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

Patti Nijhuis[a,*], Peter E. Keller[a], Sylvie Nozaradan[b], Manuel Varlet[a,c]

[a] The MARCS Institute for Brain, Behaviour and Development, Western Sydney University, Sydney, Australia
[b] Institute of Neuroscience (Ions), Université catholique de Louvain (UCL), Belgium
[c] School of Psychology, Western Sydney University, Sydney, Australia

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ABSTRACT

People have a natural and intrinsic ability to coordinate body movements with rhythms surrounding them, known as sensorimotor synchronisation. This can be observed in daily environments, when dancing or singing along with music, or spontaneously walking, talking or applauding in synchrony with one another. However, the neurophysiological mechanisms underlying accurately synchronised movement with selected rhythms in the environment remain unclear. Here we studied real and imagined sensorimotor synchronisation with interleaved auditory and visual rhythms using cortico-muscular coherence (CMC) to better understand the processes underlying the preparation and execution of synchronised movement. Electroencephalography (EEG), electromyography (EMG) from the finger flexors, and continuous force signals were recorded in 20 participants during tapping and imagined tapping with discrete stimulus sequences consisting of alternating auditory beeps and visual flashes. The results show that the synchronisation between cortical and muscular activity in the beta (14-38 Hz) frequency band becomes time-locked to the taps executed in synchrony with the visual and auditory stimuli. Dynamic modulation in CMC also occurred when participants imagined tapping with the visual stimuli, but with lower amplitude and a different temporal profile compared to real tapping. These results suggest that CMC does not only reflect changes related to the production of the synchronised movement, but also to its preparation, which appears heightened under higher attentional demands imposed when synchronising with the visual stimuli. These findings highlight a critical role of beta band neural oscillations in the cortical-muscular coupling underlying sensorimotor synchronisation.

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., 2021; Néda et al., 2000; van Ulzen et al., 2008; Varlet et al., 2020). 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., 2020).

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;

* Corresponding author at: MARCS Institute for Brain, Behaviour and Development, Western Sydney University, Locked Bag 1797, Penrith NSW 2751, Australia.
E-mail address: p.nijhuis@westernsydney.edu.au (P. Nijhuis).

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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 in 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 Bülthoff, 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 Bülthoff, 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 (Elliott 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., 2012). 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 intends 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 imaginary 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 the 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 imaginary 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 imaginary 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 where expected in the real and imaginary 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.

2. Methods

2.1. Participants

A total of 23 healthy right-handed subjects 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).

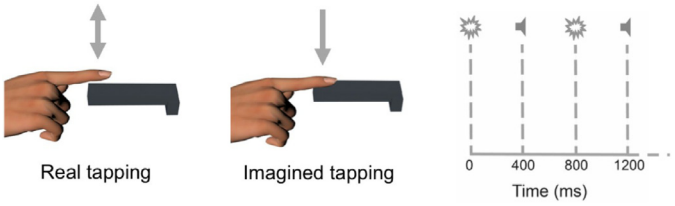

Fig. 1. Schematic representation of the Real and Imagined tapping conditions and of the interleaved audio-visual stimulus sequence.

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 Fig. 1). 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.

2.3. Apparatus

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.

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.

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.

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 the 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.

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.

2.5. Data analysis

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 (Białuńska 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).

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 4^{th} 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 4^{th} 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.

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., 2020). 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.

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 × 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 participants' 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; 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 and Shinohara, 2012; 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).

2.6. Statistical analysis

All statistical analyses were performed in jamovi version 0.9.5.12 (The jamovi project, 2019). 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).

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.

3.1. Movement synchronisation

As shown in Fig. 2A, 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 Fig. 2B and 2C).

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.

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 Fig. 3A, 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 Fig. 3A) 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 Fig. 3D, 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-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 Fig. 3B). 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-values* > .05).

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 Fig. 3B. The amplitude of EMG beta power was maximal around 250 ms before the auditory stimulus, in the Auditory

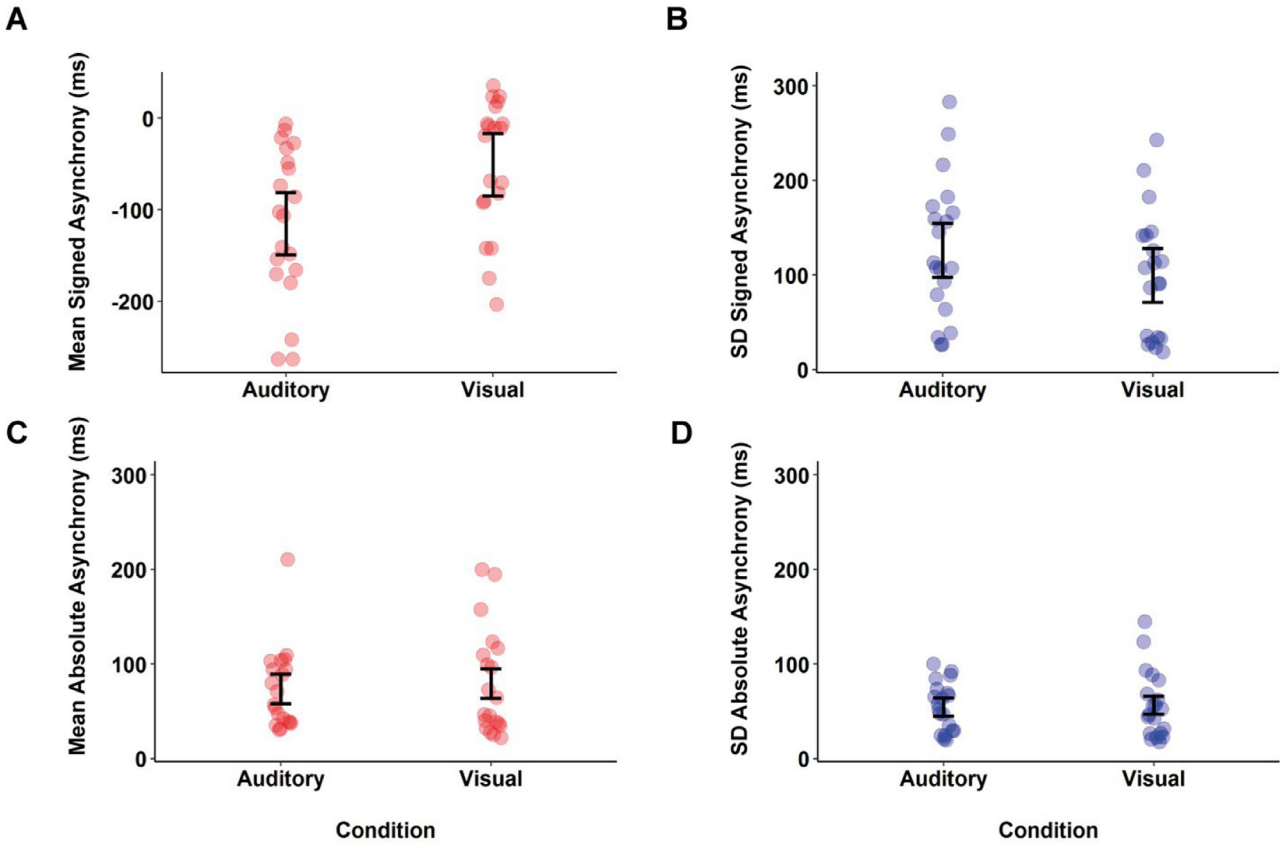

Fig. 2. Tapping performance. Mean and standard deviation of signed asynchronies (A and and B) and absolute asynchronies (C and D) for the visual and auditory conditions. Error bars represent 1 × CI of the mean computed for within-subject designs (Morey, 2008).

Tapping condition. The amplitude of EMG beta power was maximal 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 Fig. 3B) 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 Fig. 3E, 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-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 Fig. 3D). 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-values* > .05, see Fig. 3H). 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-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.

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 Fig. 3C, 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 Fig. 3C) that confirmed this effect of time (*p-values* < .05).

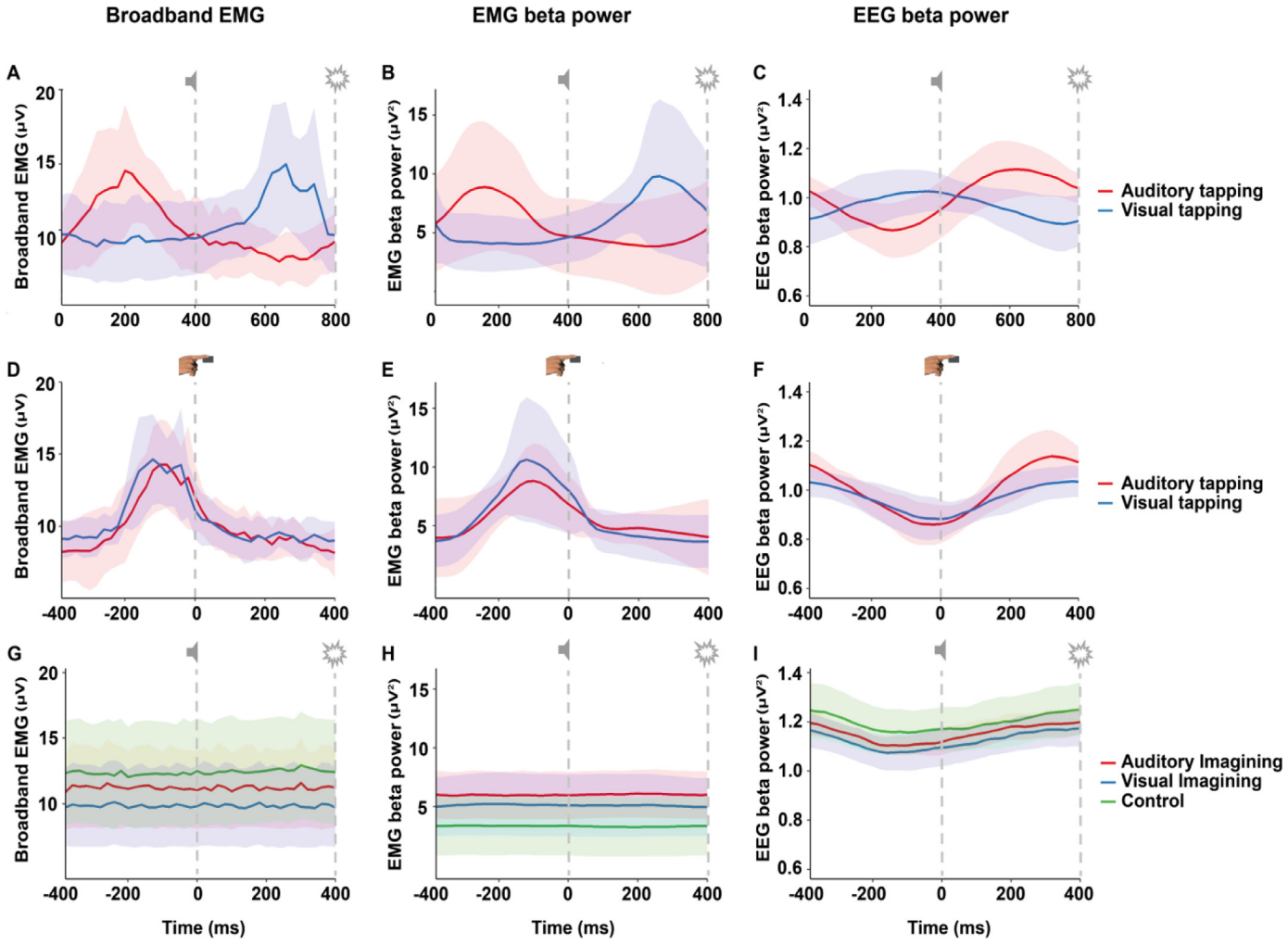

Fig. 3. Broadband EMG, EMG beta (14-38 Hz) power, and EEG beta (14-38 Hz) power as a function of time for the two tapping conditions (panels A, B, and C for stimulus-locked data, and panels D, E, and F for tap-locked data), and for the three isometric conditions (panels G, H, and I). Shaded areas represent 1 × CI of the mean computed for within-subject designs (Morey, 2008).

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-values* > .05), showing that there was no robust difference between visual and auditory conditions. As seen in Fig. 3F, 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 Fig. 3D), 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 Fig. 3I). 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 Fig. 3I) prior to the auditory stimulus (~200-400 ms, *p-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-values* > .05), suggesting that dynamic modulations exhibited at the electrodes of interest had similar temporal pattern irrespective of the instruction.

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 Fig. 4. 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).

3.4.1. Frequency response

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 $\eta^2 = .124$.

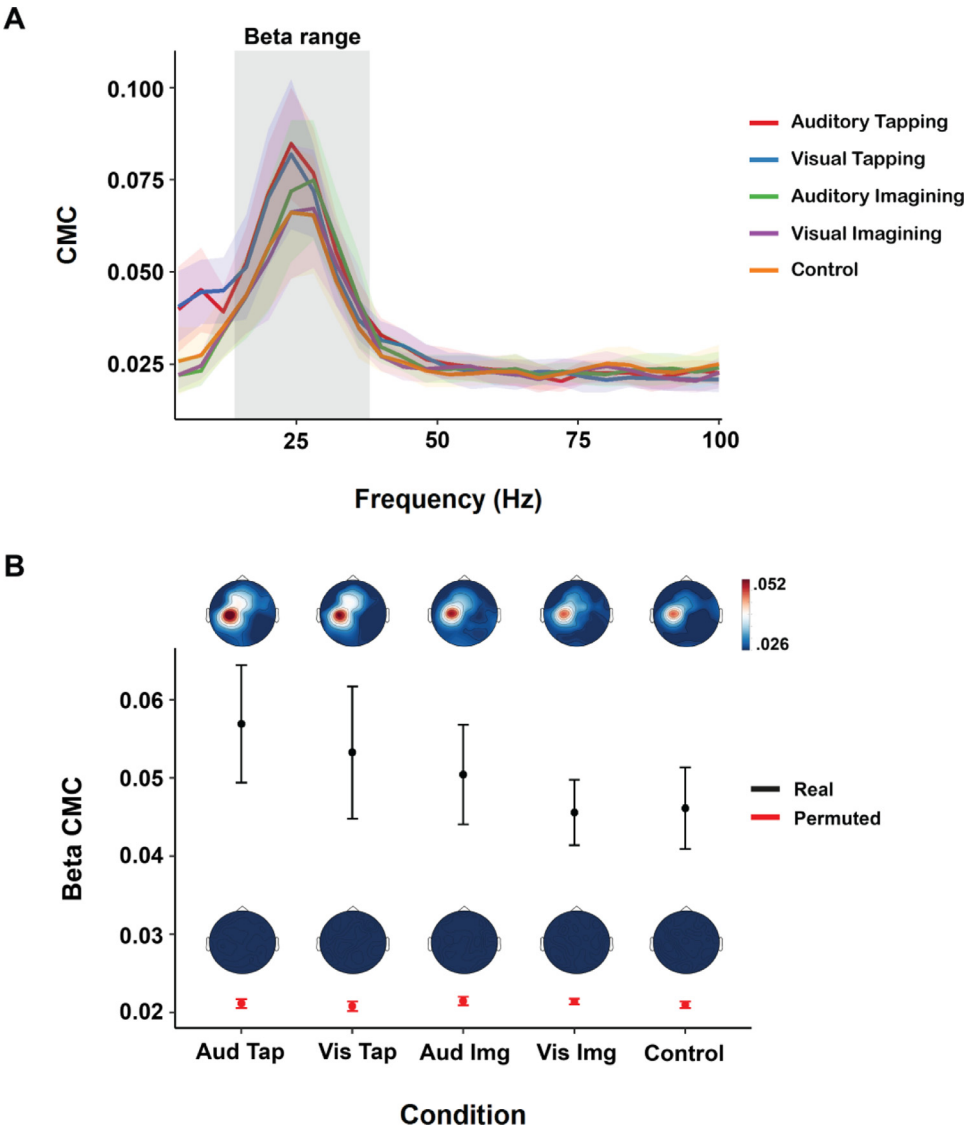

Fig. 4. CMC at the individual maximum electrode for the five conditions as a function of frequency from 0 to 100 Hz (panel A) and averaged in the beta range between 14 and 38 Hz for Real and Permuted data, with the corresponding grand average topographical maps (panel B). The colour bar represents the beta CMC amplitude on the topographical maps. Shaded areas and error bars represent 95 % confidence intervals.

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 Fig. 4. 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-values* < .05, see Fig. 4A). 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-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 and 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 higher 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 $\eta^2 = .126$.

3.4.2. Dynamic beta (14-38 Hz) CMC

As depicted in Figs. 5 and 6, 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 imaginary 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 Fig. 5A). 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 Vi-

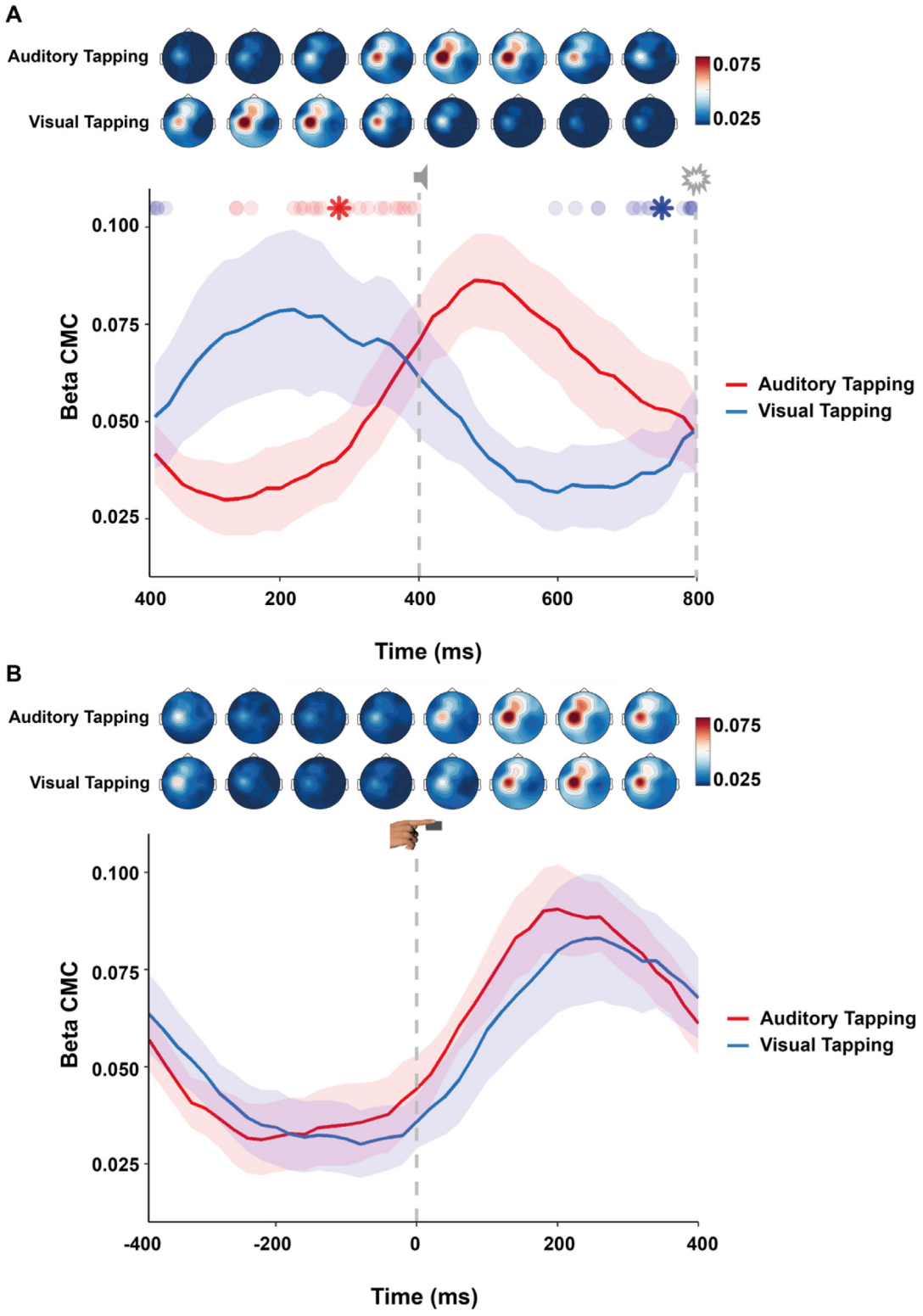

Fig. 5. Beta (14-38 Hz) CMC at the individual maximal electrode over the duration of one stimulus cycle (A) and realigned according to participants' mean tap timing (B) for the two tapping conditions, with the corresponding grand average topographical maps averaged within 100 ms time intervals. Asterisks 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.

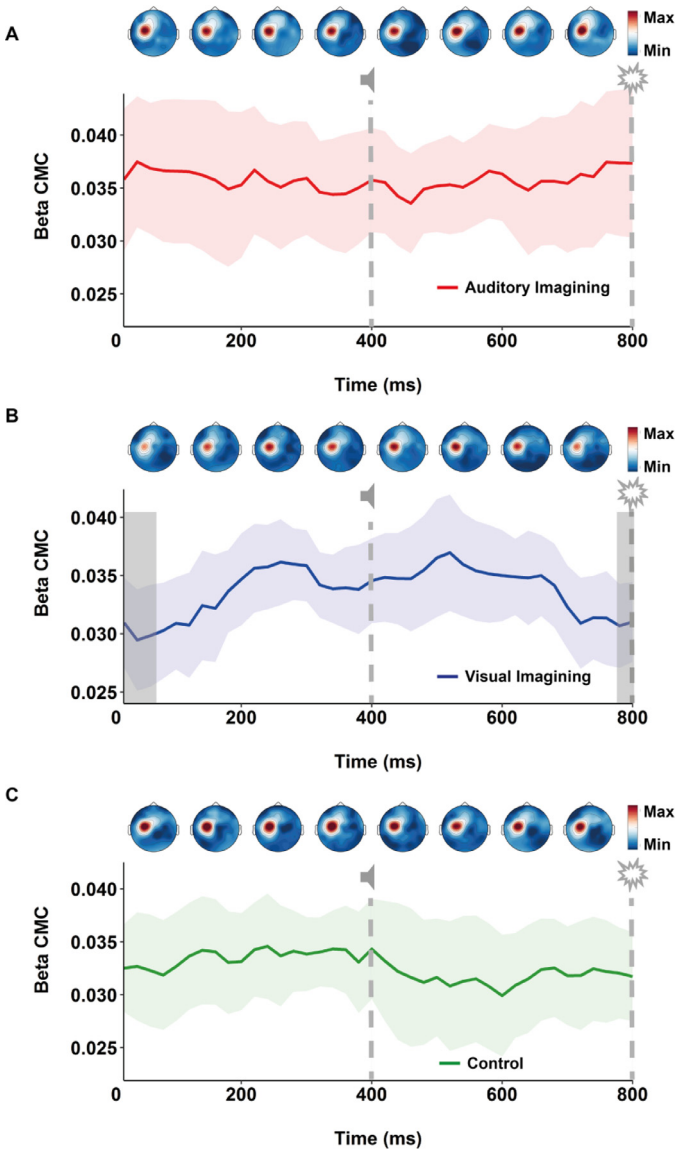

Fig. 6. Beta (14-38 Hz) CMC at the individual maximal electrode over the duration of one stimulus cycle for the three isometric conditions, (A) Auditory Imagining, (B) Visual Imagining, and (C) Control, with the corresponding grand average topographical maps averaged within 100 ms time intervals. Significant 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.

sual Tapping condition. Cluster-based permutation tests indicated large significant clusters with significant deviations from the mean (not represented in Fig. 5) that confirmed this effect of time in both real tapping conditions (*p-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-values* > .05). As seen in Fig. 5B, 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-values* > .05).

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 Fig. 6C. 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 Fig. 6A. 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 Fig. 6B), 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).

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).

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, a fine motor skill. 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 and Halsband, 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 imagined 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 related 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., 2012). 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; Loräs 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, 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 re-

sulted 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 (Białuńska et al., 2011; Hove et al., 2010; Repp, 2003; Zelic et al., 2019), which would need to be explored in future research.

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.

Data accessibility statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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References

Arnal, L.H., 2012. Predicting “when” using the motor system’s beta-band oscillations. Front. Human Neurosci. 6, 225. doi:10.3389/fnhum.2012.00225.
Baker, S.N., 2007. Oscillatory interactions between sensorimotor cortex and the periphery. Curr. Opin. Neurobiol. 17 (6), 649–655. doi:10.1016/j.conb.2008.01.007.
Bastos, A.M., Schoffelen, J.M., 2016. A tutorial review of functional connectivity analysis methods and their interpretational pitfalls. Front. Syst. Neurosci. 9, 175. doi:10.3389/fnsys.2015.00175.
Bengtsson, S.L., Ullén, F., Henrik Ehrsson, H., Hashimoto, T., Kito, T., Naito, E., Forssberg, H., Sadato, N., 2009. Listening to rhythms activates motor and premotor cortices. Cortex 45 (1), 62–71. doi:10.1016/j.cortex.2008.07.002.
Białuńska, A., Dalla Bella, S., Jaśkowski, P., 2011. Increasing stimulus intensity does not affect sensorimotor synchronization. Psychol. Res. 75 (1), 43–53. doi:10.1007/s00426-010-0282-7.
Boonstra, T.W., Breakspear, M., 2012. Neural mechanisms of intermuscular coherence: implications for the rectification of surface electromyography. J. Neurophysiol. 107 (3), 796–807. doi:10.1152/jn.00066.2011.
Bourguignon, M., Piitulainen, H., Smeds, E., Zhou, G., Jousmäki, V., Hari, R., 2017. MEG insight into the spectral dynamics underlying steady isometric muscle contraction. J. Neurosci. 37 (43). doi:10.1523/JNEUROSCI.0447-17.2017, 0447–17.
Bourguignon, M., Jousmäki, V., Dalal, S.S., Jerbi, K., De Tiège, X., 2019. Coupling between human brain activity and body movements: Insights from non-invasive electromagnetic recordings. Neuroimage 203, 116177. doi:10.1016/j.neuroimage.2019.116177.
Bouvet, C.J., Bardy, B.G., Keller, P.E., Dalla Bella, S., Nozaradan, S., Varlet, M, 2020. Accent-induced modulation of neural and movement patterns during spontaneous synchronization to auditory rhythms. J. Cogn. Neurosci. 32 (12), 2260–2271. doi:10.1162/jocn_a_01605.
Brinkman, L., Stolk, A., Dijkerman, H.C., De Lange, F.P., Toni, I., 2014. Distinct roles for alpha- and beta-band oscillations during mental simulation of goal-directed actions. J. Neurosci. 34 (44), 14783–14792. doi:10.1523/JNEUROSCI.2039-14.2014.
Burger, B., Thompson, M.R., Luck, G., Saarikallio, S.H., Toiviainen, P., 2014. Hunting for the beat in the body: on period and phase locking in music-induced movement. Front. Human Neurosci. 8, 903. doi:10.3389/fnhum.2014.00903.
Burgess, A.P., 2013. On the interpretation of synchronization in EEG hyperscanning studies: a cautionary note. Front. Human Neurosci. 7, 881. doi:10.3389/fnhum.2013.00881.
Cardellicchio, P., Dolfini, E., Hilt, P.M., Fadiga, L., D’Ausilio, A, 2020. Motor cortical inhibition during concurrent action execution and action observation. Neuroimage 208 (November 2019). doi:10.1016/j.neuroimage.2019.116445.
Carson, R.G., 1996. Neuromuscular-skeletal constraints upon the dynamics of perception-action coupling. Exp. Brain Res. 110 (1), 99–110. doi:10.1007/BF00241379.
Celma-Miralles, A., Toro, J.M., 2019. Ternary meter from spatial sounds: differences in neural entrainment between musicians and non-musicians. Brain Cogn. 136, 103594. doi:10.1016/j.bandc.2019.103594.
Chapin, H.L., Zanto, T., Jantzen, K.J., Kelso, S.J.A., Steinberg, F., Large, E.W, 2010. Neural responses to complex auditory rhythms: the role of attending. Front. Psychol. 1, 1–18. doi:10.3389/fpsyg.2010.00224.
Chen, J.L., Penhune, V.B., Zatorre, R.J., 2008. Listening to musical rhythms recruits motor regions of the brain. Cereb. Cortex 18 (12), 2844–2854. doi:10.1093/cercor/bhn042.
Chen, J.L., Penhune, V.B., Zatorre, R.J., 2009. The role of auditory and premotor cortex in sensorimotor transformations. Ann. N. Y. Acad. Sci. 1169, 15–34. doi:10.1111/j.1749-6632.2009.04556.x.
Chen, Y., Repp, B.H., Patel, A.D., 2002. Spectral decomposition of variability in synchronization and continuation tapping: comparisons between auditory and visual pacing and feedback conditions. Hum. Mov. Sci. 21 (4), 515–532. doi:10.1016/S0167-9457(02)00138-0.
Conway, B.A., Halliday, D.M., Farmer, S.F., Shahani, U., Maas, P., Weir, A.I., Rosenberg, J.R., 1995. Synchronization between motor cortex and spinal motoneuronal pool during the performance of a maintained motor task in man. J. Physiol. 489 (3), 917–924. doi:10.1113/jphysiol.1995.sp021104.
Divekar, N.V., John, L.R., 2013. Neurophysiological, behavioural and perceptual differences between wrist flexion and extension related to sensorimotor monitoring as shown by corticomuscular coherence. Clin. Neurophysiol. 124 (1), 136–147. doi:10.1016/j.clinph.2012.07.019.

De Vries, I.E.J., Daffertshofer, A., Stegeman, D.F., Boonstra, T.W, 2016. Functional connectivity in the neuromuscular system underlying bimanual coordination. J. Neurophysiol. 116 (6), 2576–2585. doi:10.1152/jn.00460.2016.

Doyle, L.M., Yarrow, K., Brown, P., 2005. Lateralization of event-related beta desynchronization in the EEG during pre-cued reaction time tasks. Clin. Neurophysiol. 116 (8), 1879–1888. doi:10.1016/j.clinph.2005.03.017.

Ehrsson, H.H., Geyer, S., Naito, E., 2003. Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. J. Neurophysiol. 90 (5), 3304–3316. doi:10.1152/jn.01113.2002.

Elliott, M.T., Wing, A.M., Welchman, A.E., 2010. Multisensory cues improve sensorimotor synchronisation. European Journal of Neuroscience 31 (10), 1828–1835. doi:10.1111/j.1460-9568.2010.07205.x.

Engel, A.K., Fries, P., 2010. Beta-band oscillations-signalling the status quo? Curr. Opin. Neurobiol. 20 (2), 156–165. doi:10.1016/j.conb.2010.02.015.

Ernst, M.O., Bülthoff, H.H., 2004. Merging the senses into a robust percept. Trends Cogn. Sci. 8 (4), 162–169. doi:10.1016/j.tics.2004.02.002.

Farah, M.J., 1984. The neurological basis of mental imagery: a componential analysis. Cognition 18 (1-3), 245–272. doi:10.1016/0010-0277(84)90026-X.

Farina, D., Negro, F., Jiang, N., 2013. Identification of common synaptic inputs to motor neurons from the rectified electromyogram. J. Physiol. 591 (10), 2403–2418. doi:10.1113/jphysiol.2012.246082.

Feige, B., Aertsen, A.D., Kristeva-Feige, R., 2000. Dynamic synchronization between multiple cortical motor areas and muscle activity in phasic voluntary movements. J. Neurophysiol. 84 (5), 2622–2629. doi:10.1152/jn.2000.84.5.2622.

Fries, P., 2005. A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. Trends Cogn. Sci. 9 (10), 474–480. doi:10.1016/j.tics.2005.08.011.

Fujioka, T., Zendel, B.R., Ross, B., 2010. Endogenous neuromagnetic activity for mental hierarchy of timing. J. Neurosci. 30 (9), 3458–3466. doi:10.1523/jneurosci.3086-09.2010.

Fujioka, T., Trainor, L.J., Large, E.W., Ross, B., 2012. Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. J. Neurosci. 32 (5), 1791–1802. doi:10.1523/JNEUROSCI.4107-11.2012.

Fujioka, T., Ross, B., Trainor, L.J., 2015. Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery. Front. Neurosci. 35 (45), 15187–15198. doi:10.3389/fnins.2016.00389.

Gan, L., Huang, Y., Zhou, L., Qian, C., Wu, X., 2015. Synchronization to a bouncing ball with a realistic motion trajectory. Sci. Rep. 5 (1), 1–9. doi:10.1038/srep11974.

Grahn, J.A., Brett, M., 2007. Rhythm and beat perception in motor areas of the brain. J. Cogn. Neurosci. 19 (5), 893–906. doi:10.1162/jocn.2007.19.5.893.

Grahn, J.A., McAuley, J.D., 2009. Neural bases of individual differences in beat perception. Neuroimage 47 (4), 1894–1903. doi:10.1016/j.neuroimage.2009.04.039.

Grahn, J.A., Henry, M.J., McAuley, J.D., 2011. FMRI investigation of cross-modal interactions in beat perception: audition primes vision, but not vice versa. Neuroimage 54 (2), 1231–1243. doi:10.1016/j.neuroimage.2010.09.033.

Halliday, D.M., Conway, B.A., Farmer, S.F., Rosenberg, J.R., 1998. Using electroencephalography to study functional coupling between cortical activity and electromyograms during voluntary contractions in humans. Neurosci. Lett. 241 (1), 5–8. doi:10.1016/S0304-3940(97)00964-6.

Halliday, D.M., Rosenberg, J.R., Amjad, A.M., Breeze, P., Conway, B.A., Farmer, S.F., 1995. A framework for the analysis of mixed time series/point process data-theory and application to the study of physiological tremor, single motor unit discharges and electromyograms. Prog. Biophys. Mol. Biol. 64 (2), 237.

Hansen, N.L., Nielsen, J.B., 2004. The effect of transcranial magnetic stimulation and peripheral nerve stimulation on corticomuscular coherence in humans. J. Physiol. 561 (1), 295–306. doi:10.1113/jphysiol.2004.071910.

Hari, R., Bourguignon, M., Piitulainen, H., Smeds, E., De Tiege, X., Jousmäki, V., 2014. Human primary motor cortex is both activated and stabilized during observation of other person's phasic motor actions. Philosoph. Trans. R. Soc. B 369 (1644), 20130171. doi:10.1098/rstb.2013.0171.

Hari, R., Salenius, S., 1999. Rhythmical corticomotor communication. Neuroreport 10 (2), 1–10.

Henry, M.J., Obleser, J., 2012. Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. Proc. Nat. Acad. Sci. 109 (49), 20095–20100. doi:10.1073/pnas.1213390109.

Hesterberg, T., Moore, D.S., Monaghan, S., Clipson, A., Epstein, R., 2005. Bootstrap methods and permutation tests. In: Moore, DS, McCabe, GP (Eds.), Introduction to the Practice of Statistics. WH Freeman and Company, pp. 1–70.

Hove, M.J., Iversen, J.R., Zhang, A., Repp, B.H., 2013. Synchronization with competing visual and auditory rhythms: bouncing ball meets metronome. Psychol. Res. 77 (4), 388–398. doi:10.1007/s00426-012-0441-0.

Hove, M.J., Keller, P.E., 2010. Spatiotemporal relations and movement trajectories in visuomotor synchronization. Music Perception 28 (1), 15–26. doi:10.1525/mp.2010.28.1.15.

Hove, M.J., Spivey, M.J., Krumhansl, C.L., 2010. Compatibility of motion facilitates visuomotor synchronization. J. Exp. Psychol. Hum. Percept. Perform. 36 (6), 1525–1534. doi:10.1037/a0019059.

Iversen, J.R., Patel, A.D., Nicodemus, B., Emmorey, K., 2015. Synchronization to auditory and visual rhythms in hearing and deaf individuals. Cognition 134, 232–244. doi:10.1016/j.cognition.2014.10.018.

Iversen, J., Repp, B., Patel, A., 2009. Top-down control of rhythm perception modulates early auditory responses. Ann. N. Y. Acad. Sci. 1169 (1), 58–73.

Jacques, C., Retter, T.L., Rossion, B., 2016. A single glance at natural face images generate larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain.. NeuroImage 137, 21–33. doi:10.1016/j.neuroimage.2016.04.045.

Janata, P., Tomic, S.T., Haberman, J.M., 2012. Sensorimotor coupling in music and the psychology of the groove. J. Experimen. Psychol. 141 (1), 54. doi:10.1037/a0024208.

Jeannerod, M., 1994. The representing brain: neural correlates of motor intention and imagery. Behav. Brain Sci. 17 (2), 187–202. doi:10.1017/S0140525X00034026.

Jeannerod, M., 1995. Mental imagery in the motor context. Neuropsychologia 33 (11), 1419–1432. doi:10.1016/0028-3932(95)00073-C.

Johnson, A.N., Shinohara, M., 2012. Corticomuscular coherence with and without additional task in the elderly. J. Appl. Physiol. 112 (6), 970–981. doi:10.1016/0028-3932(95)00073-C.

Jones, M.R., 1976. Time, our lost dimension: toward a new theory of perception, attention, and memory. Psychol. Rev. 83 (5), 323. doi:10.1037/0033-295X.83.5.323.

Kato, M., Konishi, Y., 2006. Auditory dominance in the error correction process: a synchronized tapping study. Brain Res. 1084 (1), 115–122. doi:10.1016/j.brainres.2006.02.019.

Keller, P.E., Novembre, G., Loehr, J.D., 2016. Musical ensemble performance: Representing self, other and joint action outcomes. In: Obhi, S.S., Cross, E.S. (Eds.), Shared Representations: Sensorimotor Foundations of Social Life. Cambridge University Press, pp. 280–310.

Kelso, J.A.S., Delcolle, J.D., Schoner, G.S, 1990. Action-perception as a pattern formation process. In: Jeannerod, M. (Ed.), Attention and Performance XIII. Erlbaum, Hillsdale, NJ, pp. 139–169.

Kilner, J.M., Baker, S.N., Salenius, S., Hari, R., Lemon, R.N., 2000. Human cortical muscle coherence is directly related to specific motor parameters. J. Neurosci. 20 (23), 8838–8845. doi:10.1523/JNEUROSCI.20-23-08838.2000.

Kilner, J., Bott, L., Posada, A., 2005. Modulations in the degree of synchronization during ongoing oscillatory activity in the human brain. Eur. J. Neurosci. 21 (9), 2547–2554. doi:10.1111/j.1460-9568.2005.04069.x.

Kilner, J.M., Salenius, S., Baker, S.N., Jackson, A., Hari, R., Lemon, R.N., 2003. Task-dependent modulations of cortical oscillatory activity in human subjects during a bimanual precision grip task. Neuroimage 18 (1), 67–73. doi:10.1006/nimg.2002.1322.

Kong, Y.K., Hallbeck, M.S., Jung, M.C., 2010. Crosstalk effect on surface electromyogram of the forearm flexors during a static grip task. J. Electromyogr. Kinesiol. 20 (6), 1223–1229. doi:10.1016/j.jelekin.2010.08.001.

Kristeva, R., Patino, L., Omlor, W., 2007. Beta-range cortical motor spectral power and corticomuscular coherence as a mechanism for effective corticospinal interaction during steady-state motor output. Neuroimage 36 (3), 785–792. doi:10.1016/j.neuroimage.2007.03.025.

Kristeva-Feige, R., Fritsch, C., Timmer, J., Lücking, C.H., 2002. Effects of attention and precision of exerted force on beta range EEG-EMG synchronization during a maintained motor contraction task. Clin. Neurophysiol. 113 (1), 124–131. doi:10.1016/S1388-2457(01)00722-2.

Kurgansky, A.V., 2008. Visuomotor synchronization: analysis of the initiation and stable synchronization phases. Hum. Physiol. 34 (3), 289. doi:10.1134/S0362119708030043.

Lakatos, P., Shah, A.S., Knuth, K.H., Ulbert, I., Karmos, G., Schroeder, C.E., 2005. An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. J. Neurophysiol. 94 (3), 1904–1911. doi:10.1152/jn.00263.2005.

Large, E.W., Jones, M.R., 1999. The dynamics of attending: how people track time-varying events. Psychol. Rev. 106 (1), 119. doi:10.1037/0033-295X.106.1.119.

Larsen, L.H., Zibrandtsen, I.C., Wienecke, T., Kjaer, T.W., Christensen, M.S., Nielsen, J.B., Langberg, H., 2017. Corticomuscular coherence in the acute and subacute phase after stroke. Clin. Neurophysiol. 128 (11), 2217–2226. doi:10.1016/j.clinph.2017.08.033.

Lebon, F., Ruffino, C., Greenhouse, I., Labruna, L., Ivry, R.B., Papaxanthis, C., 2019. The neural specificity of movement preparation during actual and imagined movements. Cereb. Cortex 29 (2), 689–700. doi:10.1093/cercor/bhx350.

Lenc, T., Keller, P.E., Varlet, M., Nozaradan, S., 2018. Neural tracking of the musical beat is enhanced by low-frequency sounds. Proc. Natl. Acad. Sci. 115 (32), 8221–8226. doi:10.1073/pnas.1801421115.

Lenc, T., Keller, P.E., Varlet, M., Nozaradan, S., 2020. Neural and behavioral evidence for frequency-selective context effects in rhythm processing in humans. Cerebral Cortex Commun. 1 (1), tgaa037. doi:10.1093/texcom/tgaa037.

Lorås, H., Sigmundsson, H., Talcott, J.B., Öhberg, F., Stensdotter, A.K., 2012. Timing continuous or discontinuous movements across effectors specified by different pacing modalities and intervals. Exp. Brain Res. 220 (3-4), 335–347 10.1007/s00221-012-3142-4.

Lotze, M., Halsband, U., 2006. Motor imagery. J. Physiol. Paris 99 (4–6), 386–395. doi:10.1016/j.jphysparis.2006.03.012.

Luca, C.J.De, Gilmore, L.D., Kuznetsov, M., Roy, S.H, 2010. Filtering the surface EMG signal : movement artifact and baseline noise contamination. J. Biomech. 43 (8), 1573–1579. doi:10.1016/j.jbiomech.2010.01.027.

MacRitchie, J., Varlet, M., Keller, P.E., 2017. Embodied expression through entrainment and co-representation in musical ensemble performance. In: Lesaffre, M., Leman, M., Maes, P.J. (Eds.), The Routledge Companion to Embodied Music Interaction. Routledge, London, UK, pp. 150–159.

Maier, M.A., Bennett, K.M., Hepp-Reymond, M.C., Lemon, R.N., 1993. Contribution of the monkey corticomotoneuronal system to the control of force in precision grip. J. Neurophysiol. 69 (3), 772–785. doi:10.1152/jn.1993.69.3.772.

McClelland, V.M., Cvetkovic, Z., Mills, K.R., 2012. Rectification of the EMG is an unnecessary and inappropriate step in the calculation of Corticomuscular coherence. J. Neurosci. Methods 205 (1), 190–201. doi:10.1016/j.jneumeth.2011.11.001.

McFarland, D.J., Miner, L.A., Vaughan, T.M., Wolpaw, J.R., 2000. Mu and beta rhythm topographies during motor imagery and actual movements. Brain Topogr. 12 (3), 177–186. doi:10.1023/A:1023437823106.

Mehrkanoon, S., Breakspear, M., Boonstra, T.W., 2014. The reorganization of corticomuscular coherence during a transition between sensorimotor states. Neuroimage 100, 692–702. doi:10.1016/j.neuroimage.2014.06.050.

Merletti, R., Cerone, G.L., 2020. Tutorial. Surface EMG detection, conditioning and pre-processing: best practices. J. Electromyogr. Kinesiol. 102440. doi:10.1016/j.jelekin.2020.102440.
Merletti, R., Di Torino, P., 1999. Standards for reporting EMG data. J. Electromyogr. Kinesiol. 9 (1), 3–4.
Michelon, P., Vettel, J.M., Zacks, J.M., 2006. Lateral somatotopic organization during imagined and prepared movements. J. Neurophysiol. 95 (2), 811–822. doi:10.1152/jn.00488.2005.
Miller, K.J., Schalk, G., Fetz, E.E., den Nijs, M., Ojemann, J.G., Rao, R.P., 2010. Cortical activity during motor execution, motor imagery, and imagery-based online feedback. Proc. Natl. Acad. Sci. 107 (9), 4430–4435. doi:10.1073/pnas.0913697107.
Mima, T., Hallett, M., 1999. Corticomuscular coherence: a review. J. Clin. Neurophysiol. 16 (6), 501.
Miyata, K., Varlet, M., Miura, A., Kudo, K., Keller, P.E., 2021. Vocal interaction during rhythmic joint action stabilises interpersonal coordination and individual movement timing. J. Experiment. Psychol. doi:10.1037/xge0000835.
Mizuguchi, N., Nakata, H., Kanosue, K., 2014. Activity of right premotor-parietal regions dependent upon imagined force level: An fMRI study. Front. Human Neurosci. 8 (OCT), 1–8. doi:10.3389/fnhum.2014.00810.
Morey, R.D., 2008. Confidence intervals from normalized data: a correction to Cousineau (2005). Reason 4 (2), 61–64.
Morillon, B., Baillet, S., 2017. Motor origin of temporal predictions in auditory attention. PNAS 114 (42), E8913–E8921. doi:10.1073/pnas.1705373114.
Munzert, J., Lorey, B., Zentgraf, K., 2009. Cognitive motor processes: the role of motor imagery in the study of motor representations. Brain Res. Rev. 60 (2), 306–326. doi:10.1016/j.brainresrev.2008.12.024.
Murthy, V.N., Fetz, E.E., 1992. Coherent 25- To 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys. PNAS 89 (12), 5670–5674. doi:10.1073/pnas.89.12.5670.
Myers, L.J., Lowery, M., O'malley, M., Vaughan, C.L., Heneghan, C., Gibson, A.S.C., Sreenivasan, R, 2003. Rectification and non-linear pre-processing of EMG signals for cortico-muscular analysis. J. Neurosci. Methods 124 (2), 157–165. doi:10.1016/S0165-0270(03)00004-9.
Nakagawa, K., Aokage, Y., Fukuri, T., Kawahara, Y., Hashizume, A., Kurisu, K., Yuge, L., 2011. Neuromagnetic beta oscillation changes during motor imagery and motor execution of skilled movements. Neuroreport 22 (5), 217–222.
Néda, Z., Ravasz, E., Brechet, Y., Vicsek, T., Barabási, A.L., 2000. The sound of many hands clapping. Nature 403 (6772), 849–850. doi:10.1097/WNR.0b013e328344b480.
Nozaradan, S., 2014. Exploring how musical rhythm entrains brain activity with electroencephalogram frequency-tagging. Philosoph. Transact. R. Soc. B 369 (1658), 20130393. doi:10.1098/rstb.2013.0393, –20130393.
Nozaradan, S., Peretz, I., Keller, P.E., 2016. Individual differences in rhythmic cortical entrainment correlate with predictive behavior in sensorimotor synchronization. Sci. Rep. 6 (January), 1–12. doi:10.1038/srep20612.
Omlor, W., Patino, L., Hepp-reymond, M., Kristeva, R., 2007. Gamma-range corticomuscular coherence during dynamic force output. Human Brain Mapp. J. 34 (3), 1191–1198. doi:10.1016/j.neuroimage.2006.10.018.
Ono, K., Mikami, Y., Fukuyama, H., Mima, T., 2016. Motion-induced disturbance of auditory-motor synchronization and its modulation by transcranial direct current stimulation. Eur. J. Neurosci. 43 (4), 509–515. doi:10.1111/ejn.13135.
Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci., 2011* 1. doi:10.1155/2011/156869.
Osman, A., Albert, R., Ridderinkhof, K.R., Band, G., van der Molen, M., 2006. The beat goes on: Rhythmic modulation of cortical potentials by imagined tapping. J. Exp. Psychol. Hum. Percept. Perform. 32, 986–1005. doi:10.1037/0096-1523.32.4.986.
Oullier, O., Jantzen, K.J., Steinberg, F.L., Kelso, J.A.S, 2005. Neural substrates of real and imagined sensorimotor coordination. Cereb. Cortex 15, 975–985. doi:10.1093/cercor/bhh198.
Patel, A.D., Iversen, J.R., 2014. The evolutionary neuroscience of musical beat perception: the action simulation for auditory prediction (ASAP) hypothesis. Front. Syst. Neurosci. 8, 57. doi:10.3389/fnsys.2014.00057.
Patel, A.D., Iversen, J.R., Chen, Y., Repp, B.H., 2005. The influence of metricality and modality on synchronization with a beat. Exp. Brain Res. 163 (2), 226–238. doi:10.1007/s00221-004-2159-8.
Peelle, J.E., Davis, M.H., 2012. Neural oscillations carry speech rhythm through to comprehension. Front. Psychol. 3 (SEP), 1–17. doi:10.3389/fpsyg.2012.00320.
Petersen, T.H., Willerslev-Olsen, M., Conway, B.A., Nielsen, J.B., 2012. The motor cortex drives the muscles during walking in human subjects. J. Physiol. 590 (10), 2443–2452. doi:10.1113/jphysiol.2012.227397.
Pfurtscheller, G., Solis-Escalante, T., 2009. Could the beta rebound in the EEG be suitable to realize a "brain switch"? Clin. Neurophysiol. 120 (1), 24–29. doi:10.1016/j.clinph.2008.09.027.
Pfurtscheller, G., 1981. Central beta rhythm during sensorimotor activities in man. Electroencephalogr. Clin. Neurophysiol. 51 (3), 253–264. doi:10.1016/0013-4694(81)90139-5.
Piitulainen, H., Bourguignon, M., Smeds, E., De Tiège, X., Jousmäki, V., Hari, R., 2015. Phasic stabilization of motor output after auditory and visual distractors. Hum. Brain Mapp. 36 (12), 5168–5182. doi:10.1002/hbm.23001.
Pollok, B., Gross, J., Müller, K., Aschersleben, G., Schnitzler, A., 2005. The cerebral oscillatory network associated with auditorily paced finger movements. Neuroimage 24 (3), 646–655. doi:10.1016/j.neuroimage.2004.10.009.
Pollok, B., Krause, V., Butz, M., Schnitzler, A., 2009. Modality specific functional interaction in sensorimotor synchronization. Hum. Brain Mapp. 30 (6), 1783–1790. doi:10.1002/hbm.20762.
Potter, D.D., Fenwick, M., Abecasis, D., Brochard, R., 2009. Perceiving rhythm where none exists: event-related potential (ERP) correlates of subjective accenting. Cortex 45 (1), 103–109. doi:10.1016/j.cortex.2008.01.004.
Praamstra, P., Kourtis, D., Kwok, H.F., Oostenveld, R., 2006. Neurophysiology of implicit timing in serial choice reaction-time performance. J. Neurosci. 26 (20), 5448–5455. doi:10.1523/JNEUROSCI.0440-06.2006.
Press, C., Cook, J., Blakemore, S.J., Kilner, J., 2011. Dynamic modulation of human motor activity when observing actions. J. Neurosci. 31 (8), 2792–2800. doi:10.1523/JNEUROSCI.1595-10.2011.
Quek, G., Nemrodov, D., Rossion, B., Liu-Shuang, J., 2018. Selective attention to faces in a rapid visual stream: hemispheric differences in enhancement and suppression of category-selective neural activity.. Journal of cognitive neuroscience 30 (3), 393–410. doi:10.1162/jocn_a_01220.
Repp, B.H., 2003. Rate limits in sensorimotor synchronization with auditory and visual sequences: The synchronization threshold and the benefits and costs of interval subdivision. J. Mot. Behav. 35 (4), 355–370. doi:10.1080/00222890309603156.
Repp, B.H., 2005. Sensorimotor synchronization: a review of the tapping literature. Psychon. Bull. Rev. 12 (6), 969–992. doi:10.3758/BF03206433.
Repp, B.H., Penel, A., 2002. Auditory dominance in temporal processing: new evidence from synchronization with simultaneous visual and auditory sequences. J. Exp. Psychol. Hum. Percept. Perform. 28 (5), 1085. doi:10.1037/0096-1523.28.5.1085.
Repp, B.H., Penel, A., 2004. Rhythmic movement is attracted more strongly to auditory than to visual rhythms. Psychol. Res. 68 (4), 252–270. doi:10.1007/s00426-003-0143-8.
Repp, B.H., Su, Y.H., 2013. Sensorimotor synchronization: a review of recent research (2006-2012). Psychon. Bull. Rev. 20 (3), 403–452. doi:10.3758/s13423-012-0371-2.
Reyes, A., Laine, C.M., Kutch, J.J., Valero-Cuevas, F.J., 2017. Beta band corticomuscular drive reflects muscle coordination strategies. Front. Computat. Neurosci. 11, 17. doi:10.3389/fncom.2017.00017.
Rimmele, J.M., Morillon, B., Poeppel, D., Arnal, L.H., 2018. Proactive sensing of periodic and aperiodic auditory patterns. Trends Cogn. Sci. 22 (10), 870–882. doi:10.1016/j.tics.2018.08.003.
Roland, P.E., Larsen, B., Lassen, N.A., Skinhoj, E., 1980. Supplementary motor area and other cortical areas in organization of voluntary movements in man. J. Neurophysiol. 43 (1), 118–136. doi:10.1152/jn.1980.43.1.118.
Safri, N.M., Murayama, N., Hayashida, Y., Igasaki, T., 2007. Effects of concurrent visual tasks on cortico-muscular synchronization in humans. Brain Res. 1155 (1), 81–92. doi:10.1016/j.brainres.2007.04.052.
Saleh, M., Reimer, J., Penn, R., Ojakangas, C.L., Hatsopoulos, N.G., 2010. Fast and slow oscillations in human primary motor cortex predict oncoming behaviorally relevant cues. Neuron 65 (4), 461–471. doi:10.1016/j.neuron.2010.02.001.
Salenius, S., Portin, K., Kajola, M., Salmelin, R., Hari, R., 1997. Cortical control of human motoneuron firing during isometric contraction. J. Neurophysiol. 77 (6), 3401–3405. doi:10.1152/jn.1997.77.6.3401.
Schaefer, R.S., 2014. Auditory rhythmic cueing in movement rehabilitation: findings and possible mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences 369 (1658), 20130402. doi:10.1098/rstb.2013.0402, –20130402.
Schaefer, R.S., Farquhar, J., Blokland, Y., Sadakata, M., Desain, P., 2011. Name that tune: decoding music from the listening brain. Neuroimage 56 (2), 843–849.
Schubotz, R.I., 2007. Prediction of external events with our motor system: towards a new framework. Trends Cogn. Sci. 11 (5), 211–218. doi:10.1016/j.tics.2007.02.006.
Seki, K., Fetz, E.E., 2012. Gating of sensory input at spinal and cortical levels during preparation and execution of voluntary movement. J. Neurosci. 32 (3), 890–902. doi:10.1523/JNEUROSCI.4958-11.2012.
Spackman, L., Boyd, S., Towell, T., 2006. Identification and characterization of somatosensory off responses. Brain Res. 1114 (1), 53–62. doi:10.1016/j.brainres.2005.12.135.
Stavrinou, M.L., Moraru, L., Cimponeriu, L., Della Penna, S., Bezerianos, A., 2007. Evaluation of cortical connectivity during real and imagined rhythmic finger tapping. Brain Topogr. 19, 137–145. doi:10.1007/s10548-007-0020-7.
Stephan, K.M., Fink, G.R., Passingham, R.E., Silbersweig, D., Ceballos-Baumann, A.O., Frith, C.D., Frackowiak, R.S., 1995. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. J. Neurophysiol. 73 (1), 373–386. doi:10.1152/jn.1995.73.1.373.
Steriade, M., McCormick, D.A., Sejnowski, T.J., 1993. Thalamocortical oscillations in the sleeping and aroused brain. Science 262 (5134), 679–685 10.1126/science.8235588.
Stupacher, J., Hove, M.J., Novembre, G., Schütz-Bosbach, S., Keller, P.E., 2013. Musical groove modulates motor cortex excitability: a TMS investigation. Brain Cogn. 82 (2), 127–136. doi:10.1016/j.bandc.2013.03.003.
Szameitat, A.J., Shen, S., Sterr, A., 2007. Motor imagery of complex everyday movements. An fMRI study. Neuroimage 34 (2), 702–713. doi:10.1016/j.neuroimage.2006.09.033.
Tecchio, F., Zappasodi, F., Melgari, J.M., Porcaro, C., Cassetta, E., Rossini, P.M., 2006. Sensory-motor interaction in primary hand cortical areas: a magnetoencephalography assessment. Neuroscience 141 (1), 533–542. doi:10.1016/j.neuroscience.2006.03.059.
The jamovi project (2019). *jamovi* (Version 0.9) [windows]. Retrieved from https://www.jamovi.org
Tomiak, T., Gorkovenko, A.V., Tal'nov, A.N., Abramovych, T.I., Mishchenko, V.S., Vereshchaka, I.V., Kostyukov, A.I., 2015. The averaged EMGs recorded from the arm muscles during bimanual "rowing" movements. Front. Physiol. 6, 349. doi:10.3389/fphys.2015.00349.
Torre, K., Balasubramaniam, R., 2009. Two different processes for sensorimotor synchronization in continuous and discontinuous rhythmic movements. Exp. Brain Res. 199 (2), 157–166. doi:10.1007/s00221-009-1991-2.
Tranchant, P., Vuvan, D.T., Peretz, I., 2016. Keeping the Beat: A Large Sample Study of Bouncing and Clapping to Music. PLoS One 11 (7), e0160178. doi:10.1371/journal.pone.0160178.

VanRullen, R., Busch, N., Drewes, J., Dubois, J., 2011. Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. Front. Psychol. 2, 60. doi:10.3389/fpsyg.2011.00060.

van Ulzen, N.R., Lamoth, C.J., Daffertshofer, A., Semin, G.R., Beek, P.J., 2008. Characteristics of instructed and uninstructed interpersonal coordination while walking side-by-side. Neurosci. Lett. 432 (2), 88–93. doi:10.1016/j.neulet.2007.11.070.

Varlet, M., Marin, L., Issartel, J., Schmidt, R.C., Bardy, B.G., 2012. Continuity of visual and auditory rhythms influences sensorimotor coordination. PLoS One 7 (9). doi:10.1371/journal.pone.0044082.

Varlet, M., Novembre, G., Keller, P.E., 2017. Dynamical entrainment of corticospinal excitability during rhythmic movement observation: a Transcranial Magnetic Stimulation study. Eur. J. Neurosci. 45 (11), 1465–1472. doi:10.1111/ejn.13581.

Varlet, M., Nozaradan, S., Nijhuis, P., Keller, P.E., 2020. Neural tracking and integration of 'self'and 'other'in improvised interpersonal coordination. Neuroimage 206, 116303. doi:10.1016/j.neuroimage.2019.116303.

Varlet, M., Williams, R., Keller, P.E., 2020. Effects of pitch and tempo of auditory rhythms on spontaneous movement entrainment and stabilisation. Psychol. Res. 84 (3), 568–584. doi:10.1007/s00426-018-1074-8.

von Carlowitz-Ghori, K., Bayraktaroglu, Z., Hohlefeld, F.U., Losch, F., Curio, G., Nikulin, V.V., 2014. Corticomuscular coherence in acute and chronic stroke. Clin. Neurophysiol. 125 (6), 1182–1191. doi:10.1016/j.clinph.2013.11.006.

Ward, N.J., Farmer, S.F., Berthouze, L., Halliday, D.M., 2013. Rectification of EMG in low force contractions improves detection of motor unit coherence in the beta-frequency band. J. Neurophysiol. 110 (8), 1744–1750. doi:10.1152/jn.00296.2013.

Wheaton, L.A., Carpenter, M., Mizelle, J.C., Forrester, L., 2008. Preparatory band specific premotor cortical activity differentiates upper and lower extremity movement. Exp. Brain Res. 184 (1), 121–126. doi:10.1007/s00221-007-1160-4.

Witham, C.L., Riddle, C.N., Baker, M.R., Baker, S.N., 2011. Contributions of descending and ascending pathways to corticomuscular coherence in humans. J. Physiol. 589 (15), 3789–3800. doi:10.1113/jphysiol.2011.211045.

Witte, M., Patino, L., Andrykiewicz, A., Hepp-Reymond, M.C., Kristeva, R., 2007. Modulation of human corticomuscular beta-range coherence with low-level static forces. Eur. J. Neurosci. 26 (12), 3564–3570. doi:10.1111/j.1460-9568.2007.05942.

te Woerd, E.S., Oostenveld, R., de Lange, F.P., Praamstra, P., 2018. Entrainment for attentional selection in Parkinson's disease. Cortex 99, 166–178. doi:10.1016/j.cortex.2017.11.01.

Yoshida, T., Masani, K., Zabjek, K., Chen, R., Popovic, M.R., 2017a. Dynamic increase in corticomuscular coherence during bilateral, cyclical ankle movements. Front. Human Neurosci. 11, 155. doi:10.3389/fnhum.2017.00155.

Yoshida, T., Masani, K., Zabjek, K., Chen, R., Popovic, M.R., 2017b. Dynamic cortical participation during bilateral, cyclical ankle movements: effects of aging. Sci. Rep. 7, 44658. doi:10.1038/srep44658.

Zatorre, R.J., Halpern, A.R., 2005. Mental concerts: musical imagery and auditory cortex. Neuron 47 (1), 9–12. doi:10.1016/j.neuron.2005.06.013.

Zelic, G., Nijhuis, P., Charaf, S.A., Keller, P.E., Davis, C., Kim, J., Varlet, M., 2019. The influence of pacer-movement continuity and pattern matching on auditory-motor synchronisation. Exp. Brain Res. 237 (10), 2705–2713.

Zelic, G., Varlet, M., Kim, J., Davis, C., 2016. Influence of pacer continuity on continuous and discontinuous visuo-motor synchronisation. Acta Psychol. (Amst) 169, 61–70. doi:10.1016/j.actpsy.2016.05.008.

Zelic, G., Varlet, M., Wishart, J., Kim, J., Davis, C., 2018. The dual influence of pacer continuity and pacer pattern for visuomotor synchronisation. Neurosci. Lett. 683, 150–159. doi:10.1016/j.neulet.2018.07.044.

Zoefel, B., ten Oever, S., Sack, A.T., 2018. The involvement of endogenous neural oscillations in the processing of rhythmic input: more than a regular repetition of evoked neural responses. Front. Neurosci. 12, 1–13. doi:10.3389/fnins.2018.00095.