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ORIGINAL ARTICLE

Cortical sources of electroencephalographic alpha rhythms related to the anticipation and experience of mirror visual feedback-induced illusion of finger movements

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Abstract

Mirror visual feedback (MVF) technique consists in placing a mirror in a person's body midline to induce the illusion of bilateral synchronous movements of the limbs during actual unilateral movements. A recent electroencephalographical (EEG) study demonstrated that MVF-induced illusion was related to the event-related desynchronization (ERD) of alpha (8–12 Hz) rhythms (cortical activation) at the central and parietal scalp electrodes ipsilateral to the unilateral right finger movements. In the present study, we re-analyzed those data to localize the cortical sources of alpha ERD during the anticipation and experience of the MVF-induced illusion of index finger movements. To this aim, the exact Low-Resolution Brain Electromagnetic Tomography freeware was used for the estimation of the cortical sources of the alpha ERD. Results showed that as compared to the condition without MVF, the MVF condition was characterized by greater ($p < .01$, uncorrected) alpha ERD sources in right frontopolar areas during the anticipation of the MVF-induced illusion of left movements. The MVF condition was also characterized by greater ($p < .05$, corrected) alpha ERD sources in right premotor, primary somatomotor, and posterior inferior parietal areas during both the anticipation and experience of that MVF-induced illusion. These findings suggest that the MVF-induced illusory experience of left finger movements may be due to dynamic changes in alpha ERD in associative, premotor, somatomotor, and visuomotor frontal–parietal areas located in the hemisphere contralateral to the mirrored motor acts.

KEYWORDS

alpha event-related de/synchronization (ERD/ERS), eLORETA, hhigh-density electroencephalography (HD-EEG), mirror visual feedback (MVF), sensory-motor cortex, source analysis

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1 | INTRODUCTION

Mirror visual feedback (MVF) technique consists in placing a mirror in a person's body midline to induce the illusion of bilateral synchronous movements of the limbs (usually hand or single fingers) during actual unilateral movements (Ortiz-Catalan et al., 2016; Rjosk et al., 2016). In the typical experimental approach, the mirror is positioned to produce an image of the reflected limb corresponding to the position of the limb hidden behind the mirror. While performing overt movements of the uncovered limb, the view of the image of the moving limb reflected in the mirror induces the conscious experience of the opposite limb moving in the space region compatible with the position of the unseen limb (Ding et al., 2019; Ramachandran et al., 1995; Ramachandran & Rodgers-Ramachandran, 1996). Notably, this experience was found to be associated with processes of somatomotor cortical reorganization and plasticity (Al-Wasity et al., 2019; Nojima et al., 2012; Ramachandran & Rodgers-Ramachandran, 1996), thus motivating innovative neurorehabilitation strategies for patients with chronic pain conditions such as phantom limb pain syndrome (Finn et al., 2017; Ramachandran & Rodgers-Ramachandran, 1996; Thøgersen et al., 2020), poststroke hemiparesis (Bae et al., 2012; Bartur et al., 2018; Dohle et al., 2009), complex regional pain syndrome (McCabe et al., 2003; Vladimir Tichelaar et al., 2007), and for the motor recovery of upper extremities (Bullock et al., 2020; Zhang & Fong, 2019).

Functional magnetic resonance imaging (fMRI) was used to identify the cortical and subcortical anatomical structures involved in the mentioned processes of somatomotor cortical reorganization and plasticity and explore the brain activity related to the MVF-induced illusion with a very high spatial resolution (i.e., one millimeter). The main results disclosed a major involvement of the primary motor and somatosensory (somatomotor) cortical areas during the MVF-induced illusion (Fritzsch et al., 2014; Hamzei et al., 2012; Matthys et al., 2009; Numata et al., 2013). In addition, these studies found the activation of premotor areas (Hamzei et al., 2012; Numata et al., 2013) and the superior temporal gyrus (Matthys et al., 2009), thus suggesting the involvement of a visuomotor cortical pathway in the emerging of the MVF-induced illusion. Interestingly, fMRI studies using kinesthetic illusions to investigate the neural basis of body representation unveiled the central role of a wide network encompassing the sensory-motor cortex, parietal and inferior fronto-parietal regions (for a review, see Naito et al., 2016).

Due to its intrinsic limitations in temporal resolution (i.e., one second), fMRI results could not clarify the temporal evolution of cortical areas involved in the MVF-induced illusion. Therefore, the time course of the cortical activity related to the MVF-induced illusion was investigated by electroencephalographic (EEG) techniques having a very high temporal resolution (i.e., less than one millisecond) (Kim & Lee, 2015; Light et al., 2011). Several studies used mean lateralized readiness potentials (LRPs) recorded from the central scalp regions overlying somatomotor cortical areas (Debnath & Franz, 2016; Touzalin-Chretien et al., 2009, 2010; Touzalin-Chretien & Dufour, 2008). The LRPs can be obtained by (1) averaging the ongoing EEG activity related to many repetitions of a voluntary unilateral limb movement, using the onset of the related muscle electromyographic activity or the movement onset as a zero time for that averaging, and (2) subtracting the averaged event-related potentials at the homologous central electrodes of the two hemispheres. These LRPs reflect the prominent steeper increase in the negative scalp potentials as a measure of the increasing somatomotor cortical excitability during the preparation of voluntary movements (Mittelstadt et al., 2022). LRPs showed low amplitude when unilateral hand movements were experienced as bilateral movements during the MVF-induced illusion, while they showed high amplitude during the control unilateral hand movements performed without MVF (Debnath & Franz, 2016; Touzalin-Chretien et al., 2009, 2010; Touzalin-Chretien & Dufour, 2008). Those results suggest that the MVF-induced illusion may be related to increased excitability in the somatomotor cortical areas ipsilateral to unilateral hand movements.

The temporal resolution of the EEG technique also allows the exploration of an intrinsic neurophysiological property of the cortical activity, namely its time-varying oscillation reflecting changes in the cortical excitability (Babiloni et al., 2020). In healthy adults, ongoing EEG activity shows prominent oscillations at 8–12 Hz in central and parietal scalp regions, the so-called alpha rhythms, as a sign of the inhibition of somatomotor cortical networks in the condition of psychophysical relaxation and sensory deprivation (Babiloni et al., 2020). During the preparation and execution of voluntary unilateral hand movements, EEG alpha rhythms significantly reduce in amplitude (alpha event-related desynchronization, alpha ERD) in the central and parietal scalp regions, as a sign of the enhanced cortical excitability of somatomotor and associative parietal cortical areas (Babiloni et al., 1999; Pfurtscheller & Lopes Da Silva, 1999; Pfurtscheller & Neuper, 2006). Using an MVF paradigm implemented by virtual reality, Lee and colleagues showed a central alpha ERD related to the MVF-induced illusion during unilateral voluntary self-paced hand movements (Lee et al., 2015). Bartur and colleagues found a low-frequency (8–10 Hz) alpha ERD topographically widespread to frontal, central, and parietal areas in relation to the MVF-induced illusion during unilateral voluntary self-paced hand movements (Bartur et al., 2015). Those results suggest that the MVF-induced illusion may be related to changes in specific movement-related EEG rhythms at alpha frequencies with a variable scalp topography, possibly depending on the long-time course of the movement preparation and the intrinsic bilateral representation of the alpha ERD during the preparation and execution of voluntary self-paced movements.

To better understand the above issue, we instructed healthy participants to perform auditory cue-triggered movements of the right index finger with and without MVF in a previous reference study (Rizzo et al., 2022). This kind of motor event is ideal to investigate the scalp topography of alpha ERD associated with the MVF-induced illusion of left finger movements, as the auditory-triggered right finger movements were expected to be mainly associated with the activation of the contralateral hemisphere without the MVF (noMVF). Results from our previous study (Rizzo et al., 2022) showed that in the MFV condition, the participants experienced the illusion of left finger movements while watching the moving finger in the mirror. The MVF condition was also characterized by a prominent alpha ERD (cortical activation) at bilateral central and parietal scalp electrodes during both the preparation and execution of right finger movements. In contrast, the noMVF condition was associated with a prominent alpha ERD only over the hemisphere contralateral to the right finger movements. However, the above methodological approach did not allow to make inferences about the cortical areas activated during the MVF-induced illusion as the focus of the investigation was centered on the alpha ERD distribution on the scalp rather than the mapping of the cortical sources.

In the present study, we reanalyzed the EEG data sets by the mentioned reference study (Rizzo et al., 2022) using the Exact Low-Resolution Brain Electromagnetic Tomography (eLORETA) freeware for estimating the cortical sources of the alpha ERD (www.keyinst.uzh.ch/loreta; Pascual-Marqui et al., 2002). Since the conscious experience of illusory movements entails that the visual imposition of the mirrored hand is reflected in the motor and somatic cortical areas (Ramachandran, 2005), the present study aimed at testing the hypothesis that as compared to the noMVF condition, the MVF condition may be characterized by prominent cortical sources of alpha ERD localized in primary somatomotor and lateral premotor areas of the right hemisphere ipsilateral to the true right finger movements and contralateral to the moving finger reflected in the mirror. Moreover, as the somatomotor, fronto-parietal, and posterior parietal cortical networks have been related to body awareness during kinesthetic illusion (Naito et al., 2016), the present study attempted to show that MVF-induced illusion of finger movements caused a clear change in the cortical sources of the alpha ERD situated in those specific brain regions. A special interest was focused on the dynamic changes of those alpha ERD source activity during the anticipation and the experience of the MVF-induced illusion of left finger movements.

2 | METHOD

The main procedures (such as details on participants, experimental design, and EEG recording and preprocessing) of the current study have been previously described in a previous reference study that aimed to investigate the alpha ERD/ERS at the scalp level related to the MVF-induced illusory of finger movements (Rizzo et al., 2022). A general overview of those main procedures is hereby reported.

2.1 | Participants and ethical approval

Eighteen healthy right-handed male volunteers (mean age = 28.7, *SD* = ±4.9) took part in the experiment. Primary exclusion criteria were the presence of chronic pain, nerve pain, psychiatric and neurological diseases, and current medical treatments. All experiments were conducted at the Aalborg University (Denmark), and all subjects signed an informed consent according to the Declaration of Helsinki. The study was approved by the Scientific Ethical Committee of Region Nordjylland (N-20190008).

2.2 | Experimental procedure

All the participants were seated on a chair with their arms positioned symmetrically ahead on a desk. Finger movements were triggered by auditory cues. The movement consisted of a double extension of the index finger, with a slow release toward the bottom. Every participant performed 80 trials for each condition. To induce a sort of predictability of the upcoming stimuli and obtain clear anticipatory cortical responses, a fixed inter-stimulus interval (ISI) of 10 s was used. However, to avoid systematic, overt movements anticipation, the subjects were not informed about the fixed duration of the ISI. Moreover, a 10 s interval is a sufficient period to reset the alpha rhythms synchronization (Babiloni et al., 2008). Figure 1 shows the setup during the experimental condition (*MVF*), whereby the mirror was positioned on a desk in the midsagittal plane in front of the subjects reflecting the right hand and forearm. The participants were instructed to perform the right index finger extensions in response to

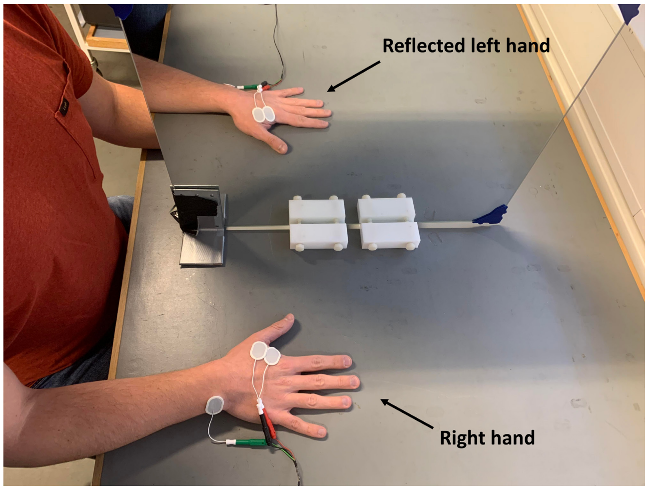

FIGURE 1 Experimental setup of the Mirror Visual Feedback procedure. The mirror is placed in the subjects' midsagittal plane, providing a view of the hidden left hand. In the control condition (no*MVF*) the mirror was removed. Electroencephalography (EEG) and electromyography (EMG) were recorded during all the conditions.

the auditory cue to induce the illusion of the left index finger movement as reflected in the mirror. The participants were instructed not to perform left-hand movements. In the control condition, the participants performed the same task (auditory-triggered right index finger movements) without the mirror (*noMVF*), hence, both hands were visible to the participants (for further details, see Rizzo et al., 2022). After the MVF condition, a revised version of the Rubber Hand Illusion Questionnaire (RHI-Q, Longo et al., 2008) was adapted to assess the subjective experience of the MVF illusion. Subjects reported their score on a numerical scale from 1 ("*I strongly disagree*") to 7 ("*I strongly agree*"). Specifically, the questionnaire assessed the sense of *ownership* (the feeling that the reflected finger belonged to the body, items 1–5) and *agency* (the feeling of moving the reflected finger, items 8–9) over the reflected hand (Longo et al., 2008). Finally, a correlation analysis (Pearson) was performed between each item of the questionnaire and the alpha ERD/ERS detected from the right somatomotor cortex (i.e., contralateral to the illusory hand). For further details, see Tables S1 and S2 in Supporting Information.

2.3 | EEG recordings and analysis

All the EEG recordings were conducted using a 64-channel active system (g.HIamp amplifier, g.tec medical engineering GmbH, Austria), installed on a standard cap according to the 10–10 international system (the sample rate was 1200 Hz and the scalp electrodes' impedance was kept under 5 kΩ). Reference electrodes were positioned on the ear lobes and the ground electrode on the forehead, whereas the frontal channels recorded the eye movements to control the blinking activity (for further details, see Rizzo et al., 2022). Offline EEG data analysis was performed by the EEGLAB (Delorme & Makeig, 2004) toolbox for MatLab (MathWorks, Inc., Natick, MA). EEG data were visually inspected, and a zero-phase basic FIR filter (passband edges between 0.3 and 40 Hz) was applied. Thus, data were resampled to 256 Hz and epoched in eighty 9 s windows. The toolbox for the independent component analysis (ICA) was used to recognize and remove EEG artifacts such as eye movements, blinking, muscular movements, etc (for further details, see Rizzo et al., 2022).

2.4 | Cortical source analysis

The artifact-free EEG data were used as input for cortical sources estimation using the freeware tool "exact Low-Resolution brain Electromagnetic Tomography" (eLORETA) (Pascual-Marqui, 2007). eLORETA is a functional imaging technique belonging to a family of standardized linear inverse solution procedures modeling the 3D distributions of the EEG sources within a head volume conductor model comparted in the scalp, skull, and brain (Pascual-Marqui et al., 1999, 2002). The eLORETA freeware solves the EEG inverse problem by estimating the cortical current density values at the voxel level. Based on the Montreal Neurological Institute (MNI152) template, eLORETA provides a brain source space restricted to the cortical gray matter of 6239 voxels with 5 mm resolution, with each voxel containing an equivalent current dipole. For each voxel, eLORETA indicates the MNI coordinates, the lobe, and the Brodmann area (BA). Since eLORETA source analysis is a reference-free method (Peng et al., 2015), the input for the sources estimation was the spectral power density computed by 62 scalp electrodes (i.e., the two reference electrodes were not considered for the cortical sources analysis). Of note, due to the lack of spatial resolution of EEG techniques, we considered Brodmann areas 1, 2, and 3 (primary somatosensory cortex) together with Brodmann area 4 (primary motor cortex), as a single functionally coherent cluster of cortical regions. The same was true in considering Brodmann area 10 together with Brodmann area 11 (polar prefrontal cortex).

2.5 | Individual alpha frequency calculation

For the quantification of the alpha band, the individual alpha frequency (IAF) peak was identified as the frequency showing the maximum power peak within the 8–12 Hz range (Klimesch, 1999). Consequently, the eLORETA solutions were individually filtered at the alpha band depending on the IAF, that is from IAF − 2 Hz to IAF + 2 Hz (mean IAF peak = 10.2; *SD* = ±1.0).

2.6 | Alpha ERD/ERS calculation

The eLORETA solutions were used to compute the cortical voxel-level event-related desynchronization/synchronization (ERD/ERS) in the alpha frequency band. Specifically, the alpha ERD/ERS was calculated by the formula: $\text{ERD/ERS\%} = (E - R)/R*100$, where E and R represent the instant power density at the "event" and "rest" periods, respectively (Del Percio et al., 2010; Pfurtscheller et al., 1997; G. Pfurtscheller & Aranibar, 1979; Pfurtscheller & Lopes Da Silva, 1999; Pfurtscheller & Neuper, 1994). The "rest" period was defined as the period from 5 to 4 s before the auditory cue (0). The anticipatory "event" period was defined as the period of 1 s before the auditory cue. Finally, the "event" period during movement execution was defined as the period from 250 to 1250 ms after the auditory cue, and the alpha ERD peak in this interval was considered for the statistical analysis. The experimental timeline is represented in Figure 2. Of note, the 250 ms after the auditory cues were intentionally excluded to remove the auditory-evoked potentials (i.e., N1-P2 complex) from the ERD/ERS analysis. Resultant negative percentage values represent the alpha power suppression (ERD, cortical activation), whereas positive percentage values indicate an increment of the alpha power synchronization (ERS) as a reflection of cortical resting state (Babiloni et al., 2006; Pfurtscheller & Lopes Da Silva, 1999; Pfurtscheller & Neuper, 1994).

2.7 | Statistical analysis

To test the hypothesis that the amplitude of the alpha ERD cortical sources was significantly higher in the *MVF* than in the *noMVF* condition, statistical nonparametric mapping using eLORETA voxel-based wise randomization tests (5000 permutations) was applied for the alpha ERD/ERS eLORETA solutions. The results obtained with this approach are equivalent to statistical parametric methods with multiple comparison corrections (Nichols, 2002). This nonparametric permutation method is particularly useful when analyzing small sample sizes with low degrees of freedom (Bian et al., 2019; Nichols, 2002). The correction of the p values for multiple testing was specifically applied for all voxels, and the outcomes are displayed as voxel-by-voxel T statistics maps with a corrected $p < .05$ (Nichols, 2002). To weaken the type II error (i.e., risk of false negatives), the uncorrected significance threshold of a more stringent $p < .01$ was also considered in the analysis. All the statistical analyses were performed using the eLORETA statistical toolbox (Pascual-Marqui, 2007).

2.8 | Control analysis

To control the eventual occurrence of muscle twitches or involuntary movements of the left hand, ongoing electromyographic (EMG) activity was recorded from the left and right hands (for further details, see Supporting Information). EMG control recordings were collected at a later stage of the data collection and data from only 9 subjects are available. A two-way ANOVA for repeated measures considering the factors *Condition* (*MVF* and *noMVF*) and *Hand* (Left and Right) was performed to show a statistically significant difference in the EMG activities between the left and the right index fingers in the MVF and noMVF conditions. The statistical analysis concerning the EMG results was performed using

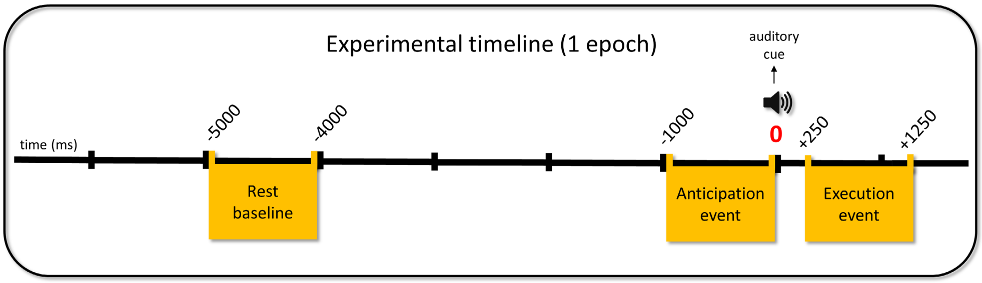

FIGURE 2 Experimental timeline. The figure illustrates the sequence of 1 trial of the experimental paradigm. During the offline analysis of the EEG datasets, 80 epochs of 9 s were extracted from each condition (the original inter-stimulus interval was constantly 10 s). In the illustration, the time is expressed in milliseconds (ms). The delivery of the auditory cue to trigger the movement was set as the 0 (zero) timepoint (in red). The ERD/ERS was calculated considering the "Rest" (or baseline) period as the time interval between 5000 and 4000 ms before the zero. The "Anticipation event" period was defined as the time interval of 1000 ms before the zero. Finally, the "Execution event" period was defined as the time interval between 250 and 1250 ms after the zero.

STATISTICA 10 software (StatSoft Inc., www.statsoft.com). Of note, our prior study included a control condition without MVF illusion wherein the participants were instructed to perform synchronous movements of both left and right index fingers (Rizzo et al., 2022). This *Bilateral* condition was introduced for a direct comparison between the sensory-motor EEG oscillations (alpha ERD) in response to illusory or actual movements. To avoid redundant results, the *Bilateral* control condition was excluded from the current re-analysis. However, as different visual inputs (i.e., mirror vs. no mirror) may represent a confounding variable, possibly affecting the somatomotor activity, a further investigation of the occipital alpha ERD (visual processes) was performed for the three conditions (*MVF*, *noMVF*, and *Bilateral*). The details of the occipital control analysis are reported in Supplementary Materials.

3 | RESULTS

3.1 | Grand average of the alpha ERD/ERS

The grand average of the eLORETA estimated cortical sources of the alpha ERD/ERS for each condition is mapped in Figure 3. During the movement anticipation phase (Figure 3, top), the noMVF condition shows alpha rhythm desynchronization (ERD) over the prefrontal, occipital, and left parietal brain areas contralateral to the movement (left hemisphere), whereas alpha ERS is visible over the right centro-parietal and left central areas. In the experimental *MVF* condition, the alpha ERD is prominent over the whole brain, with maximum peaks (<−18%) observed over the occipital and right parietal areas. A whole-brain widespread alpha ERD is visible in both conditions during the execution phase of the movement (Figure 3, bottom). In particular, the *noMVF* condition shows a clear alpha ERD over the left centro-parietal area (contralateral to the right finger movement) and moderate activity in its right counterpart, as compared to the *MVF* condition. Finally, in the execution phase of the movement, the *MVF* condition shows a bilateral alpha ERD prominent in the central and parietal areas.

3.2 | Anticipation phase

This section of the results concerns the voxel-by-voxel comparisons of the alpha ERD/ERS detected during movement preparation, between the *MVF* and *noMVF* conditions. Figure 4 illustrates the spatial distribution of the *p* values related to the Student's *t* tests (parametric statistical maps) for the eLORETA solutions of the anticipatory alpha ERD/ERS. All the significant *T* values and the relative voxels cluster size and localizations are also summarized in Table 1. As illustrated in Figure 4, the main differences appeared from the right hemisphere, contralateral to the mirrored hand.

In particular, when compared to the unilateral control condition (*noMVF*), the experimental mirror condition (*MVF*) showed the most significant *p* values ($T < -3.6$, $p < .05$ corrected) in the right somatomotor (BAs 1–2-3, and 4; peak value: $T = -3.9$) and the right parietal (BA 40; peak value: $T = -3.6$) areas (Table 1), indicating a significant increase of the centro-parietal alpha ERD when the subjects experienced the mirror illusion. Moreover, using a statistical threshold of uncorrected $p < .01$, a stronger alpha ERD has been observed in the *MVF* than *noMVF* condition in the right premotor (BA 6; peak value: $T = -3.5$) and prefrontal (BAs 10–11; peak value: $T = -3.1$) regions.

3.3 | Execution phase

The spatial distribution maps of the *p* values relative to the Student's *t* tests for the comparisons of the alpha ERD/ERS eLORETA solutions detected during movement execution are presented in Figure 5. The *T* values, the voxels cluster size, and their localization are reported in Table 2. As for the anticipatory phase, the right hemisphere exhibits all the voxel-by-voxel statistically significant differences.

Specifically, the alpha ERD in the mirror condition (*MVF*) is significantly stronger as compared to that in the control *noMVF* condition ($T < -3.4$, $p < .05$ corrected) in the right somatomotor cortex (BAs 1-2-3, and 4; peak value: $T = -3.6$) (Table 2), indicating a greater sensory-motor engagement during the mirror procedure. A stronger alpha ERD in the *MVF* than the *noMVF* condition was also observed in the right premotor (BA 6; peak value: $T = -2.9$) and parietal (BA 40; peak value: $T = -2.9$) cortices for the uncorrected significance threshold of $p < .01$.

3.4 | Control analysis

As mentioned above, EMG recording was introduced to control the possible involuntary activation of left-hand muscles during unilateral conditions. Data recorded from the right hand in 9 subjects showed no differences in the EMG amplitudes (expressed in μV) between the *MVF* and the *noMVF* conditions ($p = .639$), indicating a similar muscular activity in the task execution during the experimental and control conditions. Importantly, the analysis showed a statistically significant difference between the EMG activities recorded from the left and right index fingers ($p < .001$), thus excluding the hypothesis that the

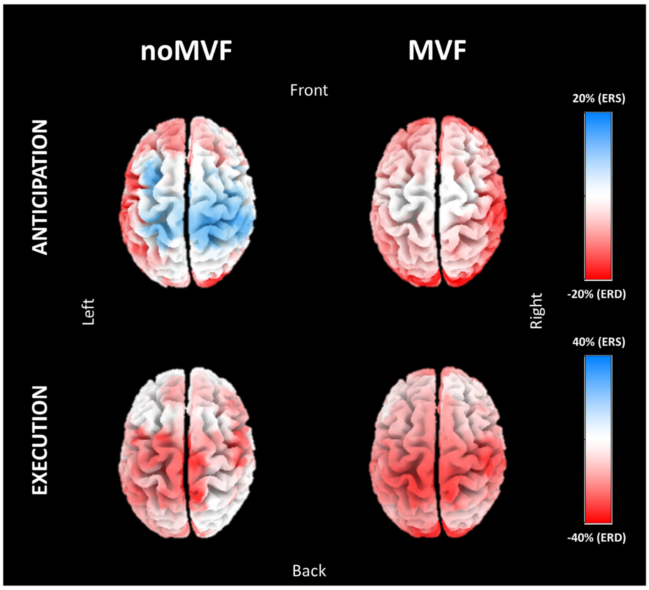

FIGURE 3 Grand average of the cortical sources of the alpha ERD/ERS values as estimated by eLORETA. The image shows the brain top view for the experimental (*MVF*) and control (*noMVF*) conditions referenced to movement preparation (top) and execution (bottom).

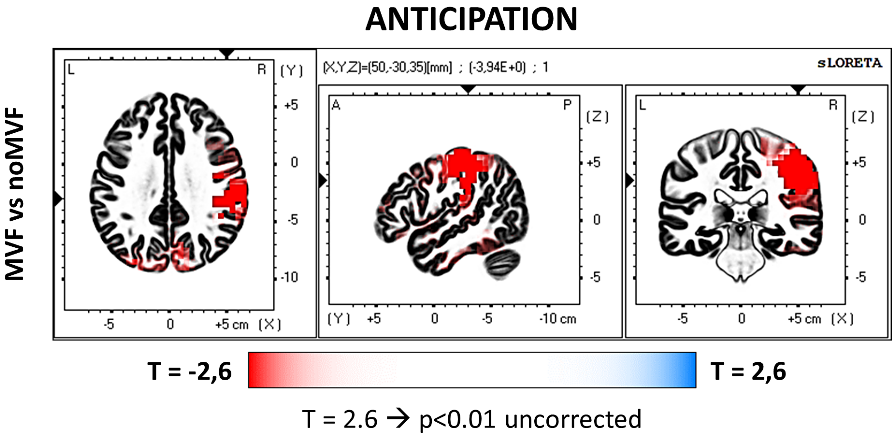

FIGURE 4 Spatial distribution of the voxel-by-voxel significant *p* values relative to the Student's *t* test for the alpha ERD/ERS eLORETA solutions during movement preparation. The axial, sagittal, and coronal sections are respectively represented. The Montreal Neurological Institute (MNI) coordinates of the voxel with the most significant *T* value are reported by eLORETA. The t value = 2.6 corresponds to the lowest significance threshold, namely the uncorrected threshold of $p < .01$. The MNI coordinates indicate the voxel position with the highest *T* value.

motor activity in the right hemisphere may be due to involuntary left-finger movements. For further details, see Figure S1 and Table S3 in Supporting Information. Finally, the analysis of the occipital visual cortex (BA 17) did not show any statistically significant difference, indicating that diverse visual input (looking at the reflected hand vs. looking at the real hand) could not explain the differences between the MVF and noMVF conditions in the central somatomotor alpha ERD (see Figure S2 in Supporting Information). Lastly, no correlations were found between the items of the revised RHI-Q and the activity recorded from the right somatomotor cortex during the MVF experience.

4 | DISCUSSION

The current study reanalyzed the EEG data of the reference EEG study (Rizzo et al., 2022) to localize the cortical sources of the alpha ERD/ERS in the MVF over the noMVF condition. A special interest was focused on the time course of the cortical sources of the alpha ERD involved during the anticipation and the experience of the MVF-induced illusion. Moreover, this re-analysis targeted the somatomotor, fronto-parietal, and posterior parietal brain regions as responsible for body awareness during kinesthetic illusions. In the recent EEG study (Rizzo et al., 2022), neurophysiological oscillatory

TABLE 1 Comparison of alpha ERD in the eLORETA cortical sources between the experimental (MVF) and control (noMVF) conditions during movement anticipation.

MVFs versus noMVF							
Anticipation							
				MNI coordinates			
BAs	**Cluster size**	**Region**	**Hemisphere**	***x***	***y***	***z***	***T* value**
1-2-3, 4	15 (97)	Central gyrus	R	65	−25	40	−3.9**
6	12	Precentral gyrus	R	35	−15	45	−3.5*
10-11	32	Frontal gyrus	R	25	50	5	−3.1*
40	3 (51)	Inferior parietal lobule	R	65	−30	40	−3.6**

Note: Voxel-based Student's *t* test analysis of alpha ERD in the Brodmann areas (BAs) of the cortical model of EEG sources in the eLORETA toolbox. The cluster size represents the number of voxels significant for the multiple comparisons' threshold (along with the number of voxels significant for the uncorrected threshold). The most statistically significant voxel is indicated by the Montreal Neurological Institute (MNI) coordinates. Alpha ERD is a negative percentage value indicating the reduction of power density at the event period with reference to the baseline. In the comparison between experimental (MVF) versus control (noMVF) conditions, a negative *T* value indicates that the alpha ERD is greater in the MVF than noMVF condition. Due to the lack of spatial resolution of EEG techniques, we considered Brodmann areas 1, 2, and 3 (primary somatosensory cortex) together with Brodmann area 4 (primary motor cortex). The same was true in considering Brodmann area 10 together with Brodmann area 11 (polar prefrontal cortex).

**Significance threshold of $p < .05$ corrected for multiple comparisons; *Significance threshold of $p < .01$ uncorrected.

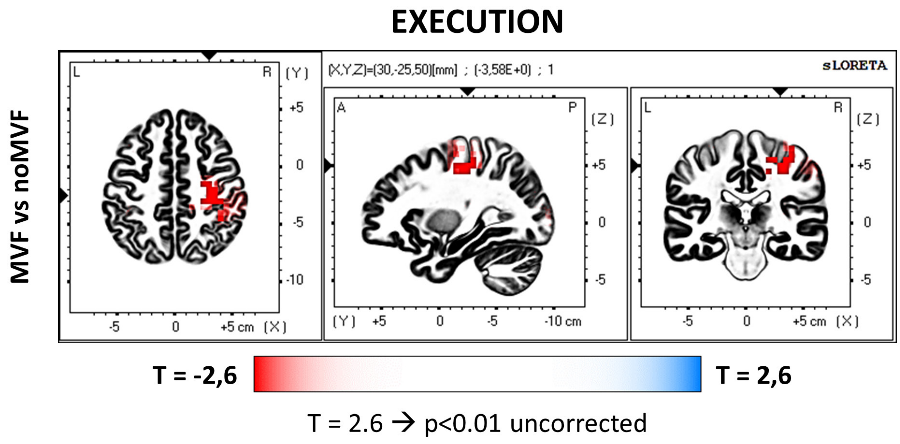

FIGURE 5 Spatial distribution of the voxel-by-voxel significant *p* values relative to the Student's *t* test for the alpha ERD/ERS eLORETA solutions during movement execution. The axial, sagittal, and coronal sections are respectively represented. The Montreal Neurological Institute (MNI) coordinates of the voxel with the most significant *T* value are reported by eLORETA. The *t* value = 2.6 corresponds to the lowest significance threshold, namely the uncorrected threshold of $p < .01$. The MNI coordinates indicate the voxel position with the highest *T* value.

mechanisms underpinning the MVF-induced illusion were investigated by the measurement of alpha ERD over the scalp in healthy adults who performed auditory-triggered unilateral right finger movements with (MVF) and without (noMVF) MVF. The scalp alpha (8–12 Hz) ERD was measured as a reflection of the underlying cortical activation (Pfurtscheller & Lopes Da Silva, 1999). In the MVF condition, the participants' mental processes may include the anticipation and the experience of an "event" formed by an auditory cue, the reaction by a right finger movement with the simultaneous observation of the motor reaction in the mirror, and the MVF-induced illusion of a simultaneous left finger movement. In that reference EEG study (Rizzo et al., 2022), the alpha ERD at ipsilateral central and parietal scalp electrodes was greater in the MVF than in the noMVF condition. Based on those results (Rizzo et al., 2022), it was speculated that the MVF-induced illusion may be related to activation in the ipsilateral premotor and primary somatomotor cortical areas contralateral to the mirrored movement. Here such speculation was transformed into the above-mentioned experimental hypothesis.

4.1 | The anticipation phase of the MVF-induced illusion

During the anticipation of the event, the cortical sources of the alpha ERD in the hemisphere ipsilateral to the right finger movements were greater in the *MVF* than in

TABLE 2 Comparison of alpha ERD in the eLORETA cortical sources between the experimental (MVF) and control (noMVF) conditions during movement execution.

MVF versus noMVF							
Execution							
				MNI coordinates			
BAs	**Cluster size**	**Region**	**Hemisphere**	***x***	***y***	***z***	***T* value**
1-2-3, 4	6 (27)	Central gyrus	R	30	−25	50	−3.6**
6	5	Precentral gyrus	R	25	−20	55	−2.9*
40	5	Inferior parietal lobule	R	40	−45	50	−2.9*

Note: Voxel-based Student's *t* test analysis of alpha ERD in the Brodmann areas (BAs) of the cortical model of EEG sources in the eLORETA toolbox. The cluster size represents the number of voxels significant for the multiple comparisons' threshold (along with the number of voxels significant for the uncorrected threshold). The most statistically significant voxel is indicated by the Montreal Neurological Institute (MNI) coordinates. Alpha ERD is a negative percentage value indicating the reduction of power density at the event period with reference to the baseline. In the comparison between experimental (MVF) versus control (noMVF) conditions, a negative *T* value indicates that the alpha ERD is greater in the MVF than noMVF condition. Due to the lack of spatial resolution of EEG techniques, we considered Brodmann areas 1, 2, and 3 (primary somatosensory cortex) together with Brodmann area 4 (primary motor cortex).

**Significance threshold of $p < .05$ corrected for multiple comparisons; *Significance threshold of $p < .01$ uncorrected.

the (control) *noMVF* condition. Specifically, there was a stronger alpha ERD in the polar prefrontal, inferior posterior parietal, lateral premotor, and primary somatomotor cortical areas of the ipsilateral hemisphere.

These cortical sources of the alpha ERD may reflect the anticipatory cortical activation before the event and may lead support to the following speculation. In the MVF condition, the activation of the ipsilateral (right) polar prefrontal cortex might underlie the participants' mental set anticipating the auditory cue, the right finger movement, the observation of that movement in the mirror, and the MVF-induced illusion. That prefrontal activation might facilitate the MVF-induced illusion during the mirrored movement by triggering an anticipatory activation of the neural representations of (1) the left finger movements and related somatosensory reafferences in the right lateral premotor and primary somatomotor cortical areas (Balconi et al., 2018, 2002; Torta & Cauda, 2011) and (2) the visuo-somatomotor transformations predicting the mirrored finger movements in the right inferior posterior parietal cortex (Arya, 2016; Babiloni et al., 2002; Lega et al., 2020). This speculation relies on previous evidence showing that the prefrontal cortex may play a top-down hierarchical role (1) in the control of hand movements in the task-switching conditions (Uehara et al., 2019) and (2) in the recruitment of the posterior parietal, lateral premotor, and motor cortical areas during voluntary motor tasks (Wager et al., 2004; Witt & Stevens, 2013). In its turn, the anticipatory activation of the posterior parietal cortex may play an important role in the subsequent multisensory integration of visuomotor and proprioceptive information, based on reciprocal functional connections with the premotor and primary somatomotor areas (Arya, 2016; Matthys et al., 2009; Medina et al., 2015; Mehnert et al., 2013).

4.2 | The execution phase of the MVF-induced illusion

During the participants' experience of the post-cued event, the cortical sources of the alpha ERD in the hemisphere ipsilateral to the right finger movements were still greater in the MVF than in the (control) noMVF condition. These sources were localized in the inferior posterior parietal, lateral premotor, and primary somatomotor cortical areas of the ipsilateral hemisphere. It can be speculated that such a dorsal-ventral cortical network might activate (1) the visual, visuospatial, motor, and somatosensory neural representations in the right inferior posterior parietal area; (2) the visuomotor and motor neural representations in the lateral right premotor area; and (3) the motor and somatosensory representations in the right primary somatomotor area. Increased cortical excitability in those areas may underpin the MVF-induced illusion of left finger movements. Moreover, it may be excluded that different visual inputs (i.e., looking at the reflected hand vs. looking at the real hand) affect the alpha ERD observed in the centro-parietal cortical areas, as shown by the control analysis of the occipital cortex.

In the MVF condition, the activation of the mentioned ipsilateral cortical network may reflect the mitigation of the inter-hemispheric inhibition mechanism typically occurring during unilateral movements (Carson, 2005; Yavuzer et al., 2008). That mechanism is typically mediated by transcallosal inhibitory signals from contralateral to ipsilateral homologous primary somatomotor and lateral premotor areas (Avanzino et al., 2014; Daskalakis et al., 2002; Ferbert et al., 1992; Hanajima et al., 2001). It can be speculated that the mitigation of the inter-hemispheric inhibition mechanism may be due to the observation of the finger movements reflected in the mirror, possibly inducing visuo-somatomotor and visuospatial processes in the lateral premotor and inferior posterior parietal areas of the right hemisphere contralateral to the mirrored movements.

Notably, the participants of the present study reported that the MVF-induced illusion included both a sense of agency (they felt moving the left finger) and a sense of ownership (they felt that the left moving finger in the mirror belonged to their bodies), as measured by the revised RHI-Q (see Supporting Information). Concerning the sense of ownership of the moving finger reflected in the mirror, it might emerge from the integration of visuomotor, visuospatial, and proprioceptive representations of the left finger in the lateral premotor, primary somatosensory, and inferior posterior parietal areas of the right hemisphere. This speculation is grounded on previous studies investigating the neural basis of the rubber hand illusion (Botvinick & Cohen, 1998; Braun et al., 2014; Kalckert & Henrik Ehrsson, 2012; Pavani & Zampini, 2007). This illusion is elicited by repeated synchronous strokes of both the true hand hidden from participants' view and a visible artificial rubber hand adequately placed to be interpreted as part of his/her body. It may be due to a proprioceptive drift produced by the synchronous integration of visual, tactile, and proprioceptive information (Botvinick & Cohen, 1998) as a function of the position and/or the size of the rubber hand (Braun et al., 2014; Ehrsson et al., 2004; Kalckert & Henrik Ehrsson, 2012; Pavani & Zampini, 2007). When the visual and tactile stimuli occurred at different times, the rubber hand illusion is practically abolished (Botvinick & Cohen, 1998; Ding et al., 2020; Reader et al., 2021). MRI studies localized the neural correlates of the rubber hand illusion in the lateral premotor, somatosensory, and posterior parietal cortical areas (Ehrsson et al., 2004). Among those areas, the posterior parietal cortex may play a causal role as its electric stimulation-induced sensations of touch and movements in patients with focal epilepsy undergoing a presurgical workup (Balestrini et al., 2015; Sun et al., 2015). In relation to the rubber hand illusion, the MVF-induced illusion may not require a proprioceptive drift due to a spatial co-localization of the left finger movements reflected in the mirror and the true position of the left finger.

From a theoretical point of view, two levels of the sense of agency were proposed, namely an implicit level based on a non-conceptual immediate raw feeling resulting from a matching between the efference copy (corollary discharge) from the active primary motor cortex and the co-occurrence of the ascending somatosensory proprioceptive afferents and an explicit higher-order integrative level (Synofzik et al., 2008). In the MVF condition, the implicit level may play a minor role as no proprioceptive afferents were generated from the periphery (the hand remains immobile). In contrast, the explicit level was demonstrated by the evidence reported in the reference study by Rizzo et al. (2022) showing ipsilateral central alpha ERD was correlated with psychometric measures of MVF-induced illusion, thus suggesting a major role of lateral premotor and primary somatomotor cortex.

Finally, the absence of correlations between the psychometric measures of the sense of ownership and agency (revised RHI-Q) with the cortical activity (alpha ERD) detected in the central right somatomotor area (i.e., contralateral to the illusory hand) might demonstrate the essential role of a wide centro-parietal network in the illusory experience, rather than the activity of single sensory-motor regions.

4.3 | Mirror neuron system versus MVF-induced illusion

Neuroimaging studies investigated the role of the so-called mirror neuron system (MNS) in the MVF-induced illusion. In humans, the core areas of the MNS include ventral frontal and posterior parietal cortical areas underpinning both the execution of goal-directed action and the observation of that action performed by other individuals (Babiloni et al., 2009; Bartur et al., 2015; Buccino et al., 2006; Deconinck et al., 2015; Matthys et al., 2009; Rizzolatti & Sinigaglia, 2010; Zhang et al., 2018).

The present experiment was focused on the localization of the cortical sources of the alpha ERD underpinning the participant's MVF-induced illusion of a self-performed finger movement, so we designed the task to minimize the confounding effects of the MNS. For this purpose, we used an “intransitive” auditory-triggered finger movement rather than a “transitive” goal-directed action of the MNS experiments in which the hand reaches and manipulates an object. Nevertheless, the findings of the present study showed that the MVF-induced illusion was related to an activation of the ipsilateral inferior parietal cortex, which is part of the MNS. No participant mentioned a “depersonalizing” experience to watching a moving finger of another person reflected in the mirror during the MVF condition (Table S1), but this fact may be due to avoiding a social stigma. Therefore, it cannot be excluded that a minor component of the mental experience of the MVF condition regarded the interpretation of the moving finger in the mirror as belonging to another person, with a related involvement of the MNS. This issue should be addressed by an experimental design in the MVF condition aimed at disentangling the mental experience of being the agent of a goal-directed action versus watching the own goal-directed action reflected in the mirror versus watching the goal-directed action performed by another person. Furthermore, specific questions about that issue will have to be asked of the participants.

4.4 | From the cortical sources of alpha ERD to a neurophysiological model of the MVF-induced illusion

In the present study, the anticipation and the experience of the MVF-induced illusion of left finger movements were related to cortical sources of alpha ERD (cortical activation) distributed in the polar prefrontal, lateral premotor, primary somatomotor, and inferior posterior parietal cortical areas ipsilateral to the true right finger movements and contralateral to their reflection in the mirror. The present findings substantially confirm previous fMRI evidence showing a major involvement of the lateral premotor (Hamzei et al., 2012; Numata et al., 2013), and primary somatomotor (Fritzsch et al., 2014; Hamzei et al., 2012; Matthys et al., 2009; Numata et al., 2013) cortical areas in the MVF-induced illusion. They also confirm the major involvement of the primary somatomotor cortex in the MVF-induced illusion of hand movements as revealed by EEG techniques by the measurement of LRPs (Debnath & Franz, 2016; Touzalin-Chretien et al., 2009, 2010; Touzalin-Chretien & Dufour, 2008) and alpha ERD (Bartur et al., 2015; Lee et al., 2015; Rizzo et al., 2022) at scalp central electrodes.

As a novelty in relation to the mentioned neuroimaging and EEG evidence, the present study allowed not only to identify of several cortical areas involved in the MVF-induced illusion of finger movements but also to explore the underlying neurophysiological oscillatory mechanisms at alpha frequencies with an unsurpassed spatial resolution based on high-density 64-electrode EEG recordings and eLORETA EEG source estimation. Let us shortly recapitulate their functional meaning. Cortical EEG alpha rhythms (8–12 Hz) result from synchronized oscillatory signals conveyed within a neural network possibly spanning cortical pyramidal, basal ganglia, reticularis thalamic, and thalamocortical neurons (Klimesch, 2012; Lopes da Silva, 1991, 2013; Lörincz et al., 2008; Pfurtscheller & Lopes Da Silva, 1999). A high level of alpha frequency synchronization within that neuronal network may reflect an inhibitory but readiness state in the involved neuronal populations while participants experience a condition of quiet wakefulness and psychophysical relaxation (Del Percio et al., 2010; Klimesch, 2012; Lörincz et al., 2008; Pfurtscheller & Lopes Da Silva, 1999). Here we posit that the anticipation and experience of the MVF-induced illusion of left finger movements during true right finger movement may be related to a prolonged block (desynchronization) of that inhibitory alpha frequency synchronization in the right frontal and parietal visuomotor and somatomotor cortical areas contralateral to the moving finger appearing in the mirror. Such a block may realize a dis-inhibition of those areas and the MFV-induced illusion, despite the immobility of the left finger. Future studies in epilepsy patients who will undergo presurgical intracerebral EEG monitoring may test the relationship between the present MVF-induced illusion and the alpha ERD located in the basal ganglia, reticularis thalamic, and thalamic relays in agreement with their potential involvement in the consciousness, voluntary movements, and the modulation of EEG alpha rhythms (Babiloni et al., 2002, 2008; Balconi et al., 2018; Pfurtscheller & Lopes Da Silva, 1999; Ribary et al., 2017).

4.5 | Methodological remarks

Despite the use of high-density EEG techniques (64 electrodes and eLORETA EEG source estimations within an average head model), we felt to have an insufficient spatial resolution to analyze separately the sources of alpha ERD located in the primary motor (BA 4) and somatosensory (BAs 1-2-3) cortical areas. For the same reason, we did not analyze separately the sources of alpha ERD located in two contiguous areas of the polar prefrontal cortex (BAs 10 and 11). Future studies may address a separate source analysis in those areas by enhanced high-density EEG techniques (e.g., 128–256 electrodes) or a multimodal approach based on the simultaneous recording of fMRI and EEG data. Moreover, the use of fMRI scans and the digital localization of the electrodes would allow the estimation of the alpha ERD sources based on individual structural head models. Finally, the EMG activity of the hands was introduced in a later stage of the data collection. Hence, only data from 9 subjects have been reported. Potential future studies should measure the individual reaction time of the movement in response to the auditory cues (namely, movement onset) to compute the alpha ERD/ERS and consider the possible variability across trials and subjects. However, Table S4 indicates moderate intertrial variability of the EMG onsets and peaks (i.e., 5–10 ms). Therefore, this variability has a negligible effect on the alpha ERD/ERS, which is a neurophysiological oscillatory phenomenon characterized by cycles of 100 ms (Başar & Golbast, 2014).

4.6 | Clinical perspectives

The present findings lead further support to the use of a procedure combining MVF-induced illusion and measures of alpha ERD in patients with a somatomotor impairment in the upper limb of one side. In this line, previous evidence showed that patients with stroke were characterized by poor movement-related EEG alpha suppression and MVF-induced illusion (Frenkel-Toledo et al., 2014). Furthermore, motor re-learning was associated with enhanced alpha

ERD in somatomotor areas in response to voluntary movements (Carino-Escobar et al., 2019; Gandolfi et al., 2015; Jochumsen et al., 2017). Finally, MVF-based therapies ameliorated the functions in the motor, sensory, and attentional domains in patients with deficits in motor preparation (Ding et al., 2018; Dohle et al., 2009). Keeping in mind these data, it can be speculated that prolonged use of MVF procedures may favor neural plasticity and cortical reorganization processes (Small et al., 2013) resulting in a thalamo-cortical motor loop reinforcement in the ipsilesional premotor, somatomotor, associative visuomotor cortices. Moreover, MVF therapies may restore the transcallosal excitatory/inhibitory interactions to enhance the activity of the impaired hemisphere and facilitate motor recovery in those patients who cannot rely upon the natural symmetric movements of the limbs.

4.7 | Conclusions

In the present study, we reanalyzed the EEG data from a previous seminal study (Rizzo et al., 2022) to localize cortical sources of alpha ERD related to unilateral right finger movements in the MVF over the noVMF condition. In the MFV condition, the participants experienced the illusion of their own left finger while watching the moving finger in a mirror adequately oriented at their body midline. A special interest was focused on the dynamic changes in the alpha ERD sources estimated during the anticipation and experience of the MVF-induced illusion.

Results showed that as compared to the noMVF condition, the MVF condition was characterized by greater alpha ERD sources in right frontopolar areas during the anticipation of the MVF-induced illusion of left finger movements. The MVF condition was also characterized by greater alpha ERD sources in right premotor, primary somatomotor, and posterior inferior parietal areas during both the anticipation and experience of the MVF-induced illusion.

These findings suggest that the MVF-induced illusory experience of left finger movements may be due to dynamic changes in alpha ERD in associative, premotor, somatomotor, and visuomotor frontal–parietal areas located in the hemisphere contralateral to the mirrored movements. Future studies may disentangle the role of MNS in the MVF-induced illusion, and the potential of alpha ERD sources estimated in the present MVF condition as endpoints for the rehabilitation of visuomotor somatomotor functions by upper limbs in patients with brain diseases.

AUTHOR CONTRIBUTIONS

Marco Rizzo: Data curation; formal analysis; methodology; software; writing – original draft. **Claudio Del Percio:** Formal analysis; software. **Laura Petrini:** Investigation; supervision; writing – review and editing. **Susanna Lopez:** Formal analysis; software. **Lars Arendt-Nielsen:** Investigation; project administration; supervision. **Claudio Babiloni:** Conceptualization; methodology; writing – review and editing.

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DATA AVAILABILITY STATEMENT

Raw data were collected at the Aalborg University. Derived data supporting the results of this study are available from the first author MR on request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

TABLE S1 List of the 19 items used to assess the illusory experience after the condition with the Mirror Visual Feedback. Subjects responded indicating a value on a numerical scale from 1 (strongly disagree) to 7 (strongly agree). Last columns report, respectively, the Pearson's correlation coefficient (*r*) and *p* values.

TABLE S2 Individual mean score for each scale included in the revised RHI questionnaire. The number of items for each scale is also reported.

FIGURE S1 Average of the EMG activity recorded from the right (dotted line) and left (dashed line) hands of nine subjects for the MVF (red) and noMVF (black) conditions. The right hand is represented by the *Y*-axes showing the power activity in microvolt, whereas the *X*-axes report the time in milliseconds. The 0 (zero) represents the auditory cue onset. The scheme shows also the "Rest" and "Event" periods considered for the alpha ERD/ERS calculation in relation to the EMG activity. Of interest, the average reaction time—corresponding to the movement onset—occurs after 250 ms from the auditory cue. This time interval was also removed from the analysis to avoid the auditory-evoked potentials disturbing the ERD/ERS final calculation.

TABLE S3 The table shows the means (±*SE*) of the EMG magnitude in microvolt of both the fingers for the *MVF* and *noMVF* conditions.

TABLE S4 The table reports the latencies (mean and standard deviations [*SD*]) in milliseconds (ms) of the movement onset and EMG activity peaks for each subject recorded from the right hand during the MVF condition.

FIGURE S2 Mean percentage (*SD*) values of the alpha ERD/ERS distribution in the occipital visual Brodmann Area 17 for each condition (noMVF, BIL, and MVF), hemisphere (left and right), and stage of the movement (anticipation and execution). No significant effects were observed in the statistical analysis.

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