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Research Report

Mu rhythm and corticospinal excitability capture two different frames of motor resonance: A TMS–EEG co-registration study

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ABSTRACT

Humans are equipped with an extraordinary ability to understand and imitate actions by mapping the observed movement onto their own cortical motor system. Long-established lines of research have identified two correlates of this motor resonance following action observation: the mu rhythm event-related desynchronization (mu-ERD) recorded through electroencephalography (EEG) and the facilitation of motor evoked potentials (MEPs) induced by transcranial magnetic stimulation (TMS) of the primary motor cortex (M1). Yet, whether mu-ERD and MEP facilitation reflect unique or distinct mechanisms is not conclusive, as prior work did not combine simultaneous TMS–EEG recording with a trial-by-trial analysis of the two markers. To address this issue, here, we used TMS–EEG co-registration while participants observed and executed finger movements. EEG was continuously recorded while single-pulse TMS was administered over the left M1 and MEPs were recorded from the right hand. We found stronger motor cortex recruitment during action execution and observation as shown by mu-ERD. MEPs instead were larger overall during action execution and showed a facilitation specific to the muscles involved in the observed movements. Interestingly, when analyzing these two parameters using a trial-by-trial statistical approach, we did not find any relationship between mu-ERD and MEPs within the action observation condition. Our findings support the notion that EEG and TMS indices of motor resonance reflect distinct neural mechanisms.

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1. Introduction

Understanding and imitating observed actions are key abilities supported by complex neural networks which include sensorimotor brain areas involved in action performance (Caspers et al., 2010; Hardwick et al., 2018; Rizzolatti & Sinigaglia, 2010, 2016). Electroencephalography (EEG) and transcranial magnetic stimulation (TMS) are two valuable, complementary non-invasive techniques that have provided important information about motor resonance. Motor resonance refers to the activation of the sensorimotor network for making actions while simply observing actions (for reviews see Fadiga et al., 2005; Pineda, 2005, 2008; Avenanti et al., 2013a; Naish et al., 2014). It is thought to reflect the activity of the mirror neuron system (di Pellegrino et al., 1992; Gallese et al., 1996; Mukamel et al., 2010) and contribute to action understanding and imitation (Avenanti el al. 2013b, 2018; Jacquet & Avenanti, 2015; Paracampo et al., 2018; Pobric & Hamilton, 2006; Tidoni et al., 2013; Urgesi et al., 2014).

Activation of sensorimotor brain areas during action observation and execution, is captured by the attenuation of the EEG mu rhythm (Arnstein et al., 2011; Cochin et al., 1999; Muthukumaraswamy & Johnson, 2004a, 2004b; Neuper et al., 2009). The mu rhythm is a spontaneous EEG oscillation in the alpha range (8–13 Hz) which is maximal over central sites overlying the sensorimotor cortex (Llanos et al., 2013; McFarland et al., 2000; Pfurtscheller et al., 2000). Following specific events, it can be temporarily altered, thus producing the so-called *event-related (de)synchronizations* (ERD/ERS) which have been interpreted as proof of motor cortex activation/inactivation, respectively (Llanos et al., 2013; McFarland et al., 2000; Pfurtscheller et al., 2000, 2006; Pfurtscheller & Neuper, 1994; Pineda, 2005).

Another classical way to assess motor resonance is through TMS targeting the primary motor cortex (M1). TMS over M1 can induce motor-evoked potentials (MEPs) from contralateral hand muscles (Barker et al., 1985; Pascual-Leone et al., 1994; Schambra et al., 2003; Stinear et al., 2001), and the amplitude of these MEPs is thought to reflect corticospinal excitability (Pascual-Leone et al., 1998; Rossini & Rossi, 1998). TMS studies have shown that observing others' actions increases the amplitude of MEPs, indicating a facilitation of corticospinal motor excitability (Avenanti et al., 2007, 2013a; Borgomaneri et al., 2012, 2015; Catmur et al., 2007; Fadiga et al., 1995, 2005).

EEG and TMS indices of motor resonance have been detected during the observation of both transitive and intransitive movements (Borgomaneri et al., 2012; Fadiga et al., 2005; Romani et al., 2005). A distinct feature of MEP indices is muscle specificity; indeed, during action observation, MEP facilitation occurs specifically in those muscles involved in the observed action (Alaerts et al., 2009'; Fadiga et al., 2005; Urgesi et al., 2006) according to their dynamic recruitment during actual execution (Alaerts et al., 2010; Gangitano et al., 2004; Tidoni et al., 2013).

Despite the large body of research using EEG and TMS techniques to investigate motor resonance in humans, only four studies have tested whether mu-ERD and MEPs could reflect the same or distinct neural process (Bekkali et al., 2021; Lapenta et al., 2018; Lepage et al., 2008; Prinsen & Alaerts, 2020). To pursue this aim, Lepage et al. (2008) recorded MEPs induced by M1 stimulation with simultaneous EEG recording during action observation and execution. In 12 participants, they reported mu-ERD in the contralateral sensorimotor cortex as well as larger MEP amplitudes for both action execution and observation relative to a resting condition. However, they found no significant correlation between the magnitude of these two parameters in this small group of participants. Both Lapenta et al. (2018) and Prinsen & Alaerts (2020), instead, tested EEG activity and TMS-induced MEPs in two separate experimental sessions where participants were asked to observe specific movements (precision grip *vs* power grip in the first study, and intransitive actions in the second one). Again, the authors found no significant correlation between mu rhythm and MEPs, thus concluding that these indices reflect distinct processes taking place in the action observation/execution matching system. Lastly, in a recent study, Bekkali et al. (2021) used simultaneous EEG and MEP recording during action observation but found no sign of mu-ERD and no relationship between EEG rhythms and MEP facilitation.

It should be noted that, in all these studies, MEPs were recorded from one muscle only and during the observation of a single action only, preventing the assessment of whether MEP facilitation truly reflects muscle-specific motor resonance or other non-specific processes such as increased arousal due to motion (Lepage et al., 2010; Naish et al., 2014). Indeed, to distinguish these possibilities, it is critical to contrast different actions that recruit distinct muscle representations (e.g., Catmur et al., 2007; Romani et al., 2005). Even more importantly, prior TMS–EEG studies analyzed the relation between EEG and TMS indices of motor resonance by averaging values of mu rhythm and MEPs in each participant and correlating these indices across participants (mean-based inter-individual correlation) – thus discarding potentially relevant information associated with trial-by-trial fluctuations of the two indices.

Considering these fluctuations is relevant, as MEPs show not only inter-subject variability (Goldsworthy et al., 2014; Iscan et al., 2016) but also consistent intra-subject variability (Goldsworthy et al., 2016; Guerra et al., 2020) that in principle could be taken into account by focusing on linear mixed models (LMM) (Madsen et al., 2019). Also, several studies have shown inter- and intra-individual differences in sensitivity in mu-ERD (Cheng et al., 2008a; Weiss et al., 2020), particularly in the alpha frequency band (8–13 Hz) (Wriessnegger et al., 2020). Therefore, to conclude that suppression of mu rhythm is not associated with facilitation of corticospinal excitability, a statistical model which accounts for intra- and inter-individual variability is needed.

In light of this scenario, a more precise and in-depth investigation into the possible relation between mu-ERD and MEP facilitation during action observation and execution is necessary. Here, we sought to address this issue by recording TMS-induced MEPs during simultaneous EEG acquisition, i.e., TMS–EEG co-registration, during different types of tasks

designed to tap into motor resonance. Specifically, participants were asked to observe and perform finger movements with the index and little fingers, as well as to remain at rest or watch a static hand. Single-pulse TMS was delivered over the left M1 while EEG activity was recorded from the scalp and MEPs were simultaneously recorded from the two corresponding muscles of the contralateral hand. In this way, we were able to assess trial-by-trial fluctuations in mu-ERD and MEPs and the association between them for the first time. Notably, by adopting a LMM statistical approach – which offers the opportunity to control for inter- and intra-individual variability – we provided powerful conditions to explore the association between mu-ERD and MEPs during action observation. Indeed, our approach offers the opportunity to test whether mu-ERD and MEP facilitations during action observation reflect a unique process or two distinct processes. If the two indices of motor resonance reflect the same process, we expected to find that larger MEP facilitations during action observation are predicted by larger mu-ERD. If, on the other hand, mu-ERD and MEPs reflect two distinct mechanisms, we expected to find no relationship between them. We therefore combined multiple statistical approaches, including Bayesian analyses, to evaluate the relative strength of evidence for the null versus alternative hypotheses of a correlation between mu-ERD and MEP indices.

2. Methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Yet, to answer our research questions we focus on a subset of conditions as we report in this section.

2.1. Participants

Twenty volunteers took part in the study (10 females; age M ± SD = 23.25 ± 2.38 years, range 20–31 years). This sample size fits well with prior mu-ERD and MEP studies on action observation (Naish et al., 2014; Pineda, 2005; Zhang et al., 2018). A post-hoc power analysis performed with the package '*simr*' (Green & MacLeod, 2016) running in R software (RStudio, Inc) revealed that, given a sample of N = 20 participants, the power (1 – β) of our linear mixed model (see Statistical analysis section for further details) was .98, which we consider highly adequate.

All participants were right-handed according to the Oldfield Handedness Inventory (Oldfield, 1971) (M ± SD = 73.53% ± 19.19% scores). None of them reported neurological or psychiatric problems or any contraindication to TMS or EEG (Rossi et al., 2009). All participants had normal or corrected-to-normal visual acuity. The experiment was approved by the Bioethical Committee at the University of Bologna and carried out in accordance with the Declaration of Helsinki. Written informed consent was obtained from each participant. The experiment was carried out at the Centre for studies and research in Cognitive Neuroscience (CsrNC) in Cesena, Department of Psychology, University of Bologna. All participants completed the experiment, and no adverse effects were reported or noticed.

2.2. Procedure

The experiment was carried out in a quiet and dark room. Participants sat at a distance of 65 cm in front of a 15″ PC monitor where visual stimuli were displayed. We followed the general procedure of a prior TMS–EEG study (Zanon et al., 2018), except that study tested other brain regions during rest and action execution only. The task used in the current study was made up of four experimental conditions (Fig. 1A–D): (i) Rest; (ii) Action Execution, during which participants were instructed to execute abduction–adduction movements either with the index or the little finger; (iii) Action Observation, during which participants observed abduction–adduction movements of a right index or little finger while remaining at rest; (iv) Static Hand Observation, during which participants remained at rest while observing the same hand in a static position.

Each condition was performed in different mini-blocks made up of 6 trials each (Fig. 1E). Every mini-block started with a 2-sec screen displaying the subsequent instruction – rest (i), action (ii), watch (iii, iv) – followed by a black screen which lasted 1–1.5 sec. Then, for the rest, static hand and action observation conditions, a fixation cross appeared at the center of the screen for 2 sec, while the specific finger to move (i.e., index or little finger) was displayed for the same time interval in the action execution condition. Subsequently, a scrambled image (obtained by scrambling the visual hand stimuli) was presented for 4 sec in the Rest and Action Execution trials. In the former, participants were instructed to relax their right hand while keeping their gaze fixated on the screen. In the latter, this image functioned as a Go signal for participants to start the required self-paced movement as soon as possible, always keeping their gaze fixated at the center of the monitor. The image of a static or dynamic hand lasting 4 sec was shown in the Static and Action Observation conditions, respectively (Fig. 1A–D). The static and dynamic hand images depicted the hands of 3 male and 3 female actors. Stimuli are openly available in Open Science Framework (OSF) at http://doi.org/10.17605/OSF.IO/9A8WB.

After 1.5/2.5 sec from the onset of the relevant visual stimulus (scrambled image/static hand/moving hand), a single pulse of active or sham TMS was applied over the left M1 (Fig. 1F). Active and sham TMS were delivered in different mini-blocks within the same experiment, but in the present article we focus on the active mode only and, therefore, the following descriptions do not cover the sham mode (see TMS section for further details). Sham data will be presented in a separate article focusing on TMS-evoked potentials and addressing a different research question.

The experiment was divided into 18 mini-blocks of each condition, in order to lighten the cognitive load – and therefore increase overall accuracy – due to the substantial number of experimental conditions and specific instructions to follow (Fig. 1E). A short break was allowed between mini-blocks. The overall task during active TMS, was made up of 432 trials divided into 108 trials for each condition, with 90 repetitions of

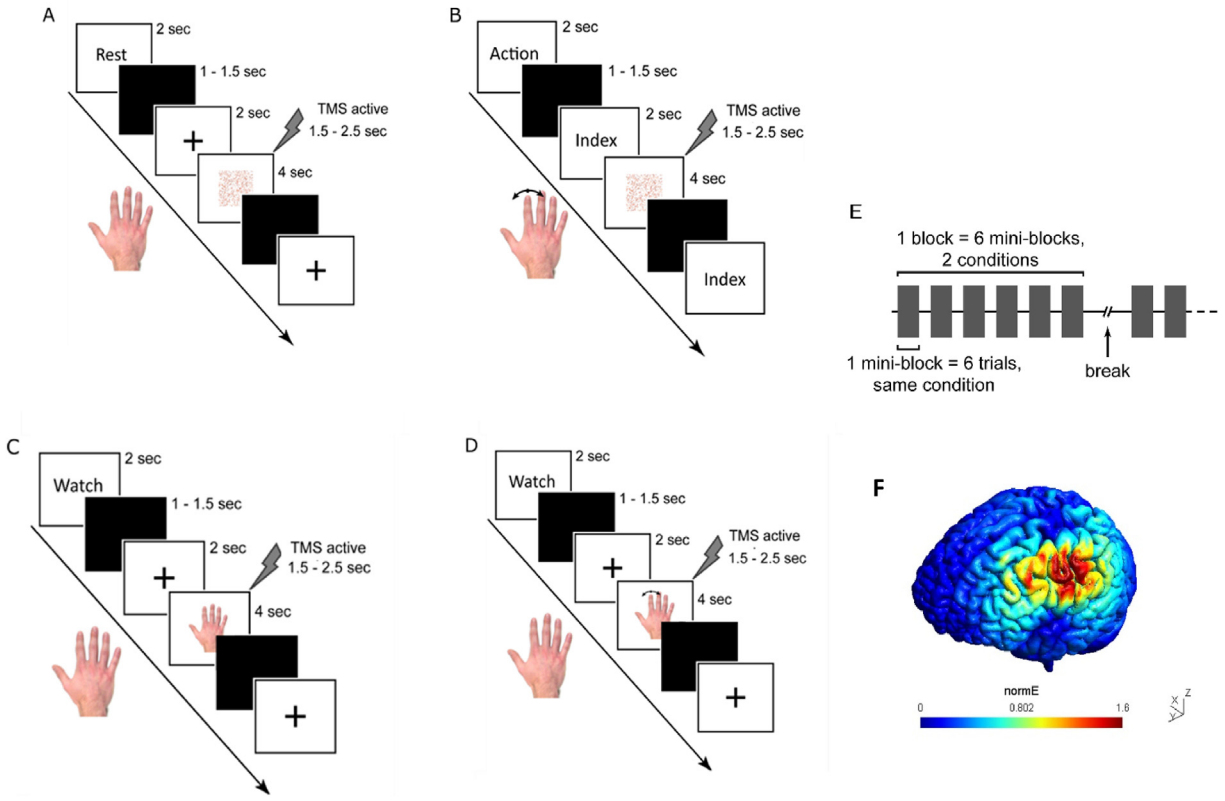

Fig. 1 – Schematic representation of the experimental design. A–D. Beginning sequences (1 complete trial) of the different conditions: (A) rest, (B) action execution, (C) static hand, (D) action observation. E. Schematic representation of trial organization in blocks and mini-blocks. F. Simulation of normalized electric field (NormE) distribution over the targeted left M1 site using SimNIBS 3.1.1. NormE intensity is color-coded from 0 to 1.6 mV/mm. Mean Talairach coordinates ± standard deviation of the targeted left M1 site were: x = −35.21 ± 7.02; y = −11.88 ± 9.4; z = 55.51 ± 4.91.

true trials and 18 of catch trials. In the small percentage of catch trials (around 17%), participants were asked to report the presence of a dot that could appear at the end of the image. This allowed us to check for an adequate level of vigilance throughout the entire task (for a similar procedure, see Zanon et al., 2018). The experiment was programmed in MATLAB (MathWorks Inc.), using the Psychophysics Toolbox extension (Brainard & Vision, 1997; Kleiner et al., 2007; Pelli & Vision, 1997) to control visual stimulus presentation and to trigger EMG, TMS and EEG. No part of the study procedures was pre-registered prior to the research being conducted.

2.3. TMS

Single monophasic magnetic pulses were administered using a 70-mm figure-of-eight coil connected to a Bistim2 TMS stimulator (MagStim Company, Ltd, UK). We placed the coil over the left M1 with the intersection of the coil aligned tangentially to the scalp and the handle pointing backward and laterally at a 45° angle away from the midline. To target the left M1, we first identified the motor hotspot of the right first dorsal interosseous (FDI) and made small adjustments to place the intersection of the coil flat against the scalp and not directly over the electrodes. The corresponding location was marked on the EEG cap to ensure proper placement of the coil throughout the experiment. To set stimulation intensity, we then determined the resting motor threshold (rMT), defined as the minimal intensity of stimulator output that produces MEPs with amplitudes of at least 50 μV with 50% probability in the FDI muscle. Because the FDI and the ADM share very similar functional topographic maps (Melgari et al., 2008), we used the FDI hotspot and rMT for both muscles.

The experimental TMS-pulse intensity was set to 105% of each individual participant's rMT. This stimulation intensity was chosen to prevent large TMS artefacts in the EEG signal (Zanon et al., 2018), and because lower TMS intensities are capable of eliciting signs of motor resonance (Loporto et al., 2013). During sham TMS, the coil was placed tangentially to the scalp, but a Plexiglas cube was attached to the coil so that it was separated from the scalp by 5 cm. Both in active and sham TMS, a thin layer of foam (50 mm) was placed between the coil and the EEG cap to mitigate the bone conduction of sound and the occurrence of trigeminal nerve stimulation (Zanon et al., 2013, 2018). Participants wore earphones throughout the experiment to attenuate the TMS click discharge sound (Ter Braack et al., 2015). Because our aim was to investigate the relationship between mu-ERD and MEP expressions of motor resonance, we analyzed active TMS trials only for this article, as no MEPs are elicited by sham TMS.

2.4. Neuronavigation

The SofTaxic NeuroNavigation System (EMS, Italy) was used in order to identify Talairach coordinates corresponding to the hand representation in the left M1 (i.e., the FDI motor hotspot). Before starting the experiment, a reconstruction of the participant's brain was computed in Talairach space based on an MRI template, 4 craniometric landmarks (nasion, inion and preauricular points) and 80 scalp points digitized with the Polaris Vicra Optical Tracking System (NDI, Canada). This procedure has been established to ensure a global localization accuracy of approximately 5 mm (Carducci & Brusco, 2012). The left M1 site stimulated during the experiment was localized at mean Talairach coordinates ± SD: x = −35.2 ± 7.0; y = −11.9 ± 9.4; z = 55.5 ± 4.9.

2.5. EMG recording and data preprocessing

Inclusion/exclusion criteria for EMG recordings were established prior to data analysis. Electromyography (EMG) was recorded using Biopac MP-35 (Biopac, USA) from the FDI and the abductor digiti minimi (ADM) muscles of the right hand, contralateral to the site of brain stimulation. The FDI and ADM muscles are responsible for controlling abduction movements of the index and little finger, respectively. EMG signal was band-pass filtered (30–500 Hz) and sampled at 5000 Hz. The absence of any voluntary contraction before the TMS pulse was visually controlled by the experimenter throughout the experiment. EMG signals were stored in a computer for offline analysis of background EMG activity (i.e., before the TMS pulse) and MEP amplitudes. EMG activity before the stimulation was root mean square (RMS) transformed and averaged in the period −100 to −1 msec prior to TMS. Because the focus of this study is on the relationship between EEG and MEPs, we focused on active TMS trials only in all analyses, as no MEP can be recorded in sham TMS trials. In each condition, trials with an EMG amplitude greater than 2 standard deviations from the mean were discarded from successive analyses (total rejection rate ~3%). For each trial involving active TMS, MEPs were induced in the two target muscles and peak-to-peak MEP amplitude (in mV) was computed in the 10–70 msec period following TMS. For each participant and condition, MEPs were normalized through logarithmic transformation (in line with Lepage et al., 2008).

2.6. EEG recording

Inclusion/exclusion criteria for EEG recordings were established prior to data analysis unless specified. EEG was acquired through a TMS-compatible EEG amplifier (BrainAmp DC, BrainProducts GmBH, Germany) along with 60 TMS-compatible sintered electrodes (EasyCap GmBH, Germany) mounted onto an elastic cap according to the 10/5 coordinate system. Additionally, two electrodes were placed on the outer canthi of the eyes to monitor saccades (hEOGI and hEORr) while another one was placed beneath the left eye to detect eye-blinks (vEOGI). Reference and ground electrodes were placed on the AFz electrode site and the right mastoid, respectively. Impedance was kept under 5Ω for each electrode. The sampling rate was set to 5000 Hz and the recorded signal was low-pass filtered at 1000 Hz (DC recording).

2.7. EEG preprocessing and data analysis

EEG recordings were analyzed using MATLAB R2019b (The MathWorks) and the Fieldtrip MATLAB toolbox (http://www.fieldtriptoolbox.org) (Oostenveld et al., 2011), in line with the pipeline reported by Herring et al. (2015) (http://www.fieldtriptoolbox.org/tutorial/tms-eeg/). First, the signal was divided into epochs of 7 s—from −3.5 to +3.5 s around the TMS pulse. Then, the TMS artefact was identified in the time interval between −2 msec and +15 msec around TMS pulse onset, and data in that interval were cut and interpolated using a cubic function (Rogasch et al., 2014; Zanon et al., 2018). The signal was downsampled to 500 Hz and noisy trials were rejected by adopting the criterion of 10^4 variance thresholds (total rejection rate: 4.4%). Independent Component Analysis (FastICA) was performed and ICA components reflecting TMS-related and other cranial muscle artefacts (Korhonen et al., 2011), as well as eye-blinks and saccades (Jung et al., 2000), were discarded through visual inspection by adopting a conservative approach to avoid dispersing relevant information (total rejection rate: <5%).

The signal was re-referenced to the channel average and high/low pass filters were applied (cutoff frequency = 100/1 Hz). TMS-locked oscillations were analyzed based on time-frequency representations (TFRs) by means of a Fast Fourier Transform (FTT). A Hanning sliding tapered time window of 50 msec was applied to the four experimental conditions by selecting 1–50 Hz frequencies in the time interval from −3 to +2 s around TMS onset. Linear trends and mean of the power were subtracted from every time window concomitantly to the time-frequency analysis (Luck, 2005). The following criteria were established following inspection of EEG signals. An absolute baseline correction was performed for each TFR by subtracting the power of the pre-TMS interval (from −3 to −2.5 s) from the whole selected time window. In the final preprocessing step, the grand average was computed for each experimental condition, excluding the vigilance trials. Lastly, by visually inspecting TF graphs as well as scalp maps of different time windows and frequency bands, we decided to focus our successive analyses on mu rhythm (8–13 Hz) in the −1.5 to −.5-s temporal window before the onset of the impulse. We thus extrapolated the power values which were averaged from C3 and CP3 electrodes over the left sensorimotor cortex.

2.8. Statistical analysis

We conducted a series of preliminary analyses to check participants' behavioral performance by assessing their accuracy in the vigilance task and EMG activity during the EEG recording. We focused on EMG activity prior to TMS pulses to ensure that participants activated their muscles in the Action Execution conditions and were at rest in the remaining conditions (e.g., during action observation). To this aim, a repeated measures analysis of variance (RM ANOVA) with the variables Condition (Rest, Action Execution, Static, Action

Observation) and Muscle (FDI, ADM) as within-subjects factors was conducted. In a further test, to ensure that muscle activation corresponded to the executed movements, we analyzed EMG activity from the FDI and ADM muscles in the Action Execution condition using a RM ANOVA with Muscle (FDI, ADM) and Movement (Congruent, Incongruent) as within-subjects factors to take correspondence with the executed movement into consideration. As a further control, we performed the same analysis on the Action Observation condition to ensure that no subtle EMG pre-activation was detected before TMS administration.

Concerning MEPs, we first carried out an exploratory 2-way RM ANOVA with Condition (Rest, Action Execution, Static, Action Observation) and Muscle (FDI, ADM) as within-subjects factors on log-transformed MEP amplitudes. Then, we tested motor resonance by assessing TMS-induced MEPs and mu-ERD. Because a main feature of motor resonance in TMS-induced MEP research is muscle congruency (e.g., Naish et al., 2014), we focused on Action Observation trials and analyzed mean MEPs using a 2-way RM ANOVA with the factors Muscle (FDI, ADM) and Movement (Congruent, Incongruent) as within-subjects factors to detect motor resonance.

For EEG data, a 1-way RM ANOVA was conducted to confirm mu-ERD in the contralateral motor cortex when performing and watching actions. Baseline-subtracted mu power was entered into the ANOVA as the dependent variable, and condition (rest, action execution, static, action observation) was entered as the within-subjects factor. Post-hoc analyses were carried out using Duncan's test. Moreover, to detect activation (i.e., ERD different from zero), one sample *t*-tests were carried out for each experimental condition. A further 2-way RM ANOVA was performed by adding the factor Hemisphere (left, right) to assess mu-ERD over the right hemisphere, as well (see Supplementary material). We also analyzed beta-ERD values to explore whether action observation and execution affected this frequency band (see Supplementary Material).

To answer our central experimental question, we computed correlation analyses between MEP indices of motor resonance (i.e., the difference in MEP amplitude between the congruent and the incongruent movement for each muscle[1]) and mu-ERD during Action Observation across subjects using averaged values; moreover, we computed correlations using all single-trial data points pooled together at the group (see below) and single-subject levels (see Supplementary Material). To match trials from EEG and EMG measurements, we discarded all trials where at least one of the two values was not present. A total rejection rate of 7.89% was achieved. We also performed Bayesian correlations in order to directly evaluate the relative strengths of evidence for the null and alternative hypotheses, thus providing quantification of the degree to which the data support either hypothesis (Dienes, 2014; Rouder et al., 2017).

Additionally, to further check for any relation between the two indices, we carried out a LMM on the single-trial data. MEP indices of motor resonance (i.e., congruent minus incongruent movements) were entered into the model as the dependent variable, with Muscle (FDI, ADM) as a fixed within-subjects factor, mu-ERD as a covariate, and subject variability as a random effect.

To ensure that the results were not affected by outliers, we repeated the main analyses (average correlations, trial-by-trial correlations, LMM) after discarding possible outlier values (see Supplementary Material). Moreover, to check not only for linear relationships, but also non-linear relationships, the LMM and the correlations were repeated with the addition of non-linear exponentials of mu-ERD values (see Supplementary Material). Finally, the main analyses (average correlations, trial-by-trial correlations, LMM) were repeated again using MEP values obtained by subtracting the average values of (i) Static and (ii) Rest conditions from congruent trials for each participant (see Supplementary Material). Significance was set at $p \leq .05$ Holm (LMM) post-hoc tests were used to follow up any significant interactions.

ANOVAs were performed using Statistica v. 12. Bayesian analyses were implemented using default priors in JASP v. 0.15.1 (Jasp Team 2021). Correlation analyses and LMMs were performed using both the '*nlme*' package (https://cran.r-project.org/web/packages/nlme/nlme.pdf) in R 1.2.5019 (RStudio, Inc) and Jamovi 1.0.7.0 (https://www.jamovi.org) software. No part of the study analyses was pre-registered prior to the research being conducted. The data that support the findings of this study are openly available in Open Science Framework (OSF) at http://doi.org/10.17605/OSF.IO/9A8WB.

3. Results

3.1. *Preliminary analyses*

First, the accuracy of participants in reporting the presence of a dot in vigilance trials was analyzed. Overall, an average accuracy of 99.05% (±.1% standard deviation) was reached at the group level. Errors included 68 missing responses (82.93% of total errors) and 14 false alarms (17.07%). No participant had an accuracy lower than 90%. Therefore, all participants were included in the subsequent analyses.

3.2. *EMG pre-activity*

Analysis of EMG activity before TMS ensured that participants were correctly activating their muscle during the experiment. The Muscle × Condition ANOVA on the EMG signal revealed a main effect of Condition ($F_{3,57} = 38.93$; $p < .001$, $\eta_p^2 = .67$) accounted for by the higher signal in the Action Execution condition (mean ± SD: .20 mV ± .11) compared to Rest (.02 mV ± .01, $p < .001$), Static (.03 mV ± .01, $p < .001$) and Action Observation (.02 mV ± .03, $p < .001$) conditions, which did not differ from one another (all $p > .60$). The main effect of Muscle and the Muscle × Condition interaction were not significant

[1] For example, for the FDI muscle, MEP indices were computed as the difference between the index finger and little finger movements, whereas for ADM MEPs, we computed the difference between the little finger and index finger movements. Then, in subsequent analyses for index finger movements, we considered FDI MEPs (index minus little finger movements), whereas for little finger movements we considered ADM MEPs (little minus index finger movements).

(all $F \leq 2.48$, all $p \geq .084$), indicating comparable muscle activations in the FDI and ADM muscles.

As expected, the two muscles were differentially activated as a function of the type of executed movement. The Muscle × Movement ANOVA showed a significant main effect of Movement ($F_{1,19} = 34.47$; $p < .001$, $\eta_p^2 = .64$) with larger signals for Congruent (.31 mV ± .19) than for Incongruent (.09 mV ± .04) movements (Fig. 2A). This effect was qualified by a Muscle × Movement interaction ($F_{1,19} = 8.42$; $p = .009$, $\eta_p^2 = .31$). Post-hoc tests confirmed larger EMG activation for congruent than for incongruent movements in both muscles (in both cases $p = .001$), but also showed that, in the congruent condition, the FDI (.34 mV ± .23) showed higher activity than the ADM muscle (.28 mV ± .17, $p = .005$), whereas in the incongruent condition, the FDI (.08 mV ± .04) and ADM (.10 mV ± .04) showed comparable activity ($p = .36$). The muscle × movement ANOVA on EMG signals during Action Observation showed no main effects or interactions (all $F \leq 1.36$, all $p \geq .26$), confirming that participants did not show pre-TMS modulation of muscle activity during action observation.

3.3. TMS-induced MEPs

The muscle × condition ANOVA conducted on MEP amplitudes showed a main effect of Muscle ($F_{1,19} = 5.30$; $p = .033$, $\eta_p^2 = .22$), with larger amplitudes in the FDI (.93 mV ± .63) than the ADM muscle (.69 mV ± .54). There was also a main effect of Condition ($F_{3,57} = 37.81$; $p < .001$, $\eta_p^2 = .67$), with larger MEPs in the Action Execution condition (1.69 mV ± 1.19) relative to all the other conditions (range: .47–.51 mV; all $p < .001$), which in turn did not differ from one another (all $p \geq .27$). These main effects were qualified by a Muscle × Condition interaction ($F_{3,57} = 10.42$; $p < .001$, $\eta_p^2 = .35$). Post-hoc analyses confirmed that, in both muscles, MEPs were larger in the Action Execution condition than in the other conditions (all $p < .001$). Moreover, relative to Rest, we observed marginally larger MEPs in the Action Observation and Static Hand conditions ($p \leq .06$), which in turn did not differ from one another (all $p \geq .40$). Finally, MEPs in the FDI and ADM were comparable during Action Execution ($p = .67$), whereas they were larger in the FDI than in the ADM muscle in the remaining conditions (all $p < .001$).

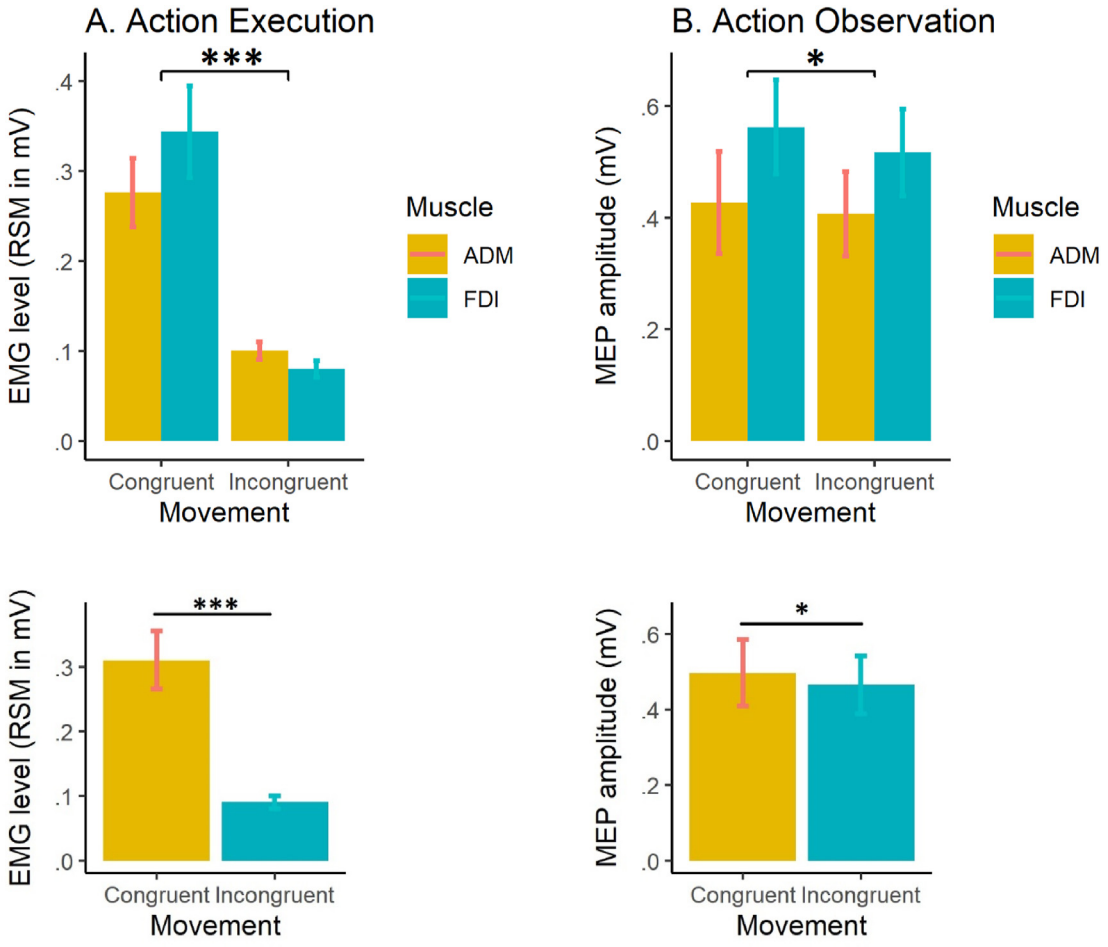

Fig. 2 – (A). EMG level during action execution. (B) MEP amplitudes during action observation. Top panels show the EMG and MEP responses separately for the two muscles. Bottom panels show the main effects of movement, indicating larger EMG activity when performing abduction/adduction movements congruent with the recorded muscle and larger MEP amplitudes when observing abduction/adduction movements congruent with the recorded muscle. Amplitudes are represented in raw values (in mV) instead of log-transformed values as used in the statistics. Error bars denote standard error of the mean.

Notably, in the previous analysis, MEPs during Action Observation were only marginally larger than MEPs during Rest and did not consistently differ from the Static Hand condition, which may suggest little or no motor facilitation and therefore no signs of motor resonance. However, a main feature of motor resonance is muscle specificity: motor facilitation should be detected only in those muscles involved in performing the observed action and not in incongruent muscles. Therefore, to address the issue of muscle congruency, in a further analysis, we focused on Action Observation trials only and distinguished between index and little finger movements. These observed movements were classified as congruent or incongruent relative to the recording muscle: for MEPs from the FDI muscle, we considered index finger abductions as congruent movements and little finger abductions as incongruent movements. Conversely, for MEPs recorded from the ADM muscle, we considered little finger abductions as congruent movements.

The Muscle × Movement ANOVA conducted on MEP amplitudes during Action Observation showed a main effect of Muscle ($F_{1,19} = 6.79$; $p = .017$, $\eta_p^2 = .26$), with larger amplitudes detected in the FDI (.54 mV ± .36) than the ADM muscle (.42 mV ± .37). Importantly, there was a main effect of Movement ($F_{1,19} = 5.05$; $p = .037$, $\eta_p^2 = .21$), showing greater amplitudes when observing congruent movements relative to the recorded muscle (.49 mV ± .36) than incongruent movements (.47 mV ± .38). That is, motor excitability was higher in the muscle corresponding to the observed movement (Fig. 2B). No interaction was found, indicating comparable motor resonance effects in the two recorded muscles ($F_{1,19} = .63$, $p = .44$, $\eta_p^2 = .03$).

3.4. *Mu rhythm*

The RM ANOVA showed a main effect of Condition ($F_{3,57} = 4.61$, $p = .006$, $\eta_p^2 = .2$; Fig. 3). Post-hoc tests showed that action observation (−.56 μV ± .96) entailed a stronger mu-ERD than static observation (−.15 μV ± .20; $p = .01$) and Rest (−.10 μV ± .33; $p = .004$), which did not differ from one another ($p = .71$). Similarly, action execution (−.45 μV ± .50) showed stronger mu-ERD than Static Observation ($p = .054$) and Rest ($p = .03$). Mu-ERD was comparable during action execution and action observation ($p = .44$). One sample *t*-tests confirmed that the mu rhythm was strongly desynchronized during action execution ($t_{19} = -3.95$, $p < .001$) and Action Observation ($t_{19} = -2.60$, $p = .018$); we also observed a small but consistent mu-ERD during static observation ($t_{19} = -3.37$, $p = .003$) but not during rest ($t_{19} = -1.35$, $p = .19$). These findings support the notion that observing actions performed by others engages the sensorimotor cortex similarly to when we perform the same actions. Mu-ERD during action observation and execution was not limited to central electrodes over the left hemisphere; rather, it extended over the right hemisphere (Fig. S1). On the other hand, further analyses showed that the beta rhythm was suppressed only during execution and not during action observation (Fig. S2).

3.5. *Relation between mu rhythm and MEPs during action observation*

The correlation analyses computed across participants on averaged individual values of mu-ERD and MEP facilitation during Action Observation showed no significant association ($r = -.095$; $p = .69$; see Fig. 4A for separate plotting of MEPs from the two muscles). Similarly, no significant correlation was observed when pooling trial-by-trial data of all participants ($r = .011$, $p = .68$). Bayesian correlations computed over these indices showed positive/strong evidence in favor of the null hypothesis (average values correlation: $BF_{01} = 3.352$; single-trial correlation: $r = .011$, $BF_{01} = 28.812$). These null results were also confirmed at a single-subject level (Fig. S3), where correlation analyses performed individually on single-trial basis did not show any significant relationship across trials within each participant.

To further test our data, we performed a LMM that showed no relation between mu rhythm and MEP facilitations during action observation ($p = .49$) (Fig. 4B) and only revealed a main effect of Muscle ($F_{1,1531} = 17.58$, $p < .001$), indicating larger

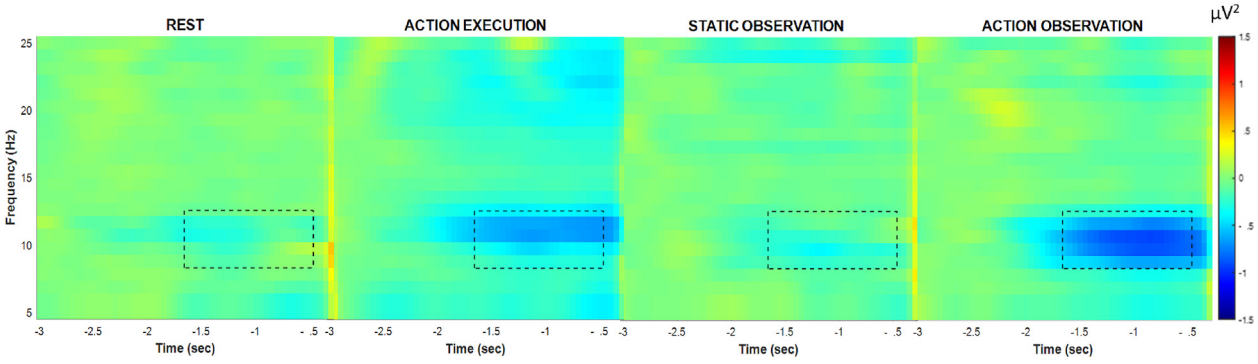

Fig. 3 – Mu rhythm oscillations in the four experimental conditions (rest, action execution, static observation and action observation). Time-frequency (TF) plots representing EEG activity before the TMS pulse averaged from electrodes C3 and CP3. The x-axis and the y-axis depict time (seconds) and frequency (Hz), respectively. The color bar on the right side ranges from −1.5 to +1.5 μV^2 of EEG power, with blue indicating desynchronization and red indicating synchronization. The dashed rectangles outline both the frequencies (8–13 Hz) and the time-window (−1.5 to −.5 sec) selected for statistical analysis. Mu-ERD is clearly visible during action execution and action observation but not during rest and static observation.

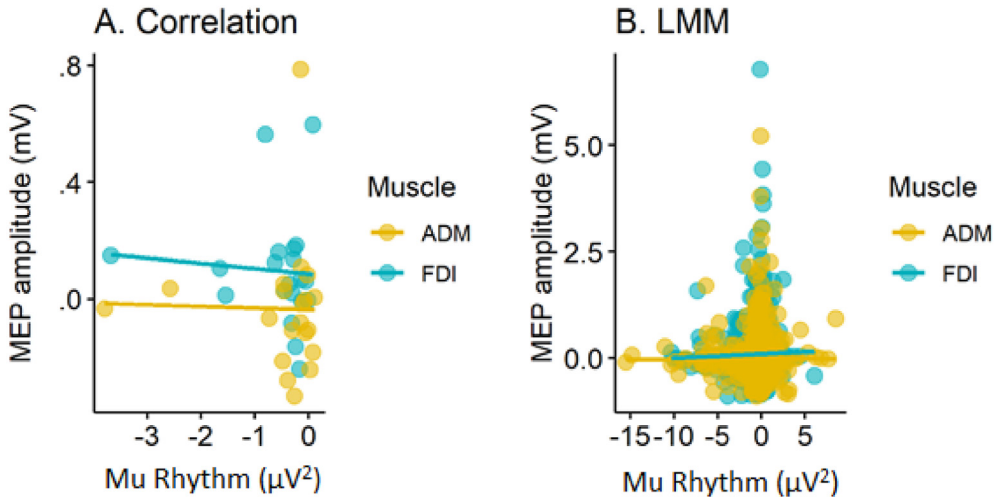

Fig. 4 – Relationship between mu rhythm and MEP indices of motor resonance in the action observation condition A) from averaged data (correlation) B) and on a trial-by-trial basis (LMM). In all graphs, the x-axis represents mu (mV^2), while MEP amplitudes (in mV) during congruent relative to incongruent movements are depicted in the y-axis. In graph A, each dot represents a single participant, while in graph B each dot represents a trial. In all graphs, dot color characterizes the specific muscle (yellow-ADM, light blue-FDI) and regression lines are shown for both muscles.

amplitudes of FDI MEPs than ADM MEPs. Additional control analyses consistently confirmed a lack of both linear and non-linear relations between mu-ERD and MEP facilitation (see Supplementary Results).

4. Discussion

Despite extensive knowledge about the involvement of the sensorimotor cortex during action observation and execution (Avenanti et al., 2013b; Caspers et al., 2010; Fadiga et al., 2005; Hardwick et al., 2018; Pineda, 2005), it remains unclear whether two key markers of motor resonance – EEG-based mu-ERD and TMS-based MEP modulations – could reflect similar or distinct neural processes (Lapenta et al., 2018; Lepage et al., 2008; Prinsen & Alaerts, 2020), as prior work did not combine TMS–EEG co-registration with a trial-by-trial analysis of the two markers to provide sensitive conditions to evaluate their association.

To answer this question, we carried out a TMS–EEG co-registration study where participants were invited to watch another person performing specific finger movements, as well as to make those movements themselves. While executing the task, single-pulse TMS was delivered over the left M1 while EEG and EMG activity were simultaneously recorded. Our results confirm that both mu-ERD and MEPs reflect motor system activation, as shown by i) the greater mu-ERD over central/centro-parietal electrodes in the action execution and action observation conditions compared to control conditions; ii) the larger MEPs recorded when executing the action with respect to all the remaining conditions, together with a muscle specificity effect revealed by MEPs in the action observation condition. However, when directly comparing mu-ERD and MEPs, we were unable to find any significant relationship between the two measures.

Concerning the first point, that is, the greater mu-ERD over the left sensorimotor cortex while executing and observing a movement, our results confirm the well-established suppression of mu frequency bands during both voluntary movement performance and action observation, especially in the contralateral sensorimotor cortex (Braadbaart et al., 2013; Frenkel-Toledo et al., 2014; McFarland et al., 2000; Pfurtscheller et al., 2000, 2006; Pineda, 2005), thus providing EEG evidence of motor resonance.

The MEP data also appear to be in line with the existing literature. Indeed, it is common knowledge that there is a strong facilitation of corticospinal excitability during action execution (Lepage et al., 2008; Prinsen & Alaerts, 2020) and a similar (although weaker) facilitation is observed during action observation (Fadiga et al., 1995; Naish et al., 2014). Interestingly, in the present study, we tested a critical feature of motor resonance, i.e., muscle specificity. While prior TMS–EEG studies assessed motor resonance by testing MEPs from a single muscle during the observation of a single type of action (Bekkali et al., 2021; Lapenta et al., 2018; Lepage et al., 2008; Prinsen & Alaerts, 2020), here, we optimized the design by testing two distinct muscles during observation of two types of actions differentially recruiting the target muscles. Our findings indicate that motor resonance occurred according to fine-grained somatotopic rules: for both muscles, we found greater corticospinal excitability during the observation of congruent than incongruent movements; that is, when participants observed index abductions/adductions, we recorded larger MEPs in the FDI muscle, while observation of little finger movements increased MEPs in the ADM muscle. These findings confirm that the MEP facilitations truly reflected motor resonance rather other non-specific processes (Lepage et al., 2010; Naish et al., 2014).

Notably, to test the relation between mu-ERD and MEPs, we combined both frequentist and Bayesian correlational

analyses and investigated trial-by-trial variability using a linear mixed model. Using multiple statistical approaches, we provided compelling evidence in favor of the independence of these two indices of motor resonance: there was no relation between mu-ERD recorded by EEG and the MEPs elicited by TMS over the left primary motor cortex when watching others' actions.

Although Lepage et al. (2008), Lapenta et al. (2018) and Prinsen & Alaerts (2020) have already found an absence of any significant correlation between these two parameters when watching others' actions, our study provided strong evidence in support of this result by adopting an extended statistical approach. Indeed, it should be noted that mu-ERD and MEPs greatly vary between participants as well as within the same participant and experimental condition (Goldsworthy et al., 2016; Madsen et al., 2019; Pfurtscheller et al., 2006). These features strongly necessitate a trial-by-trial approach when dealing with these kinds of data (for a review on LMM statistical power, see Dean & Nielsen, 2007). In accordance with this, we adopted statistical analyses (i.e., linear mixed model and single-subject correlation analysis) that allowed us control for intra-subject and trial-by-trial variability. These analyses showed no significant relation between mu-ERD and MEP facilitation during action observation. Moreover, by adopting a Bayesian approach, we also provided positive evidence supporting the null hypothesis of no relation between the two neurophysiological indices.

Therefore, we provide the first evidence of the independence of mu-ERD and MEP indices of motor resonance when directly comparing these two measures at both single-trial and single-subject levels. The independence of EEG and TMS parameters may appear puzzling, as both mu-ERD and MEPs are often interpreted as signs of motor cortex activation. Several scholars have proposed that the mu rhythm should be interpreted as more "somatosensory" than "motor" (Cheyne et al., 2003; Hari et al., 1997; Simões et al., 2004). Indeed, mu-ERD is also typically observed when sensing tactile or painful stimuli on the body (Cheyne et al., 2003; Gaetz & Cheyne, 2006; Spaccasassi et al., 2021; van Ede et al., 2010, 2011), which are conditions that engage the somatosensory cortex. In a similar vein, it is possible that, during action observation, suppression of mu rhythm would reflect activation of the somatosensory cortex. This would be in keeping with studies showing that the somatosensory cortex is consistently activated when watching others' actions (Avikainen et al., 2002, 2007; Rossi et al., 2002; Caspers et al., 2010; for a review, see Keysers et al., 2010), that it exchanges information with the rest of the action observation network (Avenanti et al., 2007; Valchev et al., 2016) and that it contributes to action recognition (Jacquet & Avenanti, 2015; Paracampo et al., 2017; Valchev et al., 2017), possibly by providing information about the somatosensory features of observed actions (e.g., Avenanti et al., 2007; Gallo et al., 2018; Keysers et al., 2010). Notably, co-registration of EEG and fMRI shows a relationship between mu-ERD over central electrodes and BOLD activity over somatosensory areas during movement observation and execution (Arnstein et al., 2011). This would be in line with the notion that the somatosensory cortex is a key source of oscillations in the 8–13 Hz frequency band (Ritter et al., 2009; Salmelin and Hari, 1994) and could have a role in the mu-ERD during action observation. Interestingly, Arnstein et al. (2011) found no consistent relation between mu-ERD and BOLD activity in a classical motor node of the mirror neuron system, i.e., the inferior frontal cortex (IFC), a site at the border between the ventral premotor cortex and the posterior inferior frontal gyrus (Avenanti & Urgesi, 2011), functionally connected with M1 (Davare et al., 2009; Fiori et al., 2016, 2018). Conversely, Avenanti and colleagues showed that downregulation of the IFC with low-frequency repetitive TMS disrupted MEP facilitation during observation of finger movements, whereas downregulation of the somatosensory cortex did not affect the magnitude of this MEP index of motor resonance (Avenanti et al., 2007, 2013a). Taken together these prior studies support the idea of dissociable neural networks driving mu-ERD and MEP facilitations during action observation, and thus converge with the present findings suggesting distinct neural mechanisms underlying these physiological responses to observed actions. Assuming that mu-ERD would reflect processing of somatosensory aspects of observed actions, one possible avenue for future research could be to try to independently manipulate the quantity of motor and somatosensory features of observed actions and test the effect on MEPs and mu-ERD (e.g., Avenanti et al., 2007; Quandt et al., 2013).

Recently, both Thies et al. (2018) and Madsen et al. (2019) tracked the relation between mu rhythm and MEPs by simultaneously collecting EEG and TMS–EMG data while participants were at rest. Thies et al. (2018) found a weak and overall positive relation between cortical oscillatory power within the alpha band (8–13 Hz) and cortical excitability as measured with TMS and MEPs. However, using a powerful statistical approach, Madsen et al., 2019 showed no evidence of a relationship between mu rhythm and MEPs at rest. Further evidence of dissociations between these EEG and MEP measures comes from studies investigating the neural correlates of empathy for pain (for a review, see Riečanský & Lamm, 2019). Indeed, while both EEG (mu-ERD) and TMS (MEP facilitation) indices of motor resonance converge toward increased cortical excitability during action observation, the same indices tend to diverge when seeing painful stimuli on the bodies of other people. Seeing pain in others induces a reduction in MEP amplitudes specific to the muscle that participants observe being painfully stimulated (Avenanti et al., 2005, 2009; Minio-Paluello et al., 2006, 2009), whereas EEG shows an attenuation of sensorimotor rhythms when watching others' pain that reflects cortical activation (Cheng et al., 2008b; Riečanský et al., 2015; Riečanský & Lamm, 2019).

Our findings further support the conclusion that mu rhythm and MEPs reflect largely independent mechanisms – at least during observation of actions. This conclusion is also supported by a recent study in which transcranial alternating current stimulation administered at 10 Hz over M1 (i.e., at the frequency of mu oscillations) did not affect the magnitude of MEP facilitation during action observation (Wang et al., 2021), whereas other transcranial stimulation protocols known to modulate M1 excitability influenced MEP facilitation (Qi et al., 2019a, 2019b; but see Avenanti et al., 2007). Thus, while M1 excitability appears relevant to the MEP index of motor resonance, oscillatory activity at a mu frequency does not.

Interestingly, Hetu et al. (2016) recently provided evidence suggesting there is no correlation between MEP facilitation due to action observation and behavioral markers of motor resonance (i.e., motor priming and interference effects during action observation). Taken together, this study and TMS–EEG experiments, including the present experiment, hint at the presence of multiple independent mechanisms underlying apparently correlated phenomena during action observation.

The independence of mu-ERD and MEP facilitation could be related to the different spatial and temporal characteristics of the two techniques. Indeed, while EEG mu-ERD would reflect slow oscillatory activity from an area wider than M1 (e.g., possibly involving somatosensory areas), TMS is able to instantaneously capture fluctuations in corticospinal excitability by stimulating discrete populations of neurons in M1. Moreover, MEP amplitudes could be affected by a spinal contribution (Baldissera et al., 2002) which is not considerably captured by EEG recordings. Additionally, watching others' actions (i.e., right hand movements) usually yields a desynchronization of sensorimotor cortices in both hemispheres, not just the contralateral one (Heida et al., 2014), as we also reported here (Fig. S1). Further, while mu-ERD is located over central areas during action execution, it involves more extensive fronto-parietal areas during action observation (Fox et al., 2016). In contrast, TMS modulations of MEPs are specific to the muscles involved in the observed actions, suggesting they reflect activity restricted to specific groups of neurons in M1.

A possible limitation of the present study is that we selected the mu rhythm band at a group level (8–13 Hz) rather than extrapolating individual mu ranges at a single-subject level (e.g., each participant could have exhibited stronger mu rhythm at a different frequency range within the 8–13 Hz band). This approach could have led to higher type II error, despite our results being in line with the previous literature (Bekkali et al., 2021; Lapenta et al., 2018; Lepage et al., 2008; Prinsen & Alaerts, 2020). Moreover, our analyses focused on mu rhythm rather than on faster activity, e.g., in the beta range (Hari et al., 1998; Wang et al., 2021). Yet, in our study, beta-ERD only occurred during action execution; we observed little or no modulation of beta rhythms during action observation (Fig. S3). It is well established that action execution robustly reduces beta activity, which cannot be merely considered as a harmonic resulting from the non-sinusoidal waveform of mu activity (McFarland et al., 2000). Moreover, despite prior research mostly focusing on mu-ERD, there is also evidence of changes in beta activity during action observation – although more consistent effects are commonly observed with goal-oriented actions (e.g., grasping or manipulating objects) rather than repetitive finger movements (e.g., Avanzini et al., 2012; Muthukumaraswamy & Johnson, 2004b). While we do not rule out that action observation could alter beta oscillations, it is possible that the type of finger movements we used in this study may have prevented us from detecting a consistent beta-ERD. Thus, one aim of future TMS–EEG research would be to further test possible relationships between neurophysiological markers of motor resonance using goal-directed actions and a trial-by-trial analysis – although, so far, TMS–EEG studies showing beta-ERD during observation of goal-directed actions reported no relationship with MEPs using averaged values (Bekkali et al., 2021; Lapenta et al., 2018).

5. Conclusion

When watching people making actions, we map the observed movements onto the corresponding areas of our own motor cortex that would have been activated if we were the agent of that action. This '*motor resonance mechanism*' is well captured by desynchronization of mu rhythm oscillations recorded through EEG as well as by facilitation of motor-evoked potentials elicited by TMS of the observer's M1. In the present work, through a TMS–EEG co-registration study, we tried to understand whether these two parameters reflect the same or distinct neural processes during action observation. Despite applying a powerful trial-by-trial statistical approach, we observed no relation between the two markers, even though both were sensitive to action observation. Our results suggest that mu-ERD and MEPs reflect two distinct processes occurring within the action observation network. We therefore confirmed William James intuition when he stated that "*every mental representation of a movement awakens to some degree the actual movement which is its object*" (James, 1890), but failed to find the red thread that binds EEG and TMS motor resonance signatures.

Author's contributions

CS: analyzed the data and wrote the manuscript. MZ: designed the experiment, collected the data and revised the manuscript. SB: collected the data and revised the manuscript. AA: conceptualized the experiment, analyzed the data and wrote the manuscript.

Open practices

The study in this article earned Open Data and Open Materials badges for transparent practices. Materials and data for the study are available at http://doi.org/10.17605/OSF.IO/9A8WB.

Declaration of competing interest

Authors have nothing to declare.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2022.04.019.

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