Corticomuscular Coherence Dependence on Body Side and Visual Feedback

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Abstract—Physiological movement develops on the basis of sensorimotor integration through synchronisation between the copy of signals sent to the effector muscles and the incoming flow of sensory information. Our aim is to study corticomuscular coherence (CMC), the most widely used measure of synchronization between brain and muscle electrical activities, in dependence on the level of visual feedback and the executing body side. We analysed CMC in 18 healthy volunteers while performing a weak isometric handgrip of an air bulb with either the right or the left hand, in either the presence or absence of visual feedback on the exerted pressure. The absence of visual feedback decreased the CMC peak frequency from 27 Hz to 23 Hz ($p < 0.001$), increased the CMC peak amplitude from 0.05 to 0.07 ($p = 0.005$) and decreased the electroencephalographic beta band power ($p = 0.005$). None of these measures changed in dependence on the performing hand ($p > 0.2$ consistently). The lack of dependence of CMC on the controlled hand involved in the movement can be considered in agreement with small hemispheric asymmetries of hand representations in primary sensorimotor cortices. Modulation of visual information changed corticomuscular synchronizations and cortical involvement, reflecting the crucial role of gaze in human behaviour. Given the fundamental role of sensory integration in motor execution, the availability of a simple index sensitive to modulations of perceptual afferents may prove useful in determining the use or the monitoring of the effects of sensory enrichments in personalized rehabilitation. © 2022 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: corticomuscolar coherence CMC, visual feedback, handedness, isometric force, electroencephalography EEG, electromyography EMG.

INTRODUCTION

The synchronization of neural activity reflects functional communication between spatially segregated regions (Gray et al., 1989), and it has been suggested that it is a basic mechanism of brain integration that mediates the formation of dynamic connections (Varela et al., 2001). The synchronization mechanisms sustaining motor control began to be elucidated by studies of single motor units in different muscles (Farmer et al., 1993a; Farmer et al., 1993b) while the connection between central and peripheral connectivity was first observed by magnetoencephalography (MEG) in 1995 (Conway et al., 1995). Since then, an increasing number of studies have probed the details of this connection, both in physiological and pathological conditions by MEG and electroencephalography (EEG), two techniques with an optimal temporal resolution for assessing those synchronizations (Liu et al., 2019; Porcaro et al., 2020).

The typical assessment of the cortex-muscles synchronization during a motor task is the spectral coherence known as cortico-muscular coherence (CMC) - between the EEG/MEG signals from the contralateral sensorimotor cortex and the electromyography (EMG) from the prime mover muscle recorded simultaneously (Gerloff et al., 2006; Tecchio et al., 2006b; 2008a). The

CMC reflects the interaction and the flow of information between the cerebral cortex sending commands to muscle tissue and the afferent feedback from the controlled districts (Airaksinen et al., 2015).

As recently reviewed by (Liu et al., 2019), consistently, in physiological conditions, CMC is maximal in the beta band (14–30 Hz) when studied movements involve a static force, while CMC prevails in gamma band (above 30 Hz) during movements changing in time. Furthermore, stronger forces correspond to smaller CMC amplitudes.

Many physiological parameters influence the cortico-muscular synchronizations indexed by CMC. First of all, ageing, which is associated with a reduction of CMC, despite increased beta-band EEG, during sustained contractions of upper limb muscles (Graziadio et al., 2010; Bayram et al., 2015).

In particular, CMC increases with individual maturation from childhood to adulthood, indicating that beta-band synchronisation mirrors the development of hand movement control abilities (Graziadio et al., 2010). Consistently, higher CMC amplitude associates with better motor control performance (Kristeva et al., 2007; Desmyttere et al., 2018).

Also, the respiratory cycle modifies CMC, in addition to maximal muscle strength (Li and Laskin, 2006) and oculomotor control (Rassler and Raabe, 2003). By a MEG study, the authors of (Kluger and Gross, 2020) showed that beta-band CMC reduced during voluntary deep breathing compared to normal involuntary breathing. Moreover, CMC amplitude was modulated by the phase of breathing, being reduced during inspiration and increased during expiration. As expected, the sleep state alters cortico-muscle communication, with the brain-muscle network showing high connectivity and strong network links during wakefulness, which weaken as sleep enters deeper stages (Rizzo et al., 2020). All these pieces of evidence reveal the deep interdependence of the body-brain system's functions within his nature of complex system (Bashan et al., 2012; Bartsch et al., 2015).

The brain controls the body mainly contralaterally, despite ipsilateral projections, thus, the left hemisphere controls the right hemi-body and vice versa (Becker, 1953). Several studies have focused on assessing the CMC in relation to bilateral or unilateral tasks (Chen et al., 2013). Despite the clear right handedness dominance, the literature does not report a CMC asymmetry in hand control in healthy people (Tecchio et al., 2006a). Nevertheless, notably, after a monolateral stroke, in which the function of one cerebral hemisphere may be partially compromised, an asymmetry in CMC between the contralateral and ipsilateral side of the lesion emerges (Mima et al., 2001). As would be expected, CMC from both sides of the tongue during protrusion was achieved with no hemispheric asymmetries. Specifically, CMC was detected bilaterally at two different frequency bands (Maezawa et al., 2014, 2017). The results concerning the symmetry/asymmetry of synchronization phenomena as expressed in the CMC in the control of specific body districts lead us to pone the working hypothesis that, in a physiological state, there is no dependence of CMC on the moved hand.

Sensory and proprioceptive feedback is inherently part of motor control (Rossi et al., 1998; Fink et al., 2014) and modulates the CMC (Riddle and Baker, 2005; Witham et al., 2011). Definitely, visual feedback is a crucial modulator of our everyday gestures, with gaze anticipating whatever we are about to do (Johansson et al., 2001). The integration of information across different sensory modalities optimizes the timing of motor commands (Elliott et al., 2011), as well as multimodal feedback increases the accuracy of the activities execution. As a correlate of CMC, in a tapping task, beta CMC increased when visual rhythmic cues led the motor execution (Laine et al., 2014; Nijhuis et al., 2021). This suggests the working hypothesis that visual feedback modulates cortico-muscular synchronisation.

In the present study, we aimed at assessing whether CMC is sensitive to manual dominance and visual sensory feedback within the internal dynamics underlying continuous motor control. EEG and EMG were collected while participants performed a weak handgrip with the right or the left hand (separately), in the two conditions of presence/absence of visual feedback about the exerted pressure.

To study such modulations of CMC, we conducted our experiments using a common movement in our lives, a light handgrip that requires a fixed level of pressure exerted as when we hold cutlery.

EXPERIMENTAL PROCEDURES

Study design

This proof of principle study was approved by the Ethical Committee of S. Giovanni Calibita Hospital, Rome, Italy.

Participants

Eighteen healthy and drug-free volunteers (10 females and 8 males, age range from 20 to 48 years, mean 29 ± 7 years) participated in the study after signing a written informed consent. All subjects were right-handed (as tested by Edinburgh Handedness Questionnaire Oldfield, 1971) and had normal or corrected-to-normal vision.

Fine hand motor ability quantification

The fine hand-motor control was evaluated with the 9-hole peg test (9-HPT) conducted with the dominant arm first. A practiced trial (for each arm) preceded the actual timed test. Subjects were given the following instructions: "Pick one peg up using only your right (left) hand and put it into one of the holes, no matter which one. Repeat until all holes are filled. Then, remove the pegs, one at a time, in any order, and return them to the container. Stabilize the pegboard with your left (right) hand. You can now perform a practice trial. See how fast you can put all the pegs in the container and take them out of it. Are you ready? Go!" After the subject had performed the practice trial, the experimenter would say: "Now, this will be the actual test. Perform the same actions as in the practice test as quickly as you can. Are you ready? Go!". Timing, executed by the experimenter

with a stopwatch, started when the subject touched the first peg and stopped when the subject placed the last peg back in the container. As test score, we used the total time in seconds to put and remove the nine pegs, as typically done for healthy subjects.

Electrophysiological investigation

EEG, EMG, EOG, and ECG data recordings. The subjects' EEG was recorded using a 64-channel acti-CHamp System (Brain Products GmbH, Munich, Germany, Fig. 1), with electrodes positioned according to the 10–10 EEG International System and referenced to the Fz electrode. Electrode impedances were maintained below 5 kΩ. Surface EMG – recorded by using Ag–AgCl cup electrodes – of the right and left opponents pollicis muscle (EMG_{OPr} and EMG_{OPl}) were recorded with a belly tendon montage (2.5 cm inter-electrode distance). An electrooculogram (EOG) and an electrocardiogram (ECG) were recorded to check for eye blinking and cardiac interferences. EEG, EOG, ECG and EMG were all sampled at 5 kHz (pre-sampling analogical band pass filtering 0.1–2000 Hz) and stored for off-line processing.

Motor task. Each subject sat comfortably on a chair in front of a monitor about 1 m away (Fig. 1A). The subject performed a handgrip against the resistance of a semi-compliant air-bulb, connected to a digital board that recorded the exerted pressure while giving the subject a visual feedback (Interactive Pressure Sensor, InPresS) (Tomasevic et al., 2013). For right and left hands separately, after determining handgrip maximum voluntary contraction (MVC), a rest period of at least 2 min was provided. Then, a green visual signal indicated the subject to start the 20 s block of weak isometric handgrip and a red visual signal indicated to stop, initiating a 10 s block of complete relaxation (Fig. 1B). Each succession of contraction and rest sequences lasted about 5 min, thus executing about 10 blocks of contraction (300 s/(20 s movement + 10 s rest)). The target level was set to 5% MVC, to minimize weariness related to the task.

Online visual feedback was shown as a horizontal black segment that moved up and down according to the pressure exerted. Subjects were asked to match their pressure by fitting the target level – indicated by the lateral segments – and to maintain the target pressure as consistently and accurately as possible. The visual feedback amplitude consisted of about 0.9° of visual angle for 1% of MVC. The task was executed in presence of visual feedback and, thereafter, in absence of it, with an identical setting but with the horizontal bar fixed in the central position.

The four handgrips (about 5 min each), were executed in the same order in all subjects: first with the dominant hand with visual feedback (DxYes), then without (DxNo), thereafter with the non-dominant hand with (SnYes) and without visual feedback (SnNo). The EEG-EMG session lasted about 30 min overall.

Data analysis

EEG data pre-processing. EEG data were filtered (1–250 Hz) before the analysis. A semi-automatic fast independent component analysis (fastICA)-based procedure (Barbati et al., 2004) was applied to the whole recordings to identify biological (cardiac, ocular, and muscular) and non-biological (power line, instrumental and environmental noise) artifacts, which allowed removing them from the signals. For each subject we selected 180 s of artifact-free signal for carrying out the analysis.

CMC estimate. Since in the diverse conditions we were interested more in the neurodynamics than in the spatial changes, we avoided localization analysis of our data, while we estimated the coupling between brain and muscles as the spectral coherence function between the EMG_{OPr} and a single representative bipolar EEG derivation (Wang et al., 2007). To obtain this representative derivation, we preliminary selected the maximal coherence with $EMG_{OPr/l}$ among all the bipolar derivations in antero-occipital and medio-lateral directions between the first nearest channels, to ensure comparable amplitudes across conditions (Lou et al., 2008; Graziadio et al., 2010; Tomasevic et al., 2013; Jacobs et al., 2015). CMC was scored by the amplitude and the frequency of the maximum amplitude peak (Fig. 2).

CMC was estimated by Welch procedure to obtain the EEG and EMG spectra and cross-spectra (1024 ms duration, Hanning window, 50% overlap) omitting the first and the last second of each contraction block, not to include the transients. The CMC peak was investigated in the beta band, between 15 to 33 Hz.

The plots show an example, in the four conditions of interest, of the power spectral density of EMG and EEG as well as the CMC as a function of frequency. In the topographical representation of the 64 EEG recording channels, we coloured in red those considered to estimate the bipolar derivation displaying highest CMC during the task with the contralateral hand. In the CMC plots, the bold dot and the vertical segment highlight the peak submitted to the analysis.

EEG and EMG activities. As a control about the CMC behavior, we evaluated the power spectral density (PSD) of EEG and the EMG in dependence on the moved hand and the presence/absence of visual feedback.

Exerted pressure. We estimated the level of pressure maintained along the duration of the isometric contraction as the average of the rectified EMG from the thumb opponent. For small muscles, such as hand muscles with narrow motor unit recruitment and force ranges, the relationship between force and the average rectified value of surface EMG is linear (Lawrence and De Luca, 1983). We previously confirmed this relationship in a group of 13 subjects (age range 6–80 years) performing a similar task (Graziadio et al., 2010).

Task performance. We estimated the quality of execution by using the variation index of the rectified
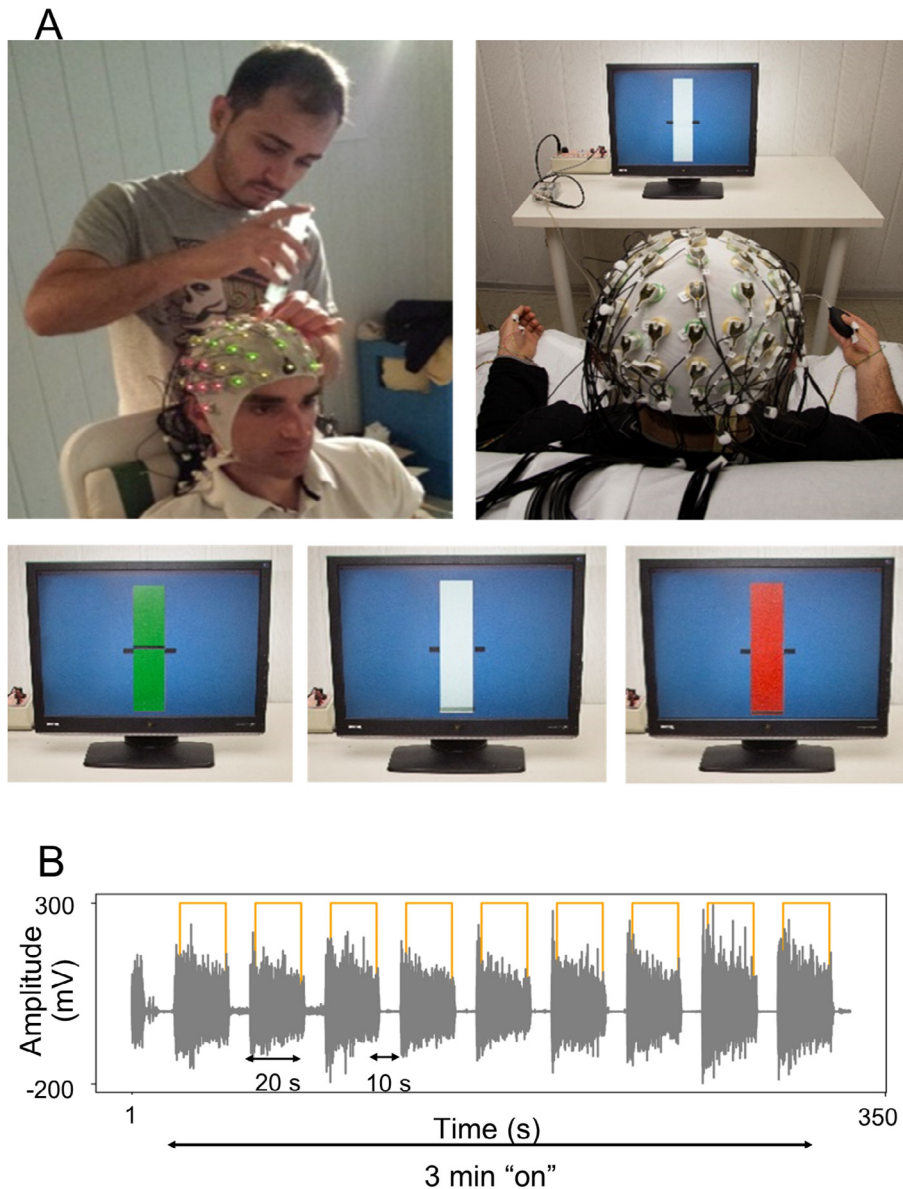
To evaluate the impact of several parameters on the sensorimotor task, we applied a mixed-model with the conditions of interest as fixed-effects and the single subject data as random-effect. We submitted the variable to an analysis of variance (ANOVA) with *Hemi-body* (left hemisphere-right hand, right hemisphere-left hand) and *Visual feedback* (Yes, No) as within-subject factors. We focused mainly on the two *Hemi-body* and *Visual feedback* effects, pointing out that CMC differed for the control of the dominant and non-dominant hand and it also differed for the presence of visual feedback.

We considered similar models for the CMC peak frequency, CMC peak amplitude, PSD of EEG and EMG in the beta band, exerted pressure, task performance and 9HPT execution times to score the behavioral quality of fine motor hand control.

Fig. 1. Experimental settings. **(A)** EEG recordings and task. The general set-up to record the EEG during the weak hand grip (see methods) executed in sequences of 20 s starting with a go signal (green rectangle) and ending with a stop signal (red rectangle) intermingled by 10 s at rest. During the hand grip, a horizontal oscillating (blocked) segment indicates the level of exerted pressure on the bulb in the condition with (without) visual. **(B)**. Example of EMG acquisition during isometric contraction execution. In grey the EMG trace of opponents pollicis (OP) muscle in one representative subject, for the whole task duration, with 20 s contraction sequences intermingled by 10 s at rest. Orange line indicates the temporal portions selected for analysis. Each subject performed at least 6 sequences of artefact free contractions.. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

EMG (Graziadio et al., 2010), that is the ratio of the standard deviation over the mean, along the whole isometric contraction duration.

Statistical analysis

The statistics were executed by SPSS 26.

The distribution of each variable was checked for normality by the Shapiro–Wilk test and homogeneity of variance by Levene's test.

RESULTS

The selection of the bipolar derivations with maximal peak amplitude of CMC in beta band resulted in the case with visual feedback to one of the two channels typically C3 for the right hand movement (13 out of 18, 4 CZ, 1 F3) and C4 for the left (17 out of 18, 1 P4) with somewhat more variable second channel (right hand movement: 7 FC1, 4 CP3, 2 FC3, 2 CP1, 1 CP5, 1 C5, 1 C1; left hand: 9 FC2, 4 FC6, 2 CP2, 1 C2, 1 CP4, 1 FC4). A similar emergence of channels composing the bipolar derivation resulted when the movement was executed without visual feedback: right hand movement: 13 C3 out of 15, 1 F3, 1 CZ against the second channel: 7 FC1, 5 CP5, 2 CP3, 1 FC5. Left hand movement: 10 C4 out of 16, 3 CZ, 2 F4, 1 P4 against 7 FC2, 2 CP2, 3 C2, 1 CP4, 1 FC6, 1 FC4, 1 CP2).

We tested by Shapiro–Wilk statistics the distribution shape of the 24 variables, that are the 6 measures (CMC peak frequency, CMC peak amplitude, EEG beta PSD, EMG beta PSD, exerted pressure, task performance) in the 4 conditions (DxYes, DxNo, SnYes, SnNo). Twenty-three out of the 24 did not differ from
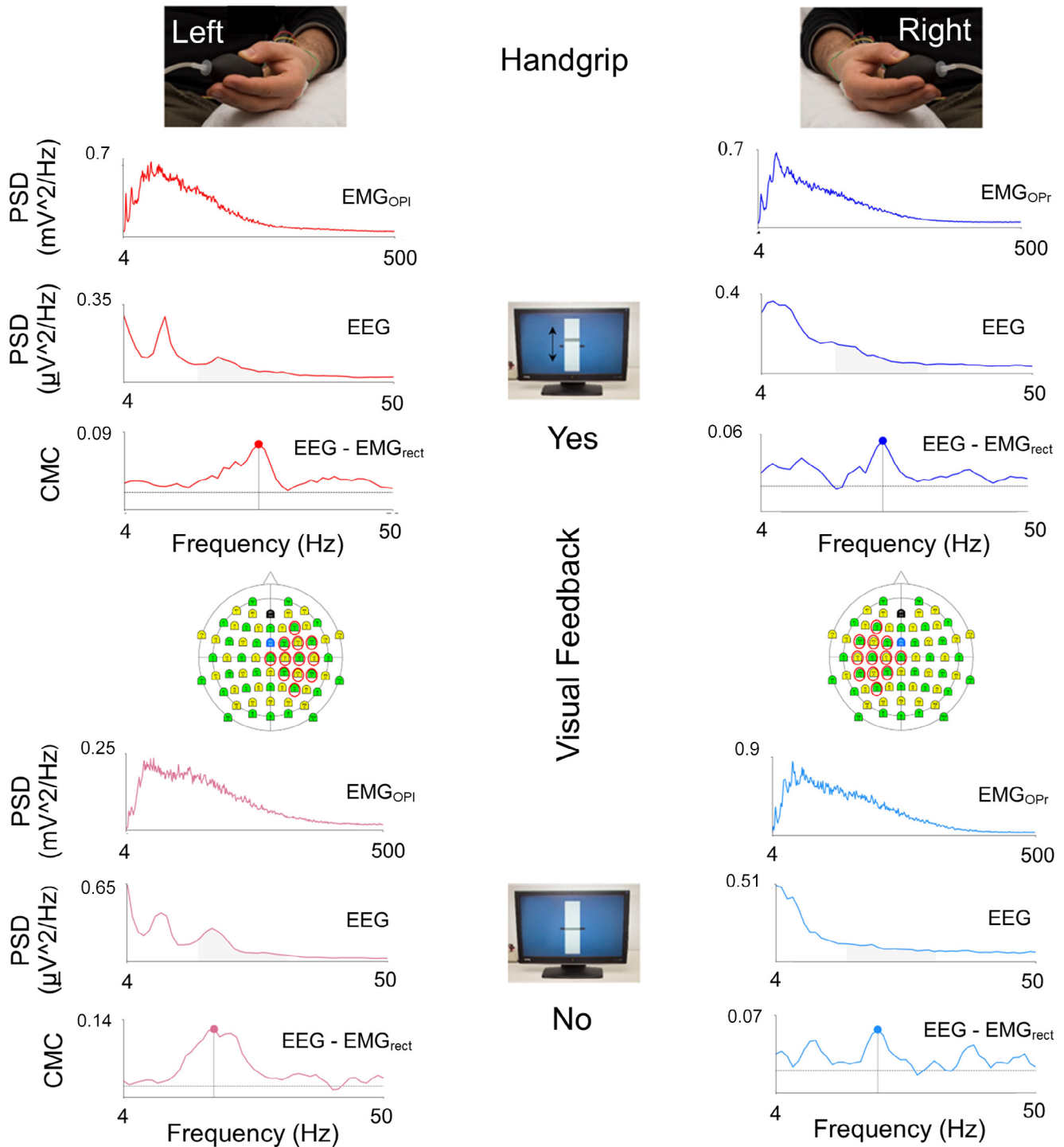
Fig. 2. Variables of interest. The plots show an example, in the four conditions of interest, of the power spectral density of EMG and EEG as well as the CMC as a function of frequency. In the topographical representation of the 64 EEG recording channels, we coloured in red those considered to estimate the bipolar derivation displaying highest CMC during the task with the contralateral hand. In the CMC plots, the bold dot and the vertical segment highlight the peak submitted to the analysis.

normality after proper transformation and outliers exclusion ($p > 0.2$ consistently). We applied natural logarithmic transformation to all variables but the CMC frequency, which was transformed by square function. For some variables, we had to exclude outliers indicated by the test, never remaining with less than 15 subjects but the CMC amplitude for the right hand with feedback, which remained with 12 cases. Although in the single case of CMC frequency in SnNo condition the distribution differed from a normal distribution even after

Table 1. Demographic and CMC peak features

			Cortico-muscular coherence (CMC) peak							
			Right hand				Left hand			
			With Vf		Without Vf		With Vf		Without Vf	
Sex		Age	Freq (Hz)	Amp	Freq (Hz)	Amp	Freq (Hz)	Amp	Freq (Hz)	Amp
10 F 8 M	**Mean**	29	26.9	0.05	23.1	0.07	27.6	0.06	22.0	0.08
	SD	6	3.8	0.04	3.2	0.04	3.9	0.05	4.2	0.05

M = male, F = female; Mean and standard deviations (SD) of cortico-muscular coherence peak frequency (Freq, Hz) and amplitude (Amp, dimensionless) in the experimental conditions of interest. For amplitudes the value is the exponential transformation of the mean of logarithmic transformed values. For frequency the square root of the averages of the squared values.

the transformation (no outliers appeared), we applied ANOVA also including this variable and we felt that the obtained behavior is reliable, as we show reporting single subjects' data in the results section.

Levene's tests indicated that the four conditions displayed variances not inhomogeneous for each of the six measures under study ($p > 0.2$).

CMC peak frequency

The ANOVA with *Hemi-body* (left hemisphere-right hand, right hemisphere-left hand) and *Visual feedback* (Yes, No) as within-subjects factors indicated a clear *Visual feedback* effect [$F_{1,14} = 36.099$, $p < 0.001$] reflecting a higher frequency of the CMC peak in presence of the visual feedback (27.3 Hz) with respect to the absence of it (22.6 Hz). The CMC peak frequency did not differ when moving the right or the left hand, as indicated by absence of *Hemi-body* effect [$F_{1,14} = 0.030$,

$p = 0.866$]. Lack of interaction effect *Visual feedback*Hemi-body* [$F_{1,14} = 1.057$, $p = 0.321$] indicated that the influence of visual feedback on CMC peak frequency did not differ in dependence of the moved hand (Table 1, Figs. 3A and 4A).

CMC peak amplitude

A clear *Visual feedback* effect [$F_{1,11} = 12.197$, $p = 0.005$] showed that in absence of visual feedback CMC had higher amplitudes (Figs. 3A and 4B, Table 1). A trend of the *Hemi-body* Visual feedback* interaction effect [$F_{1,11} = 4.818$, $p = 0.051$] suggested that the CMC amplitude difference between presence and absence of visual information was more pronounced for the right than the left movement. A trend of the *Hemi-body* effect [$F_{1,11} = 4.303$, $p = 0.062$] suggested higher CMC amplitudes for the left than right movement.

Beta band PSD of EEG and EMG

EEG beta PSD. A clear *Visual feedback* effect [$F_{1,14} = 11.175$, $p = 0.005$] showed that with visual feedback, PSD of EEG in beta band is lower (0.09 $\mu V^2/Hz$) than in absence of it (0.13 $\mu V^2/Hz$) (Fig. 4C). No *Hemi-body* effect [$F_{1,14} = 0.273$, $p = 0.609$] indicated that the PSD of EEG in beta band did not change when moving the right or left hand. The *Hemi-body*Visual feedback* interaction effect [$F_{1,14} = 5.423$, $p = 0.035$] indicated that change between presence and absence of visual information was more pronounced for the right than for the left movement.

EMG beta PSD. No effect was observed, with a trend of *Visual feedback* factor [$F_{1,13} = 4.060$, $p = 0.065$] suggesting that with visual feedback, PSD of EMG in beta band is lower (0.55 mV^2/Hz) than
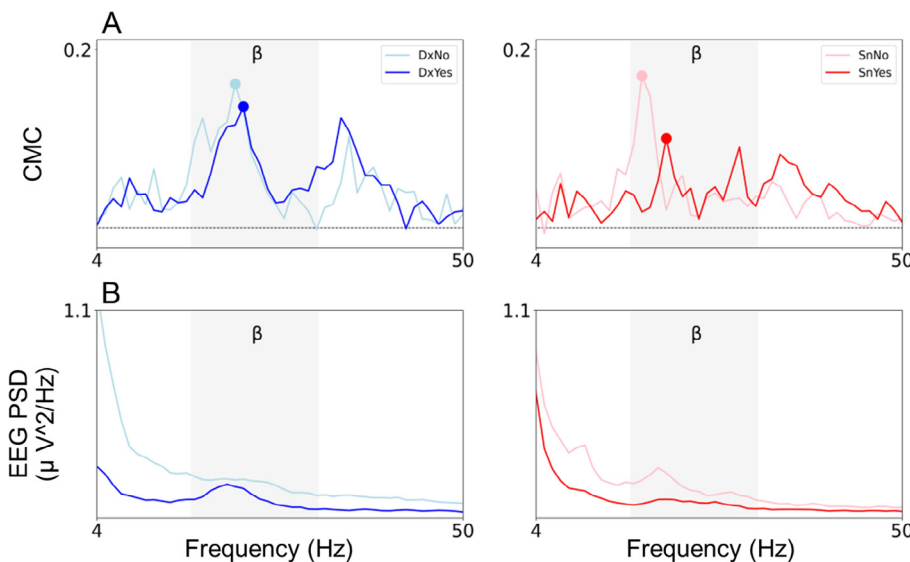

Fig. 3. Example of visual feedback effect on CMC and PSD of EEG in beta band. **(A)** CMC. In a representative subject, CMC when moving the right hand with (blue) and without (cyan) visual feedback [left side] and the left hand with (red) and without (pink) visual feedback [right side]. The colored dots highlight the CMC peak in beta band. Dx and Sx codes in the legends stand for right (destra) and left (sinistra) hand movement, Yes and No indicate presence and absence of visual feedback respectively. The grey area in the plots bounds beta band. **(B)** EEG PSD. With the same color coding and nomenclature as in the panel A, PSD of the bipolar derivation EEG used to estimate CMC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
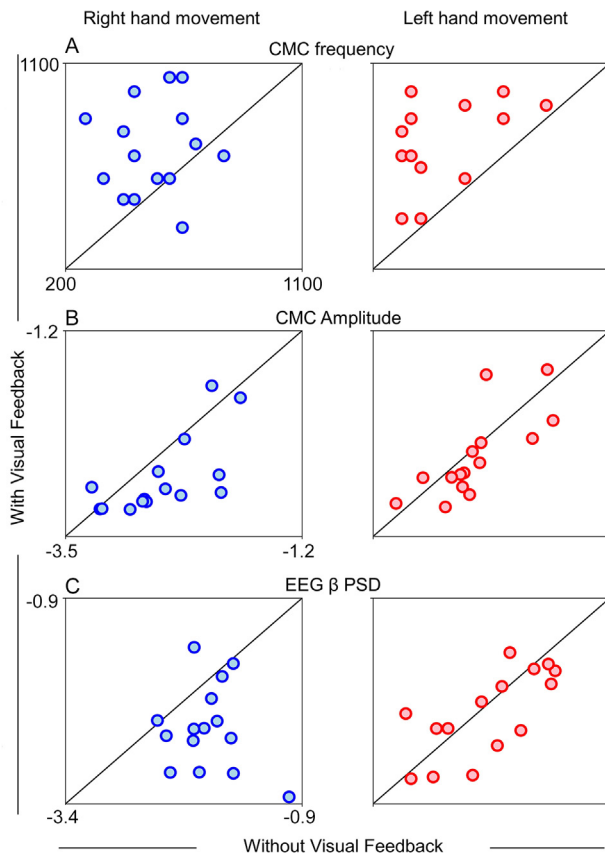
Fig. 4. Distribution across population of the Visual feedback effect on CMC and PSD of EEG in beta band. **(A)** CMC peak frequency. For each single subject, we plot the CMC peak frequency in beta band with visual feedback (ordinate axis) vs that without (abscise axis). Color coding always is blue for right and red for left hand movement. The values of axes are frequency transformed by square function. Below the bisector values in absence of feedback are smaller than those with feedback. Almost all subjects had CMC peak frequency without visual feedback lower than with it. **(B)** CMC peak amplitude. As in panel **(A)** but for CMC amplitude. On both the axes we report the natural logarithm of the CMC peak amplitude. The scatter plot highlights that, for both hands, the CMC peak amplitude was higher in the absence of visual feedback. **(C)** PSD of EEG in beta. As in panel **(A)** but for PSD of EEG in beta band. On both the axes we report the natural logarithm of the PSD. It is evident, especially for the right hand movement, that EEG PSD in beta band was higher in absence than in presence of visual feedback.

in absence of it (0.72 mV^2/Hz). No *Hemi-body* [$F_{1,13}$ = 0.649, p = 0.435] or *Hemi-body*Visual feedback* [$F_{1,13}$ = 0.121, p = 0.733] factors were found.

Exerted pressure. No effect was observed, with no significance of *Visual feedback* [$F_{1,14}$ = 2.862, p = 0.113], *Hemi-body* [$F_{1,14}$ = 0.645, p = 0.435] or *Hemi-body*Visual feedback* [$F_{1,14}$ = 0.819, p = 0.381] factors indicating that the task was executed exerting comparable pressures in the four conditions.

Task performance. No effect was observed, with all *Visual feedback* [$F_{1,14}$ = 0.195, p = 0.666], *Hemi-body* [$F_{1,14}$ = 0.001, p = 0.973] or *Hemi-body*Visual feedback* [$F_{1,14}$ = 0.203, p = 0.660] factors

definitely absent, indicating that the execution quality was comparable in the four conditions.

Fine hand motor ability quantification. ANOVA with Hand (right, left) and Repetition (1st, 2nd) as within-subject factors of the execution time of the 9-HPT indicated a clear *Hand* effect [$F_{1,15}$ = 8.42, p = 0.011] corresponding to quicker execution with the right (16.1 ± 0.4 s) than with the left hand (17.5 ± 0.3 s).

DISCUSSION

Here, while we confirmed that CMC is not sensitive to manual dominance, we learned that the CMC peak in beta band appears higher in amplitude and at lower frequencies when sensory feedback is impoverished omitting visual information. At the same time, lack of visual information results in a reduced cortical involvement as expressed by higher EEG PSD in beta band. Overall, the exerted pressure and the execution quality were similar for the two hands and the different type of feedback.

The eye-movement coordination

A distinguishing feature of all exploratory human behaviours is that the spatiotemporal pattern of the incoming inputs is unavoidably shaped by overt movements (Tomassini et al., 2020). In performing a movement, planning and execution, neurons send a message to the muscles and simultaneously to the neurons that receive information from the world (Scott et al., 2015). The levels of synchronization between the sensory and motor areas (Tecchio et al., 2008b) determine whether the movement continues as planned or is corrected and refined (Wolpert et al., 2011). While proprioceptive and sensory feedback is crucial in determining trajectory and executive fluency (Fink et al., 2014), it is the gaze that precedes and guides the planning of all our actions (Flanagan and Johansson, 2003). During motor execution, the visual feedback integrates via the implementation of eye motor programs the acquired representations of the actions being performed. This supports the hypothesis that action is based on a direct correspondence mechanism that maps the visual representation of the observed action onto a motor representation of the same action. Visual information is used in the control of prehension grasping (Jeannerod, 1986; Johansson et al., 2001), and pinch grip, with the amount of visual feedback modulating beta-band corticomuscular and intermuscular coherences differently in dependence on aging (Watanabe et al., 2020).

A key role of gaze emerges not only in the actual movement realization. The relationship that animals engage with the environment they inhabit is a practical one. A specific class of neurons called 'visuo-motor' were discovered, encoding consistently both the execution of a specific motor act, and the simple observation of objects that display physical features that in turn imply the same motor act (Rizzolatti and Craighero, 2004). Such brain organization inscribes a special role of vision within the continuous feedback

dependent interaction with the environment. Yet, the activity of bimodal 'visuo-motor' neurons (Rizzolatti et al., 1997a,b), which encode a set of movements that allow interaction with the environment independently of the effector they are performed by, suggest that eye and hand movements are implemented in dynamic synergy so that visual cues are also integrated into the programming of manipulative forces. In agreement with such notion, we observed that in absence of visual information the primary sensorimotor cortex was less active than monitoring the ongoing result of the action. Notably, while in the acquisition of a new skill, people strongly rely on multimodal feedback, the feedback-dependent gain is reduced when the task is acquired (Kasuga et al., 2018). In agreement, we observed that in simple movements typical of everyday life, the lack of visual feedback did not impair the execution quality.

Proprioceptive afferents in providing task-appropriate feedback are expressed over a wide range of frequencies (Fink et al., 2014). In the present work, we explored the effects of the failure of the physiologically expected visual feedback by performing the precision hand grip first with visual information about the expressed pressure and then in the absence of this sensory information. The result found indicated higher frequencies of synchronization between muscular and cortical activity with smaller amplitude of the synchronization in presence of visual feedback. The change in corticomuscular coherence frequency is in agreement with corticomuscular synchronous oscillation shifting from beta band to higher frequencies (principally gamma) when increasing the subject's attention (Pittaccio et al., 2011; Li et al., 2020), if we consider that executing the isometric contraction in presence of visual feedback people focus more their attention to the task. Furthermore, Omlor and colleagues (Omlor et al., 2007) show that time evolving compressions express at higher CMC frequency and we can speculate that lack of visual feedback in an everyday simple task sets the system to a more simple sensorimotor processing condition inducing a lower frequency CMC. Furthermore, we observed stronger cortical involvement in presence of visual feedback as expressed by higher beta-band EEG reactivity, here seen as lower beta band PSD with visual feedback than without (Pfurtscheller and Lopes Da Silva, 1999). In fact, considering similar resting-state powers in the two conditions, lower beta band power in presence of visual feedback implies higher cortical involvement. This is consistent with higher attention as mentioned above, as well as higher sensorimotor processing in matching the visually provided information. Consistently, we can report a result that we obtained when we executed an fMRI study investigating the same comparison of an isometric handgrip executed in the presence or absence of visual information about the exerted pressure (Mayhew et al., 2017). Notably, despite a wider higher activation without rather than with visual feedback, selectively in the primary motor cortex, we found higher activation in presence of it. Higher CMC amplitude in absence of visual feedback with respect to with, while executing tasks at the same level of performance, is particularly interesting if considered together with this reduced cortical involvement. These two behaviours can indicate effects of learning, where well acquired movements recruit more efficiently the same neuronal networks, with a lower cortical involvement more synchronized with the involved muscles. In other words, the execution of a movement well represented within the everyday motor repertoire, that does not require matching with visual adjunctive information, seems to involve a more efficiently recruited network.

Hemispheric asymmetries and CMC

It was 1967 when Eason and his colleagues published their paper in which they confirmed that the amplitude of evoked responses in the human occipital cortex depended on the visual field in which the stimulus was presented and in which they correlated left or right lobe activation to handedness (Eason et al., 1967). Since then, many researchers tried to study brain activations, hemispheric asymmetries, and manual dominance. We now know that there is a strong interhemispheric asymmetry related to language with substantial loss of language for left temporal lesion and unaltered language for homologous right lesion (Landrigan et al., 2021). This asymmetry, however, is relatively limited in the case of the cortical representation of the hand, as we can infer from the evidence that a unilateral stroke impairs control of the contralateral hand similarly, irrespective of whether the lesion affects the right or left hemisphere. (Tecchio et al., 2006c; Finkelsteyn et al., 2019). We found that manual dominance does not reflect in CMC features. Certainty the cortex plays a key role in handedness, with more synchronized networks consistently typical of the dominant hand representation both in sensory (Theuvenet et al., 2005; Tecchio et al., 2007) and motor areas (Mac donell et al., 1991; Solodkin et al., 2001). Nevertheless, the overall position and dimension of the hand representation express minimal asymmetries in the two hemispheres (Jung et al., 2008; Rossini and Tecchio, 2008; Finkelsteyn et al., 2019).

Where handedness is one of the fundamental dimensions of brain organization, CMC is not sensitive to this feature, suggesting the need to find new measures that quantify the phenomena of dynamic synchronization underlying behaviour, in general, and manual control specifically. Behaviourally, in the present work we were able to witness by the 9hole peg test the higher functional dexterity of the right with respect to the left hand. Considering the well-established notion that neural networks at rest express characteristics dependent on their ability to perform the behaviour in which they are involved (Kim and Kang, 2018; Doucet et al., 2022; Deco and Corbetta, 2011; Bansal et al., 2021), we expect that there will be functional measures that differ between the dominant and non-dominant hand cortical representation even if tested via a simple task. In fact, in our experience with the primary somatosensory area, the activation properties of networks with different levels of ability, in particular the thumb and little finger representation networks, differed even when tested while responding to elemental galvanic stimulation (Tecchio et al., 2007). Based on this reasoning, we expect that

even via a simple handgrip we can sense the different ability of the left and right hand representation networks. Possibly, more sensitive measures of cortico-muscular synchronizations taking into account the neurodynamics patterns in connected areas could highlight minimal differences reflecting the greater control ability of the dominant hand (Porcaro et al., 2018; Tecchio et al., 2020).

In conclusion, we observed that primary sensorimotor cortex activity and synchronization with the muscle are sensitive to the lack of visual ongoing information. We revealed that online visual monitoring of exerted pressure modifies the cortico-muscular synchronizations controlling the motor execution, consistently with incoming inputs integrating previsions into the descending motor commands, effectively regulating the flow of information within the multimodal, multi-scale sensorimotor loop. Given the central role that asymmetries have in every system and the centrality of the handedness concept as the basis of human behaviour, we suggest overcoming cortico-muscular coherence insensitivity searching for more suitable indices of the synchronization phenomena between cortex and muscles that subtend every behavioural expression.

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REFERENCES

Airaksinen K, Lehti T, Nurminen J, Luoma J, Helle L, Taulu S, Pekkonen E, Mäkelä JP (2015) Cortico-muscular coherence parallels coherence of postural tremor and MEG during static muscle contraction. Neurosci Lett 602:22–26. Available at: https://pubmed.ncbi.nlm.nih.gov/26116820/ [Accessed May 26, 2021].

Bansal K, Garcia JO, Lauharatanahirun N, Muldoon SF, Sajda P, Vettel JM (2021) Scale-specific dynamics of high-amplitude bursts in EEG capture behaviorally meaningful variability.. Neuroimage 241.

Barbati G, Porcaro C, Zappasodi F, Rossini PM, Tecchio F (2004) Optimization of an independent component analysis approach for artifact identification and removal in magnetoencephalographic signals. Clin Neurophysiol 115:1220–1232.

Bartsch RP, Liu KKL, Bashan A, Ivanov PC (2015) Network physiology: how organ systems dynamically interact Perc M, ed. PLoS One 10 e0142143.

Bashan A, Bartsch RP, Kantelhardt JW, Havlin S, Ivanov PC (2012) Network physiology reveals relations between network topology and physiological function. Nat Commun 3:1–9.

Bayram MB, Siemionow V, Yue GH (2015) Weakening of corticomuscular signal coupling during voluntary motor action in aging. J Gerontol - Ser A Biol Sci Med Sci 70:1037–1043. Available at: https://pubmed.ncbi.nlm.nih.gov/25779095/ [Accessed May 26, 2021].

Becker RF (1953) The cerebral cortex of man. By Wilder Penfield and Theodore Rasmussen. The Macmillan Company, New York, N.Y. 1950. 248 pp. Am J Phys Anthropol 11:441–444. Available at: https://onlinelibrary.wiley.com/doi/full/10.1002/ajpa.1330110318 [Accessed May 26, 2021].

Chen S, Entakli J, Bonnard M, Berton E, De Graaf JB (2013) Functional corticospinal projections from human supplementary motor area revealed by corticomuscular coherence during precise grip force control. PLoS One 8. Available at: https://pubmed.ncbi.nlm.nih.gov/23555945/ [Accessed January 18, 2022].

Conway BA, Halliday DM, Farmer SF, Shahani U, Maas P, Weir AI, Rosenberg JR (1995) Synchronization between motor cortex and spinal motoneuronal pool during the performance of a maintained motor task in man. J Physiol 489:917–924. Available at: https://pubmed.ncbi.nlm.nih.gov/8788955/ [Accessed May 19, 2021].

Deco G, Corbetta M (2011) The dynamical balance of the brain at rest.. Neuroscientist 17:107–123. https://doi.org/10.1177/1073858409354384.

Desmyttere G, Mathieu E, Begon M, Simoneau-Buessinger E, Cremoux S (2018) Effect of the phase of force production on corticomuscular coherence with agonist and antagonist muscles. Eur J Neurosci 48:3288–3298. Available at: https://europepmc.org/article/med/30141828 [Accessed November 26, 2021].

Doucet Gaelle E, Hamlin Noah, West Anna, Kruse Jordanna A, Moser Dominik A, Wilson Tony W (2022) Multivariate patterns of brain-behavior associations across the adult lifespan. Aging 44 (1):161–194. https://doi.org/10.18632/aging.203815.

Eason RG, Groves P, White CT, Oden D (1967) Evoked cortical potentials: relation to visual field and handedness. Science (80-) 156:1643–1646.

Elliott MT, Wing AM, Welchman AE (2011) The eVect of ageing on multisensory integration for the control of movement timing. Exp Brain Res 213:291–298. Available at: https://pubmed.ncbi.nlm.nih.gov/21688143/ [Accessed May 26, 2021].

Farmer SF, Bremner FD, Halliday DM, Rosenberg JR, Stephens JA (1993a) The frequency content of common synaptic inputs to motoneurones studied during voluntary isometric contraction in man. J Physiol 470:127–155. Available at: https://pubmed.ncbi.nlm.nih.gov/8308721/ [Accessed May 19, 2021].

Farmer SF, Swash M, Ingram DA, Stephens JA (1993b) Changes in motor unit synchronization following central nervous lesions in man. J Physiol 463:83–105. Available at: https://pubmed.ncbi.nlm.nih.gov/8246205/ [Accessed May 19, 2021].

Fink AJP, Croce KR, Huang ZJ, Abbott LF, Jessell TM, Azim E (2014) Presynaptic inhibition of spinal sensory feedback ensures smooth movement HHS Public Access. Nature 509:43–48.

Finkelsteyn AM, Saucedo MA, Miquelini LA, Chertcoff A, Bandeo L, Pacha S, León Cejas L, Uribe Roca C, Fernández Pardal M, Reisin R, Bonardo P (2019) Ischemic stroke of the ''hand knob area'': a case series and literature review. J Clin Neurosci 65:100–105. Available at: https://pubmed.ncbi.nlm.nih.gov/30910548/ [Accessed November 25, 2021].

Flanagan JR, Johansson RS (2003) Action plans used in action observation. Nature 424:769–771. Available at: https://pubmed.ncbi.nlm.nih.gov/12917683/ [Accessed May 26, 2021].

Gerloff C, Braun C, Staudt M, Hegner YL, Dichgans J, Krägeloh-Mann I (2006) Coherent corticomuscular oscillations originate from primary motor cortex: evidence from patients with early brain lesions. Hum Brain Mapp 27:789–798. Available at: https://pubmed.ncbi.nlm.nih.gov/16475178/ [Accessed May 26, 2021].

Gray CM, König P, Engel AK, Singer W (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. Nature 338:334–337.

Graziadio S, Basu A, Tomasevic L, Zappasodi F, Tecchio F, Eyre JA (2010) Developmental tuning and decay in senescence of oscillations linking the corticospinal system. J Neurosci 30:3663–3674.

Jacobs JV, Wu G, Kelly KM (2015) Evidence for beta corticomuscular coherence during human standing balance: effects of stance width, vision, and support surface. Neuroscience 298:1–11. Available at: https://pubmed.ncbi.nlm.nih.gov/25869620/ [Accessed January 18, 2022].

Jeannerod M (1986) Mechanisms of visuomotor coordination: a study in normal and brain-damaged subjects. Neuropsychologia 24:41–78. Available at: https://pubmed.ncbi.nlm.nih.gov/3517680/ [Accessed May 26, 2021].

Johansson RS, Westling G, Bäckström A, Randall Flanagan J (2001) Eye-hand coordination in object manipulation. J Neurosci 21:6917–6932.

Jung P, Baumgärtner U, Magerl W, Treede RD (2008) Hemispheric asymmetry of hand representation in human primary somatosensory cortex and handedness. Clin Neurophysiol 119:2579–2586. Available at: https://pubmed.ncbi.nlm.nih.gov/18786858/ [Accessed May 26, 2021].

Kasuga S, Momose N, Ushiyama J, Ushiba J (2018) Corticomuscular coherence reflects somatosensory feedback gains during motor adaptation. Neurosci Res 131:10–18. Available at: https://pubmed.ncbi.nlm.nih.gov/29030077/ [Accessed November 25, 2021].

Kim J, Kang E (2018) Strength of resting-state functional connectivity associated with performance-adjustment ability. Behavioural brain research 347:377–384. https://doi.org/10.1016/J.BBR.2018.02.024.

Kluger DS, Gross J (2020) Depth and phase of respiration modulate cortico-muscular communication. Neuroimage 222. Available at: https://pubmed.ncbi.nlm.nih.gov/32822811/ [Accessed May 26, 2021].

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 36:785–792.

Laine CM, Yavuz ŞU, Farina D (2014) Task-related changes in sensorimotor integration influence the common synaptic input to motor neurones. Acta Physiol 211:229–239. Available at: https://pubmed.ncbi.nlm.nih.gov/24620727/ [Accessed May 26, 2021].

Landrigan J-F, Zhang F, Mirman D (2021) A data-driven approach to post-stroke aphasia classification and lesion-based prediction. Brain.

Lawrence JH, De Luca CJ (1983) Myoelectric signal versus force relationship in different human muscles. J Appl Physiol 54:1653–1659. Available at: https://pubmed.ncbi.nlm.nih.gov/6874489/ [Accessed November 24, 2021].

Li S, Fan M, Yu H, Gao L (2020) Gamma frequency band shift of contralateral corticomuscular synchronous oscillations with force strength for hand movement tasks. Neuroreport 31:338–345. Available at: https://pubmed.ncbi.nlm.nih.gov/32058430/ [Accessed November 25, 2021].

Li S, Laskin JJ (2006) Influences of ventilation on maximal isometric force of the finger flexors. Muscle Nerve 34:651–655. Available at: https://pubmed.ncbi.nlm.nih.gov/16770794/ [Accessed May 26, 2021].

Liu J, Sheng Y, Liu H (2019) Corticomuscular coherence and its applications: a review. Front Hum Neurosci 13. Available at: https://pubmed.ncbi.nlm.nih.gov/30949041/ [Accessed May 19, 2021].

Lou B, Hong B, Gao X, Gao S (2008) Bipolar electrode selection for a motor imagery based brain-computer interface. J Neural Eng 5:342–349. Available at: https://pubmed.ncbi.nlm.nih.gov/18756030/ [Accessed January 17, 2022].

Mac donell RA, Shapiro BE, Chiappa KH, Helmers SL, Cros D, Day BJ, Shahani BT (1991) Hemispheric threshold differences for motor evoked potentials produced by magnetic coil stimulation. Neurology 41:1441–1444 Available at: https://pubmed.ncbi.nlm.nih.gov/1891095/ [Accessed May 26, 2021].

Maezawa H, Mima T, Yazawa S, Matsuhashi M, Shiraishi H, Hirai Y, Funahashi M (2014) Contralateral dominance of corticomuscular coherence for both sides of the tongue during human tongue protrusion: an MEG study. Neuroimage 101:245–255. Available at: https://pubmed.ncbi.nlm.nih.gov/25038437/ [Accessed May 26, 2021].

Maezawa H, Oguma H, Hirai Y, Hisadome K, Shiraishi H, Funahashi M (2017) Movement-related cortical magnetic fields associated with self-paced tongue protrusion in humans. Neurosci Res 117:22–27. Available at: https://pubmed.ncbi.nlm.nih.gov/27888072/ [Accessed May 26, 2021].

Mayhew SD, Porcaro C, Tecchio F, Bagshaw AP (2017) fMRI characterisation of widespread brain networks relevant for behavioural variability in fine hand motor control with and without visual feedback. Neuroimage 148:330–342. Available at: https://pubmed.ncbi.nlm.nih.gov/28093359/ [Accessed January 18, 2022].

Mima T, Toma K, Koshy B, Hallett M (2001) Coherence between cortical and muscular activities after subcortical stroke. Stroke 32:2597–2601. Available at: https://www.ahajournals.org/doi/abs/10.1161/hs1101.098764 [Accessed November 29, 2021].

Nijhuis P, Keller PE, Nozaradan S, Varlet M (2021) Dynamic modulation of cortico-muscular coupling during real and imagined sensorimotor synchronisation. Neuroimage:118209. Available at: https://linkinghub.elsevier.com/retrieve/pii/S1053811921004869 [Accessed May 31, 2021].

Omlor W, Patino L, Hepp-Reymond MC, Kristeva R (2007) Gamma-range corticomuscular coherence during dynamic force output. Neuroimage 34:1191–1198.

Pfurtscheller G, Lopes Da Silva FH (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin Neurophysiol 110:1842–1857. Available at: https://pubmed.ncbi.nlm.nih.gov/10576479/ [Accessed January 12, 2022].

Pittaccio S, Zappasodi F, Viscuso S, Mastrolilli F, Ercolani M, Passarelli F, Molteni F, Besseghini S, Rossini PM, Tecchio F (2011) Primary sensory and motor cortex activities during voluntary and passive ankle mobilization by the SHADE orthosis. Hum Brain Mapp 32:60–70.

Porcaro C, Cottone C, Cancelli A, Salustri C, Tecchio F (2018) Functional semi-blind source separation identifies primary motor area without active motor execution. Int J Neural Syst 28.

Porcaro C, Mayhew SD, Bagshaw AP (2020) Role of the ipsilateral primary motor cortex in the visuo-motor network during fine contractions and accurate performance. Int J Neural Syst. Available at: https://pubmed.ncbi.nlm.nih.gov/33622198/ [Accessed May 31, 2021].

Rassler B, Raabe J (2003) Co-ordination of breathing with rhythmic head and eye movements and with passive turnings of the body. Eur J Appl Physiol 90:125–130. Available at: https://pubmed.ncbi.nlm.nih.gov/12827368/ [Accessed May 26, 2021].

Riddle CN, Baker SN (2005) Manipulation of peripheral neural feedback loops alters human corticomuscular coherence. J Physiol 566:625–639. Available at: https://pubmed.ncbi.nlm.nih.gov/15919711/ [Accessed May 26, 2021].

Rizzo R, Zhang X, Wang JWJL, Lombardi F, Ivanov PC (2020) Network physiology of cortico–muscular interactions. Front Physiol:11. Available at: https://pubmed.ncbi.nlm.nih.gov/33324233/ [Accessed May 26, 2021].

Rizzolatti G, Craighero L (2004) The mirror-neuron system. Annu Rev Neurosci 27:169–192. Available at: https://pubmed.ncbi.nlm.nih.gov/15217330/ [Accessed November 30, 2021].

Rizzolatti Giacomo, Fadiga Luciano, Fogassi Leonardo, Gallese Vittorio (1997) The Space Around Us. Science 277 (5323):190–191. https://doi.org/10.1126/science.277.5323.190.

Rizzolatti Giacomo, Fogassi Leonardo, Gallese Vittorio (1997) Parietal cortex: from sight to action. Neurobiology 7(4):562–567. https://doi.org/10.1016/S0959-4388(97)80037-2.

Rossi S, Pasqualetti P, Tecchio F, Sabato A, Rossini PM (1998) Modulation of corticospinal output to human hand muscles following deprivation of sensory feedback. Neuroimage 8:163–175.

Rossini PM, Tecchio F (2008) On primary cortical hand representation in the left and right hemispheres. Clin Neurophysiol 119:2421–2423.

Scott SH, Cluff T, Lowrey CR, Takei T (2015) Feedback control during voluntary motor actions. Curr Opin Neurobiol.

Solodkin A, Hlustik P, Noll DC, Small SL (2001) Lateralization of motor circuits and handedness during finger movements. Eur J Neurol 8:425–434. Available at: https://pubmed.ncbi.nlm.nih.gov/11554905/ [Accessed May 26, 2021].

Tecchio F, Cecconi F, Colamartino E, Padalino M, Valci L, Reinert M (2020) The morphology of somatosensory evoked potentials during middle cerebral artery aneurysm clipping (MoSAC): a pilot study. Clin EEG Neurosci 51:130–136.

Tecchio F, Graziadio S, Barbati G, Sigismondi R, Zappasodi F, Porcaro C, Valente G, Balsi M, Rossini PM (2007) Somatosensory dynamic gamma-band synchrony: a neural code of sensorimotor dexterity. Neuroimage 35:185–193.

Tecchio F, Melgari JM, Zappasodi F, Porcaro C, Milazzo D, Cassetta E, Rossini PM (2008a) Sensorimotor integration in focal task-specific hand dystonia: a magnetoencephalographic assessment. Neuroscience 154:563–571.

Tecchio F, Porcaro C, Zappasodi F, Pesenti A, Ercolani M, Rossini PM (2006a) Cortical short-term fatigue effects assessed via rhythmic brain-muscle coherence. Exp Brain Res 174:144–151.

Tecchio F, Zappasodi F, Melgari JM, Porcaro C, Cassetta E, Rossini PM (2006b) Sensory-motor interaction in primary hand cortical areas: a magnetoencephalography assessment. Neuroscience 141:533–542. Available at: https://pubmed.ncbi.nlm.nih.gov/16713107/ [Accessed May 26, 2021].

Tecchio F, Zappasodi F, Porcaro C, Barbati G, Assenza G, Salustri C, Maria Rossini P (2008b) High-gamma band activity of primary hand cortical areas: a sensorimotor feedback efficiency index. Neuroimage 40:256–264.

Tecchio F, Zappasodi F, Tombini M, Oliviero A, Pasqualetti P, Vernieri F, Ercolani M, Pizzella V, Rossini PM (2006c) Brain plasticity in recovery from stroke: an MEG assessment. Neuroimage 32:1326–1334.

Theuvenet PJ, Van Dijk BW, Peters MJ, Van Ree JM, Lopes Da Silva FL, Chen ACN (2005) Whole-head MEG analysis of cortical spatial organization from unilateral stimulation of median nerve in both hands: No complete hemispheric homology. Neuroimage 28:314–325. Available at: https://pubmed.ncbi.nlm.nih.gov/16040256/ [Accessed May 26, 2021].

Tomasevic L, Zito G, Pasqualetti P, Filippi MM, Landi D, Ghazaryan A, Lupoi D, Porcaro C, Bagnato F, Rossini PM, Tecchio F (2013) Cortico-muscular coherence as an index of fatigue in multiple sclerosis. Mult Scler J 19:334–343.

Tomassini A, Maris E, Hilt P, Fadiga L, D'Ausilio A (2020) Visual detection is locked to the internal dynamics of cortico-motor control. PLoS Biol 18. Available at: https://pubmed.ncbi.nlm.nih.gov/33079930/ [Accessed May 26, 2021].

Varela F, Lachaux JP, Rodriguez E, Martinerie J (2001) The brainweb: phase synchronization and large-scale integration. Nat Rev Neurosci 2:229–239. Available at: https://pubmed.ncbi.nlm.nih.gov/11283746/ [Accessed May 19, 2021].

Wang Y, Hong B, Gao X, Gao S (2007) Design of electrode layout for motor imagery based brain-computer interface. Electron Lett 43:557–558.

Watanabe T, Nojima I, Mima T, Sugiura H, Kirimoto H (2020) Magnification of visual feedback modulates corticomuscular and intermuscular coherences differently in young and elderly adults. Neuroimage 220. Available at: https://pubmed.ncbi.nlm.nih.gov/32592849/ [Accessed June 10, 2021].

Witham CL, Riddle CN, Baker MR, Baker SN (2011) Contributions of descending and ascending pathways to corticomuscular coherence in humans. J Physiol 589:3789–3800. Available at: https://pubmed.ncbi.nlm.nih.gov/21624970/ [Accessed April 1, 2021].

Wolpert DM, Diedrichsen J, Flanagan JR (2011) Principles of sensorimotor learning. Nat Rev Neurosci 12:739–751.