Fetz, 1992; Schmied et al., 2000).

In addition, a proof-of-concept study showed that people can be trained with neurofeedback to voluntarily modulate their level of CMC independently of motor control (von Carlowitz-Ghori et al. 2015). This implies that participants acquired self-regulation of CMC amplitude using mental processes that could be related to attention or cognitive effort, specifically motor imagery (Jeannerod, 1995; Solodkin et al., 2004), motor attention (Rushworth et al., 2001, 2003), or somatosensory attention (van Ede and Maris, 2013).

As an extension to the level of perceived difficulty of the motor task proposed by Divekar and John (2013), these findings suggest that cortico-muscular coherence can also reflect the *cognitive effort* needed to maintain isometric muscle contraction.

2.5.7 Training and expertise

With the observation of increased CMC alongside increased motor performance, the question of motor expertise related to CMC arises. A handful of studies have explored the relationship between motor expertise and CMC magnitude (e.g., Dal Maso et al., 2017;

Ushiyama et al., 2010). Although results are varied, there seem to be changes in CMC related to motor expertise, and some have even shown that CMC can increase with training (Larsen et al., 2016; Mendez- Balbuena et al., 2012; Perez et al., 2006).

CMC is thought to be reduced in long-term specialisation of muscles due to training. For example, the dominant hand has been found to display lower magnitude motor unit beta coherence between motor unit pairs in the first dorsal interosseous (FDI) muscle than the non-dominant hand in untrained individuals (Semmler et al., 2004). Furthermore, musicians, i.e. highly trained individuals, had even lower (motor unit) beta coherence than untrained people in both hands (Semmler et al., 2004). Ushiyama et al. (2010) also reported a reduction in CMC in response to specialised training. Ballet dancers and weightlifters showed lower magnitude of beta CMC than untrained controls (Ushiyama et al., 2010). Both ballet and weightlifting are classified as anaerobic exercise, and anaerobic strength training has been associated with higher CMC than aerobic endurance training, showing specificity for training-induced adaptations (Dal Maso et al., 2017).

Not only power or endurance training changes CMC magnitude, training of perceptual-motor skills has also been shown to improve CMC magnitude. Fifteen years ago, Perez et al. (2006) already reported an increase of the beta-range CMC after visuo-motor skill learning and suggested that the increased CMC reflects tighter cortical control of the muscle activity in relation to the acquisition of the task. Hence, increased CMC may reflect a more efficient corticospinal interaction. Mendez-Balbuena et al. (2012) showed that all of their participants increased both CMC and motor performance on a visuo-motor task, i.e. isometric compensation of a static or dynamic force. Most recently, using visuo-motor pinching task, Larsen et al. (2016) showed that tablet-based motor practice is associated with both increased motor performance and increased CMC involved in manual dexterity. Possibly these changes reflect sensorimotor integration processes between the cortex and muscles as part of the

motor learning process (Perez et al., 2006). Together these results suggest that an increase of CMC is linked to improving sensorimotor skills, but that this increase might disappear after learning has occurred and people have become experts at a skill (Dal Maso et al., 2017; Ushiyama et al., 2010).

Due to the involvement of CMC in perceiving sensory events (Hariri et al., 2014; Piitulainen et al., 2015; Safri et al., 2006, 2007), rhythmic movement production (Castermans and Duvinage, 2013; Petersen et al., 2012; Yoshida et al., 2017) and the combination of the two in perceptual-motor learning (Perez et al., 2006), CMC could provide insight into motor control mechanisms underlying the dynamical processes involved in movement synchronisation with external rhythms.

2.6 Thesis overview

The current thesis aims to understand the role of cortico-muscular coupling during SMS. Using CMC, the following two experiments will study cortico-muscular modulation at different levels of engagement of the motor system by testing music listening, imagined and executed sensorimotor synchronisation. First, spontaneously induced changes of CMC magnitude during music listening, without any movement intention, are evaluated in three conditions of varying levels of motor engagement. For this first experiment, musical groove, i.e. an acoustic quality that induces an urge to move, known to elicit high levels of movement facilitation is manipulated (Janata et al., 2012; Stupacher et al., 2013). This study examines whether spontaneous movement facilitation induced by different levels of musical groove, i.e. high and low, is associated with spontaneous modulation of overall CMC magnitude. Then, CMC is examined dynamically during three different states of motor system engagement: passively perceiving, imagining synchronisation with, and executing synchronisation with

sensory rhythms. In this second experiment, CMC is examined over time to investigate how CMC dynamics aligns with external rhythms and/or imagined and executed synchronised movement. In addition, CMC dynamics are examined with bimodal audio-visual sequences in this study, to investigate the underlying processes of the superiority of the auditory modality for SMS. This second study therefore examines: (i) Is CMC dynamically modulated during sensorimotor synchronisation?; (ii) Do such dynamic modulations occur when executing as well as imagining the synchronous movement?; (iii) Do such dynamic modulations become selectively aligned with the stimuli individuals intend to synchronise with?; and (iv) Are such dynamic modulations facilitated with auditory stimuli compared to visual stimuli?

Together, the aim of these experiments is to explore the role that cortico-muscular coupling - in the form of CMC - plays in sensorimotor synchronisation and if motor facilitation observed at the level of the brain extends to the neuromuscular coupling. The prospective findings of this research will further our understanding of motor control and the outcomes of this project might inform the development of new perspectives for motor training and rehabilitation.

It should be noted that the experiments have been written up as papers and are published or currently under review. Hence there is some overlap between the introductions of each experiment and the general introduction.

Chapter 3: Null effects of musical groove on cortico-muscular coherence

Chapter 3 is currently under review as: Nijhuis, P., Keller, P. E., Nozaradan, S., and Varlet, M. (2021). Null effects of musical groove on cortico-muscular coherence. *NeuroImage: Reports*.

3.1 Introduction

People have a natural tendency to move to music (Janata et al., 2012; Zentner and Eerola, 2010). Children already show movement to music from a very young age (Fujii et al., 2014; Honing et al., 2009; Huron, 2006; Witek et al., 2014; Zentner and Eerola, 2010). When listening to rhythmic music, it is often difficult to suppress the natural urge to tap the feet or fingers along with the beat. This urge to move to music is often ascribed to the tight coupling between the auditory and motor system and the active role of the motor system in the perception of musical rhythms (Zatorre et al., 2007). While a growing number of studies corroborate the evidence for an engagement of the motor system in the brain when listening to music (e.g., Särkämö et al., 2016), how this effect transfers through the body to the muscles even when no movement is intended remains unknown. Here we combine Electroencephalography (EEG) and Electromyography (EMG) techniques to investigate changes along the cortico-muscular pathway induced by music listening while maintaining an isometric contraction, especially high-groove music characterised by stronger induction of spontaneous movement.

The active role of the motor system in music and rhythm perception has been shown in numerous studies that revealed that even without actual movement the perception of auditory rhythms activates motor regions in the brain, including premotor cortices, supplementary motor areas (SMA), and the basal ganglia (Bengtsson et al., 2009; Chen et al., 2008a; Chen et al., 2006; Grahn and Brett, 2007; Kornysheva et al., 2010; Schubotz et al., 2000), with stronger activity for musicians compared to non-musicians (Cameron and Grahn, 2014; Chen et al., 2008b). Studies have also shown music-induced modulations in the amplitude of neural oscillations in the beta band (≈ 20 Hz), which are critical for movement production and control (Engel and Fries, 2010; Khanna and Carmena, 2015; Pfurtscheller, 1981). Such motor activity suggests that temporal features of music, such as the ongoing rhythm, directly engage auditory-motor links that facilitate moving in time with the music. Furthermore, auditory-motor interactions and movement facilitation have been shown to be stronger with extensive musical training (Chen et al., 2008b, Rosenkranz et al., 2007, see Zatorre et al., 2007 for a review).

Motor regions have been suggested to play a critical role in extracting the beat from the music and forming an internal temporal representation (Araneda et al., 2017; Bengtsson et al., 2009; Grahn, 2009, 2012; Grahn and Rowe, 2009; Chapin et al., 2010; Wiener et al., 2010; Teki et al., 2011, 2012; McAuley et al., 2012). The motor system has been argued to be involved in generating temporal predictions via covert and unconscious action simulation to predict when future (auditory) events will occur (Arnal, 2012; Cannon and Patel, 2021; Patel and Iversen, 2014; Keller et al., 2007; Pecenka et al., 2013; Ross et al., 2016; Schubotz, 2007). This is supported by work showing that temporal predictions in the context of regular auditory stimuli are driven by motor signals to the auditory cortex (Morillon and Baillet, 2017). In the context of beat perception, the efferent signals of these covert actions may act as

an internal representation of the beat, or ‘pacing signal’, informing beat-based expectations and in turn facilitating movement to a beat (Kotz et al., 2016).

Interestingly, certain types of music are particularly enticing to move to, and more potent at inducing synchronised movement than other music (Janata et al., 2012). Such music is considered high in groove, and yields a pleasurable experience (Janata et al., 2012).

Properties of the musical structure and acoustic properties, such as rhythmic and harmonic complexity (Matthews et al., 2019), syncopation (Sioros et al., 2014; Witek et al., 2014; 2017) and spectral flux (Burger et al., 2013; Stupacher et al., 2016) seem to play a crucial role in the experience of groove and the induction of movement. In particular, a moderate degree of rhythmic (and harmonic) complexity, including syncopation, is thought to induce groove (Huron and Ommen, 2006; Keller and Schubert, 2011; Matthews et al., 2020; Witek et al., 2014). It has been suggested that deviations from a predictable rhythm cause the listener to make a greater effort, i.e. increasing their predictive engagement, to follow the rhythm than with a simple and fully predictable isochronous metronome (Levitin et al., 2017). According to Iyer (2002), this “active” listening experience through increased predictive engagement would be essential to the experience of groove, and a medium rhythmic complexity strikes a balance between satisfying and violating rhythmic expectations. This theory of medium (rhythmic) complexity as the crucial characteristic of groove to optimally engage prediction processes is supported by a study by Matthews et al. (2020) that found medium complexity rhythms scored high on groove ratings and led to increased activity in areas that are critical for generating an internal representation of the beat, including the putamen, caudate, SMA and dorsal premotor areas (see Araneda et al., 2017; Grahn and Rowe, 2009; Merchant et al., 2015). In addition to an increase in activity, higher complexity rhythms that were correlated with higher groove ratings have also been

linked to stronger neural entrainment, i.e., entrainment of ongoing neural oscillations to regularities in stimulus rhythms (Cameron et al., 2019).

Therefore, it is well established that the motor system is actively involved in music listening, and inducing groove in particular (generating the pleasurable urge to move along), through its involvement in time-keeping and temporal prediction. However, the involvement of the motor system during music listening beyond cortical and subcortical regions remains unknown. It is unclear how music, especially high-groove music characterised by high movement induction, spontaneously modulates activity along the cortico-muscular pathway, and thus, intrinsic behavioural motor functioning.

Of particular interest in the present study is cortico-muscular coherence (CMC), a measure that quantifies the degree of synchronisation between cortical and muscular activities, which has been shown to play a critical role in movement production and control (Halliday et al., 1995). CMC is used to assess the communication between cortical regions and muscles, and can be obtained by combining EEG or MEG with EMG (Fries, 2005). CMC, which is usually measured best during low-intensity isometric contraction, has been found to peak over primary motor regions contralateral to the active limb, and in the beta frequency range around 20 Hz (Conway et al., 1995; Feige et al., 2000; Halliday et al., 1998; Hari and Salenius, 1999; Salenius et al., 1997; Witham et al., 2011; for reviews see Bourguignon et al., 2019; Mima and Hallett, 1999).

CMC has been shown to be relevant for understanding motor control. It has been suggested that increased CMC occurs when higher level of control (measured as perceived task difficulty) is required, when maintaining a stable motor output, for instance (Divekar and John, 2013). Increased CMC has also been found to be associated with more accurate motor performance (i.e., motor precision) in certain scenarios, suggesting more effective

communication between the brain and the muscles (Kristeva-Feige et al., 2002; Kristeva et al., 2007; Witte et al., 2007).

Previous research has shown that CMC is sensitive to surrounding environmental stimuli, even if an individual is not moving and is required to maintain a steady isometric contraction. Piitulainen et al. (2015) found pronounced increases in CMC following the presentation of unexpected auditory and visual distractors. Changes in CMC have also been shown during the observation of human actions (Hari et al., 2014) and the presentation of simple predictable audio-visual sequences (Piitulainen et al., 2015; Safri et al., 2006, 2007; Varlet et al., 2020b). These results suggest that music, especially high-groove music characterised by stronger movement induction, might spontaneously modulate the strength of cortico-muscular synchronisation even if there is no intended movement.

Transcranial Magnetic Stimulation (TMS) research supports this possibility, revealing enhanced cortico-muscular facilitation with music compared to white noise, as indicated by larger Motor Evoked Potentials (MEP) in EMG recordings following TMS pulses during passive music listening (Stupacher et al., 2013) and foot tapping to music (Wilson and Davey, 2002). In these studies, cortico-muscular facilitation was stronger for high-groove than low-groove music and was found for both upper and lower limbs, in line with previous behavioural research that showed similar effects of groove levels on movement entrainment for both the hands and the feet, although the absolute amount of movement or synchronisation performance to the beat might differ between hands and feet (Janata et al., 2012; Tranchant et al., 2016). These results are particularly relevant here because it has been previously shown that the amplitude of TMS-induced MEPs is linked to the magnitude of beta band CMC (Schulz et al., 2014), suggesting that the connectivity between the brain and the muscles for upper and lower limbs might be modulated by music, especially high-groove music.

The current study tested this hypothesis in order to better understand the effects of music on the motor system by examining the strength of CMC between EEG and EMG recordings from the upper and lower limbs of participants listening to either no music, low-groove music, or high-groove music while instructed to maintain a steady isometric contraction. Because groove induces feelings of wanting to move and because this spontaneous movement planning may act as a time-keeping mechanism allowing temporal prediction and actual spontaneous movement, groove was expected to modulate the strength of the cortico-muscular coupling even if participants were not moving and were instructed to maintain an isometric contraction. More specifically, because high-groove music results in stronger motor engagement and higher motor excitability, it was hypothesised that listening to high-groove music would result in stronger CMC than listening to low-groove music and no music. This effect was expected to occur for both lower and upper limbs and to be stronger in participants with musical experience due to increased motor engagement and enhanced temporal predictions.

3.2 Method

3.2.1 Participants

Eighteen healthy right-handed participants volunteered in this study (age: 18-45 years old, $M = 26.7 \pm 6.1$; 13 females, 5 males). The sample size was chosen based on an a priori power analysis to detect medium effect sizes ($f = .25$) with at least 80 % power, in line with effect sizes previously reported in CMC and groove studies (e.g., Safri et al., 2006; Stupacher et al., 2013; Varlet et al., 2020b).

None of the participants had any history of hearing, motor, neurological, or psychiatric disorders. This study was approved by the Human Research Ethics Committee of

Western Sydney University and was performed in accordance with the ethical standards of the Declaration of Helsinki. All participants gave written informed consent prior to participation and were debriefed after the study.

To control for the effect of musical experience, a dichotomous between-subject factor Musical Experience (high and low) was used where participants were assigned to one of the two groups post-hoc depending on whether they had more or less than five years of combined musical and dance experience, as self-reported (Grahn and Rowe, 2009; Zhang et al., 2018). The low Musical Experience group had an average of 1.000 ± 1.483 years of musical experience, whereas the high Musical Experience group had an average of 8.571 ± 2.370 years of musical experience.

3.2.2 Musical stimuli

The stimuli consisted of 50 musical excerpts of 30 s each, from which 25 were categorised as high-groove and 25 were categorised as low-groove. Forty excerpts were derived from the Janata et al. (2012) database. Twenty high-groove excerpts were chosen from the forty highest rated excerpts and twenty low-groove excerpts were derived from the forty lowest rated excerpts from this database. An extra ten musical excerpts (5 high-groove and 5 low-groove) from contemporary music (2010-2018) were also included (i.e., high-groove: Uptown Funk, Call Me Maybe, Shape of You, Despacito, Sorry – low-groove: Lovely London Sky, Opposite of Loving Me, I Miss Her, Mark My Words, Love Drought). These new contemporary excerpts were pilot tested on 9 participants, asking how much participants felt like moving on a 7-point Likert scale (“very much” - “not at all”), to confirm that the newly selected high-groove and low-groove excerpts differed significantly in

perceived groove ($p < .001$). All the musical excerpts were obtained from the previews accessible on the iTunes Music Store.

The musical excerpts in this study varied in their genre (rock, soul, jazz) and had a wide range of tempi (from 66 to 159 bpm). The high-groove ($M = 106$, $SD = 16$ bpm) and low-groove ($M = 113$, $SD = 26$ bpm) excerpts were balanced as closely as possible for their tempo, as operationalised by the beats per minute. The excerpts were also matched for perceived loudness using adobe audition CS6. The musical stimuli were presented at a comfortable hearing level using ER-1 in-ear phones (Etymotic Research Inc, Illinois, USA).

In addition to the 50 musical excerpts, 25 control trials consisting of 30 s of silence were presented. The 75 trials were presented to the participants in random order. To ensure an equal distribution of the excerpts over time, the presentation order was blocked into sets of three. In each block a random high-groove, low-groove and control trial was assigned in random order.

3.2.3 Apparatus

During the experiment participants were seated on an armless chair, in front of a computer screen, with their right forearm placed on a table adjacent to them, with their elbow joint making approximately a 90 degrees angle and the hand palm facing down. Their right index finger was placed on a force sensor on the table. The left foot was placed on a pedal that measured plantar flexion force.

3.2.3.1 Force

The force exerted by the participant's right index finger and left foot was recorded at a sampling frequency of 60 Hz using two wide bar load cells (HTC-Sensor TAL201, Colorado,

USA), one on the table and one for the foot pedal. The cells were connected to an Arduino Duemilanove board (Arduino, Ivrea, Italy) via an amplifier shield (Load Cell / Wheatstone Amplifier Shield, RobotShop, Mirabel, Quebec, Canada). The Arduino board was connected to a MacBook Pro laptop (Apple, Cupertino, CA, USA) via USB. The load cells were calibrated for linearity.

3.2.3.2 EEG and EMG recording

EEG and EMG signals were recorded at a sampling rate of 2048 Hz using a BioSemi Active-Two system (BioSemi, Amsterdam, Netherlands). EEG was recorded with 64 Ag-AgCl electrodes placed over the scalp of the participant according to the international 10/20 system. EMG signals were recorded using BioSemi flat electrodes with a standard belly-tendon montage. After preparing the participant's skin using alcohol swabs, a pair of electrodes was placed on the right forearm to record the right Flexor Digitorum Superficialis (FDS) muscle, involved in maintaining continuous finger pressure (Cardellicchio et al., 2020; Kong et al., 2010). A second pair of electrodes was placed on the participant's Gastrocnemius Medialis (GM) muscle on the left calf, involved in maintaining the foot pressure (Hermens et al., 1999).

3.2.4 Procedure

Before commencing the experiment, participants were asked to complete a short questionnaire concerning demographic information including age, gender, handedness, and information regarding their level of expertise in music and dancing.

Prior to data collection, the force sensors for both hand and foot were calibrated for each participant by asking the participants to place their right index finger and their left foot on the sensors without applying any force, thereby subtracting the relative weight of participants' relaxed limbs on the sensors. Then, the participant's maximal voluntary contraction (MVC) was measured. The participants were instructed to put as much pressure on the sensors as they could for approximately 3 seconds. This was repeated three times and the average of the three maximum forces was considered to be the MVC, which was used in the following experimental trials.

3.2.4.1 Task

Participants were instructed to sustain an isometric contraction of the right index finger and left foot throughout the 30 s trials, corresponding to the duration of the musical excerpts. The target force for the hand and the foot was calculated as 7 % of the MVC (Kristeva-Feige et al., 2002; Kristeva et al., 2007; Safri et al., 2006, 2007). Low-intensity isometric contraction was chosen to study CMC with line with previous research suggesting that the motor cortex is particularly involved with the coding of weak forces (Maier et al., 1993). It also provides the required level of muscular activity to gather EMG signals while preventing dynamic fluctuations in CMC related to movements (Halliday, 1995). Isometric contractions of both the hand and the foot enabled testing systemic effects of groove through the whole body, expected to propagate from central level to all distal body parts in line with previous research (e.g., Burger et al., 2013; Cameron et al., 2019; Matthews et al., 2020; Wilson and Davey, 2002).

Participants were instructed to focus on the musical excerpts and keep the pressure on the force sensors as stable as possible. Participants' force levels applied with the hand and the foot had to be within a 5 % accuracy range of their respective target force defined as 7 % of

their MVC (Conway et al., 1995; Kristeva-Feige et al., 2002, Kristeva et al., 2007; Safri et al., 2007; Witte et al., 2007; Varlet et al., 2020b). Feedback of the participant's force level was visually presented between trials, and the following trial could only be started by the experimenter once the participant was within a 5 % accuracy range of the target force for both the hand and the foot.

The visual feedback for each limb corresponded to a red bar that changed in length in real-time depending on participant's exerted force and turned green when the exerted force was within the 5 % accuracy range of the target force. The target force was indicated by a white line on the bar. The force feedback disappeared as soon as the experimenter started the trials to avoid distracting the participants from focusing on the musical excerpts. Several practice trials were performed to familiarise participants with the experiment until they managed to hold steady forces of approximately 7 % of MVC for both the hand and the foot.

3.2.4.2 Survey items

Perceived groove, loudness, familiarity, effort to sit still, and enjoyment were evaluated on a seven-point scale (where 1 = “not at all” and 7 = “very much”) via the computer display at the end of each musical excerpt. The following survey items were presented on the screen: 1) How much did you feel like moving? (groove); 2) How loud was the music? (loudness); 3) How familiar were you with the music? (familiarity); 4) How hard did you find it to sit still while listening to the music? (effort to sit still); and 5) How much did you enjoy the music you just heard? (enjoyment). Participants reported their answer to the experimenter who entered the values into the computer. Participants were also asked to report some lyrics to the experimenter at the end of each musical excerpt to make sure they paid attention to the stimuli. For this attention check, a dichotomous answer was used, participants

either did (7) or did not (1) remember lyrics. When the excerpt had no lyrics, 7 was awarded when participants reported correctly that there were no lyrics.

To minimise the source of artefacts in EEG signals during trials, participants were also instructed to focus their gaze on a cross at the centre of the screen, to relax their upper body and to refrain from moving their head, talking, swallowing, coughing, clenching their jaw, and blinking excessively. Participants were allowed to take as many breaks as necessary in between trials. The experimental task and procedure were explained to the participants in detail before the commencement of the experiment. The total experiment, including EEG and EMG preparation, lasted approximately 2 hours.

3.2.5 Data analysis

The surface EEG and EMG were processed and analysed using MATLAB 2017a (The MathWorks, Inc., Natick, MA).

3.2.5.1 EEG pre-processing

EEG signals were first (i) high-pass filtered using a 4th order Butterworth filter with a cut-off frequency of .2 Hz to remove very slow drifts in the recorded signals and (ii) segmented into 30 s epochs locked to the onset of each trial.

After the initial filtering, EEG channels containing excessive artefacts or noise were identified based on visual inspection and interpolated with neighbouring channels (i.e., an average of 1.389 [SD = 1.253] interpolated electrodes per participant, and never more than 5 electrodes). The EEG signals were then decomposed by an independent component analysis (FastICA), as implemented in Fieldtrip (Oostenveld et al., 2011), to remove muscular activity

related to eye movement artifacts. Based on visual inspection of the topography and time-course of independent components, components reflecting eye-blinks and lateralised eye movements were removed from the data. EEG data were then (i) re-referenced to the average of all scalp electrodes (Snyder et al., 2015), (ii) notch filtered to remove 50 Hz (and harmonics up to 200 Hz) electrical power contamination with a bandwidth of 1 Hz, and (iii) low-pass filtered at 195 Hz to exclude high frequency noise (de Cheveigné and Nelken et al., 2019; Kerrén et al., 2018).

3.2.5.2 EMG pre-processing

EMG signals for FDS and GM muscles were first (i) high-pass filtered using a 4th order Butterworth filter with a cut-off frequency of .2 Hz to remove very slow drifts in the recorded signals and (ii) segmented into 30 s epochs locked to the onset of each trial. The EMG signals were then re-referenced to their respective reference electrode, notch filtered to remove 50 Hz (and harmonics up to 200 Hz) electrical power contamination with a bandwidth of 1 Hz, and high-pass filtered using a 4th order Butterworth filter with a cut-off frequency of 10 Hz to remove movement artifacts (de Luca et al., 2010; de Vries et al., 2016; Merletti and Di Torino, 1999; Tomiak et al., 2015). The EMG signals were then rectified and low-pass filtered at 195 Hz to remove high frequency noise in line with previous EMG and EEG/MEG-EMG coherence studies (Bourguignon et al., 2017; Piitulainen et al., 2015; Varlet et al., 2020b). Although its benefits remain debated, rectifying EMG signals has been shown to be particularly appropriate to examine CMC for low exerted forces (Boonstra and Breakspear 2012; Farina et al. 2013; McClelland et al., 2012; Ward et al. 2013). We also examined EMG broadband amplitude in separate analyses to investigate overall amplitude of muscular activity across conditions. EMG broadband amplitude was computed as the mean

envelope of the rectified EMG (10-195 Hz) signals using the Hilbert transform. Finally, the pre-processed EEG and EMG signals were down-sampled to 500 Hz to reduce computational load.

3.2.5.3 Cortico-muscular coherence analysis.

Cortico-muscular coherence (CMC) and the time-frequency spectra required for coherence analysis were both calculated using the FieldTrip toolbox (Oostenveld et al., 2011). For each participant, CMC was calculated between all EEG electrodes and the FDS muscle (hand-EEG coherence), and the GM muscle (foot-EEG coherence). To do so, the EEG and EMG power spectra and their cross-spectrum were calculated over the whole 30 s trial using a Fast-Fourier transform based time-frequency analysis between 0 and 50 Hz. The time-frequency analysis was computed using fixed-length windows of 1000 ms giving a frequency resolution of 1 Hz with 800 ms overlap (Bourguignon et al., 2013; Piitulainen et al., 2018). A multitaper approach was used in order to improve CMC estimation using 3 Slepian tapers, resulting in ± 1.5 Hz frequency smoothing for the computation of power- and cross-spectra (Reyes et al., 2017). Then, coherence was calculated from the cross-spectrum, normalised by the auto-spectrum as described by Halliday (1995). This operation results in coherence values between 0 and 1 for each frequency bin, where 1 corresponds to perfect synchrony and 0 corresponds to no synchrony between the EEG and EMG signal.

Further analyses of coherence focused on the beta range between 15 and 35 Hz. This relatively large range allowed variability within and between participants to be captured at the frequencies at which CMC usually occurs (Hansen and Nielsen, 2004; Mehrkanoon et al., 2014; Murthy and Fetz, 1992, 1996; Omlor et al., 2007; Salenius et al., 1997; Varlet et al., 2020b). Beta range CMC for the hand has been shown to occur in contralateral motor regions

with C3 electrode being most commonly reported, whereas the foot has a more central topographical distribution with Cz electrode being most commonly reported (Kristeva-Feige et al., 2002; Mehrkanoon et al., 2014; Petersen et al., 2012; Safri et al., 2007). Therefore, the C3 electrode (hand) and the Cz electrode (foot) were selected for further analyses.

3.2.5.4 Statistical analysis

3.2.5.4.1 Subjective ratings

2×2 mixed model ANOVAs with the within-subject factor Groove (high-groove and low-groove) and the between-subject factor Musical Experience (high and low) were used to test for differences between the high-groove and low-groove excerpts in subjective ratings of groove, loudness, familiarity, effort to sit still and enjoyment, as well as to test the effect of Musical Experience on the subjective ratings. In addition, to check if the newly added excerpts were as effective at inducing groove as the high-groove excerpts retrieved from Janata et al. (2012), *t*-tests were used to examine differences in subjective ratings between the 5 new high-groove contemporary excerpts and the high-groove excerpts retrieved from Janata et al. (2012). Where necessary, *t*-tests were adjusted for unequal variances using the Welch test.

Groove, familiarity and enjoyment are strongly correlated and therefore thought to be part of the experience of groove (Janata et al., 2012). Thus, we attempted to capture an overall construct of “groove” by performing an orthogonal Principal Component Analysis (PCA) for each participant on all 5 subjective items and 50 excerpts. The first principal component (PC1) was then used for further analyses, as described below.

3.2.5.4.2 Cortico-muscular coherence

A $2 \times 3 \times 50 \times 2$ mixed model ANOVA with the factors Limb (hand and foot), Groove (high-groove, low-groove, and control), Frequency (1 to 50 Hz), and Musical Experience (high and low) was first used on the CMC frequency spectrum across all frequency bins to detect a peak in the spectrum (Hanslmayr et al., 2005). A $2 \times 3 \times 2$ mixed model ANOVA with the factors Limb (hand and foot), Groove (high-groove, low-groove, and control), and Musical Experience (high and low) was then used to examine beta CMC (averaged coherence across the 15-35 Hz frequency range) more specifically. Because groove is a subjective experience, it was expected that the highest rated excerpts might differ for each participant. Hence, subjective high-groove and low-groove categories were also tested based on the average of individual's 20 highest and lowest rated excerpts for Groove, Loudness, Familiarity, Effort to sit still, Enjoyment, and PC1. To confirm that the changes in CMC were due to actual changes in synchronisation between EEG and EMG signals and did not originate from time-locked amplitude modulations in the EEG and/or EMG signals, CMC was also calculated on permuted data. For each participant and each condition, the EEG signals of each trial were randomly matched with the EMG signal from another trial (von Carlowitz-Ghori et al., 2014; Hesterberg et al., 2005; Yoshida et al., 2017a). Beta CMC was calculated for 1000 permutations of the 75 trials and compared to real coherence values in a $2 \times 2 \times 3$ repeated-measures ANOVA with the factors Dataset (real, permuted), Limb (hand and foot) and Groove (high-groove, low-groove, and control).

3.2.5.4.3 EEG and EMG

A $2 \times 3 \times 2$ mixed model ANOVA with the factors Limb (hand and foot), Groove (high-groove, low-groove, and control), and Musical Experience (high and low) was also

used on beta EMG power, beta EEG power, and broadband EMG (envelope of the 10-195 Hz rectified signal) amplitude averaged over the duration of the trials.

3.2.5.4.4 Mean and variability of Force

A $2 \times 3 \times 2$ mixed model ANOVA was also used on Mean Force and Force variability computed as the mean and standard deviation of participant's exerted force over the duration of the trials and expressed as a percentage of the instructed target force.

3.2.5.4.5 Correlation between subjective ratings and physiological measures

To further explore the relation between the subjective ratings (i.e., groove, familiarity, loudness, effort to sit still, enjoyment, and PC1) and the physiological measures (i.e., beta CMC, beta EEG power, beta EMG power, broadband EMG amplitude, Mean Force, and Force variability), Pearson correlations between them were calculated, both across participants and across excerpts. For the between-subject correlations, all variables were averaged across the low-groove and high-groove conditions. For the between-excerpt correlations, all variables were averaged across the participants.

All statistical analyses were performed in JASP (0.12.2.0). In addition to the frequentist statistics, Bayes Factors were calculated for all analyses with the default priors in JASP. The Bayes factor is a likelihood ratio that compares the evidence in favour of a null hypothesis H_0 to an alternative hypothesis H_1 , i.e., the adequacy of the null model prediction and the alternative model prediction (Berger, 2006; Schönbrodt and Wagenmakers, 2018). Depending on the order of numerator and denominator in the ratio, the Bayes factor is either denoted as BF_{01} (“ H_0 over H_1 ”) or as its inverse BF_{10} (“ H_1 over H_0 ”). When the Bayes factor BF_{01} equals 4, this indicates that the data are four times more likely under H_0 than under H_1 ,

meaning that H_0 has issued a better probabilistic prediction for the observed data than did H_1 . In contrast, when BF_{01} equals 0.25, the data support H_1 over H_0 . Specifically, the data are $1/BF_{01} = BF_{10} = 4$ times more likely under H_1 than under H_0 (Schönbrodt and Wagenmakers, 2018). In other words, any $BF_{01} < 1$ supports H_1 over H_0 , whereas it is the opposite in case of $BF_{01} > 1$.

The benefit of Bayes factors is that their predictive underpinnings entail that neither H_0 nor H_1 need be “true” for the Bayes factor to be useful. The Bayes factor does not force an all-or-none decision, but instead coherently reallocates belief on a continuous scale, allowing the Bayes factor to distinguish between absence of evidence and evidence of absence (e.g., Dienes 2014, 2016). Although Bayes factors are defined on a continuous scale, several papers have proposed to subdivide the scale in discrete evidential categories (Jeffreys, 1961; Lee and Wagenmakers, 2013). Evidence in favour of an effect is considered anecdotal for $BF < 3$, moderate for $3 < BF < 10$, strong for $10 < BF < 30$, very strong for $BF > 30$, and extremely strong for $BF > 100$.

3.3 Results

3.3.1 Groove ratings

The perceived groove ratings were significantly higher for musical stimuli in the high-groove condition ($M = 4.280$) than for the low-groove condition ($M = 2.798$), $F(1,16) = 38.121$, $p < .001$, partial $\eta^2 = .704$, $BF_{10} > 100$, indicating that the manipulation of induced groove was successful (see Figure 2). The subjective groove ratings were not affected by musical experience, no main effect of Musical Experience was found, $F(1,16) = 1.824$, $p = .196$, partial $\eta^2 = .102$, $BF_{01} = .940$ and no interaction with Groove was found $F(1,16) = 2.455$, $p = .137$, partial $\eta^2 = .133$, $BF_{01} = .573$.

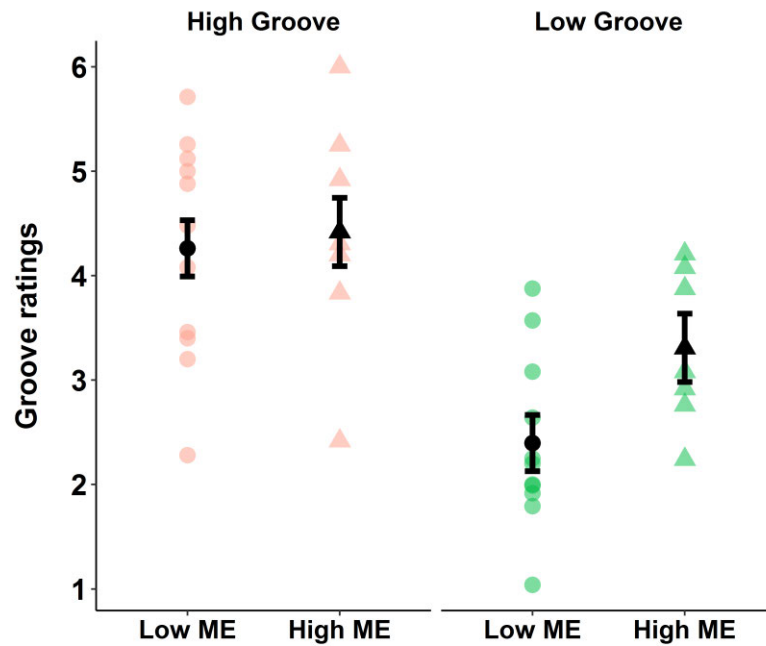


Figure 2. Mean subjective groove ratings across the high-groove and low-groove conditions for the low Musical Experience (Low ME) and high Musical Experience group (High ME).

The results also indicated that high-groove conditions scored higher than low-groove conditions on their subjective ratings of familiarity (high-groove; $M = 3.651$, low-groove; $M = 1.689$), $F(1,16) = 193.952$, $p < .001$, partial $\eta^2 = .924$, $BF_{10} > 100$, perceived effort to sit still (high-groove; $M = 4.212$, low-groove; $M = 3.274$), $F(1,16) = 21.097$, $p < .001$, partial $\eta^2 = .569$, $BF_{10} > 100$, enjoyment (high-groove; $M = 4.676$, low-groove; $M = 3.910$), $F(1,16) = 21.474$, $p < .001$, partial $\eta^2 = .573$, $BF_{10} > 100$, and PC_1 (high-groove; $M = 1.546$, low-groove; $M = -1.106$), $F(1,16) = 60.188$, $p < .001$, partial $\eta^2 = .817$, $BF_{10} > 100$, but not on perceived loudness (high-groove; $M = 3.649$, low-groove; $M = 3.433$), $F(1,16) = 3.488$, $p = .08$, partial $\eta^2 = .179$, $BF_{01} = .806$. No main effect of Musical Experience was found on any of the subjective ratings, nor did the effect of Groove interact with Musical Experience for

any of the subjective ratings (p -values $> .05$, see Figure 3).

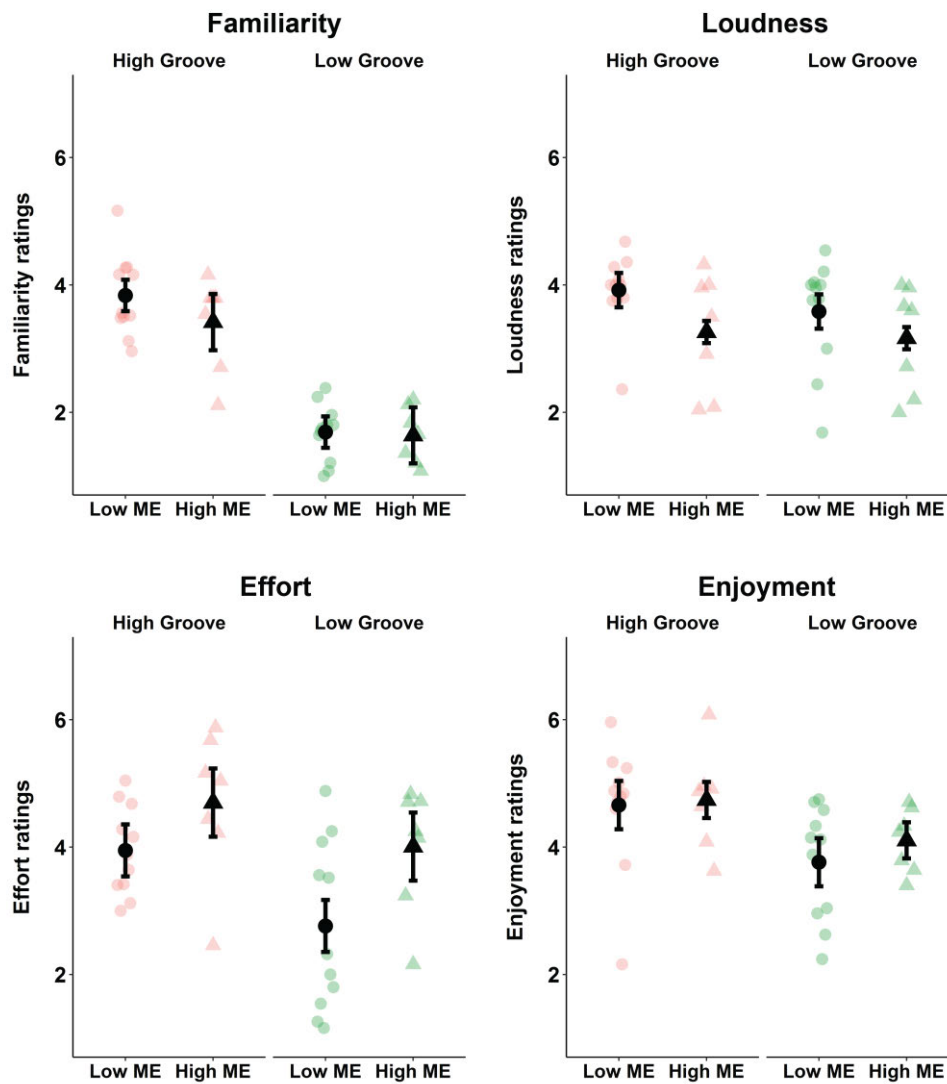


Figure 3. Mean subjective familiarity, loudness, effort, and enjoyment ratings across the high-groove and low-groove conditions for the low Musical Experience (Low ME) and high Musical Experience group (High ME).

The average groove ratings for each excerpt as well as the familiarity, loudness, effort to sit still, and enjoyment ratings are shown in Figure 4.

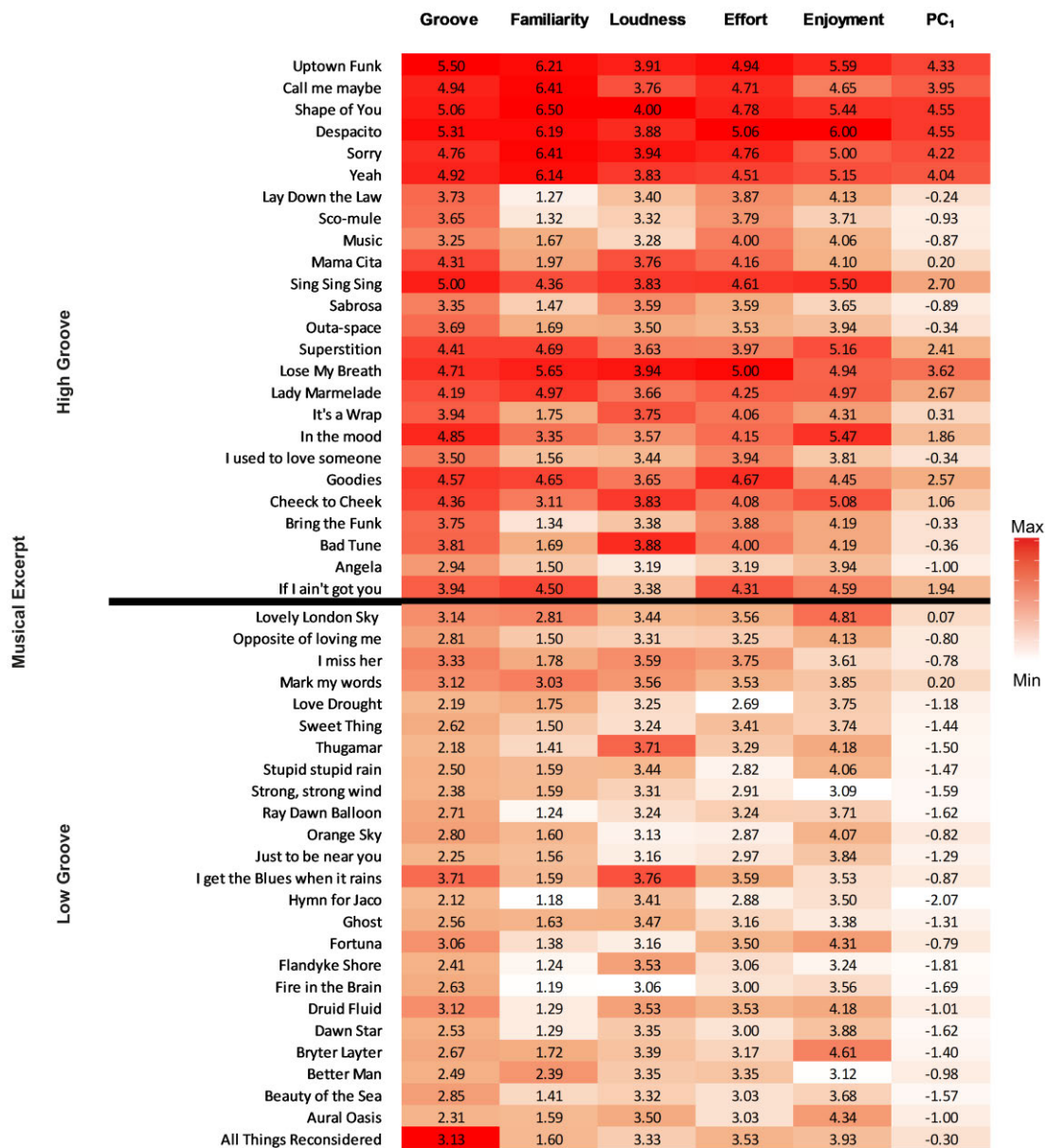


Figure 4. Subjective ratings (on a 7-point Likert scale) for high-groove excerpts (above the line) and low-groove excerpts (below the line). The cell colour is scaled according to the values of the dependent variable, ranging from minimum to maximum for each column.

3.3.1.1 New excerpts

The results also suggest that the five new contemporary excerpts scored higher for perceived groove, $t(23) = 3.963, p < .001, d = 1.982$, familiarity $t(19.585) = 8.950, p < .001, d = 2.847$, effort to sit still $t(23) = 3.935, p < .001, d = 1.967$, enjoyment, $t(23) = 2.918, p = .008, d = 1.459$, the first principal component PC₁, $t(23) = 2.738, p = .012, d = 1.369$, and even perceived loudness, $t(18.619) = 5.011, p < .001, d = 1.853$, than the other high-groove excerpts previously used by Janata et al. (2012).

3.3.2 Exerted Force

A $2 \times 3 \times 2$ mixed model ANOVA on the mean force and force variability (expressed as the percentage of instructed force), with the within-subject factors Limb (hand and foot) and Groove (high-groove, low-groove, and control), and between-subject factor Musical Experience (high and low), indicated a significant main effect of Limb on mean force, $F(1,16) = 35.962, p < .001$, partial $\eta^2 = .692$, $BF_{10} > 100$, and force variability, $F(1,16) = 19.026, p < .001$, partial $\eta^2 = .543$, $BF_{10} > 100$. As depicted in Figure 5, the foot showed significantly higher force and lower force variability. There was no main effect of Groove on the mean force, $F(1.417, 22.669) = 1.436, p = .254$, partial $\eta^2 = .082$, $BF_{01} = 20.843$, and force variability, $F(1.490, 23.847) = .901, p = .392$, partial $\eta^2 = .053$, $BF_{01} = 17.050$, nor was there an interaction between the factors Groove and Limb for mean force, $F(2,32) = .066, p = .936$, partial $\eta^2 = .004$, $BF_{01} = 30.149$, and force variability, $F(2,34) = 1.056, p = .360$, partial $\eta^2 = .062$, $BF_{01} = 21.762$. No main effect of Musical Experience was observed for mean force, $F(1,16) = .022, p = .883$, partial $\eta^2 = .001$, $BF_{01} = 2.830$, and force variability, $F(1,16) = .696, p = .417$, partial $\eta^2 = .042$, $BF_{01} = 2.718$, nor were there any significant interactions with Musical Experience (p -values $> .05$).

ANOVAs conducted on high-groove and low-groove force data selected based on each participant's subjective ratings (i.e., groove, loudness, familiarity, effort, enjoyment, and PC1) also did not show any significant effects of Groove on mean force and force variability (p -values $> .05$ and $BF_{01} > 3$).

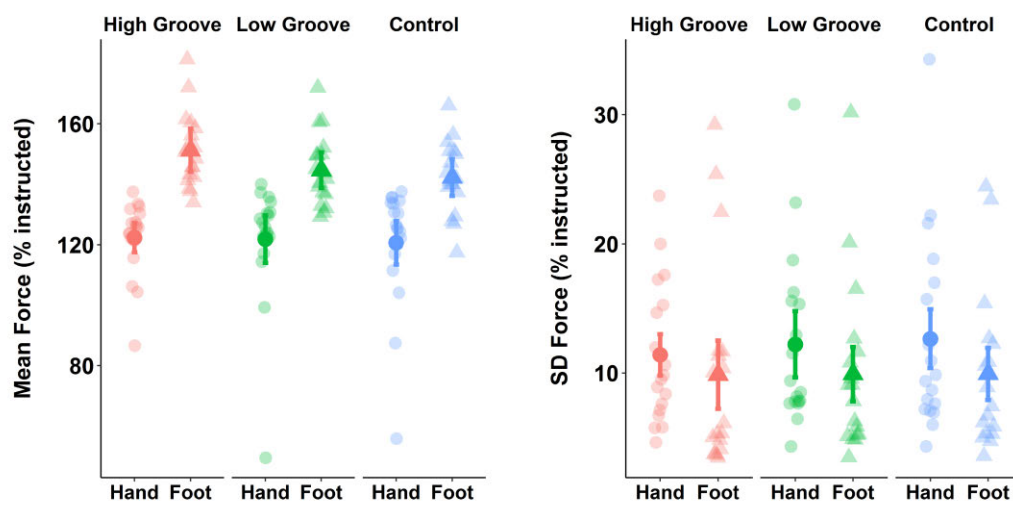


Figure 5. Mean (A) and Standard Deviation (B) of the instructed force (7 % of an individual's maximum force) for the hand and the foot across the different groove conditions.

3.3.3 Cortico-muscular Coherence

A $2 \times 3 \times 50 \times 2$ mixed model ANOVA on coherence values at the respective electrodes for each limb (i.e., C3 and Cz), with the within-subject factors Limb (hand and foot), Groove (high-groove, low-groove, and control) and Frequency (0 to 50 Hz in 1 Hz bins), and the between-subject factor Musical Experience (high and low), indicated a significant main effect of Frequency, $F(49,833) = 6.201, p < .001$, partial $\eta^2 = .267$, $BF_{10} > 100$, but not of Groove, $F(2,34) = 2.221, p = .124$, partial $\eta^2 = .013$, $BF_{01} > 100$, or Limb, $F(1,17) < .001, p = .765$, partial $\eta^2 < .001$, $BF_{01} = 8.962$, and no significant interactions between the factors Limb, Groove, and Frequency (p -values $> .05$; see Figure 6 for individual's coherence spectra and Figure 7 for coherence spectra in the different Groove conditions). Musical Experience did not have a significant effect on CMC, $F(1,16) = .304, p = .589$, partial $\eta^2 = .019$, $BF_{01} = 5.685$, nor did Musical Experience interact with the factors Limb, Groove, and Frequency (p -values $> .05$). However, the three-way interaction between Limb, Groove, and Musical Experience was significant, $F(1,16) = 4.138, p = .025$, partial $\eta^2 = .205$, but post-hoc testing with Bonferroni correction did not show any significant comparisons (p -values $> .05$) and Bayesian analysis indicated extremely strong evidence for the exclusion of the three-way interaction, $BF_{01} > 100$ in favour of the null hypothesis.

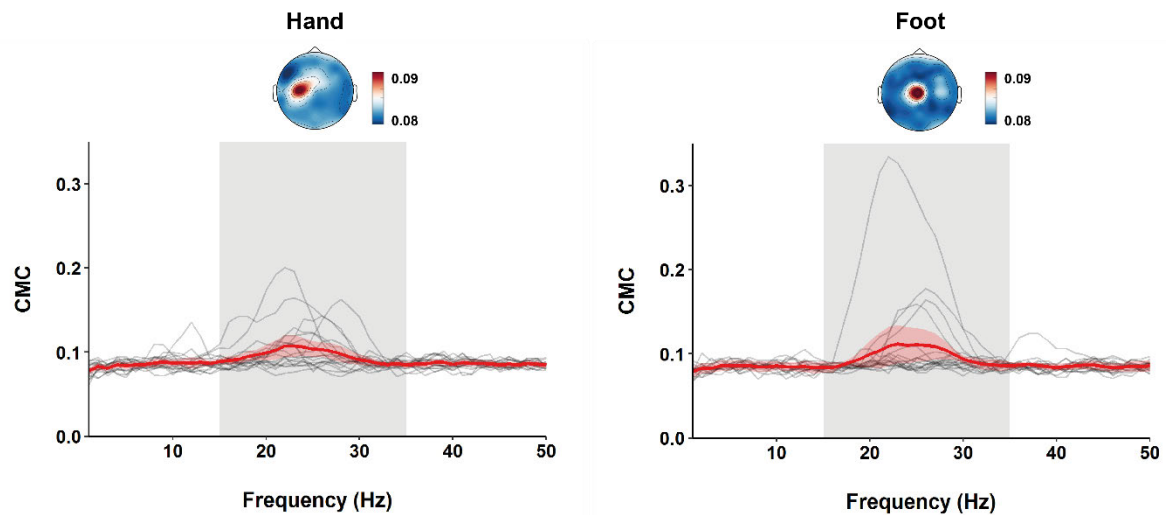


Figure 6. EEG-EMG coherence spectra averaged across conditions for the hand and foot. Red lines represent the average of the three Groove conditions with shading representing 95% confidence intervals (CI) and grey lines representing individual participants. Grey shaded areas represent the selected beta range (15-35 Hz) and the topographical maps show the distribution of coherence values averaged within this range across participants.

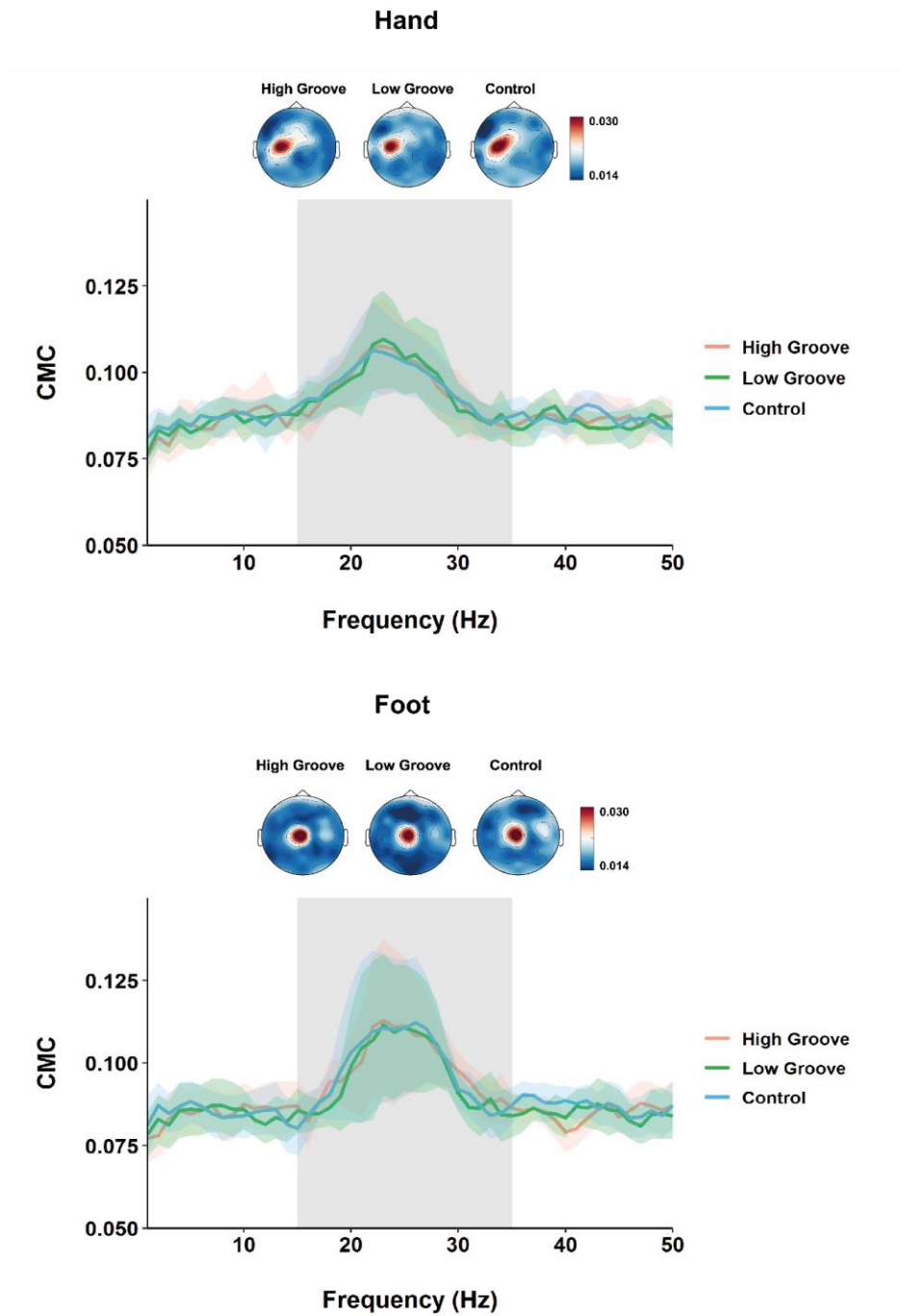


Figure 7. Coherence spectra for the hand (top) and foot (bottom). Coloured lines represent the coherence values for the different experimental conditions averaged across participants with the corresponding 95% confidence intervals. Grey shaded areas represent the selected beta range (15-35 Hz) with the corresponding topographical map for each groove condition.

3.3.3.1 Beta CMC

A $2 \times 2 \times 3$ repeated measures ANOVA on CMC in the beta (15-35 Hz) frequency range, with the factors Dataset (real and permuted), Limb (hand and foot) and Groove (high-groove, low-groove, and control), indicated a significant main effect of Dataset, $F(1,17) = 14.128$, $p = .002$, partial $\eta^2 = .454$, $BF_{10} > 100$, showing that coherence captures genuine synchronisation between EEG and EMG activity.

A $2 \times 3 \times 2$ mixed model ANOVA on beta CMC, with the within-subject factors Limb (hand and foot) and Groove (high-groove, low-groove, and control) and the between-subject factor Musical Experience (high and low) indicated no significant effect of Limb, $F(1,16) < .001$, $p = .995$, partial $\eta^2 = .004$, $BF_{01} = 4.512$, Groove, $F(2,32) = .785$, $p = .477$, partial $\eta^2 = .045$, $BF_{01} = 26.911$, or Musical Experience, $F(1,16) = .221$, $p = .645$, partial $\eta^2 = .014$, $BF_{01} = 4.352$. No interaction between Limb and Groove was observed, $F(2,32) = 1.138$, $p = .333$, partial $\eta^2 = .066$, $BF_{01} = 6.587$ (see Figures 7 and 9A). The average beta CMC for each excerpt can be found in Figure 8.

No interaction between Limb and Musical experience, $F(1,16) = 1.138$, $p = .259$, partial $\eta^2 = .079$, $BF_{01} = 86.143$, or Groove and Musical Experience was observed, $F(1,16) = .482$, $p = .622$, partial $\eta^2 = .029$, $BF_{01} = 62.695$. The three-way interaction between Limb, Groove, and Musical Experience, however, was significant, $F(1,16) = 4.601$, $p = .018$, partial $\eta^2 = .223$, but post-hoc tests with Bonferroni correction did not show any significant comparisons (p -values $> .05$) and Bayesian analysis indicated extremely strong evidence for the exclusion of the three-way interaction ($BF_{01} > 100$).

ANOVAs conducted on high-groove and low-groove CMC data selected based on each participant's subjective ratings (i.e., groove, loudness, familiarity, effort, enjoyment, and PC1) also did not reveal any significant effects of Groove (p -values $> .05$ and $BF_{01} > 3$).

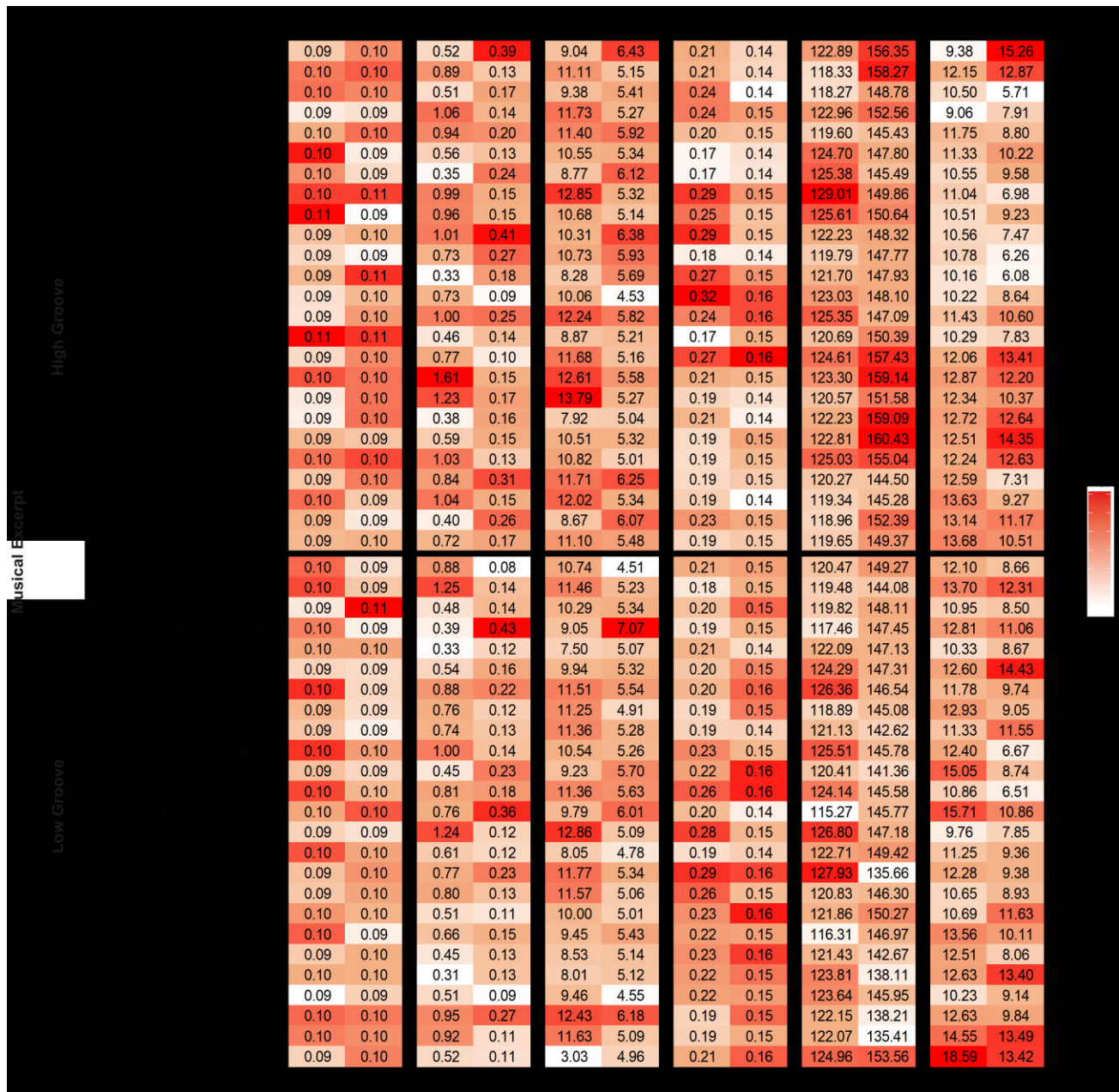


Figure 8. Physiological measures for high-groove excerpts (above the line) and low-groove excerpts (below the line). The cell colour is scaled to the values of the dependent variable, ranging from minimum to maximum for each column.

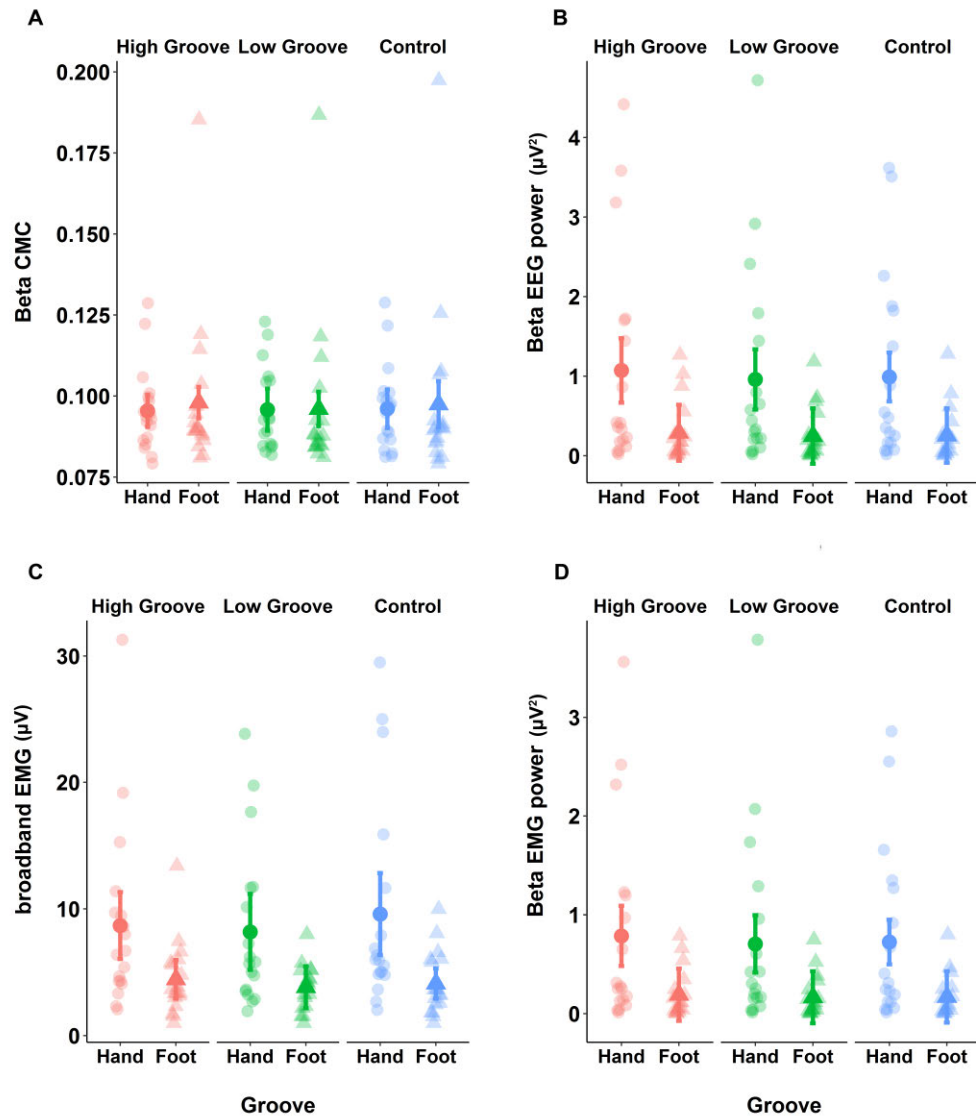


Figure 9. Mean beta (15-35 Hz) CMC (A), Mean beta (15-35 Hz) EEG power (B), Mean broadband EMG (C), and Mean beta (15-35 Hz) EMG power (D) as a function of the limb and experimental conditions. Error bars represent 95 % confidence intervals (CI). Individual data points are shaded.

3.3.4 EMG

A $2 \times 3 \times 2$ mixed model ANOVA, with the within-subject factors Limb (hand and foot) and Groove (high-groove, low-groove, and control) and the between-subject factor Musical Experience (high and low), indicated a significant main effect of Limb on the mean beta EMG power, $F(1,16) = 5.201, p = .037$, partial $\eta^2 = .245$, $BF_{10} > 100$, and broadband EMG, $F(1,16) = 13.227, p = .002$, partial $\eta^2 = .453$, $BF_{10} > 100$. No effect of Groove was found on the mean beta EMG power, $F(2,32) = 1.794, p = .183$, partial $\eta^2 = .101$, $BF_{01} = 24.597$, and broadband EMG, $F(1.441,23.049) = .292, p = .677$, partial $\eta^2 = .018$, $BF_{01} = 9.439$. The average broadband EMG and beta EMG power for each excerpt can be found in Figure 8. No effect of Musical Experience was found on mean beta EMG power, $F(1,16) = .006, p = .937$ partial $\eta^2 < .001$, $BF_{01} = 4.876$, and broadband EMG, $F(1,16) = .508, p = .486$, partial $\eta^2 = .031$, $BF_{01} = 9.429$. No interaction between Limb and Groove was observed either for mean beta EMG power, $F(2,32) = .574, p = .569$, partial $\eta^2 = .035$, $BF_{01} = 32.981$, and the broadband EMG, $F(1.335,21.367) = .302, p = .654$, partial $\eta^2 = .019$, $BF_{01} = 6.178$ (see Figure 9C and 9D). No interactions with Musical Experience were observed (p -values $> .05$).

ANOVAs conducted on high-groove and low-groove EMG data selected based on each participant's subjective ratings (i.e., groove, loudness, familiarity, effort, enjoyment, and PC1) also did not show any significant effects of Groove on broadband EMG or mean beta EMG power (p -values $> .05$ and $BF_{01} > 3$).

3.3.5 EEG

Similar to the EMG beta power, a $2 \times 3 \times 2$ mixed model ANOVA on the mean beta EEG power, with the within-subject factors Limb (hand and foot) and Groove (high-groove, low-groove, and control), and the between-subject factor Musical experience (high and low)

indicated a significant main effect of Limb, $F(1,16) = 14.535$, $p = .002$, partial $\eta^2 = .476$, $BF_{10} > 100$. No effect of Groove on mean beta EEG power was found, $F(2,32) = .191$, $p = .827$ partial $\eta^2 = .012$, supported by strong evidence in favour of the null-hypothesis, $BF_{01} = 24.075$. The average beta EEG power for each excerpt can be found in Figure 8. No effect of Musical Experience on mean beta EEG power was found, $F(1,16) = .183$, $p = .183$ partial $\eta^2 = .108$, $BF_{10} = 4.285$. No interaction between Groove and Limb was observed either, $F(2,32) = .545$, $p = .585$, partial $\eta^2 = .033$, $BF_{01} = 28.980$ (see Figure 9B). No significant interactions with Musical Experience were observed (p -values $> .05$).

Although ANOVAs conducted on high-groove and low-groove EEG data selected based on each participant's subjective ratings (i.e., groove, loudness, familiarity, effort, enjoyment, and PC1) did show significant main effects of Groove on mean beta EEG power for the subjective excerpt selection based on groove ($p = .014$), familiarity ($p = .011$), and enjoyment ($p = .006$) ratings, all of them yielded evidence in favour of the null-hypothesis ($BF_{01} > 3$).

3.3.6 Correlations between subjective ratings and physiological measures

To explore the relation between subjective ratings and physiological measures across participants, Pearson correlations were calculated to address whether participants who perceived higher levels of Groove also had higher CMC. Out of the 60 correlations only three were significant, as depicted in Figure 10. CMC for the hand was negatively correlated with the effort to sit still, $\rho(17) = -.564$, $p = .009$, but CMC for the foot was not, $\rho(17) = -.372$, $p = .116$. Additionally, a significant negative correlation between EMG beta power and familiarity was observed for the foot, $\rho(17) = .520$, $p = .024$, but not for the hand, $\rho(17) = .070$, $p = .702$. In addition to the lack of consistency of these significant effects across

effectors, it can be noted that none of these correlations remains significant when corrected for multiple comparisons using Bonferroni correction, which brings the significance threshold to .0008.

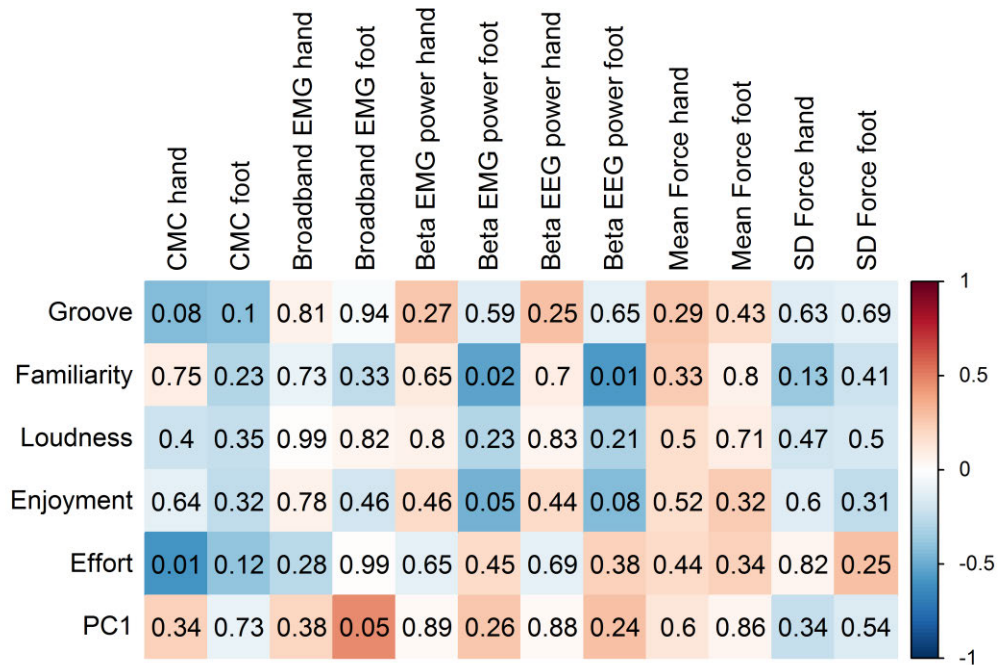


Figure 10. Correlation matrix between subjective ratings and physiological responses across participants. The colour scale represents the correlation coefficient (ρ), whereas the numbers represent p -values.

Additionally, Pearson correlations were calculated between excerpts to address whether excerpts that scored higher on subjective Groove ratings were associated with higher CMC. Out of the 60 correlations, eight were significant, but no consistency across the hand and foot was found. Furthermore, none of these correlations remained significant when corrected for multiple comparisons (which brings the significance threshold to .0008). Groove, familiarity, effort to sit still, and PC1 were all negatively correlated with the EEG beta power of the foot, $\rho(49) = -.319, p = .024$, $\rho(49) = -.304, p = .031$, $\rho(49) = -.340, p = .016$, $\rho(49) = -.360, p = .010$, respectively, but not with EEG beta power of the hand, $\rho(49) =$

- .136, $p = .347$, $\rho(49) = -.209$, $p = .145$, $\rho(49) = -.227$, $p = .113$, $\rho(49) = -.167$, $p = .246$, respectively (see Figure 11). Additionally, familiarity and effort to sit still were positively correlated with broadband EMG of the foot, $\rho(49) = .280$, $p = .048$, $\rho(49) = .324$, $p = .022$, respectively, but not for the hand, $\rho(49) = -.031$, $p = .829$, $\rho(49) = .140$, $p = .332$, respectively. Finally, the subjective ratings of groove, effort to sit still and PC1 were significantly correlated with the Mean Force of the hand, $\rho(49) = .373$, $p = .008$, $\rho(49) = .355$, $p = .011$, and $\rho(49) = .310$, $p = .029$, respectively, but not with the Mean Force of the foot, $\rho(49) = -.078$, $p = .592$, $\rho(49) = -.045$, $p = .754$, and $\rho(49) = -.046$, $p = .751$, respectively.

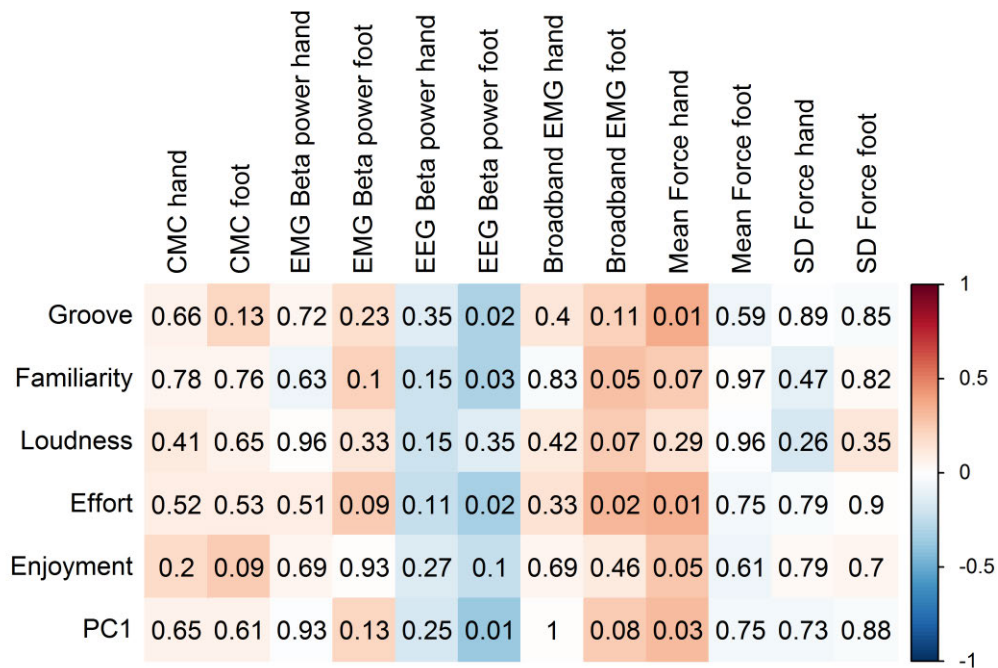


Figure 11. Correlation matrix between subjective ratings and physiological responses across excerpts. The colour scale represents the correlation coefficient (ρ), whereas the numbers represent p -values.

3.4 Discussion

The current study aimed to better understand the effects of music on the motor system by examining the strength of CMC between EEG and EMG recordings from the upper and lower limbs of participants listening to either no music, low-groove music, or high-groove music. It was hypothesised that listening to high-groove music would result in stronger CMC than listening to low-groove music and no music due to increased engagement of the motor system through predictive timing mechanisms and/or effort to sit still with high-groove music. Although different levels of groove were successfully induced while instructed to maintain an isometric contraction, no effect of groove was found on participants' CMC and capacity to maintain a steady force for both upper and lower limbs irrespective of participants' musical expertise.

The results show that the presented sounds successfully modulated the experience of groove but this occurs without actual changes in force and cortico-muscular coupling. The five newly added high-groove excerpts also successfully led to higher experience of groove with even greater magnitude than the previous excerpts from Janata et al. (2012). This is likely due to their familiarity for our relatively young participant sample, as this is a well-established relationship (Janata et al., 2012; Leow et al., 2015; Senn et al., 2018, 2019). These new highly groovy excerpts would therefore make a useful contribution in future studies of groove. Musical excerpts that yield high-groove ratings have been previously associated with better movement entrainment and more spontaneous movement (Janata et al., 2012). However, high-groove excerpts in the current study did not invoke changes in the mean and variability of participants' force. Thus, regardless of different levels of 'wanting to move', people were rather successful at suppressing spontaneous behavioural motor responses when asked to. Hence, these results support theories of groove induction through active listening that propose that moving to the rhythm is not a necessary component of

experiencing different levels of groove (Levitin et al., 2017; Madison, 2006; Madison et al., 2011; Witek et al., 2014).

The lack of an effect of groove on CMC could be related to the general lack of modulation in participants' force in response to the groove conditions. CMC has been shown to vary during dynamic movement or changes in exerted force (Kilner, 2000; Petersen et al., 2012; Reyes et al., 2017; Ushiyama et al., 2017; Yoshida et al., 2017a). CMC correlates with force levels and fluctuations (Conway et al., 1995; Baker et al., 1997; Kilner et al., 1999, 2000, 2003; Baker, 2007; Kristeva et al., 2007; Ushiyama et al., 2017; Witte et al., 2007). Specifically, CMC increases when force levels and/or fluctuation increases. In addition, Stupacher et al. (2013) also argued that Motor Evoked Potentials elicited by TMS could be lower for high groove stimuli than low groove stimuli in non-musicians due to the effort that they invested in suppressing movement. Although we did not find an effect of musical experience, participants in our study's high Musical Experience group still had significantly less experience than the musicians in the study by Stupacher et al. (2013) and the current task constraints may have annulled the effect of musical experience. Therefore, the successful suppression of force modulations in the current study, despite different levels of experienced groove, might have led to the current null-effects on CMC.

However, with the successful induction of groove, even without spontaneous modulation in participants' force, it remains possible that CMC could have been increased with high-groove music for two main reasons. The first is the increased effort to maintain a stable force output whilst 'wanting to move'. Several studies support the hypothesis that the effort required to maintain stable motor output correlates with CMC magnitude (Divekar and John, 2013; Safri et al., 2006), suggesting top-down regulation of CMC. Divekar and John (2013) proposed that CMC is not directly dependent on the precision of the motor output, but rather on the (perceived) task difficulty and the required effort to perform the task. In

addition, cognitive factors such as attention to the task have been shown to affect CMC magnitude (Kristeva-Feige et al., 2002; Safri et al., 2006, 2007). Here we found no differences in the mean and variability of participants' force but it remains possible that maintaining a stable force with high-groove excerpts was more difficult, as indicated by the increased subjective urge to move and effort to sit still. Therefore, according to the top-down view of CMC being driven by subjective task difficulty, CMC could have increased for the high-groove excerpts compared to low-groove and silence. Yet we did not find such results; no difference in CMC was found between conditions, even though participants did report they found it more difficult to sit still during the high-groove excerpts. These results do not support strong top-down influence on CMC mediated by task difficulty or effort.

The second reason CMC was expected to increase with groove is the involvement of the motor system in predictive timing processes, which has been suggested to be stronger with high-groove music. Again, no effect of groove on CMC was found, including in participants with musical expertise despite them being known to have stronger temporal prediction and being better at time-keeping (e.g., Doelling and Poeppel, 2015; Repp, 2005). In the current study, however, subjective groove was induced without following any rhythmic instructions or allowing movement. Thus, the used task did not require the same degree of active temporal prediction as would be needed to move in time with music. The lack of difference in both EEG and CMC over motor areas in response to different levels of groove and silence, suggests that motor engagement or attention was not modulated by music listening, which might have contributed to the null-effects on CMC. The current control for vigilance was based on the lyrics to prevent artificial rhythmic interference if a specific counting or rhythmic task was given. Perhaps, participants' attention could have been drawn more to temporal structures of the music in a way that would require more active temporal prediction, i.e., a more active listening experience. This could have increased the covert

predictive activity in the motor system, as observed by Matthews et al. (2020), leading in turn to amplitude modulations in beta EEG and increased CMC.

Alternatively, there might have been (enough) predictive motor engagement in the current design to affect cortico-muscular pathways, as indicated by the differences in subjective feelings of groove and effort to sit still. Instead, cortico-muscular responses could have been dynamic, rather than a static increase in CMC baseline. Dynamic modulations of CMC aligned with the beat, increased on the beat and decreased off the beat, for example, was not captured in this study. Dynamic cortico-muscular responses to audio-visual rhythms have previously been reported (Varlet et al., 2020b), but examining CMC dynamically comes with some practical limitations. In order to calculate CMC reliably, a large number of time windows is required (Bastos and Schoffelen, 2016; Carter et al., 1973). Since the excerpts were pieces of music with variations in tempo, loudness and pitch, windows cannot be stacked within a single trial or excerpt and would require the excerpts to be played many times to generate multiple windows at each time-point. It was therefore not possible to capture CMC dynamic modulations with the current design. Future studies should consider testing rhythmic musical stimuli with a controlled period to explore CMC dynamics.

Although neither hand nor foot was affected by musical groove, some differences between the two limbs can be noted. The mean exerted force, expressed as the percentage of the target force, was significantly higher for the foot than the hand. This suggests that fine motor control at lower intensity with the foot might have been more challenging compared to the hand (Volz et al., 2015). Lower EMG and EEG activity for the foot compared to the hand was also observed, leaving unclear whether larger force was actually applied with the foot compared to the hand, although a wide range of factors, such as the absolute maximum recorded force, might have influenced these measures. Interestingly, these differences in force, EMG, and EEG amplitude did not transfer to beta CMC magnitude, which further

supports that CMC is sensitive to the synchrony between EEG and EMG signals rather than their amplitude, as underscored by the permutation analyses. More generally, further investigation of CMC at the level of the hand and the foot will be needed in future research to better understand whether musical groove affects the coupling between the brain and muscles across the different body parts.

Particularly important for future research would be to further investigate the role of movement in the experience of groove and the modulation of the cortico-muscular coupling. Indeed, even if the experience of groove was successfully induced while participants maintained an isometric contraction, it remains possible that stronger effects of groove, including significant effects on CMC, might have occurred if participants were allowed to move with the music (Manning and Schutz, 2013). There are conflicting theories about the role of movement in the experience of groove, but some consider that moving in time with the music is an essential component of the groove experience (e.g., Roholt, 2014), and therefore, suggest that a steady isometric contraction might have limited groove induction and contributed to the current-null effect. However, investigating the effects of groove on CMC while moving in time with music will result in methodological challenges that future research will need to address. CMC is largely modulated when moving, which might involve bottom-up processes that differ from, and even mask, top-down control processes that were targeted in the current study (Nijhuis et al., 2021; Petersen et al., 2012; Yoshida et al., 2017a, 2017b).

In sum, this study found no evidence for an effect of music listening, high-groove music in particular, on cortico-muscular coupling and participants' capacity to maintain a steady force despite an increase in participants' urge to move and difficulty to stay still. These results do not support a top-down influence of groove on cortico-muscular coupling, although it remains possible that such influence might have occurred in the form of dynamic

modulations and/or with more active listening. Therefore, these results encourage further research to better understand the effects of groove on the motor system at central but also peripheral level and the exact function of cortico-muscular coherence.

Chapter 4: Transition 1

Experiment 1 tested the effect of musical groove on cortico-muscular facilitation by measuring CMC whilst listening to high-groove and low-groove musical excerpts compared to silence. Experiment 1 showed no difference between high-groove, low-groove and silence conditions, hence no effect of musical rhythms on CMC was observed. However, the null-effect of groove on CMC brought up additional questions. For example, can CMC be modulated by sensory rhythms at all? Or, might the rhythmic stimuli translate to rhythmic modulation of CMC, considering the rhythmic component of the stimuli, similar to movement being facilitated on-the-beat rather than off-beat? Furthermore, is mere sensory stimulation “active” enough to modulate the cortico-muscular coupling, i.e., CMC? Could, instead, movement intention modulate CMC? Or is overt movement required to modulate CMC?

4.1 Do sensory rhythms affect cortico-muscular coupling?

Experiment 1 attempted to test hypothesis (i): “Rhythms in the environment, such as music, spontaneously modulate cortico-muscular coupling”. The null-result, in particular the lack of a difference between silence and the musical groove conditions, suggests that musical rhythms do not spontaneously affect the overall cortico-muscular coupling.

CMC varies widely between individuals, both in strength and peak frequency, i.e. the frequency at which CMC is highest for an individual. Therefore, additional analyses on individual differences in CMC strength and peak frequency were explored. The three groove conditions were, for example, compared using ANOVAs across each individual's beta CMC value at their respective maximum frequency. Additionally, subselections of participants with clear beta CMC peaks (based on visual inspection and several threshold criteria) were looked into. Neither the selection of a peak frequency nor the selection of participants showing clear CMC peaks changed the null-result or provided additional insight.

Although study 1 had a particular focus on beta range CMC, analyses of other frequency ranges were also explored. In particular, the Alpha band (8-13 Hz), or mu rhythm, is of interest for passive listening to music, as alpha band activity has recently been shown to suppress overt movement in passive listening (Ross et al., 2022), which explains why it decreases during executed sensorimotor synchronisation compared to passive observation (Chen, Ding, et al., 2002). However, neither the alpha nor gamma band showed any effect of musical groove on CMC. Although CMC in these bands remained unaffected in study 1, CMC in other frequency bands should remain of interest for future research to study motor engagement during passive (and active) auditory-motor tasks.

However, the CMC *dynamics* in response to those musical rhythms were not investigated. It is possible that the cortico-muscular coupling was modulated dynamically. For example, peaks aligned with musical beats, similar to the dynamics observed in neural entrainment to external rhythms, may have prevented the discovery of any changes in the whole trial-average CMC used in Experiment 1. Studies have previously found such dynamic changes to CMC when presenting visual and auditory stimuli (Piitulainen et al., 2015; Varlet et al., 2020).

The excerpts in Experiment 1 were pieces of music with variations in tempo, loudness and pitch. Thus, they cannot be segmented in “equal” windows that can be stacked within a single trial or excerpt and would require the excerpts to be played many times to generate multiple windows at each time-point, required to calculate CMC (Bastos and Schoffelen, 2016; Carter et al., 1973). Thus, in Experiment 2, the selected rhythms will consist of clearly separable stimulus cycles, in the form of audio-visual metronomes to be able to assess CMC dynamics as well.

4.2 The active role of the motor system in CMC

The second hypothesis tested was: “Movement intention modulates cortico-muscular coupling”. In Experiment 1, groove generated a “passive” intention to move by inducing a sense of “wanting to move” to the musical excerpts (Janata et al., 2012). The urge to move along and effort to sit still whilst listening to the high-groove musical excerpts was expected to modulate CMC magnitude, as an extension of cortical motor entrainment. This hypothesis was based on previous evidence that sensory rhythms engaged the motor system and entrained motor cortical activity (Fujioka et al., 2012, 2015; Nozaradan, 2014), as well as increased corticomotor excitability in musicians when listening to high-groove music

(Stupacher et al., 2013). However, CMC magnitude was not modulated in Experiment 1. Hence, CMC could potentially be a mechanism unlike neural entrainment that requires more active movement rather than mere “active” listening to be modulated. Another method to induce a stronger sense of movement intention without actual movement is motor imagery. Motor imagery (MI) has been shown to activate the motor system similarly to executed movement, albeit at lower magnitude (Miller et al., 2010; Osman et al., 2006; Oullier et al., 2005; Stavrinou et al., 2007). MI has also been shown to modulate the dynamics of cortical beta activity induced by sensory rhythms (Fujioka et al., 2014). To systematically manipulate the movement intention, active motor imagery will be implemented in Experiment 2, as well as the execution of movements, to investigate CMC dynamics.

4.3 Dynamics of CMC

As CMC dynamics will be investigated in Experiment 2, it is important to note that in addition to the CMC dynamics observed in perceptual tasks, dynamic changes in CMC have been observed during executed (dynamic) movement (Kilner et al., 2000, 2003; Omlor et al., 2007; Petersen et al., 2012; Yoshida et al., 2016, 2017). During the active movement phase, CMC is seemingly ‘abolished’ (Baker et al., 1997; Kilner et al., 1999; Feige et al., 2000). During *rhythmic* movement however, CMC does not disappear. Instead, recent studies have shown CMC to be dynamic in rhythmic movement tasks such as walking and ankle circling (Petersen et al., 2012; Yoshida et al., 2016, 2017).

4.4 Visual-motor synchronisation

In Experiment 1, auditory musical rhythms were tested. However, sensorimotor synchronisation (SMS) is not limited to the auditory modality. Studies have demonstrated

SMS with visual, auditory and tactile rhythms (e.g., Ammirante et al., 2016; Iversen et al., 2015). For sequences comprised of discrete events (such as a metronome) an auditory dominance is commonly reported due to higher temporal resolution in the auditory domain compared to other modalities (e.g., Chen et al., 2002; Dunlap, 1910; Loras, 2012; Sugano et al., 2012).

Because the auditory rhythms did not modulate CMC in Experiment 1, it is worth testing if this generalises to other sensory modalities. In particular, visuo-motor synchronisation is of interest, as it is relevant to everyday coordination (Schmidt et al., 2007), such as in instances of joint action where visual information guides movement coordination with others (Schmidt et al., 1990). We effectively synchronise with dance partners, synchronise our steps when walking side-by-side (van Ulzen et al., 2008) or members of our musical ensembles based on auditory and visual information (Keller et al., 2014). Compared to audio-motor synchronisation, visuo-motor synchronisation traditionally resulted in “worse” synchronisation performance, i.e. larger asynchronies and variability and lower rate limits (e.g., Repp, 2003; Repp and Penel, 2002). Auditory dominance is not surprising when testing discrete rhythms (e.g., flashing light versus isochronous metronome), as it has often been stressed that the auditory domain has higher temporal resolution and is therefore better suited for precise synchronisation (e.g., Fendrich and Colballi, 2001; Myers et al., 1981; Ruspantini et al., 2011). Synchronisation with visual sequences can, however, drastically increase when those stimuli are continuous and spatial information is added (Gan et al., 2015; Hove et al., 2013; Iversen et al., 2015; Silva and Castro, 2016; Varlet et al., 2012a; Zelic et al., 2016).

Of particular relevance for Experiment 2 is the different neural responses to auditory and visual stimuli. It has been reported that visual stimuli evoke stronger cortical responses than auditory stimuli, although stimulus intensity was often uncontrolled (e.g., Arrubla et al.,

2013; Gawel et al., 1981; Tasman et al., 1999). Visual stimuli may therefore more strongly modulate the cortical activity, and thereby CMC. In fact, most studies that have found effects of sensory stimuli on CMC have all included visual stimuli (Hari et al., 2014; Safri et al., 2006, 2007; Varlet et al., 2020b), suggesting CMC might show modality specific effects. Therefore, Experiment 2 will compare the effect of both auditory and visual rhythms on CMC.

4.5 Selective attention

Regardless of modality specific effects, both auditory and visual rhythmic streams can entrain cortical activity (Fujioka et al., 2012, 2015; Power et al., 2012). The two streams can compete for processing, for example in incongruent visual and auditory speech or when following/anticipating a conductor's visual cues whilst playing in an orchestra. Selective attentional entrainment can help to suppress the processing of unattended and/or irrelevant stimulus streams during the low excitability phase (Lakatos et al., 2005, 2008, 2013).

When presenting concurrent visual information, Safri et al. (2006) observed an increase in CMC as a result of selective attention. As previously stated in Chapter 2, there is evidence that CMC is sensitive to attention (Johnson et al., 2011; Johnson and Shinohara, 2019; Kristeva-Feige et al., 2002; Safri et al., 2006), with increased cognitive effort leading to increased CMC (Divekar et al., 2013). A potential way to actively modulate attention is to compare the auditory and visual modality in situations where they compete for attention and processing resources. Selectively attending to intermixed auditory and visual streams has shown larger attentional effects on cortical (beta) activity for the visual stream (te Woerd et al., 2018). Experiment 2 will therefore not only include a comparison between the auditory and visual domain, but also include attentional effects by asking participants to selectively

focus on either the auditory or visual stream when presented with intermixed auditory and visual metronomes.

4.6 Summary

In summary, Experiment 2 will test all three outlined hypotheses by extending Experiment 1 to the visual domain, manipulating movement intention, and investigating CMC dynamics. Hypothesis (i): “Rhythms in the environment, such as music, spontaneously modulate cortico-muscular coupling”, which was not supported in Experiment 1, will be tested in the visual modality and CMC dynamics will be studied, to see if there is any dynamical modulation of CMC induced by sensory rhythms. Hypothesis (ii): “Movement intention modulates cortico-muscular coupling, i.e., rhythmic movement as well as motor imagery in time with a metronome.” was previously touched on in Experiment 1, as the musical rhythms considered to be high-groove induce an urge to move, which did not seem to affect CMC. However, in Experiment 2 movement intention will be systematically manipulated by comparing passive listening and observation of sensory rhythms with active imagining of movement as well as executed movement. Finally, Experiment 2 will investigate dynamic changes of CMC instead of overall changes in CMC during SMS, addressing hypothesis (iii): “Cortico-muscular coupling is dynamically modulated during sensorimotor synchronisation time-locked to the stimulus rhythm.”

Chapter 5: Dynamic modulation of cortico-muscular coupling during real and imagined sensorimotor synchronisation

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5.1 Introduction

People commonly move along or in synchrony with the environmental rhythms they encounter. This can easily be observed in daily environments, either intentionally, when dancing or singing to music (Burger et al., 2014; Keller et al., 2016; Tranchant et al., 2016), or unintentionally, when we talk, walk, or applaud with one another (Miyata et al., 2020; Néda et al., 2000; van Ulzen et al., 2008; Varlet et al., 2020c). These examples demonstrate the natural and intrinsic ability of humans for coordinating bodily movements with rhythms surrounding them, and are referred to as sensorimotor synchronisation (Repp and Su, 2013).

After decades of research, benefits and practical applications, such as the use of rhythms for movement rehabilitation in the context of neurological disorders (for a review see Schaefer, 2014), have been found for sensorimotor synchronisation, but questions remain about how we achieve it accurately (Repp and Su, 2013). In particular, it is still unclear what the neural mechanisms underlying sensorimotor synchronisation are. A growing body of studies has reported that the brain tracks auditory rhythms such as music and speech, as well as visual rhythms such as dance (Bouvet et al., 2020; Celma-Miralles and Toro, 2019;

Fujioka et al., 2012; 2015; Lenc et al., 2018; Nozaradan, 2014; Nozaradan et al., 2016; Peelle and Davis, 2012; Press et al., 2011; Varlet et al., 2020a).

The tracking of these rhythms by the brain does not only involve the sensory system but the motor system as well. An individual's motor system becomes activated when listening to auditory rhythms or observing visual rhythms in the absence of produced movement, typically implicating the basal ganglia, cerebellum, SMA, pre-SMA, and PMC (Bengtsson et al., 2009; Chapin, et al., 2010; Chen et al., 2008, 2009; Grahn and Brett, 2007; Grahn and McAuley, 2009). These motor regions have been suggested to play a critical role in extracting regularities from rhythmic stimuli and generating temporal predictions of future events via covert and unconscious action simulation (Arnal, 2012; Morillon and Baillet, 2017; Patel and Iversen, 2014; Rimmele et al., 2018; Schubotz, 2007). These same regions are activated when an individual imagines producing a movement without external sensory input (Farah, 1984; Lotze and Halsband, 2006; Munzert et al., 2009). For rhythmic finger tapping in particular, overlapping neural substrates, which are similar to those reported in rhythm perception tasks, were found in covert (imagined) and overt tapping, albeit with lower activation while imagining than executing tapping (Miller et al., 2010; Osman et al., 2006; Oullier et al., 2005; Stavrinou et al., 2007).

The contribution of the motor system in rhythm perception is also reflected by dynamic modulations in motor cortical activity that occur in synchrony with external stimuli (Fujioka et al., 2012; Praamstra, et al., 2006; Saleh et al., 2010). Previous research has shown that amplitude modulations in beta-band oscillations (~20 Hz), which are generally associated with producing and sustaining movement (Engel and Fries, 2010; Pfurtscheller, 1981) as well as imagining movement (Brinkman et al., 2014; McFarland et al., 2000; Pfurtscheller and Solis-Escalante, 2009), become time-locked to periodic sequences even in the absence of movement (Fujioka et al., 2012; 2015). It has been proposed that such modulations serve to

focus neuronal excitability on time-points at which external stimuli are expected and thereby to facilitate related processing in both sensory and motor areas (Henry and Obleser, 2012; Lakatos et al., 2005; Steriade, et al., 1993; VanRullen et al., 2011; te Woerd et al., 2018; Zoefel et al., 2018). This alignment of neural oscillations with external periodic stimuli is line with the Dynamic Attending Theory, which proposes that attentional oscillations entrain to regular external rhythms, in turn facilitating the processing of events that are in phase with those rhythms (Jones, 1976; Large and Jones, 1999).

Although the relation between cortical synchronisation to rhythms in the environment and synchronised rhythmic movement has been far less studied, this theoretical framework has relevance for understanding behavioural entrainment phenomena, including sensorimotor synchronisation. Previous research using Electroencephalography (EEG) has linked the strength of the neural tracking of auditory rhythms, measured as the amplitude of EEG activity at the frequencies corresponding to these auditory rhythms, to an individual's capacity to synchronise movements with these rhythms (Bouvet et al., 2020; Lenc et al., 2020; Nozaradan et al., 2016). There is also evidence from Transcranial Magnetic Stimulation (TMS) studies suggesting that such dynamic modulation at cortical level might transfer to cortico-muscular coupling underpinning movement synchronisation. Stupacher et al. (2013) found an increased “readiness to move” with high groove music, as indicated by increased motor evoked potentials (MEPs) induced by TMS, in line with behavioural studies that showed stronger movement synchronisation to high groove music (Janata et al., 2012). Stupacher et al. (2013) also observed larger MEPs when TMS pulses were delivered at particular time points corresponding to the musical beat compared to when the TMS pulses were delivered off those beat time points. This suggests that cortico-muscular coupling can be periodically modulated in accordance with the period of the auditory rhythm, consistent with previously reported modulations at the cortical level, which could explain facilitated

movement synchronisation on this external period (Carson, 1996; Fujioka et al., 2010; 2015; Iversen et al., 2009; Kelso et al., 1990; Potter et al., 2009; Schaefer et al., 2011). Temporal coordination between cortical, muscular and movement responses to external sequences are further evidenced by TMS results indicating dynamic modulations in cortico-muscular coupling during passive observation of visual rhythms that correspond with preferred movement patterns during actual synchronisation (Varlet et al., 2017).

A promising index for examining whether dynamic modulations at the cortical level extend to cortico-muscular mechanisms is cortico-muscular coherence (CMC), obtained by combining EEG or Magnetoencephalography (MEG) with Electromyography (EMG) to quantify the connectivity between cortical and muscular activities (Halliday et al., 1995). CMC is a measure of synchronisation, and thus, of the communication between cortical regions and muscles (Fries, 2005). Previous research has shown that CMC usually occurs over primary motor regions, as indicated by its distribution over the central EEG electrodes contralateral to the active limb, and peaks in the beta-band frequency range around 20 Hz (Conway et al., 1995; Feige et al., 2000; Halliday et al., 1998; Hari and Salenius, 1999; Salenius et al., 1997; Witham et al., 2011; for reviews see Bourguignon et al., 2019; Mima and Hallett, 1999). CMC has also been shown to have relevance for understanding optimal motor control. Increased CMC has been associated with accurate motor performance, suggesting more effective communication between the brain and the muscles (Kristeva-Feige et al., 2002; Kristeva et al., 2007; Witte et al., 2007). It has also been suggested that it is the subjective perception of the task difficulty rather than the actual motor precision that might drive increased CMC (Divekar and John, 2013).

In a study that involved tapping along with auditory rhythms, Pollok et al. (2005) found significant MEG-EMG coherence over the contralateral motor areas, but they did not examine dynamic changes in CMC over time, i.e., whether there were dynamic changes in

CMC that matched movement dynamics. For other rhythmic movement patterns such as walking and foot circling, for instance, CMC has been reported to elicit similar rhythmic patterns, to those of the movement, demonstrating that CMC can be time-varying (i.e., dynamic) rather than being increased in a static and constant way during movement execution (Petersen et al., 2012; Yoshida et al., 2017a; 2017b). For example, Yoshida et al. (2017a) reported time-locking between CMC and flexion of the foot, with maximum coherence observed with the Tibialis Anterior muscle when the foot reaches maximum flexion. Moreover, previous research has shown that CMC is sensitive to surrounding environmental stimuli. Piitulainen et al. (2015) found that the presentation of unexpected auditory and visual distractors results in a salient increase in an individual's CMC, even if they are not moving and are maintaining steady isometric contraction. Such findings support the validity of this measure for understanding the underlying mechanisms of sensorimotor synchronisation.

Importantly, everyday sensorimotor synchronisation is often achieved in complex multisensory environments where simultaneously presented multimodal rhythms might compete for our attention (Ernst and Bühlhoff, 2004; Repp and Penel, 2002, 2004). In such environments, an individual is often required to synchronise movements selectively with specific events that might be conveyed by auditory or visual information (Ernst and Bühlhoff, 2004; Repp and Su, 2013). For example, during musical ensemble performance, musicians might have to selectively synchronise with the visual cues provided by the conductor more so than auditory sounds produced by other musicians (e.g., if separate parts have complex rhythmic relations), or in contrast, selectively synchronise with the sounds produced by other musicians while ignoring surrounding visual information related to other musicians' unrelated movements (Keller et al., 2016; MacRitchie et al., 2017). When there are multiple stimulus streams, selective neural tracking might facilitate the processing of the relevant stimulus stream by aligning the oscillatory phase corresponding to high cortical excitability

with the relevant stimuli (te Woerd et al., 2018), which could transfer to cortico-muscular coupling. In settings where competing auditory and visual temporal information is present together, such selective neural tracking has been found to be better for auditory rhythms than visual rhythms (Kato and Konishi, 2006; Repp and Penel, 2002; 2004). Auditory rhythms have been shown to allow better movement synchronisation than visual rhythms due to higher temporal resolution of the auditory system (Elliot et al., 2010; Hove et al., 2013; Patel et al., 2005; Repp, 2003), although this auditory facilitation appears restricted to discrete stimuli, as indicated by similar synchronisation performance when visual rhythms contain more real-life-like continuous motion (e.g., Gan et al., 2015; Hove et al., 2013; Hove and Keller, 2010; Varlet et al., 2012a). These findings suggest modality specific control mechanisms for sensorimotor synchronisation that might be reflected in CMC.

Therefore, the goal of the current study was to investigate whether cortico-muscular coupling is dynamically modulated during sensorimotor synchronisation, and determine more specifically whether such dynamic modulations (i) occur when executing as well as imagining the synchronisation, (ii) become selectively aligned with the stimuli an individual intend to synchronise with, and (iii) are facilitated with auditory discrete stimuli compared to visual discrete stimuli. EEG-EMG coherence (CMC) in the beta frequency band was used to examine the dynamic changes in cortico-muscular coupling when participants were asked to synchronise or imagine synchronising finger taps with either periodic auditory or visual stimuli embedded in a bimodal isochronous sequence. Such a sequence with intermixed auditory and visual stimuli was used to make it possible to determine whether the selective neural tracking and synchronisation with auditory or visual stimuli would extend to CMC, while ensuring that external sensory inputs that could result in spurious changes in CMC (Bastos and Schoffelen, 2016; Burgess, 2013), were kept the same across all conditions. In two real tapping conditions, participants were instructed to actively produce finger taps in

synchrony with the auditory or visual rhythm, and in two imagined tapping conditions, participants were asked to imagine tapping with the auditory or visual rhythm while maintaining a constant isometric finger pressure. Finally, in a fifth control condition, participants were presented with the bimodal sequence without movement instructions, except to maintain constant isometric finger pressure.

It was hypothesised that dynamic modulations occurring at cortical level would transfer to the cortico-muscular coupling underlying sensorimotor synchronisation, as indicated by dynamic modulations in CMC time-locked with the stimuli participants were instructed to tap with. Selective dynamic modulations in CMC were not only expected in the real tapping conditions but also in the imagined tapping conditions, in accordance with previous research showing activity in the motor system when imagining movement, and its central role in temporal prediction through action simulation (Arnal, 2012; Miller et al., 2010; Morillon and Baillet, 2017; Oullier et al., 2005; Stavrinou et al., 2007). Similar patterns of CMC modulation were expected in real and imagined tapping conditions due to shared mechanisms (Oullier et al., 2005; Stavrinou et al., 2007), although differences in the amplitude and/or temporal patterning of these modulations remained possible due to differences in actual movement (Kilner et al., 2003, 2000; Miller et al., 2010; Oullier et al., 2005). These dynamic modulations in CMC were expected to be of lower amplitude, or even vanish, in the control condition due to a lack of active motor engagement without actual or imagined tapping.

Additionally, modality-specific modulations in CMC were expected in the real and imagined tapping conditions, consistent with previous studies showing facilitated movement synchronisation with auditory rhythms compared to visual rhythms, and results suggesting that greater motor control might be underpinned by stronger CMC (Hove et al. 2010; Kristeva-Feige et al., 2002; Kristeva et al., 2007; Patel et al., 2005; Pollok et al., 2009; Witte

et al., 2007). Accordingly, it was hypothesised that the magnitude of CMC and its dynamic modulations when tapping and imagining tapping would differ between auditory and visual conditions due to the superiority of the auditory modality for temporal predictions and sensorimotor synchronisation.

5.2 Methods

5.2.1 Participants

A total of 23 healthy right-handed participants volunteered to participate in this study. All participants had normal or corrected-to-normal vision. None of them had any history of hearing, motor, neurological, or psychiatric disorders. This study was approved by the Western Sydney University Human Research Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of Helsinki. All participants gave written informed consent prior to participation and were debriefed at the end of the experiment. Three participants were excluded because they produced periodic force modulations while instructed to maintain a constant force as detailed below, leading to a final sample of 20 participants (28.35 ± 5.34 years old, 7 females and 13 males).

5.2.2 Stimuli

The stimulus sequences presented to the participants alternated between 83 ms auditory (pure 400 Hz sine tone, 5 ms ramps) beeps and 83 ms visual flashes (red dot; approximately 3° visual angle) at 2.5 Hz, so that the time interval between two events of the same modality was 800 ms (1.25 Hz) and the interval between the different modalities was 400 ms (see Figure 12). The stimulus sequence was presented continuously for 120 s in each trial and was the same across all experimental conditions. This ensured that the sensory input was consistent across all conditions.

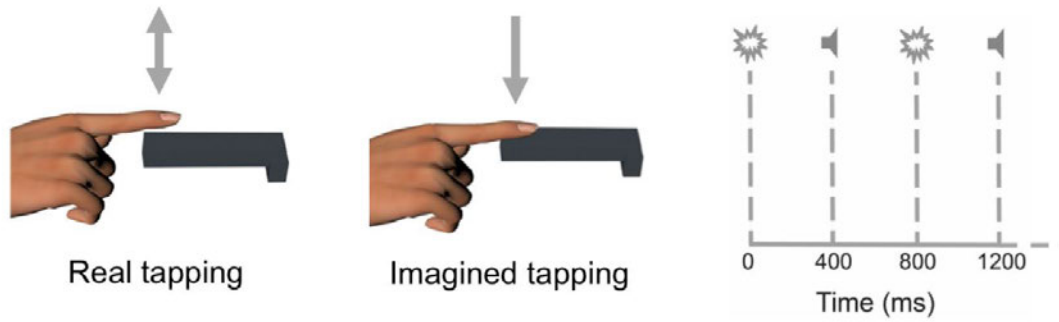


Figure 12. Schematic representation of the Real and Imagined tapping conditions and of the interleaved audio-visual stimulus sequence.

5.2.3 Appartatus

To avoid noise interference, the experiment was conducted in a closed and soundproof booth. During the experiment participants were seated on a chair with a backrest and a custom-built forearm support to ensure comfort and a stationary right arm position to help them to stay still and relaxed in order to prevent muscular interference.

5.2.3.1 Stimulus presentation

The visual stimulus sequence was presented on a 1920×1200 resolution ViewPixx monitor (VPixx Technologies inc., Quebec, Canada) while the auditory stimulus sequence was simultaneously presented via ER2 insert earphones (Etymotic Research Inc, IL, USA). The auditory stimuli were presented at a comfortable intensity for the participant (approximately 70 dB), which was kept the same for all trials. The timing of both visual and auditory stimuli was controlled at the 60 Hz refresh rate of the monitor such that the 800 ms stimulus inter-onset intervals and the 83 ms stimulus duration corresponded to an exact number of frames.

5.2.3.2 Force recording

Attached to the armrest of the chair was a wide bar load cell (HTC-Sensor TAL201, Colorado, USA) connected to an Arduino Duemilanove board (Arduino, Ivrea, Italy) via an amplifier shield (Load Cell / Wheatstone Amplifier Shield, RobotShop, Mirabel, Quebec, Canada) to record the force exerted by participant's right index finger at a sampling frequency of 60 Hz (i.e., the refresh rate of the monitor). Force measures therefore had a precision of 16.7 ms. The Arduino board was connected to a MacBook Pro laptop (Apple, Cupertino, CA, USA) via USB. The load cell was calibrated for linearity and positioned on the custom forearm support of the chair on which the participant was seated.

5.2.3.3 EEG and EMG recording

EEG and EMG signals were recorded at a sampling rate of 2048 Hz using a Biosemi Active-Two system (Biosemi, Amsterdam, Netherlands). EEG was recorded with 64 Ag-AgCl electrodes placed over the scalp of the participant according to the international 10/20 system. EMG signals of the right Flexor Digitorum Superficialis (FDS) muscle were recorded using BioSemi flat electrodes after preparing participant's skin using alcohol swabs. A pair of electrodes was placed on the participant's right forearm in a standard belly-tendon montage (Cardellicchio et al., 2020; Kong et al., 2010). A custom C++ program ensured that all EEG and EMG recordings received triggers at the start of each trial from the ViewPixx monitor controlling the timing of stimulus presentation and the force recordings.

5.2.4 Procedure

At the start of the test session, the experimental task and procedures were explained before participants were asked to complete an informed consent form as well as a short demographic questionnaire.

There were five conditions: 1) synchronising finger tapping with the auditory beeps (Auditory Tapping), 2) synchronising finger tapping with the visual flashes (Visual Tapping), 3) imagining synchronising finger tapping with the auditory beeps (Auditory Imagining), 4) imagining synchronising finger tapping with the visual flashes (Visual Imagining), and 5) passive listening and observation of the audio-visual sequence (Control). Participants were instructed to tap as close as possible to the auditory or visual events for the Auditory Tapping and Visual Tapping conditions, respectively. Discrete tapping was executed by lifting the finger from the force sensor and striking the force sensor in synchrony with the instructed stimuli. For the Auditory and Visual Imagining conditions participants were instructed to imagine they were tapping to the auditory or visual events, respectively, while maintaining a constant exerted force with their right index finger on the force sensor. For the control condition participants were instructed to attend to the stimulus sequence while again keeping the force exerted with their right index finger as stable as possible.

For the duration of the experiment participants were asked to sit on the chair in front of the monitor, place their right forearm on the arm rest, rest their elbow at approximately 90 degrees with the hand palm facing down. Their right index finger was placed on the force sensor. The experimenter was in the room with the participant and made sure that the participant remained focussed on the task.

Prior to data collection, the participant's maximal voluntary contraction (MVC) was measured. The participants were instructed to put as much pressure on the force sensor as they could with their right index finger for approximately 3 s. This task was repeated three

times and the average of the three maximum forces was considered to be the MVC. Then, the target force was calculated as 7 % of the MVC (Kristeva-Feige et al., 2002; Kristeva et al., 2007; Safri et al., 2007), in line with research suggesting that the motor cortex is most concerned with the coding of weak forces (Maier et al., 1993).

Participants could then see on the monitor a visual feedback of the force exerted with their index finger. The visual feedback corresponded to a red bar that changed in length in real-time depending on participant's exerted force and turned green when the exerted force was within a 5 % accuracy range of the target force. The target force was indicated by a white line on the bar. The force feedback was displayed before each trial in which participants needed to hold an isometric contraction (i.e., the Imagining and Control conditions). Those trials could only start once participants were within the 5 % accuracy range of their target force. The force feedback disappeared as soon as the trials started to avoid distracting the participants from focusing on the audio-visual sequence. Participants were allowed to practice the isometric contraction until they managed to hold a steady force of approximately 7 % of MVC.

Twenty trials of 120 s were presented in four blocks that included one trial for each of the five experimental conditions to ensure an equal distribution of the conditions over time. Within the blocks the presentation order was randomised. Participants were allowed to take as many breaks as necessary in between trials. The total experiment, including the EEG and EMG preparation, took about 120 minutes.

5.2.5 Data analysis

5.2.5.1 Movement synchronisation

The accuracy and stability of synchronisation with the stimulus sequence in the auditory and visual trials were measured as the mean and standard deviation of the signed and absolute asynchronies (Repp, 2005). First, tap onsets were extracted from the force signal as the first sample above the sensor baseline + 0.25 N. The asynchronies were then calculated as the difference between the stimulus onset and the tap onset, for which the absolute closest tap was selected (Białyńska et al., 2011; Zelic et al., 2016, 2019). The first four taps were excluded to account for transient behaviour (e.g., Hove et al., 2010; Iversen et al., 2015; Zelic et al., 2016; 2018). Asynchronies larger than half the inter-onset interval (i.e., 400 ms) or larger than 3 standard deviations were removed as they likely resulted from missed taps or double taps (Ono et al., 2016; Zelic et al., 2018; 2019).

5.2.5.2 EEG and EMG pre-processing

The EEG and EMG data were processed using MATLAB 2017a (The MathWorks, Inc., Natick, MA). Both EEG and EMG data were first (i) high-pass filtered using a 4th order Butterworth filter with a cut-off frequency of .2 Hz to remove slow drifts in the recorded signals and (ii) segmented into 120s-trials. Zero-phase digital filtering was used. Based on visual inspection, channels containing excessive artifacts or noise were then interpolated with the neighbouring channels (i.e., an average of 1.279 [SD = 1.133] interpolated electrodes per participant, and never more than 5 electrodes).

After filtering, the EEG signals were decomposed using an independent component analysis (FastICA), as implemented in Fieldtrip (Oostenveld et al., 2011) to remove eye movement artifacts. Based on visual inspection of the topography and time-course of

independent components, components reflecting eye-blinks and lateralised eye movements were removed from the data. EEG data were then (i) re-referenced to the average of all scalp electrodes and (ii) notch filtered to remove 50 Hz (and corresponding harmonics) electrical power contamination with a bandwidth of 1 Hz.

After the initial filtering, the EMG signals were re-referenced to their respective reference electrode, notch filtered to remove 50 Hz (and corresponding harmonics) electrical power contamination with a bandwidth of 1 Hz, and high-pass filtered using a 4th order Butterworth filter with a cut-off frequency of 10 Hz to remove movement artifacts (Merletti and Di Torino, 1999; de Vries et al., 2016; Tomiak et al., 2015). The EMG signals were then rectified and low-pass filtered at 195 Hz. EMG rectification has been suggested to be an important step for the examination of CMC, enhancing the power spectral density of the EMG signal at a frequency of common input that recruits the constituent motor units (Yoshida et al., 2017a). This assumption is supported by experimental evidence and computational modelling (Myers et al., 2003; Ward et al., 2013). Although its benefits remain debated, rectifying EMG signals has been shown to be appropriate when examining CMC for low exerted forces (Boonstra and Breakspear 2012; Farina et al. 2013; McClelland et al., 2012; Ward et al. 2013). We also examined EMG broadband amplitude in separate analyses to further investigate changes in muscular activity in the tapping conditions and to control for uninstructed periodic modulations synchronised with the stimuli in the static conditions, as detailed below. EMG broadband amplitude was computed as the envelope of the rectified EMG (10-195 Hz) signals using the Hilbert transform. Finally, the pre-processed EEG and EMG signals were down-sampled to 500 Hz.

5.2.5.3 Data exclusion

Despite being instructed to maintain a constant force in the isometric (Imagining and Control) conditions, periodic modulations in participants' force and muscular activity synchronised with the stimuli were found in some trials. Therefore, preliminary analyses were conducted on the continuous force and EMG envelope to exclude segments that exhibited periodic activity at the stimulus frequency, and to exclude participants when they had a large number of segments to exclude. For each trial, the 116.8 s data segment left after removing the first four 800 ms stimulus cycles (1.25 Hz period) was first separated into eight non-overlapping segments of 14.6 s. Segments were excluded when they showed significant activity at the stimulus frequency (1.25 Hz) or its first harmonic (2.5 Hz) in the frequency spectrum of the continuous force or EMG envelope calculated using Fast Fourier Transforms (FFTs). In line with previous studies that used frequency-tagging techniques, force and EMG amplitude at the 1.25 Hz and 2.5 Hz frequency bins were considered to be significant when the Z-score value was greater than 3.1 ($p < .001$, one-tailed), which indicated signal amplitude significantly larger than the background noise (Jacques et al., 2016; Quek et al., 2018). The Z-scores were computed at each frequency bin as the difference in amplitude between a given frequency bin and the mean of its 10 neighbouring frequency bins (i.e., 5 on each side, excluding the two immediately adjacent frequency bins), divided by the standard deviation of those 10 neighbouring bins (Quek et al., 2018; Varlet et al., 2020a). Data were excluded for participants who had significant periodic activity in the equivalent of more than one of the four trials in any of the three isometric (Imagining and Control) conditions (i.e., more than 8 segments in one of the three conditions, one full trial [116.8 s] in total). This procedure thus ensured that the participants retained for further analyses performed the task correctly at least in 75 % of the trials per condition. Three participants were excluded based on this criterion. Twenty participants were kept, with some segments exhibiting significant

periodic activity (77 segments of 14.6 s, 4 % of the total data) removed from further analyses, as detailed below.

5.2.5.4 Cortico-muscular coherence

Cortico-muscular coherence (CMC) was computed to measure changes in the synchronisation between EEG and EMG signals across the different experimental conditions, over the time-course of the 800-ms stimulus cycle in particular. For each participant, CMC was calculated between each EEG electrode and the EMG recorded from the FDS muscle using the FieldTrip toolbox with a Fast Fourier Transform based time-frequency analysis (Oostenveld et al., 2011).

The EEG and EMG power spectra and their cross-spectrum required to compute CMC were calculated over the time-course of each 800-ms stimulus cycle using a sliding fixed-length window of 250 ms with 20 ms increments, resulting in 40 time-points per stimulus cycle and a frequency resolution of 4 Hz (1/0.250 s window). This window size was chosen to avoid overlap between consecutive stimuli and to make it possible to examine within-cycle modulations with sufficient temporal and frequency resolution. A multitaper approach was taken in order to improve CMC estimation using 3 Slepian tapers, resulting in a ± 6 Hz frequency smoothing for the computation of power- and cross-spectra (Reyes et al., 2017).

Coherence was computed for each of the 40 time-points of the stimulus cycle using the 584 corresponding EEG-EMG cross-spectra, and EEG and EMG auto-spectra (4 trials \times 146 stimulus cycles per trial) to ensure reliable synchronisation estimation (Bastos and Schoffelen, 2016). Data corresponding to the first four cycles were removed from this analysis to avoid transient behaviour in line with movement analyses. Data corresponding to segments that were excluded because of periodic changes in participant's force and/or EMG activity in the isometric (Imagining and Control) conditions were discarded from the analysis

to make sure CMC was computed on movement-free data in these conditions. These segments were removed for all three isometric (Imaging and Control) conditions (231 segments of 14.6 s, 12 % of the data in total) to ensure that CMC was computed on the same number of cross-spectra and auto-spectra (Bastos and Schoffelen, 2016), resulting in an average of 515 (SD = 43, 438-584) per condition. This operation resulted in coherence values between 0 and 1 for each frequency bin and time-point, where 1 indicates perfect synchronisation between EEG and EMG signals and 0 indicates no synchronisation.

Coherence was selected for further analyses in the beta range between 14 and 38 Hz. This range allowed variability within and between participants to be captured at the frequencies at which CMC usually occurs (Hansen and Nielsen, 2004; Mehrkanoon et al., 2014; Murthy and Fetz, 1992, 1996; Omlor et al., 2007; Salenius et al. 1997a). Beta range CMC has been shown to occur in contralateral motor regions. For the right finger/hand in particular, electrode C3 on the left hemisphere is most commonly reported (Johnson et al., 2011; Kristeva-Feige et al., 2002; Safri et al., 2007). Therefore, C3 and its surrounding 8 electrodes (i.e., FC1-5, C1-5, CP1-5) were selected as our area of interest. For each participant the electrode with the highest time-averaged CMC within the area of interest was selected for further analyses (Bourguignon et al., 2017; Larsen et al., 2017).

5.2.6 Statistical Analysis

All statistical analyses were performed in jamovi (0.9.5.12). For the tapping, the mean and SD of signed and absolute asynchronies were compared in Visual and Auditory Tapping using paired t-tests.

To obtain the beta CMC as well as beta EMG and EEG power, values in the beta range (14-38 Hz) were averaged. For the broadband EMG amplitude, the 10-195 Hz filtered and rectified EMG signal was down sampled to 50 Hz to match the 40 time-points of the

CMC as well as EMG and EEG power. Beta (14-38 Hz) CMC, beta (14-38 Hz) EMG and EEG power, and broadband EMG amplitude (envelope of the 10-195 Hz filtered and rectified signal) were compared in the different conditions with repeated-measures ANOVAs.

To test the hypothesis of dynamic (i.e., time-varying) changes in CMC, EMG and EEG, repeated-measures ANOVAs including a factor Time with 40 levels (i.e., increments of 20 ms) were used to test significant differences within the stimulus cycle. Because of EMG, EEG and CMC responses of large magnitude in the tapping conditions due to the moving finger, tapping conditions were separated from the Imagining and Control conditions (isometric conditions) in the statistical analyses that included Time as a factor. This allows better assessment of the potential temporal dynamics in the Imagining and Control conditions, without being obfuscated by the large responses in the tapping conditions.

2×40 ANOVAs with the factors Movement Condition (Auditory Tapping and Visual Tapping) and Time (increments of 20 ms) were used to compare the two tapping conditions. To further explore dynamic modulations in CMC, EEG and EMG in the tapping conditions, and more specifically differences between stimulus-locked and tap-locked fluctuations, 2×40 ANOVAs were also conducted with participants' data realigned according to their respective mean tap timing, i.e., tap-locked EMG beta power, broadband EMG, EEG beta power and CMC. 3×40 ANOVAs with the factors Movement Condition (Auditory Imagining, Visual Imagining and Control) and Time (increments of 20 ms) were used to compare the three isometric conditions.

Where applicable, the effect of time was further explored using cluster-based permutation testing using point-by-point t-tests and ANOVAs with Letswave6 (www.letswave.org) in MATLAB to identify significant clusters (Oostenveld et al., 2011). Point-by-point one sample t-tests were used on demeaned EMG, EEG, and CMC data to test significant deviations from 0. Point-by-point paired t-tests were used to compare the two

tapping conditions and point-by-point ANOVAs were used to compare the three isometric (Imagining and Control) conditions where necessary. Clusters of adjacent time-points above the critical t -value or F -value ($\alpha = .05$) were determined and the magnitude of each cluster by calculating the sum of the absolute t -values or F -values constituting each cluster. A thousand random permutations for each participant's time-series were calculated to obtain a reference distribution of maximum cluster magnitude. Clusters in observed data were considered to be significant if they had a magnitude larger than the threshold of the 95th percentile of the permutation distribution.

The frequency spectrum of CMC averaged across time was tested in a 5×25 ANOVA with the factors Movement Condition (Auditory Tapping, Visual Tapping, Auditory Imagining, Visual Imagining and Control) and Frequency (0 to 100 Hz in 4 Hz bins) to confirm the largest magnitude of CMC in the beta range.

To confirm that the changes in CMC were due to actual changes in synchronisation between EEG and EMG signals and not driven by time-locked amplitude modulations in EEG and EMG signals, CMC was also calculated on permuted data (Burgess et al., 2013; Hari et al., 2014). For each participant and condition, the EEG signals of each trial were randomly matched with the EMG signal from another trial (von Carlowitz-Ghori et al., 2014, Hesterberg et al., 2005). By assigning time-series that were not recorded simultaneously while preserving any possible stimulus-locked amplitude modulations in the EEG and EMG signals, permuted data allowed to control for the magnitude of CMC and its dynamic modulations that could occur by chance, and thus, determine genuine changes in CMC. Coherence was calculated for all possible permutations of the 4 trials within the same condition. Coherence values obtained from these 3 possible permutations were then averaged and used to test differences with coherence values computed on real data (Yoshida et al., 2017a).

5.3 Results

The series of analyses presented below aimed to compare sensorimotor synchronisation across modalities, and cortico-muscular responses across modalities, over time, and between real and imagined conditions. First, the results for movement synchronisation performance, EMG activity, and EEG activity are presented, followed by the results for CMC.

5.3.1 Movement synchronisation

As shown in Figure 13A, the mean of signed asynchronies indicated that participants tapped significantly earlier with auditory stimuli compared to visual stimuli, $t(19) = -2.800$, $p = .011$, $d = .626$. However, neither the accuracy of tapping, as measured by the mean of absolute asynchronies, nor the stability of tapping, as measured by the standard deviation of signed asynchronies and the standard deviation of absolute asynchronies, differed significantly between auditory and visual conditions, $t(19) = 1.390$ $p = .181$, $d = .310$; $t(19) = -.525$, $p = .606$, $d = .117$; and $t(19) = .884$, $p = .388$, $d = .198$; respectively (see Figure 13B and 13C).

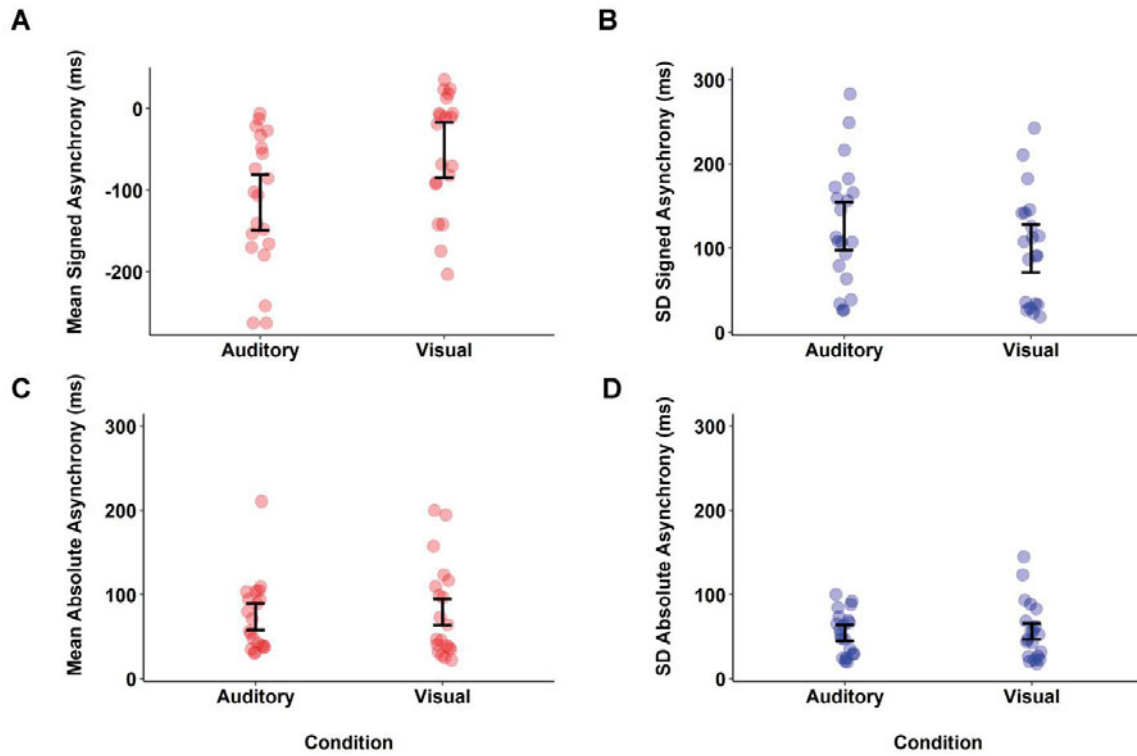


Figure 13. Tapping performance. Mean and standard deviation of signed asynchronies (A and B) and absolute asynchronies (C and D) for the visual and auditory conditions. Error bars represent $1 \times \text{CI}$ of the mean computed for within-subject designs (Morey, 2008).

5.3.2 Muscular responses

The analyses of muscular responses, for both broadband and beta EMG data, revealed no differences in mean amplitude between the two tapping conditions and between the three static finger pressure (isometric) conditions. As expected, the analyses also indicated dynamic modulations (i.e., time-varying differences), for both broadband and beta EMG data, in muscular activity, time-locked to auditory and visual stimuli in the two tapping conditions but not in the three isometric static conditions.

5.3.2.1 Broadband EMG

The 2×40 ANOVA with the factors Movement Condition (Auditory Tapping and Visual Tapping) and Time (increments of 20 ms) on broadband EMG (10-195 Hz, rectified) indicated no difference between the two tapping conditions, $F(1,19) = .181$, $p = .675$, partial $\eta^2 = .009$, but a significant effect of Time, $F(39,741) = 2.597$, $p < .001$, partial $\eta^2 = .120$, and interaction between Movement Condition and Time, $F(39,741) = 6.667$, $p < .001$, partial $\eta^2 = .260$. These results show that there was no reliable difference in the mean amplitude of broadband EMG between the two tapping conditions but there were dynamic modulations (i.e., time-varying differences) depending on the sensory modalities. Separate one-way ANOVAs to test the effect of Time for each tapping condition yielded a significant main effect for Auditory Tapping, $F(39, 741) = 5.390$, $p < .001$, partial $\eta^2 = .221$, and Visual Tapping, $F(39,741) = 5.340$, $p < .001$, partial $\eta^2 = .219$, both showing significant dynamic modulations (i.e., time-varying differences) in broadband EMG amplitude over the time of the stimulus cycle.

As depicted in Figure 14A, these dynamic modulations appeared to be time-locked to the onset of the stimuli participants were instructed to synchronise with, hence showing an antiphase relation between auditory and visual conditions. The amplitude of broadband EMG was maximal at around 200 ms before the auditory stimulus, in the Auditory Tapping condition. The amplitude of broadband EMG was maximum at around 150 ms before the visual stimulus, in the Visual Tapping condition. This effect of time was confirmed by the cluster-based permutation tests, which indicated large significant clusters with significant deviations from the mean (not represented in Figure 14A) in both conditions (p -values $< .05$).

When realigned to individual participants' mean tap timing, broadband EMG data did not show any significant difference between visual and auditory conditions, as indicated by a significant main effect of Time, $F(39, 741) = 7.645$, $p < .001$, partial $\eta^2 = .287$, but no main

effect of Movement Condition, $F(1,19) = .181$, $p = .675$, partial $\eta^2 = .009$ or interaction between Time and Movement Condition, $F(39,741) = 1.348$, $p = .079$, partial $\eta^2 = .066$, in the ANOVA. As depicted in Figure 14D, broadband EMG showed a deflection starting about 200 ms prior to the tap and peaking about 100 ms prior to the tap, and this was similar across both tapping conditions. Cluster-based permutation tests that compared broadband EMG data realigned to the participant's mean tap timing in the two tapping conditions did not indicate any significant clusters either ($p\text{-values} > .05$).

The 3×40 ANOVA with the factors Movement Condition (comparing across the three isometric conditions: Auditory Imagining, Visual Imagining and Control) and Time (increments of 20 ms) yielded no differences between the three isometric conditions, $F(2,38) = .544$, $p = .585$, partial $\eta^2 = .028$, no significant modulations of EMG amplitude over time, $F(39,741) = 1.022$ $p = .435$, partial $\eta^2 = .051$, and no significant interaction between Movement Condition and Time, $F(78,1482) = .996$ $p = .489$, partial $\eta^2 = .050$ (see Figure 14B). These results show that there were no reliable differences in the amplitude of broadband EMG between the three isometric conditions, supporting the premise that participants (who were not excluded) were doing the task as instructed, i.e., they were not systemically moving along with the stimuli in these conditions. Cluster-based permutation analyses on demeaned EMG data testing for significant deviations from zero supported this result with no significant clusters in any of the three isometric conditions ($p\text{-values} > .05$).

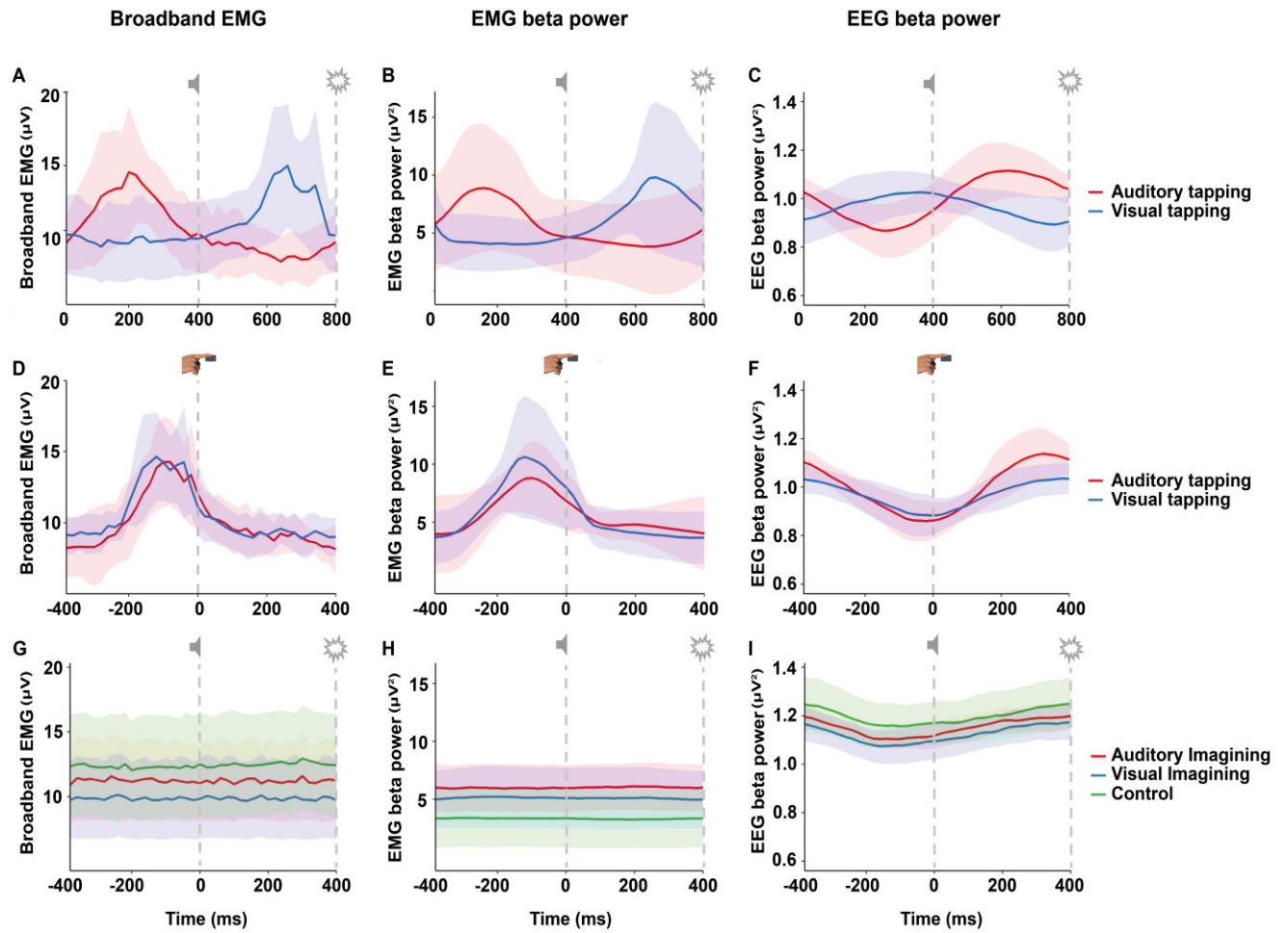


Figure 14. Broadband EMG, EMG beta (14-38 Hz) power, and EEG beta (14-38 Hz) power as a function of time for the two tapping conditions (panels A, B, and C for stimulus-locked data, and panels D, E, and F for tap-locked data), and for the three isometric conditions (panels G, H, and I). Shaded areas represent 1 \times CI of the mean computed for within-subject designs (Morey, 2008).

5.3.2.2 EMG beta (14-38 Hz) power

Similar to broadband EMG, the 2×40 ANOVA with the factors Movement Condition (Auditory Tapping and Visual Tapping) and Time (increments of 20 ms) on the EMG beta (14-38 Hz) power yielded no significant main effect of Movement Condition, $F(1,19) = .026$, $p = .873$, partial $\eta^2 = .001$, but a significant main effect of Time, $F(39,741) = 2.422$, $p < .001$, partial $\eta^2 = .113$, and interaction between Time and Movement Condition, $F(39,741) = 3.112$, $p < .001$, partial $\eta^2 = .141$. Separate one-way repeated-measures ANOVAs for Auditory Tapping and Visual Tapping conditions both indicated a significant main effect of Time, $F(39,741) = 3.590$, $p < .001$, partial $\eta^2 = .159$, and $F(39,741) = 2.640$, $p < .001$, partial $\eta^2 = .122$, respectively. These results suggest that there was no difference in the mean EMG beta power between the two tapping conditions but dynamic modulations in both conditions that were time-locked to the corresponding auditory and visual stimuli in the sequence, as shown in Figure 14B. The amplitude of EMG beta power was maximum around 250 ms before the auditory stimulus, in the Auditory Tapping condition. The amplitude of EMG beta power was maximum around 150 ms before the visual stimulus, in the Visual Tapping condition. Cluster-based permutation tests indicated large significant clusters with significant deviations from the mean (not represented in Figure 14B) that confirmed this effect of time (p -values $< .05$).

When realigned to individual participants' mean tap timing, EMG beta power did not reveal any significant difference between visual and auditory conditions, as shown by the ANOVA indicating a significant main effect of Time, $F(39,741) = 3.938$, $p < .001$, partial $\eta^2 = .172$, but no main effect of Movement Condition, $F(1,19) = .026$, $p = .873$, partial $\eta^2 = .001$, or interaction between Time and Movement Condition, $F(39,741) = 1.348$, $p = .079$, partial $\eta^2 = .066$. As depicted in Figure 14E, EMG beta power peaked about 125 ms prior to the tap and this was similar for both tapping conditions. Cluster-based permutation testing

that compared EMG beta power data realigned to the participant's mean tap timing in the two tapping conditions did not indicate any significant cluster either ($p\text{-values} > .05$).

Also in accordance with broadband EMG, the 3×40 repeated-measures ANOVA with the factors Movement Condition (Auditory Imagining, Visual Imagining and Control) and Time (increments of 20 ms) on the EMG beta (14-38 Hz) power indicated no main effect of Movement Condition, $F(2,38) = 2.355$, $p = .109$, partial $\eta^2 = .110$, and no main effect of Time, $F(78,1482) = .533$, $p = .992$, partial $\eta^2 = .027$ (see Figure 14D). The ANOVA indicated a significant interaction between the two factors, $F(2,38) = 1.399$, $p = .014$, partial $\eta^2 = .069$ but post-hoc comparisons with Bonferroni correction did not reveal any significant difference between the different conditions at any time-point ($p\text{-values} > .05$, see Figure 14H). In addition, none of the separate one-way ANOVAs for the Auditory Imagining, Visual Imagining, and Control conditions indicated a significant main effect of Time, $F(39,741) = 1.33$, $p = .088$, partial $\eta^2 = .065$; $F(39,741) = 1.090$, $p = .326$, partial $\eta^2 = .054$; $F(39,741) = .823$, $p = .771$, partial $\eta^2 = .042$, respectively. Cluster-based permutation analyses likewise found no significant clusters in any of the three isometric conditions ($p\text{-values} > .05$). There was, therefore, no evidence for a difference in EMG amplitude between the three isometric conditions or for systematic muscular modulations along with visual and auditory stimuli in participants' data retained after the exclusion procedure.

5.3.3 EEG responses

The 2×40 ANOVA with the factors Movement Condition (Auditory tapping and Visual tapping) and Time (increments of 20 ms) on the EEG beta (14-38 Hz) power yielded no significant main effect of Movement Condition, $F(1,19) = 1.420$, $p = .248$, partial $\eta^2 = .069$, but a significant main effect of Time, $F(39,741) = 5.010$, $p < .001$, partial $\eta^2 = .209$, and

interaction between Time and Movement Condition, $F(39,741) = 4.770, p < .001$, partial $\eta^2 = .201$. Separate one-way repeated-measures ANOVAs for Auditory Tapping and Visual Tapping conditions both indicated a significant main effect of Time, $F(39,741) = 6.200, p < .001$, partial $\eta^2 = .246$, and $F(39,741) = 2.320, p < .001$, partial $\eta^2 = .109$, respectively. These results show that there was no difference in mean EEG beta power between the two tapping conditions but dynamic modulations in both conditions. As shown in Figure 14C, the EEG beta power was time-locked to the corresponding auditory and visual stimuli in the sequence, with maximum amplitude around 200 ms after the auditory stimulus, in the Auditory Tapping condition, and around 350 ms after the visual stimulus, in the Visual Tapping condition. Cluster-based permutation testing indicated large significant clusters with significant deviations from the mean (not represented in Figure 14C) that confirmed this effect of time ($p\text{-values} < .05$).

The ANOVA on EEG beta power realigned to the participant's mean tap timing indicated a significant main effect of Time, $F(39,741) = 6.600, p < .001$, partial $\eta^2 = .258$, and no main effect of Movement Condition, $F(1,19) = 1.420, p = .248$, partial $\eta^2 = .069$. The ANOVA indicated a significant interaction between Time and Movement Condition, $F(39,741) = 8.770, p < .001$, partial $\eta^2 = .316$, but cluster-based permutation tests that compared tap-locked EEG beta power between the two tapping conditions did not indicate any significant cluster ($p\text{-values} > .05$), showing that there was no robust difference between visual and auditory conditions. As seen in Figure 14F, EEG beta power peaked about 325 ms after the tap in both tapping conditions.

The 3×40 repeated-measures ANOVA with the factors Movement Condition (Auditory Imagining, Visual Imagining and Control) and Time (increments of 20 ms) on the EEG beta (14-38 Hz) power indicated no main effect of Movement Condition, $F(2,38) = 1.279, p = .290$, partial $\eta^2 = .063$, a significant main effect of Time, $F(39,741) = 11.895, p <$

.001, partial $\eta^2 = .385$ (see Figure 14D), and no significant interaction between the two factors, $F(2,38) = .951$, $p = .600$, partial $\eta^2 = .048$. Separate one-way ANOVAs for the Auditory Imagining, Visual Imagining, and Control conditions indicated a significant main effect of Time, $F(39,741) = 9.060$, $p < .001$, partial $\eta^2 = .323$; $F(39,741) = 9.090$, $p < .001$, partial $\eta^2 = .324$; $F(39,741) = 9.350$, $p < .001$, partial $\eta^2 = .330$, respectively (see Figure 14I). These dynamic modulations were confirmed in the three conditions by cluster-based permutation tests showing significant clusters with significant decrease from the mean (not represented in Figure 14I) prior to the auditory stimulus (~200-400 ms, $p\text{-values} < .05$). Cluster-based permutation tests that directly compared the three conditions did not reveal any difference at any time-point between the Auditory Imagining, Visual Imagining, and Control conditions ($p\text{-values} > .05$), suggesting that dynamic modulations exhibited at the electrodes of interest had similar temporal pattern irrespective of the instruction.

5.3.4 Cortico-muscular coherence responses

In line with previous studies the results indicated larger CMC in the beta frequency band and at electrodes positioned over the contralateral cortical motor regions, as seen in Figure 15. Maximum beta (14-38 Hz) coherence was found at C1 (4 participants), C3 (9 participants), FC1 (2 participants), FC3 (1 participants), CP1 (3 participants), and CP3 (1 participant).

5.3.4.1 Frequency responses

The 5×25 ANOVA on coherence values at these electrodes, with the factors Movement Condition (Auditory Tapping, Visual Tapping, Auditory Imagining, Visual Imagining and Control) and Frequency (0 to 100 Hz in 4 Hz bins), indicated a significant main effect of Frequency, $F(24,456) = 27.470$, $p < .001$, partial $\eta^2 = .591$, of Movement

Condition, $F(4,76) = 3.410$, $p = .013$, partial $\eta^2 = .152$, and a significant interaction between the two factors, $F(96,1824) = 2.690$, $p < .001$, partial $\eta^2 = .124$. The main effect of Frequency confirms that the magnitude of CMC is frequency dependent, with largest CMC values observed around 25 Hz, as depicted in Figure 15. Post-hoc comparisons with Bonferroni correction to further explore the significant interaction indicated differences between the tapping conditions and the isometric (Imagining and Control) conditions at the two lowest frequency bins (0-8 Hz, $p\text{-values} < .05$, see Figure 15A). However, this frequency range is outside of our region of interest (14-38 Hz), because (i) the high-pass filtering at 10 Hz applied to the EMG signals in line with previous research (de Luca et al., 2010; Merletti and Cerone, 2020; Merletti and Di Torino, 1999; de Vries et al., 2016) may have biased this low frequency range, and (ii) CMC values in this range did not differ from those computed from permuted data ($p\text{-values} > .05$), suggesting that these CMC differences were spurious and driven by amplitude differences in EMG due to the produced movement.

Coherence values at the maximum electrode averaged between 14 and 38 Hz were then kept for further analyses. A 5×2 repeated-measures ANOVA with the factors Movement Condition (Auditory Tapping, Visual Tapping, Auditory Imagining, Visual Imagining and Control) and Data Type (Real, Permuted) showed no significant main effect of Movement Condition, $F(4,76) = 1.260$, $p = .294$, partial $\eta^2 = .062$, confirming the absence of difference in mean beta coherence between the five different conditions. The ANOVA also yielded a significant main effect of Data Type, $F(1,19) = 49.31$, $p < .001$, partial $\eta^2 = .722$, showing larger coherence in Real data than Permuted data. No significant interaction between Movement Condition and Data Type was found, $F(1.94,32.95) = 2.740$, $p = .083$, partial $\eta^2 = .126$.

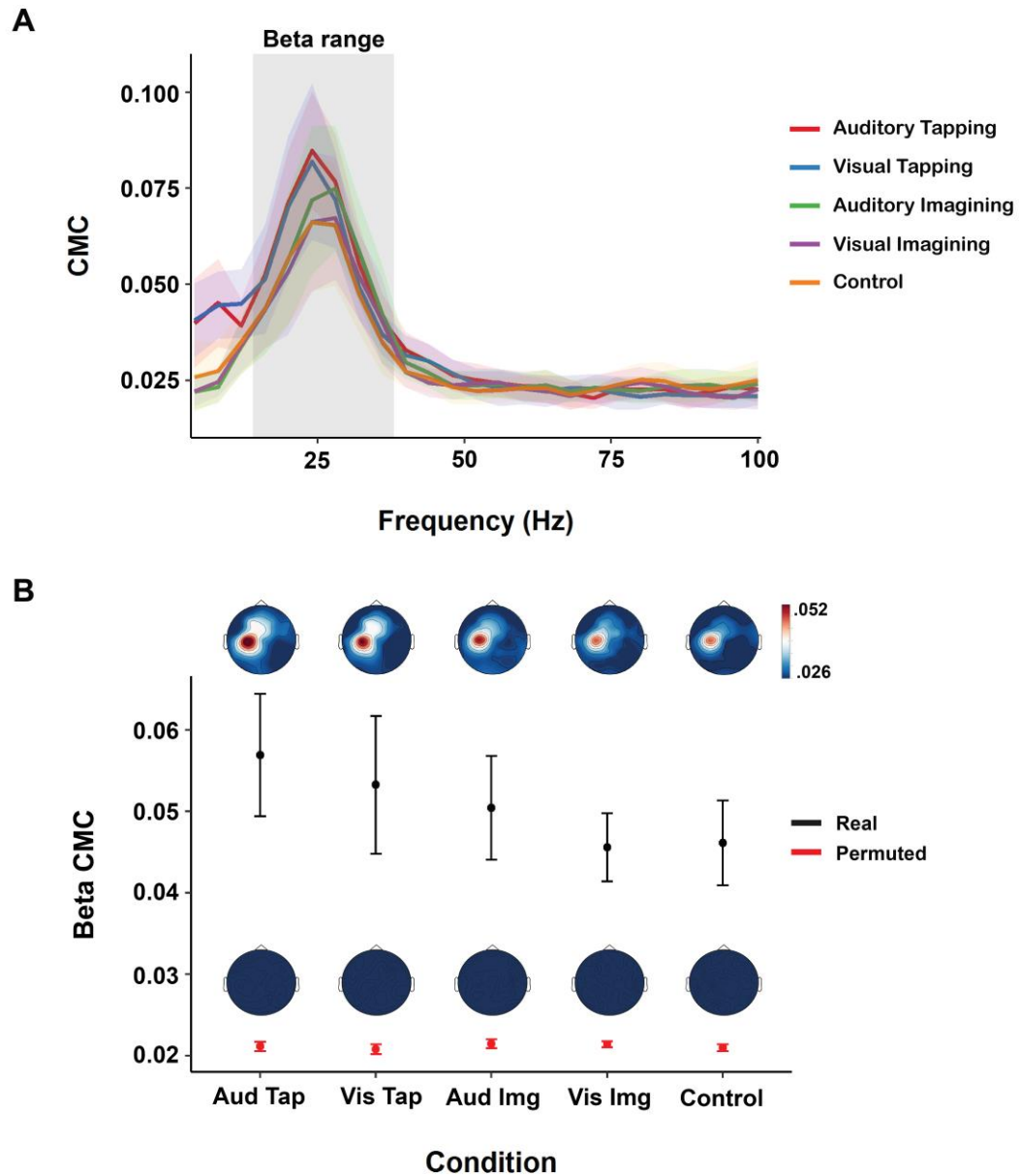


Figure 15. CMC at the individual maximum electrode for the five conditions as a function of frequency from 0 to 100 Hz (panel A) and averaged in the beta range between 14 and 38 Hz for Real and Permuted data, with the corresponding grand average topographical maps (panel B). The colour bar represents the beta CMC amplitude on the topographical maps. Shaded areas and error bars represent 95 % confidence intervals.

5.3.4.2 Dynamic beta (14-38 Hz) CMC

As depicted in Figures 16 and 17, CMC exhibited dynamic modulations time-locked to the stimuli within the sequences and/or produced taps. In contrast to EMG, these modulations did not only occur during actual tapping but also during imagined tapping with visual stimuli.

These observations were confirmed by the 2×40 ANOVA with the factors Movement Condition (Auditory Tapping and Visual Tapping) and Time (increments of 20 ms), which indicated no significant main effect of Movement Condition, $F(1,19) = .597, p = .449$, partial $\eta^2 = .030$, a significant main effect of Time, $F(39,741) = 6.663, p < .001$, partial $\eta^2 = .260$, and a significant interaction between the two factors, $F(39,741) = 16.186, p < .001$, partial $\eta^2 = .460$. Separate one-way ANOVAs for each tapping condition showed that significant modulations time-locked to their respective modality in the stimulus sequence occurred for both Auditory Tapping and Visual Tapping, $F(39,741) = 14.300, p < .001$, partial $\eta^2 = .430$, and $F(39, 741) = 10.600, p < .001$, partial $\eta^2 = .359$, respectively (see Figure 16A). Maximum CMC occurs around 100 ms after the auditory stimulus, in the Auditory Tapping condition, and around 250 ms after the visual stimulus, in the Visual Tapping condition. Cluster-based permutation tests indicated large significant clusters with significant deviations from the mean (not represented in Figure 16) that confirmed this effect of time in both real tapping conditions ($p\text{-values} < .05$).

The 2×40 ANOVA on CMC realigned to the individual participants' mean tap timing revealed a significant main effect of Time, $F(39,741) = 29.474, p < .001$, partial $\eta^2 = .608$, and no main effect of Movement Condition, $F(1,19) = .597, p = .449$, partial $\eta^2 = .030$. Although the interaction between Time and Movement Condition was significant, $F(39,741) = 1.755, p = .003$, partial $\eta^2 = .085$, post-hoc comparisons indicated no significant difference between Auditory and Visual tap-locked CMC at any time-point ($p\text{-values} > .05$). As seen in

Figure 16B, tap-locked CMC strongly decreases 200 ms prior to the tap and rebounds to peak around 200 ms after the tap, which was similar for both tapping conditions. Cluster-based permutation tests that compared tap-locked CMC between the visual and auditory tapping conditions confirmed this result with no significant clusters ($p\text{-values} > .05$).

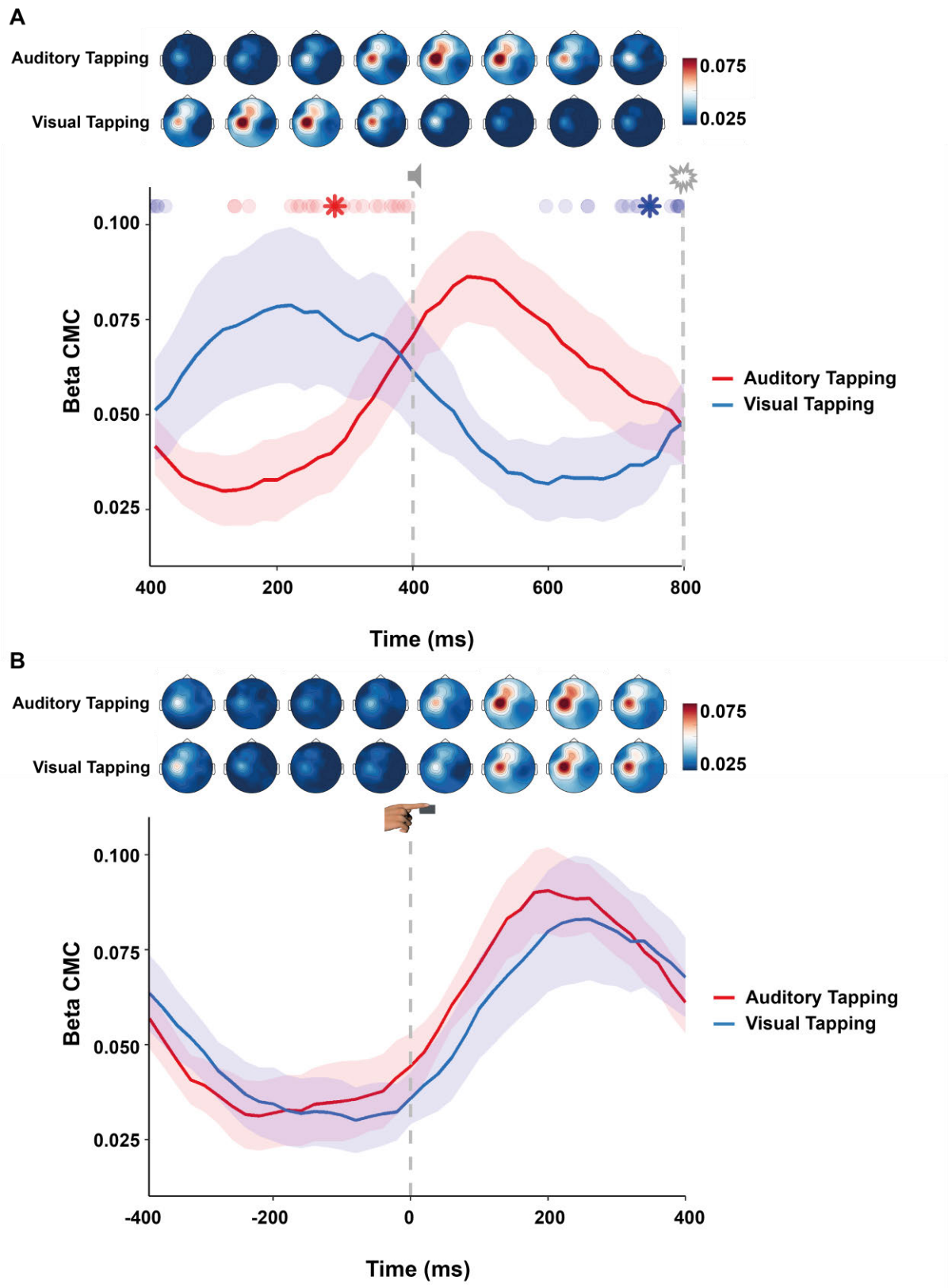


Figure 16. Beta (14-38 Hz) CMC at the individual maximal electrode over the duration of one stimulus cycle (A) and realigned according to participants' mean tap timing (B) for the

two tapping conditions, with the corresponding grand average topographical maps averaged within 100 ms time intervals. Asterisks and dots represent grand average and individual mean tapping positions, respectively, for the Auditory Tapping (red) and Visual Tapping (blue) conditions. Shaded areas represent 95 % confidence intervals. The colour bar represents the beta CMC amplitude on the topographical maps.

The 3×40 repeated-measures ANOVA with the factors Movement Condition (Auditory Imagining, Visual Imagining and Control) and Time (increments of 20 ms) indicated no significant main effect of Movement Condition, $F(2,38) = 2.722$, $p = .079$, partial $\eta^2 = .125$, no significant main effect of Time, $F(39,741) = .781$, $p = .830$, partial $\eta^2 = .039$, and no significant interaction between the two factors, $F(78,1482) = 1.065$, $p = .332$, partial $\eta^2 = .053$. With the particular interest in CMC dynamics that motivated this study, the dynamics of CMC were explored in all three isometric conditions separately. As expected, the Control condition did not show any significant modulations of CMC over time, $F(39,741) = .649$, $p = .953$, partial $\eta^2 = .033$, as depicted in Figure 17C. The Auditory Imagining condition showed no significant modulations of CMC over time either, $F(39,741) = .309$, $p = 1.000$, partial $\eta^2 = .016$, as depicted in Figure 17A. However, the Visual Imagining condition did show a significant modulation of CMC over time, $F(39,741) = 2.250$, $p < .001$, partial $\eta^2 = .106$ (see Figure 17B), with maximal CMC occurring around 250 ms before the visual stimulus. Cluster-based permutation testing on (demeaned) CMC for the Visual Imagining condition indicated significant deviations from the mean at 0-60 and 780-800 ms (p -values $< .05$). Cluster-based permutation testing did not indicate any significant deviations in the Auditory and Control conditions (p -values $> .05$).

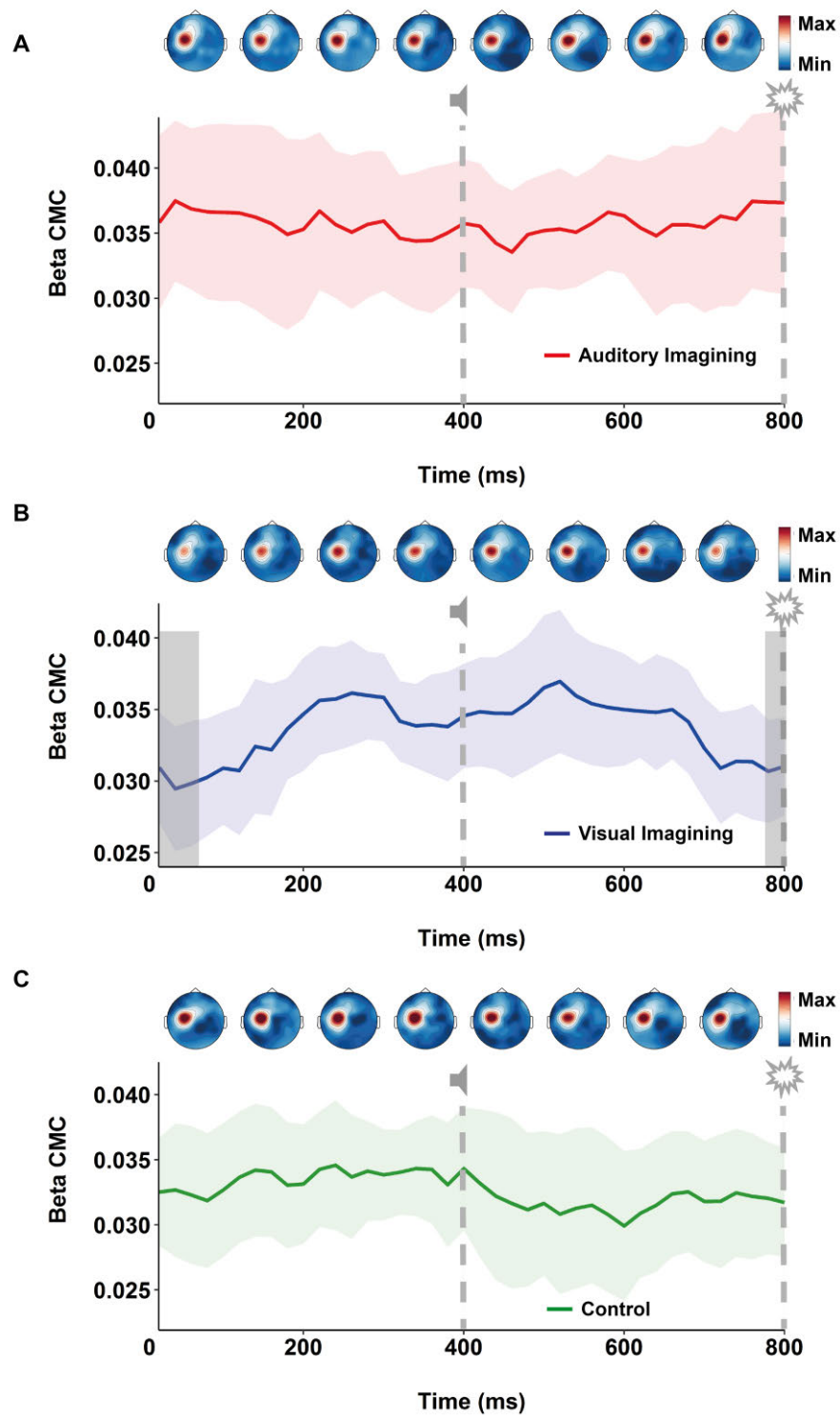


Figure 17. Beta (14-38 Hz) CMC at the individual maximal electrode over the duration of one stimulus cycle for the three isometric conditions, (A) Auditory Imagining, (B) Visual Imagining, and (C) Control, with the corresponding grand average topographical maps averaged within 100 ms time intervals. Significant deviations from the mean CMC,

as indicated by cluster-based permutation tests, are highlighted with the grey rectangles.

Shaded areas around the graph line represent 95 % confidence intervals.

5.3.4.3 Permuted cortico-muscular coherence

Time-locked responses were not present in the Permuted data, showing that they originated from genuine changes in EEG-EMG synchronisation rather than systematic changes in EEG and EMG signal amplitude. Two separate repeated-measures ANOVAs for the tapping and isometric conditions did not find any significant effects. The 2×40 ANOVA with the factors Movement Condition (Auditory Tapping and Visual Tapping) and Time (increments of 20 ms) indicated no main effect of Movement Condition, $F(1,19) = .074$, $p = .789$, partial $\eta^2 = .004$, or of Time, $F(39,741) = .615$, $p < .970$, partial $\eta^2 = .031$, and no significant interaction between the two factors, $F(39,741) = .885$, $p = .673$, partial $\eta^2 = .044$. The 3×40 ANOVA with the factors Movement Condition (Auditory Imagining, Visual Imagining and Control) and Time (increments of 20 ms) indicated no significant main effect of Movement Condition, $F(2,38) = .251$, $p = .779$, partial $\eta^2 = .013$, no significant main effect of Time, $F(39,741) = .707$, $p = .911$, partial $\eta^2 = .036$, and no significant interaction between the two factors, $F(78,1482) = .741$, $p = .955$, partial $\eta^2 = .038$. None of the five separate ANOVAs on the Permuted data yielded a significant main effect of Time either (p -values $> .05$), which was also confirmed by the cluster-based permutation analyses that did not reveal significant clusters (p -values $> .05$).

5.4 Discussion

The current study investigated the dynamic changes occurring in cortico-muscular connectivity, using EEG-EMG coherence, during real and imagined finger tapping synchronised to environmental rhythms. Participants were presented with isochronous sequences consisting of interleaved auditory and visual stimuli while either actually producing finger taps or maintaining constant isometric finger pressure with the right hand in imagining and control conditions. The results revealed that modulations of CMC in the beta band (14-38 Hz) frequency range over contralateral cortical motor regions were selectively time-locked to taps executed in synchrony with the stimuli. Furthermore, time-locked modulations of CMC were found to occur not only during actual finger tapping but also during imagined finger tapping. This modulation was only observed for imagined taps with visual stimuli and was of lower magnitude with a different temporal profile compared to that exhibited during actual tapping, suggesting different processes for executed and imagined tapping modulated by the stimulus sensory modality, as discussed below.

These results extend previous findings of dynamic CMC modulations with continuous rhythmic movement such as walking and cyclical ankle movements (Petersen et al., 2012; Yoshida et al. 2017a, 2017b) to finger tapping. In the current study, no difference between the auditory and visual modality was found for tap-locked CMC, suggesting no effect of the stimulus modality on CMC during real tapping. This result is also in line with the view that dynamic modulation of CMC is mostly driven by motor processes, as proposed by Yoshida et al. (2017) who showed no difference between self- and externally-paced circling ankle movements. In the current study, CMC between EEG and the FDS muscle was found to increase immediately after the tap to peak 200 ms after the tap, irrespective of the modality of the stimulus (i.e., visual or auditory) participants were instructed to synchronise with. More specifically, the time course of CMC for the FDS muscle seemed to increase during finger

extension and to decrease during finger flexion. These dynamic modulations are in line with the hypothesis that CMC has a critical function in stabilising movement (Reyes et al., 2017). It has been argued that during sustained contraction of a muscle, groups of sensorimotor neurons oscillate in synchrony to maintain the current motor state (Engel and Fries, 2010), while synchrony decreases and can even vanish during dynamic movements (e.g., Kilner et al., 2003; Mehrkanoon et al., 2014; Omlor et al., 2007). The peak in CMC with the FDS muscle after the tap likely represents the stabilisation of the finger in the extension position while waiting for the next tap to be triggered. Such finger deceleration and stabilisation towards maximal extension have been previously reported in finger tapping studies (e.g., Torre and Balasubramaniam, 2009), encouraging further investigations of CMC in the future together with motion-capture recordings of the entire finger trajectory.

The current study also extends previous research by demonstrating that dynamic modulations in CMC can also occur when the movements are imagined. Our results show significant modulations of CMC in the beta band while imagining tapping with the visual stimuli, even if no evidence for change in the amplitude of muscular activity over time was found, suggesting that CMC might capture top-down control mechanisms of the movement. Jeannerod (1994,1995) argued that motor imagery represents the result of conscious access to the content of the intention of a movement, which is usually performed unconsciously during movement preparation. Conscious motor imagery and unconscious motor preparation can be considered to share common mechanisms and are functionally equivalent. Recent studies using brain-imaging techniques, such as fMRI, MEG, and PET, have provided plenty of evidence supporting this possibility. Motor imagery and execution tasks have been found to share similar activity in the motor system and functional networks (Lotze et al., 2006), especially in the posterior SMA and the premotor cortex (Ehrsson et al., 2003; Miller et al., 2010; Roland et al., 1980; Stephan et al., 1995). Szameitat et al. (2007) also found that more

complex imagined everyday movements use the same cortical networks involved in motor preparation and overt motor performance, and Mizuguchi et al. (2014) even showed that such motor activity scales to the imagined force. The current findings further support the existence of a link between the underlying mechanisms of motor imagery and execution. They indicate that shared mechanisms between the two might not be restricted to the brain but also extend to the coupling between the brain and the muscles.

Importantly, the modulations found in CMC during real and imagined tapping with visual stimuli had different dynamics, suggesting that they might reflect different processes. Although the significant trough in CMC for imagined taps is close to that for executed taps in visual conditions, the time-locked oscillations in beta CMC during the imagining tapping had much lower magnitude and displayed peaks at different time-points relative to the visual stimuli. During tapping, CMC peaked 100-200 ms after the visual stimuli whereas CMC peaked around 250 ms before the visual stimuli participants were instructed to imagine tapping with. These differences might be indicative of different underlying processes. The most prominent difference between motor imagery and execution is the discharge of motor units and the somatosensory feedback provided during execution (Baker, 2007; McClelland et al., 2012). Such discharge and/or kinaesthetic feedback relative to the position of the moving finger might have contributed to the CMC modulations observed during actual tapping. Somatosensory feedback due to finger contact on the force sensor during the actual tapping could also have modulated CMC (Spackman et al., 2006; Tecchio et al., 2006) but the CMC peak about 200 ms after the taps does not support this possibility. In contrast, CMC modulations when imagining tapping might have reflected movement preparation which is considered to be the main mechanism responsible for motor activity during motor imagery (Jeannerod, 1994,1995; Lebon et al., 2019; Michelon et al., 2006). The pre-stimulus CMC increase occurring when imagining in the current study, which we argue might reflect motor

preparation, is in line with changes in EEG beta power reported in previous studies prior to movement (Doyle et al., 2005) and during motor imagery (McFarland et al., 2000; Nakagawa et al., 2011). These changes in beta power are usually considered to reflect increased activity in the sensorimotor cortex related to movement preparation (Kilner et al., 2005; Seki and Fetz, 2012; Wheaton et al., 2008). There is no direct evidence for such changes in EEG beta power at the electrodes of interest in the current study, but more advanced analyses using source localisation to disentangle visual, auditory and sensorimotor responses might help in future work to fully address the link between beta power and CMC. More direct comparisons between the temporal patterns of CMC during real and imagining tapping could also help in future studies to confirm the difference in the processes involved, although experimental settings allowing more robust and less variable CMC responses when imagining might need to be developed.

Also particularly noteworthy is that modulations in CMC during imagined tapping were found when participants were instructed to imagine tapping with the visual stimuli in the sequence but not with the auditory stimuli. This difference might have occurred because tapping with discrete visual stimuli is more difficult than tapping with auditory stimuli due to lower temporal resolution of the visual system (Repp 2005; Repp and Su 2013; Varlet et al., 2012a). Signed asynchronies indicated that participants tapped earlier, i.e., anticipated more, with auditory stimuli compared to visual stimuli in accordance with previous studies (Kurgansky, 2008; Lorås et al., 2012; Pollok et al., 2009; Repp and Su, 2013). However, there was no difference of synchronisation stability between auditory and visual conditions, an absence of auditory facilitation that has also been reported previously when both visual and auditory information were available (Chen et al., 2002; Grahn et al., 2011). The stimulus sequence in the current study always contained both auditory and visual events, and the auditory events provided temporal reference points that have likely helped to synchronise

with the visual events (Grahn et al., 2011). Although behavioural performance might have been similar, processing both auditory and visual information to enable equally accurate timing performance with visual sequences, might have led to increased attentional demands that may have affected CMC.

Kristeva-Feige et al. (2002) have previously shown that increased levels of attention lead to increased levels of CMC. In addition, increased (perceived) difficulty of motor control, rather than an actual increase of motor control performance itself (e.g., precision), has been argued to result in increased CMC (Divekar and John et al., 2013). Therefore, increased task difficulty and attentional demands when synchronising with visual stimuli in the sequence may have elicited higher levels and/or clearer time-locking of CMC. These results are also in line with studies that reported larger modulations in brain activity and connectivity with visual rhythms, especially in the beta frequency band (Pollok et al., 2009; te Woerd et al., 2018). Pollok et al. (2009) for example found greater activity in the ventral premotor cortex (PMv), as well as stronger beta coherence between PMv and the thalamus for sensorimotor synchronisation with visual than auditory rhythms. Using an audio-visual bimodal sequence similar to the one used in the present study, te Woerd et al. (2018) also showed that attending to the visual stimuli resulted in larger amplitude modulations of beta activity in the motor regions. As discussed above, further analyses allowing visual, auditory and sensorimotor responses to be disentangled would be needed in future studies to clarify the exact nature of the link between beta band amplitude and CMC. Nevertheless, together these results suggest that higher cognitive demands imposed by the processing of visual stimuli due to the lower temporal resolution of this modality, and more generally top-down mechanisms, might lead to stronger modulations in beta amplitude and coherence at central and peripheral levels.

Using experimental stimuli that enable visual, auditory and sensorimotor responses to be teased apart could also be informative in future studies. Interleaved stimuli as used in the current study are particularly interesting because they allow the stimuli to be kept the same across all conditions, thereby allowing relatively direct CMC comparisons. However, such interleaved stimuli make it difficult to disentangle modality specific responses. Presenting visual and auditory stimuli in separate conditions might help with disentangling these responses but also makes comparisons across conditions more difficult, as different stimuli would result in large differences in EEG beta band amplitude that might influence CMC irrespective of genuine changes in the synchronisation between EEG and EMG (Bastos and Schoffelen, 2016; Burgess, 2013). A promising alternative for future research could involve presenting interleaved visual and auditory stimuli but with different frequencies for the two modalities, which would help tease apart the different responses while keeping the same sensory input across conditions.

Such designs might also help to enhance differences in tapping performance between visual and auditory conditions during real tapping, including at the level of CMC, where no difference between the two modalities was found in the current study. A difference between the auditory and visual conditions was only observed when imagining tapping. It is possible that this difference in CMC, originating from higher cognitive demand involved in the processing of visual stimuli, was also present during actual tapping but was largely hidden by much larger modulations induced by actual movement. Enhancing modality specific effects by further separating visual and auditory stimuli might therefore help to reveal them at the level of CMC, especially during actual tapping performance.

Having different frequencies for the visual and auditory streams might also help to control that participants correctly follow the instructions in imagining conditions, as more distinctive responses would be expected between conditions or modalities based on the

specific period for each sensory stream. Indeed, controlling if participants are correctly imagining is a challenging issue (see Zatorre and Halpern, 2005), and using experimental stimuli that allow more distinctive responses between conditions when participants perform the task adequately is critical for future research on imagined sensorimotor synchronisation.

Finally, further manipulations of basic features of visual and auditory stimuli could help in future research to better understand the extent of these differences between visual and auditory modalities. While decreased synchronisation performance with the visual modality compared to the auditory modality observed here is generally in line with previous research (Chen et al. 2002, Repp and Penel, 2002, 2004), differences between these two modalities could also have been influenced by basic features of the selected stimuli such as their intensity, continuity, and tempo (Białyńska et al., 2011; Hove et al., 2010; Repp, 2003; Zelic et al., 2019), which would need to be explored in future research.

5.5 Conclusion

In sum, the current findings show that the synchronisation between cortical and muscular activity in the beta frequency band is dynamically modulated not only when actively tapping with external sequences but also when imagining tapping with visual sequences. The results suggest that dynamic modulations in CMC might not only reflect changes related to movement production—that is, to the discharge of the motor units and somatosensory feedback in particular—but also to movement preparation. Moreover, differences between synchronisation with auditory and visual stimuli suggest that CMC is modulated by higher attentional demand and/or the task difficulty, further supporting the importance of top-down mechanisms in CMC. Therefore, these findings help understand the

control mechanisms linking brain and behaviour to support movement synchronisation with environmental rhythms.

Chapter 6: Transition 2

Experiment 2 manipulated movement intention at three levels: “passive” listening and observing, motor imagery, and movement execution. In addition, modality and attention were manipulated to measure the effect on CMC dynamics. Therefore, Experiment 2 addressed all 3 main hypotheses:

- (i) Rhythms in the environment, such as music, spontaneously modulate cortico-muscular coupling.
- (ii) Movement intention modulates cortico-muscular coupling, i.e., rhythmic movement as well as motor imagery in time with a metronome.
- (iii) Cortico-muscular coupling is dynamically modulated during sensorimotor synchronisation time-locked to the stimulus rhythm.

In sum, hypothesis (i) was not supported by the findings of Experiment 2; passive perception of auditory and visual rhythms was insufficient to spontaneously modulate average CMC magnitude or dynamics. Yet, rhythms in the environment might still modulate CMC when there is intention to move. The outcomes of Experiment 2 support hypothesis (ii) and (iii), as the visual imagining condition showed that movement intention can modulate CMC dynamics. Furthermore, Experiment 2 showed that rhythmic movement results in CMC dynamics time-locked to the movement dynamics.

6.1 Sensory Rhythm & CMC

Experiment 2 extended hypothesis (i) to the visual domain and found, in line with Experiment 1, no spontaneous modulation of CMC in response to auditory and visual

rhythms when no movement intention was present. Whereas CMC dynamics could not be explored in Experiment 1, Experiment 2 was specifically designed to examine CMC dynamics within a stimulus sequence. Yet, no dynamic modulations in CMC were found during passive listening and observation of auditory and visual sequences. Neither the visual nor the auditory modality was sufficient to spontaneously modulate CMC. Therefore, no evidence to support hypothesis (i); “Rhythms in the environment, such as music, spontaneously modulate cortico-muscular coupling”, was found in Experiment 1 and 2. Instead, more active involvement of the perceiver was required, and movement intention seems to be one of the factors modulating CMC (dynamics). This is supported by the view that CMC is modulated by the effort of the task, which might require more active motor involvement (Divekar and John, 2013).

Nonetheless Varlet et al. (2020b) have shown CMC modulation through passive perception of bimodal metronomes. A possible limitation in Experiment 2 might be the long trials that were used, which may explain the difference with the study by Varlet et al. (2020b). Varlet et al. (2020b) used short trials, i.e. 16 stimulus cycles (approximately 16 and 8 s, respectively). Experiment 2 had very long trials in comparison, lasting 120 seconds. These long trials may cause fatigue and slow drifts in the executed force that might affect CMC. Moreover, it is difficult to sustain attention during such long trials (Langner and Eickhof, 2013). The short trials in the study by Varlet et al. (2020b) may have allowed more attention to be paid to the stimuli, and thus be less passive. As discussed in section 2.5.6, attention has previously been shown to impact CMC magnitude (Johnson et al., 2011; Johnson and Shinohara, 2012; Kristeva-Feige et al., 2002; Safri et al., 2006). Thus, the long trials could have decreased attentional engagement and in turn not show any modulations in CMC dynamics.

6.2 Movement intention & CMC

Active movement intention through motor imagery did affect CMC. Time-locked modulation of CMC was observed during imagined sensorimotor synchronisation with visual sequences. Hypothesis (ii): “Movement intention modulates cortico-muscular coupling, i.e., rhythmic movement as well as motor imagery in time with a metronome.” was thus partially supported, as imagined movement modulated CMC, but only in the visual modality. This extends the findings of passive neural entrainment with sensory rhythms to more active cortico-muscular coupling when movement intention is present. The effect of movement intention on CMC dynamics furthermore suggests that top-down influences can modulate CMC, extending the scope of previous studies showing top-down contributions to CMC (Brown et al., 1998; Gross et al., 2000; Murayama et al., 2001; Salenius et al., 1997).

6.3 Movement & CMC dynamics

The investigation of CMC dynamics in Experiment 2 allowed hypothesis (iii): “Cortico-muscular coupling is dynamically modulated during sensorimotor synchronisation”, to be tested. The outcomes of Experiment 2 supported this hypothesis, as Experiment 2 showed dynamical CMC modulations during tapping in synchrony with the auditory or visual sequences. However, CMC was not time-locked to the stimulus rhythm. Instead, it was time-locked to the executed movement (i.e., the taps). No further differences were observed between CMC dynamics for auditory and visual tapping, when aligned to the tap. These findings seem to indicate that CMC mainly reflects some motor processes that are thus strongly modulated by movement. In addition, the CMC modulations were much clearer and stronger in executed movement than imagined movement, indicating a significant role for the integration of proprioceptive and/or somatosensory feedback.

When the dynamic modulations of CMC are considered in relation to the movement phases of (repeated) discrete movements, Experiment 2 showed lowest CMC during the execution phase of the tap, and peak CMC during the recovery phase. First, in the preparatory phase, i.e. initiating finger flexion, CMC with the FDS muscle decreases. This is followed by the execution phase, i.e. force production of the finger upon contact with the sensor, at which point CMC is at its lowest. Finally, CMC increases towards its peak in the recovery phase, i.e. post-tap return to finger extension.

The decrease of beta CMC during the initiation and execution of the tap is in line with beta CMC and cortical beta dynamics previously reported during dynamic movements (e.g., Kilner et al., 2003; Mehrkanoon et al., 2014; Omlor et al., 2007). The CMC peak during the recovery phase, in which the finger is being stabilised in the extended position (Torre & Balasubramaniam, 2009), is in line with a proposed critical function of CMC in stabilising movement (Reyes et al., 2017), related to cortical beta oscillations synchronising to maintain the current motor state (Engel & Vries, 2010). The similarities in CMC dynamics to cortical dynamics during active dynamic movement seems to indicate that beta CMC dynamics are related to (or an extension of) cortical EEG dynamics in the beta range.

As mentioned in section 5.4 and 6.2, beta CMC dynamics are less pronounced and show different patterns during imagined sensorimotor synchronisation, yet we can see a similarity between the CMC dynamics in executed and imagined movement. If we now consider the *imagined* movement phases, beta CMC is also lowest around the visual stimulus presentation, i.e. when participants imagined the execution of the tap in synchrony with the visual stimulus. Beta CMC then also shows a rebound after the imagined movement has occurred, i.e. during the imagined recovery phase, in a similar timeframe as the executed movement, around 200 ms after the imagined tap.

The difference in CMC dynamics between imagined and executed movement lies mainly in the timing of the CMC peak. As mentioned, CMC peaked around 200 ms after execution of the tap, in line with cortical beta rebound and the recovery phase of movement, whereas CMC peaked around 250 ms before the visual stimuli participants were instructed to imagine tapping with, aligning peak CMC with the preparation phase of the movement. Therefore, the CMC dynamics during imaginary movement are argued to reflect the movement preparation, as considered to be the main mechanism responsible for motor activity during motor imagery (Jeannerod, 1994,1995; Lebon et al., 2019; Michelon et al., 2006), stemming from increased activity in the sensorimotor cortex related to movement preparation (Kilner et al., 2005; Seki and Fetz, 2012; Wheaton et al., 2008).

6.4 Modality & CMC

Although neither auditory nor visual rhythms spontaneously modulated CMC during passive listening and observation or during movement execution, differences between the auditory and visual domains were observed during motor imagery. Only imagined synchronised movement with visual rhythms modulated the CMC dynamics. Two reasons for this effect have been noted: (1) higher attentional demands for (imagined) visual SMS and (2) stronger cortical response to visual than auditory stimuli. This difference indicates that there are modality specific effects for CMC. This might indicate that visuo-motor and audio-motor coupling, although similar in performance in Experiment 2, are not necessarily similar in neuro-muscular coupling.

A proposed explanation for this, as discussed in section 5.4, is the higher difficulty of synchronisation with visual metronomes than auditory metronomes, which commonly results in decreased synchronisation performance (e.g., Kurgansky, 2008; Lorås et al., 2012; Pollok

et al., 2009; Repp and Su, 2013). More effortful performance would be required in the visual synchronisation task to achieve similar movement synchronisation performance with the visual modality and the auditory modality, as was the case in Experiment 2. Therefore, a more effortful performance with additional attentional demands in the visual synchronisation task may have led to the modulation of CMC dynamics. This interpretation is consistent with Divekar and John (2013), who argued that CMC magnitude increases with the attentional demand of the motor task.

Ultimately, other factors might contribute to the difference in CMC dynamics between the visual and auditory modality. For example, the generation of vocal images alongside auditory tones (Pruitt, 2019), differences in processing speed (Robinson et al., 2018) and subcortical (basal ganglia) activity (Hove et al., 2013), are other factors that might play a significant role and that deserve further attention in future research.

Chapter 7: General Discussion

7.1 Sensorimotor synchronisation and CMC

The aim of this thesis was to investigate the role of cortico-muscular mechanisms underlying the ubiquitous phenomenon of SMS. In particular, this thesis aimed to test if cortico-muscular coupling (CMC) can be modulated, either spontaneously by rhythms in the environment, or more actively by movement intention, and whether such rhythmic engagement of the motor system affects the cortico-muscular dynamics.

Two experiments were executed to assess CMC during SMS at three levels of motor engagement; passive rhythm perception, motor imagery of SMS and performed SMS.

Experiment 1 and 2 tested three main hypotheses:

- (i) Rhythms in the environment, such as music, spontaneously modulate cortico-muscular coupling.
- (ii) Movement intention modulates cortico-muscular coupling, i.e., rhythmic movement as well as motor imagery in time with a metronome.
- (iii) Cortico-muscular coupling is dynamically modulated during sensorimotor synchronisation time-locked to the stimulus rhythm.

Experiment 1 tested the effect of different levels of groove, i.e. the urge to move, on CMC, whilst Experiment 2 tested the effect of movement intention through motor imagery and execution on CMC dynamics in both the auditory and visual modality. As discussed in Chapters 4 and 6, hypothesis (i) was not supported for passive listening in either the auditory or visual modality. However, results suggest that the effect that rhythms in the environment have on CMC might be modulated by movement intention. Hypothesis (ii) was supported, as movement intention modulated CMC. Imagining tapping along to a visual metronome

dynamically modulated CMC, and CMC dynamics were time-locked to taps during tapping movement, partially supporting hypothesis (iii). Most notably, dynamic changes in CMC were time-locked to the movement dynamics rather than stimulus events, showing that CMC is more strongly modulated by rhythmic movement than rhythm perception. Moreover, CMC dynamics were more strongly modulated during motor execution than motor imagery, indicating a role for bottom-up proprioceptive and/or somatosensory feedback in CMC.

Neither experiment found a direct relation between motor performance and CMC, as neither average force, nor force fluctuation, nor synchronised tapping accuracy and variability, were related to CMC magnitude. However, the findings do suggest that CMC dynamics might play a role in the control of rhythmic movement synchronised to sensory rhythms, as CMC dynamics were seen to be tightly linked to movement dynamics and are not present in similar form during imagined synchronised movement.

7.2 Effect of rhythms on CMC

As stated previously, the passive listening and/or observation of sensory rhythms was insufficient to spontaneously modulate CMC. This finding seems to contradict previous studies that have found effects of sensory (auditory and visual) stimuli on CMC (Piitulainen et al., 2015; Safri et al., 2006, 2007; Varlet et al., 2020b). However, those studies did not “passively” present sensory stimuli, as was the case in Experiments 1 and 2. Safri et al. (2006, 2007) implemented an attentional task, as concurrent visual stimuli needed to be ignored, which elicited additional attentional demands, rather than “passive” observation of rhythmic stimuli. This is in line with Divekar and John’s (2013) view on CMC that proposes CMC magnitude to be modulated by the effortfulness of the performed task. Hence, increased CMC was observed for the conditions where visual stimuli needed to be ignored, i.e., the most effortful conditions, in Safri et al. (2006, 2007).

Piitulainen et al. (2015), in similar fashion, presented auditory and visual distractors. The distractors even showed a startle-like response in the EMG. In contrast, during both Experiment 1 and 2 in this thesis, EMG magnitude was measured and successfully kept steady across trials. The stimuli used in Experiment 1 and 2 were mostly predictable, as they contained a repeating rhythmic structure, therefore not startling participants, as distractor stimuli might (Piitulainen et al., 2015).

Varlet et al. (2020b) seems to be the only study that found CMC to be modulated by passive rhythmic sensory stimulation, i.e., there was no motor or cognitive-attentional task required. Thus, this study found spontaneous dynamic CMC modulations due to stimulation with sensory rhythms. Varlet et al. (2020b) found no differences in overall CMC magnitude, which is in line with the findings of Experiment 1. Instead, changes in CMC dynamics time-locked to a bimodal (audio-visual) metronome were observed. This could explain the lack of modulation of CMC in Experiment 1 and 2, as unimodal auditory and visual stimuli were used.

Varlet et al. (2020b) found a rather small effect, only in the bimodal condition at 2 Hz. Unimodal conditions of auditory-only and visual-only metronomes did not induce similar changes in CMC, neither did presentation at 1 Hz, not even in the bimodal condition. This is in line with the findings of Experiment 2 where passive listening and observation did not modulate CMC, as participants were attending the metronomes unimodally. Although both visual and auditory information were presented in the same trials in Experiment 2, they appeared interleaved rather than bimodal, i.e. they were not integrated in perception as originating from a single event. Thus, the results from Varlet et al. (2020b) might be explained by a benefit due to stronger neural responses that are specific to the bimodal rhythm. This could be supported by beta EEG power changes accompanying dynamical CMC modulations in Varlet et al. (2020b), whereas in Experiments 1 and 2 no differences between

(time-averaged) EEG beta power were observed. An additional difference was the short trials (16 stimulus cycles) in Varlet et al. (2020b), compared to the long trials in both Experiment 1 and 2, which suggests that attentional engagement, fatigue, or slow drift in contraction force might be affecting the observed CMC dynamics. Moreover, a letter detection task was included in Varlet et al. (2020b) to ensure high vigilance during the stimulus presentation, which might have contributed to further attentional engagement.

The finding by Varlet et al. (2020b) that the effect was sensitive to stimulus frequency could also explain findings in both Experiment 1 and 2. In Experiment 1 the tempo was controlled for, only in the sense that high-groove and low-groove conditions had a similar mean and spread of tempi. However, all excerpts had a different tempo. As previously explained in Chapter 3, the dynamics could thus not be examined, and a lack of difference between the average beta CMC magnitude is in line with the findings of Varlet et al. (2020b). In Experiment 2, the presentation frequency was 1.25 Hz, which was based on comfortable synchronisation with both visual and auditory sequences (Patel et al., 2005). Compared to the observation of Varlet et al. (2020b), this might not be the ideal frequency to modulate CMC magnitude or dynamics. The stimulus frequency specific effect found by Varlet et al. (2020b) was argued to be related to the preferred movement frequency of the body (2 Hz), which is thought to relate to the biomechanical properties of human locomotion (Bouvet et al., 2019a, 2019b; Large, 2008; MacDougall and Moore 2005; Todd and Lee 2015;). This finding shows that the CMC modulation of finger muscles is specific to a systemic frequency, i.e. 2 Hz, rather than eigenfrequencies for individual limbs (Damm et al., 2019), as the natural oscillator frequency of the finger lies around 4 Hz (Collyer et al., 1992, 1994), which suggests that the facilitation effect of 2 Hz might be related to the system's general processing preferences (Michaelis et al., 2014).

In sum, passive listening and/or observation of sensory rhythms did not modulate CMC, possibly due to an attenuated EEG response, as a result of predictability, fatigue, and/or slow stimulus frequency.

7.3 The effect of movement intention on CMC (dynamics)

To test hypothesis (ii): “Movement intention modulates cortico-muscular coupling, i.e., rhythmic movement as well as motor imagery in time with a metronome”, the effect of movement intention was studied at three different levels across the experiments: First by passively perceiving rhythms that induce different intensities of the urge to move, i.e. high and low groove, second by imagining synchronised movement, and third by performing synchronised movements.

In Experiment 1, the passively induced urge to move was not sufficient to modulate CMC. The results of Experiment 2, on the other hand, did support hypothesis (ii). Motor imagery was sufficient to affect CMC dynamics, although only when imagining movement with visual sequences. Nonetheless, this suggests that CMC *can* be modulated by top-down influences, such as movement intention. Possible reasons for this discrepancy between modalities have been discussed in Chapter 5, and include the magnitude of evoked neural responses and level of cognitive and/or attentional demands for coordinated movement timing that might be modality dependent.

Executed and imagined movement was found to modulate CMC dynamics rather than overall CMC magnitude, partially supporting hypothesis (iii). For executed movement, CMC was time-locked to movement dynamics, as has been previously found for non-isometric hand movements (Glories et al., 2021; Kilner et al., 2003) and other rhythmic movement tasks, such as walking (Artoni et al., 2017; Petersen et al., 2012) and ankle circling (Yoshida et al., 2017a, 2017b). CMC peaked during the stabilising part of the movement, mimicking

the EEG beta power trajectory, in line with previous research (Artoni et al., 2017; Kilavik et al., 2013; Roeder et al., 2020). This finding underscores views like those expressed by Bourguignon et al. (2019), who argue that CMC is a by-product of motor activity structured after the 20 Hz component of the mu rhythm, rather than reflecting motor processes playing a critical role in cortico-muscular coupling.

Although the CMC dynamics were clearly in line with known and observed EEG beta power dynamics such as a clear drop during movement and a post-movement rebound (Kilavik et al., 2013), the CMC modulations were much larger and clearer than the measured EEG dynamics in Experiment 2. These clear cortico-muscular dynamics provide an argument that CMC is a valuable tool in studying cortical dynamics in motor control (Bourguignon et al., 2019). Beta band cortical activity (~ 20 Hz) can be contaminated by a variety of sources, most commonly by nearby distinct neuronal populations. It is difficult, if not impossible, to separate such nearby sources based on their topography (Bourguignon et al., 2019). Source localisation could provide additional insight here, but CMC is also a very effective tool to separate cortical sources of nearby muscles. EMG activity contains 20 Hz beta activity free from cortical cross-contamination from nearby, yet distinct, sources. It is specific to the given muscle and the cortical motor neurons projecting to the motor pool of this muscle (Bourguignon et al., 2019). Thus, coherence between EMG and EEG activity is an effective tool to assess fluctuations in motor cortical dynamics for specific muscles or coordination between muscle pairs. CMC can, for example, be used in more complex tasks such as reaching and grasping (Fang et al., 2009) to assess agonist-antagonist cortico-muscular dynamics (Desmyttere et al., 2018; Fang et al., 2009).

The additional value of CMC is underscored by the observation that the beta EEG power dynamics did not differ for any of the imagined and control conditions, in contrast

with the CMC dynamics. This finding indicates that CMC dynamics are either more sensitive or hold additional information compared to EEG dynamics.

7.4 Mechanisms of CMC

7.4.1 Top-down

In line with several top-down views on CMC (e.g., Brown et al., 1998; Gross et al., 2000; Murayama et al., 2001; Salenius et al., 1997), Experiment 2 provided some evidence for CMC being a top-down efferent mechanism, as motor imagery was sufficient to modulate CMC. However, it should be noted that there were clear differences between modulation magnitude and timing compared to executed movement, providing evidence for other mechanisms affecting CMC.

Many studies have advocated for a top-down regulated mechanism of CMC driven by cortico-spinal efference (Brown et al., 1998; Gross et al., 2000; Murayama et al., 2001; Salenius et al., 1997). Several other studies have shown that top-down factors can modulate CMC. For example, Kristeva-Feige et al. (2002) showed decreased CMC when attention was divided between a motor precision and mental arithmetic task, and Johnson et al. (2011) showed a decrease of CMC with both motor and cognitive dual tasks.

The results of Experiment 2 might support the view that CMC reflects the 20 Hz motor rhythm, and that lower CMC magnitude is due to a lack of ~20-Hz bursts in EMG (Bourguignon et al., 2017). The idea that CMC is driven by efferent motor commands is reinforced by the result of the tapping conditions showing CMC modulations time-locked to the movement dynamics. However, the large difference in modulation magnitude between imagined and executed movement clearly indicates additional contributions to CMC during movement execution. The main difference, as discussed in Chapter 5, is the displacement of the finger, the discharge of motor-neurons, and the somatosensory and/or proprioceptive

feedback this provides. This finding therefore suggests an additional role for bottom-up proprioceptive and/or somatosensory feedback to modulate CMC.

7.4.2 Bottom-up

As elaborated in section 7.2, Experiment 1 and 2 did not find any effects of external auditory or visual stimulus sequences on CMC. Instead, bottom-up somatosensory and/or proprioceptive feedback might be highly relevant to CMC (Gwin and Ferris, 2012; Kilner et al., 2004). As previously shown by several studies, bottom-up somatosensory feedback plays a significant role in CMC and can modulate CMC magnitude. For example, Kilner et al. (2004) found that a closed sensorimotor loop was necessary for the appearance of CMC in a de-afferent case. Fisher et al. (2002) showed a significant decrease in CMC when the digital nerve was blocked from providing somatosensory feedback. Several analyses using Granger causality also showed both efferent and afferent contributions to CMC (Lim et al., 2014; Tsujimoto et al., 2009; Witham et al., 2011, 2010).

From the observations in Experiment 1 and 2, the strongest modulation of beta CMC was seen during executed movement. As noted in section 5.4, the difference between imagined and executed movement is the somatosensory and/or proprioceptive resulting from the executed movement. Experiment 1 and 2 showed no effect of external rhythmic stimuli on CMC and only a small modulation of CMC during motor imagery, compared to executed movement. These results indicate that somatosensory and/or proprioceptive feedback might be one of the strongest possible modulators of CMC during motor tasks.

7.4.3 Somatosensory feedback gain

Experiment 2, as well as other studies, have shown both top-down and bottom-up influences on CMC. That is, top-down influences of attention and movement intention (Divekar and John, 2013; Johnson et al., 2011; Kristeva-Feige et al., 2002) and a clear

influence of somatosensory feedback (e.g., Fisher et al., 2002; Kilner et al., 2004), as described in sections 7.4.1 and 7.4.2. Thus, CMC might reflect a more bidirectional mechanism, potentially involved in the coupling of top-down and bottom-up information, i.e. sensorimotor binding (Gerlof, 2002; Kasuga et al., 2018; Witham et al., 2011).

Sensorimotor integration during movement tasks, i.e. the coupling between motor activity and its sensory feedback, has previously been attested by CMC (Witham et al., 2007, 2010, 2011). Sensorimotor and parietal areas have shown significant beta-band cortico-muscular coherence during finger movements (Witham et al., 2010), even with larger amplitude than CMC in the primary motor area (Witham and Baker, 2007). Moreover, Witham et al. (2010) found stronger beta-band coherence from the primary somatosensory cortex to the primary motor cortex, than in the reverse direction. This suggests that beta-band cortical oscillations are involved in sensorimotor feedback and may contribute to the integration of motor output and sensorimotor input (Kasuga et al., 2018). The effective integration of sensory and motor information is particularly relevant for adapting to a novel environment or a highly demanding motor task, providing appropriate motor adaptations (Kasuga et al., 2018).

Motor adaptations can be achieved through scaling (somato)sensory feedback gain (Azim and Seki, 2019). The precision of the executed movement would then be a measure of the effectiveness of sensorimotor integration and its motor adaptations, through somatosensory feedback gain. This could explain some of the differences in CMC magnitude between participants (Mendez-Balbuena et al., 2012) and the increase of CMC with motor learning. For instance, early adaptation that disappears with motor expertise (Dal Maso et al., 2017; Ushiyama et al., 2010), as motor adaptations have occurred and somatosensory feedback gains have ceased (Kasuga et al., 2018). Somatosensory feedback gains can then also explain Divekar and John's (2013)'s account of CMC being related to "effortfulness" of

the motor task, as feedback gains are enhanced during demanding tasks or in novel movement contexts (Azim and Seki, 2019). Somatosensory feedback gains might thus explain the dynamical modulation found only in the visual imagining condition in Experiment 2, as visual-motor synchronisation is more challenging than auditory-motor synchronisation. Moreover, dysfunctional feedback gains, lead to a variety of movement pathologies (Azim and Seki, 2019), explaining decreased and altered CMC in Parkinson's (Roeder et al., 2020; Salenius et al., 2002), post-stroke (Fang et al., 2009; Guo et al., 2020; Krauth et al., 2019; Rossiter et al., 2013), and cerebral palsy patients (Riquelme et al., 2014).

7.5 CMC function

CMC magnitude did not relate to movement performance in Experiment 1 and 2. That is, CMC was not correlated with mean force, force variability or synchronised tapping performance. These results are in line with previous studies demonstrating no effect of changes in CMC magnitude on contraction force (Hari et al., 2014; Piitulainen et al., 2015; Tecchio et al., 2006). Therefore, the results from Experiment 1 and 2 do not provide evidence for CMC being a direct motor performance indicator and it is not very likely that CMC is directly involved in motor control per se. This is in line with several accounts of CMC, including the previously mentioned by Bourguignon et al. (2019). In their review, Bourguignon et al. (2019) posit that CMC reflects the 20 Hz structuring of motor commands, rather than motor control processes per se. However, their view clearly posits CMC as a top-down mechanism, arguing that CMC is mainly driven by efferent (20 Hz) signals and the “burstiness” of the ~20 Hz sensorimotor rhythm, and rejects the view of CMC being a binding mechanism. Instead, Bourguignon et al. (2017) argue that “the cortex sends population-level motor commands that tend to structure according to the ~20 Hz

sensorimotor rhythm, and that it dynamically adapts these commands based on the <3 Hz fluctuations of proprioceptive feedback”. Therefore, they presume that although the motor command is adapted based on proprioceptive feedback, cortical activity drives the periphery, and CMC does not reflect feedback from the periphery. This is quite an elegant, minimalist view of mechanisms underlying CMC, however it does not fully acknowledge the previously mentioned studies providing evidence for somatosensory and/or proprioceptive contributions to CMC. In particular, Kasuga and colleagues’ (2018) evidence for CMC’s sensitivity to feedback gains. It is clear that a consensus on the mechanisms and function of CMC is yet to be formed. Based on the findings from the two studies in this thesis and the wider literature, such consensus is likely to include some form of integration of efferent motor commands and afferent feedback.

7.6 Relevance of CMC for SMS

As discussed in 7.5, CMC magnitude did not relate to movement performance in these two studies. That is, an individual’s CMC magnitude was not related to mean force, force variability or synchronised tapping performance. Therefore, it is unlikely that CMC is a direct movement performance indicator. Understanding its underlying mechanisms might nonetheless be relevant for the future study of motor control and movement performance, considering that abnormal CMC is associated with movement pathology. Gaining a deeper understanding of CMC would provide a more precise understanding of pathological motor control.

Furthermore, CMC dynamics were clearly linked to movement dynamics. Thus, CMC might be a unique measure to study dynamic cortical motor control (Bourguignon et al.,

2019). Potentially, in the future, through its links with movement dynamics, CMC dynamics could inform on motor control or performance parameters.

7.6.1 Training and expertise

Based on the lack of correlation between movement performance and CMC magnitude from Experiment 1 and 2, there seems to be no need to aim for a particular increase or decrease in CMC to increase movement performance. However, understanding the mechanisms behind CMC for motor functioning and control can have implications for athletes aiming to improve their movement performance. Although not specifically covered in the two experiments in this thesis, inter-individual differences have been uncovered in CMC. Individuals vary in their relative ratio of top-down to bottom-up contributions to CMC (Riddle and Baker, 2005; Witham et al., 2011), which might be related to the individual's scaling of feedback gains (Kasuga et al., 2018). CMC has been shown to indicate individual-dependent efficiency of motor command delivery to the periphery (Bourguignon et al., 2017), which might explain vastly different CMC values for similar force levels between participants in Experiment 1. Further understanding of the origin and function of the mechanisms underlying CMC might ultimately aid athletes and other movement experts in improving their performance as a function of cortico-muscular efficiency and/or motor learning.

7.6.2 Pathology

Compared to the healthy population, altered CMC, usually decreased CMC magnitude, has been observed for many clinical populations, such as post-stroke patients (Fang et al., 2009; Guo et al., 2020; Krauth et al., 2019; Rossiter et al., 2013), Parkinson's patients (Roeder et al., 2020; Salenius et al., 2002), and cerebral palsy patients (Riquelme et al., 2014). Therefore, much is to be gained for these populations from understanding the mechanisms behind CMC and the factors that might modulate it. The benefits of

understanding CMC mechanisms also extend to the wider population of healthy older adults. Healthy older adults undergo similar decreases in CMC as certain clinical populations, such as Parkinson's patients (Roeder et al., 2020). Ultimately benefits of understanding CMC could include the possibility to increase or alter CMC and in turn motor function. It would further provide a deeper understanding of the problems encountered in motor control processes experienced by clinical populations plagued by pathologically low CMC.

The findings of Experiment 1 and 2 imply that clinical populations with altered, often decreased magnitudes of CMC, might benefit more from motor imagery, and even more from integrated motor practice with rhythmic stimulation, than passive exposure to rhythm. This finding is supported by research on the effectiveness of rhythmic auditory stimulation in Parkinson's rehabilitation (Schaefer et al., 2014) and motor imagery strategies in post-stroke patients (Pichiorri et al., 2015).

The indication of somatosensory feedback gains playing a crucial role in CMC modulation during movement might suggest that decreased motor performance, accompanied by decreased CMC, might partly be due to the loss of somatosensory integration in clinical populations. This is underscored by a recent review by Pillette et al. (2020) on motor rehabilitation in stroke patients. The review states that somatosensory impairments are common and diverse in stroke patients and affect motor rehabilitation outcomes (Pillette et al., 2020). Moreover, somatosensory stimulation has been shown to increase excitability of the motor cortex and improve motor function of post-stroke patients (Edwards et al., 2019; Kessner et al., 2016). In Parkinson's patients, a pathological decline in haptic feedback and somatosensory integration was also observed (Konczak et al., 2012). The authors argued that common sensorimotor problems in Parkinson's disease may have a sensory origin. Further, observations in cerebral palsy patients highlight the importance of sensorimotor integration impairments and somatosensory deficits (Kurz et al., 2014, 2015; Riquelme and Montoya,

2010; Wingert et al., 2009). These somatosensory impairments and related sensorimotor integration abnormalities, found in pathological motor control related to clinical populations with altered CMC, support the view that the integration of (somato)sensory feedback is an essential component of healthy cortico-muscular coupling, giving rise to CMC dynamics.

The finding of Experiment 2, that motor execution provides stronger CMC modulation than motor imagery alone, supports the idea of developing post-stroke rehabilitation including motor imagery and integrated somatosensory feedback. Such rehabilitation strategies have shown stronger improvement than motor imagery alone (Pichiorri et al., 2015). It would be of further interest to study the effect of somatosensory impairment on CMC magnitude and dynamics in clinical populations prior, during, and after motor rehabilitation. Brain Computer Interface (BCI) based rehabilitation strategies would be of particular interest as they allow for co-activation of ascending (i.e., somatosensory) and descending (i.e., motor) networks. Using BCIs has proven to be an effective tool for motor rehabilitation, inducing significant functional motor improvement, as well as significant sensorimotor-related neurophysiological changes (Pilletto et al., 2020).

7.7 Future directions

Future investigations could use CMC as a tool to further study cortical and cortico-muscular dynamics of movement execution and explore a wider variety of motor tasks that are tightly controlled and standardised. Current literature still largely focusses on static isometric tasks. However, more studies that clearly show dynamic CMC during dynamic movement are emerging, including Experiment 2. These studies encourage cortical and cortico-muscular dynamics of a wider variety of complex motor tasks to be explored. CMC provides great opportunities to study the cortical drive to separate muscles that is

uncontaminated by other nearby sources of cortical activity to investigate agonist-antagonist dynamics. For example, agonist-antagonist CMC could be studied in a finger tapping task such as Experiment 2, or in more complex motor actions, such as reaching and grasping. Further synchronised movements to external rhythms could be investigated in a more continuous paradigm, like continuous force fluctuations. In such complex motor tasks, the effect of motor imagery on CMC strength could further be explored to provide a greater understanding of top-down and bottom-up contributions to CMC during active movement and synchronisation with the environment.

7.8 Conclusion

In conclusion, the current thesis provided insight on the dynamic cortico-muscular activity involved in SMS. Although the current findings require caution when interpreting, indications have been given of a role for both top-down, and somatosensory and/or proprioceptive (bottom-up) contributions to CMC during SMS, as conceptualised in Figure 1. Further investigations to understand the mechanisms and function of CMC within and outside of SMS paradigms are necessary, because they have implications for clinical and elderly populations with decreased or otherwise abnormal CMC, as well as for optimisation of movement performance in elite athletes.

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