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ORIGINAL ARTICLE

Early modulations of neural oscillations during the processing of emotional body language

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Abstract

The processing of threat-related emotional body language (EBL) has been shown to engage sensorimotor cortical areas early on and induce freezing in the observers' motor system, particularly when observing fearful EBL. To provide insights into the interplay between somatosensory and motor areas during observation of EBL, here, we used high-density electroencephalography (hd-EEG) in healthy humans while they observed EBL stimuli involving fearful and neutral expressions. To capture early sensorimotor brain response, we focused on P100 frontocentral event-related potentials (ERPs) and event-related desynchronization/synchronization (ERD/ERS) in the mu-alpha (8–13 Hz) and lower beta (13–20 Hz) bands over the primary motor (M1) and somatosensory (S1) cortices. Source-level ERP and ERD/ERS analyses were conducted using eLORETA. Results revealed higher P100 amplitudes in motor and premotor channels for 'Neutral' compared with 'Fear'. Additionally, analysis of ERD/ERS showed increased beta band desynchronization in M1 for 'Neutral', and the opposite pattern in S1. Source-level estimation showed significant differences between conditions mainly observed in the beta band over sensorimotor areas. These findings provide high-temporal resolution evidence suggesting that seeing fearful EBL induces early activation of somatosensory areas, which in turn could suppress M1 activity. These findings highlight early dynamics within the observer's sensorimotor system and hint at a sensorimotor mechanism supporting freezing during the processing of EBL.

KEYWORDS

beta rhythm, EEG, emotional body language, emotions, event-related potential, fear, mu rhythm

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1 | INTRODUCTION

The understanding of nonverbal emotional cues has become a cornerstone of biological sciences since the seminal work of Darwin in the 19th century (Darwin, 1872). Although for decades the main interest of researchers was focused on emotional facial expressions, cognitive neuroscience investigation of emotional body language (EBL) is now attracting comparable attention as studies on face perception (de Gelder, 2009). EBL is rapidly processed in the observer's brain (Borhani et al., 2015; van Heijnsbergen et al., 2007). Like other emotional signals, EBL has been shown to prime the body for action (de Gelder, 2009; Frijda, 2009; Lang et al., 2000). Especially when it comes to fearful EBL, studies have reported consistent modulations of sensorimotor brain networks on early time windows (i.e., at ~100–150 ms after stimulus presentation; (Borgomaneri, Vitale, Gazzola, & Avenanti, 2015; Botta et al., 2022; van Heijnsbergen et al., 2007), with the earliest motor modulations reported already at 70–90 ms after stimulus presentation (Borgomaneri et al., 2015b, 2015c, 2017), well before the conscious perception of the stimulus (Dehaene et al., 2014; Thorpe et al., 1996).

Transcranial magnetic stimulation (TMS) studies have shown that static pictures of fearful EBL exert an inhibitory, rapid effect on corticospinal excitability as well as on intracortical facilitatory mechanisms within the primary motor cortex (M1) of the observer (Borgomaneri et al., 2015b, 2015c, 2017) when compared with positive EBL and nonemotional body movements. Furthermore, in a previous TMS work by our group, we found that fearful EBL stimuli, differently from positive and nonemotional stimuli, enhance short-latency somatosensory afferent inhibition (SAI) at 120 ms after the stimulus onset, hence demonstrating that the observation of fearful EBL produces an early reduction of M1 excitability mediated by sensorimotor integration mechanisms involving the primary somatosensory cortex (S1) (Botta et al., 2022). Moreover, in behavioral tasks, EBL static pictures induced shorter response times, when compared with positive EBL and nonemotional body language (Borgomaneri et al., 2020; Botta et al., 2021). These results suggest that the observation of fear-related behavior induces an early, transient, decrease of M1 excitability reflecting a 'freezing-like' response to threat-related information, which in turn is followed by a speed-up effect on behavioral motor response – observed at longer latencies, i.e., 700–800 ms.

Interestingly, our recent TMS-SAI study (Botta et al., 2022) suggests that early freezing response to fear EBL may reflect increased S1 activity, which in turn would contribute to inhibiting M1. S1 is increasingly recognized as a key brain region for perceiving and understanding others' actions, and sensory and emotional states (Adolphs et al., 2000; Bufalari et al., 2007; Gazzola et al., 2012; Keysers et al., 2010; Paracampo et al., 2017; Pitcher et al., 2008). Increased somatosensory activity during observation of fear expressions stimuli is supported by several behavioral studies showing enhanced performance at somatosensory tasks following observation of such stimuli (Bertini & Làdavas, 2021), and is in keeping with the notion that fear and threat-related stimuli enhance sensory vigilance and attention (Davis & Whalen, 2001; Kret et al., 2013; Phelps et al., 2006). Yet, to date, no study has directly tested whether observation of fear EBL induces enhanced S1 activity (in addition to decreased M1) within an early time window.

To result in fast sensorimotor responses, fearful cues have to be rapidly processed by visual regions. Electroencephalography (EEG) studies using event-related potentials (ERPs) to EBL stimuli have shown that the first responses to fearful stimuli start showing a positive deflection in a similar time window as the earliest motor responses detected with TMS (Borgomaneri et al., 2015b, 2015c, 2017), and peak at ~110 ms after picture onset on posterior cortical areas (Meeren et al., 2005; van Heijnsbergen et al., 2007). Due to its latency, this ERP response has been identified as a P100 component. Moreover, in the comparison between nonemotional and fearful body stimuli, longer latencies for neutral stimuli have been reported but no differences in terms of P100 amplitudes were recorded in the posterior areas, interpreting such results as a processing advantage for fearful EBL (van Heijnsbergen et al., 2007).

EBL intrinsically carries motor information about another's body movements, which can be reflected in the modulation of neural activity in sensorimotor areas. Interestingly, the P100 component was shown to have a sensorimotor counterpart during the visual processing of action-related information. Kiefer and collaborators described an early ERP component peaking in the time window of the P100 (i.e., between 85 to 115 ms) positively over posterior electrodes and negatively over fronto-central electrodes. The fronto-central (negative) counterpart of the P100 was selectively modulated by action-related visual stimuli, with cortical sources encompassing S1 and M1 (Kiefer et al., 2011; Sim et al., 2015). Yet, whether similarly, early negative components over primary sensorimotor areas are sensitive to EBL remains to be clarified.

To test this hypothesis, here, we first investigated early ERP response to fearful EBL and neutral body movements over fronto-central (sensorimotor) areas. In addition, we took advantage of the high temporal resolution and improved spatial resolution of high-density EEG (hd-EEG) coupled with source estimation to further investigate the timeline of modulation of specific EEG oscillations over sensorimotor areas.

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We recorded event-related desynchronization/synchronization (ERD/ERS) in the mu-alpha (8–13 Hz) and lower beta (13–20 Hz) frequency bands over M1 and S1. Indeed, these oscillations have shown sensitivity both to action observation and EBL. In particular, the mu rhythm – a well-known oscillation in the alpha band (i.e., 8–13 Hz) recorded over central sensors – shows a consistent ERD during action execution and observation (Bommarito et al., 2020; Debnath et al., 2019; Oberman et al., 2005; Pineda, 2005). This activity reflects motor resonance, i.e., the mapping of observed motor actions onto one's motor representations – a phenomenon occurring later than the early freezing response to EBL (Borgomaneri et al., 2015a; Spaccasassi et al., 2022). Interestingly, studies have reported stronger mu-ERD during the observation of low arousal EBL (e.g., neutral or romantic EBL) relative to high arousal body movements (e.g., angry or erotic EBL) (Schubring & Schupp, 2019; Siqi-Liu et al., 2018). Moreover, studies have reported that negative EBL-induced modulations of fronto-central activity in the lower beta band (16–20 Hz) (Siqi-Liu et al., 2018). Yet, these EEG studies (Schubring & Schupp, 2019; Siqi-Liu et al., 2018) did not focus on fearful EBL and reported changes in brain oscillations occurring within a much later temporal window (between ~600 to 3000 ms) compared with the TMS studies reported above.

Summing up, considering the fast temporal dynamics of EBL processing (van Heijnsbergen et al., 2007), and in particular the early motor (Borgomaneri et al., 2015b, 2015c, 2017) and sensorimotor responses to fearful expressions (Botta et al., 2022), it seems plausible to expect a decreased M1 activity in response to fearful EBL in the temporal window of the P100 (Kiefer et al., 2011; Sim et al., 2015). We also expect to observe increased activity in the mu-alpha and/or beta frequency bands over primary somatosensory areas in the early phases of fearful EBL processing at the expense of reduced activity over motor areas.

2 | MATERIALS AND METHODS

2.1 | Participants

Seventeen healthy, right-handed, individuals (9 females, mean age ± SD: 22.9 ± 3.3 years) were enrolled in the study. All participants were in good health, without any nervous, muscular, orthopedic, or cognitive disorders. Right-handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). The sample size was chosen based on a previous study by Boudewyn et al. (2018). In this methodological study, the authors computed the minimal number of participants needed in an ERP study to observe a difference in a within-group experimental design. Based on their results, to observe a $p < .05$ based on a difference of at least 0.75 μV in ERP's amplitude between two observed conditions, and several trials equal to 90 trials per condition, a sample size of 16 subjects would have been necessary to observe a significant difference between conditions with a probability higher than 80% (Boudewyn et al., 2018). In our case, we planned to have 150 trials per condition and 17 subjects, meaning that our sample size should be acceptable for our study design. The experimental protocol was approved by the ethics committee of the University of Genoa and was performed in agreement with legal requirements and international norms stated in the adjourned declaration of Helsinki (World Medical Association Declaration of Helsinki, 2001).

2.2 | Experimental design and procedure

All participants were asked to sit on an armless chair and passively observe the 15.6 inches screen located 1 m in front of them. After a brief explanation of the experiment, the set-up of the 128-channel hd-EEG system was performed. The experiment was composed of three trains of 100 randomized fearful/neutral visual stimuli, for a total of 300 EBL stimuli (150 fearful and 150 nonemotional). Each visual stimulus had a duration of 500 ms with an interstimulus interval (ISI) of 1500 ms where a black cross on a white blank screen was shown to the participants. The duration of the whole experiment was approximately 80 min.

2.3 | Visual stimuli

Visual stimuli were presented on a 15.6-inch computer screen with a resolution of 1920 × 1200 pixel and a refresh rate of 60 Hz. We utilized a total of 60 EBL visual stimuli comprising 30 fearful and 30 neutral images (for example Appendix S1).

EBL pictures were selected from a validated database (Borgomaneri et al., 2012; Botta et al., 2021). The pictures featured four actors in different postures with negative and neutral valence, fifteen depicting fearful EBL, and fifteen with no emotional significance. The actors were not handling objects and their face was blanked out. Noteworthy, the pictures used in our study underwent rigorous control for valence, arousal, perceived implied motion, and emotional content, and have been validated in numerous studies (for more detailed information, see Borgomaneri et al., 2012, 2015c; Borhani et al., 2016; Botta et al., 2021). Additionally, to eliminate potential confounding factors related to the intrinsic visual properties of the images, all stimuli had the same resolution (1000 × 1500 pixels)

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and underwent control for RGB values, perceived luminance, contrast, and visual complexity (for details, see Appendix S1).

Of the 60 EBL pictures used in the experiment, half of the stimuli were the original pictures and the other half were mirror-reflected copies (Borgomaneri et al., 2020; Borhani et al., 2015). By using these mirror-reflected copies, we ruled out the possibility that any lateralized changes in sensorimotor activity could be due to any difference in the amount of implied motion of the models' left or right arms, regardless of the emotional content.

To reach a congruous number of trials, each picture was presented 5 times following a pseudorandomized order, so that the total number of stimuli per trial was sufficient to study electrophysiological correlates of emotional processes and weighted to maintain the same number of visual stimuli for the two conditions examined (i.e., Fear and Neutral).

Visual stimuli were presented via E-Prime 3.0 (Psychology Software Tools).

2.4 | Data collection

EEG data were recorded via a 128-channel hd-EEG data at a 1 kHz sampling rate amplified by an ActiCHamp amplifier (Brain Products GmbH). Electrode impedance was kept below 5 kΩ. Electrooculographic (EOG) signals were recorded to monitor for vertical (VEOG) and horizontal (HEOG) eye movement. The EOG recordings were subsequently used for EEG artifact removal.

2.5 | Data analysis

A validated workflow for hd-EEG analysis recorded during task execution recording was used (Marino et al., 2019; Samogin et al., 2019; Zhao et al., 2019). The aforementioned workflow included different steps such as data preprocessing, head modeling based on an MRI template, and source-space estimation for ERP and ERD/ERS analysis.

2.6 | Data pre-processing

Data pre-processing implied corrections for bad channels, artifact removal EEG data re-referencing. Bad channel detection was performed via a validated procedure which included a Pearson correlation analysis of each channel against the others in a fixed frequency band ranging from 1 to 50 Hz and a 200–250 Hz frequency band noise variance (Liu et al., 2017; Zhao et al., 2019). Bad channels were then reconstructed starting from neighboring channels (Oostenveld et al., 2011). EEG signals were then band-passed (1–80 Hz), and artifact removal was performed via a multi-step blind source separation-based approach to decompose the channel signals in independent components, which were then classified in either artefactual or neuronal depending on artifact-specific parameters (kurtosis, sample entropy and power ratio in gamma band for eye, movement and muscular artefacts respectively) (Zhao et al., 2021). Components with relevant artefactual activity derived from ocular movements or environmental noise were subsequently excluded from the analysis. Lastly, average re-referencing was run on EEG data (Liu et al., 2015).

2.7 | ERP analysis

The cleaned and re-referenced EEG data used for ERP analysis were first band-pass filtered (1–40 Hz). Recorded data were then segmented into epochs of 500 ms based on triggers related to the two different experimental conditions (i.e., fearful and neutral), starting 100 ms before the presentation of the visual stimulus until 400 ms after stimulus onset. The time window from −100 to 0 ms served as a baseline. Early fronto-central EEG activity was studied as the mean amplitude within the temporal window of the P100, i.e., from 80 to 150 ms after stimulus presentation, specifically on channels C3, C4, Fc3 and Fc4 (Kiefer et al., 2011; Sim et al., 2015).

Statistical analysis of ERP data was performed on two levels. To rule out any potential influence of the mirror-reflected copies of EBL stimuli (for details see section 2.3 'Visual stimuli'), we performed two-way analysis of variance (ANOVA) on ERP amplitudes with MIRROR (Original and Mirrored) and CHANNEL (C3, C4, Fc3, Fc4) as within-subjects factors. Subsequently, we performed a two-way analysis of variance (ANOVA) on ERP amplitudes and latencies with EMOTION (Fear and Neutral) and CHANNEL (C3, C4, Fc3, Fc4) as within factors. Before running the ANOVA, all data were checked for normality (Shapiro–Wilk test) and sphericity (Mauchly test). Greenhouse–Geisser's correction was applied whenever needed. Post hoc analysis was performed by means of the Bonferroni correction method for multiple comparisons. Statistical analysis of ERP data was run via SPSS Statistics 23.0 (IBM). *p*-values of .05 were considered as the threshold for statistical significance.

2.8 | Source-space estimation

Source localization of EEG signals was based on MRI templates taken from previous studies (for more details see Liu

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et al., 2017). Brain activity related to source space was reconstructed via the exact low-resolution brain electromagnetic tomography (eLORETA) method (Cao et al., 2018; Pascual-Marqui et al., 2011; Zhao et al., 2019). Considering previous studies (Botta et al., 2022; Sim et al., 2015) and the main research question we aimed to explore, the ROIs taken for the time-frequency analysis were the left and right M1 (lM1 and rM1, respectively) and the left and right S1 (lS1 and rS1). Coordinates for each ROI were taken from the Neurosynth website (https://neurosynth.org/) based on the paper of Mayka and colleagues for the motor area (Mayka et al., 2006) and from Roux et al. (2018) for the somatosensory area. Coordinates for each area can be found in the legend of Figure 1. MNI coordinates of each ROI were then transformed to individual space and the voxels within 6 mm from the ROI were selected (Zhao et al., 2019).

2.9 | ERD/ERS analysis

Frequency-dependent modulations of brain regions were assessed by conducting an ERD/ERS analysis on reconstructed neural signals. We first performed an ERD/ERS analysis for selected ROIs, and we then calculated ERD/ERS spatial maps. Time-frequency analysis was performed both at a whole-brain level and for the four ROIs (see section above) separately, using a short-time Fourier transform, with a moving window of 1 s, with an overlap between adjacent windows of 900 ms. The bands taken into account for the analysis were the mu-alpha band (8–13 Hz) (Debnath et al., 2019) and the lower beta-band (13–20 Hz) (Siqi-Liu et al., 2018). The timeframes of interest for the ERD/ERS analysis lasted from −500 s to +1000 ms after the stimulus onset. Activity in the first 500 ms before the stimulus presentation was taken as the baseline. More in detail, a spectrogram in the aforesaid timeframe [−500 ms, +1000 ms] centred on the emotional stimulus presentation was computed for all the frequencies ranging from 8 to 20 Hz at steps of 1 Hz and a time resolution of 10 ms. The ERD/ERS intensity was then calculated via the following formula:

$$\mathrm{ERD}/\mathrm{ERS}(f,t) = \frac{P(f,t) - P_B(f)}{P_B(f)} \times 100\,\%$$

where $P(f, t)$ is the power as a function of a given frequency and time and $P_B(f)$ is the average power in the [−500 ms, 0 ms] time window (i.e., baseline) (Zhao et al., 2019). Subsequently, we restricted the time window to the first 200 ms after stimulus onset.

The same procedure was then used to perform a time–frequency analysis on all voxels included in the source space so that it was possible to obtain a spatial map of the time-frequency activity all over the brain by applying a nonrigid deformation using MRI templates (Zhao et al., 2019). Specifically, we reconstructed two spatial maps where to observe early changes in neural oscillations, we focused our attention on the differences in whole-brain activity in the mu-alpha and the beta bands between the 'Fear' and the 'Neutral' conditions in the first 200 ms after stimulus onset.

To establish differences in ERD/ERS whole-brain activity between conditions we analyzed all voxels in the source space for 'Fear' and the 'Neutral' in the [0 ms, 200 ms] timeframe and computed the t-maps of the differences between the two experimental conditions separately for the frequency bands of interest. Group-level analyses were performed on the ERD/ERS spatial maps by using a random-effect analysis. Specifically, a two-tailed t test across participants was calculated for each of the two conditions in each frequency band of interest. Finally, a spatial map showing the differences in the ERD/ERS activity between conditions was computed between conditions so to clarify which condition showed the highest activity in the ROIs.

Correction for multiple comparisons was performed via the false discovery rate (FDR) method for all analyses (Benjamini & Hochberg, 1995). The significance level for the t test was set at $p < .05$ and so was the p-value after correction for multiple comparisons. All analyses were conducted with MATLAB® (R2016a, Math-Works).

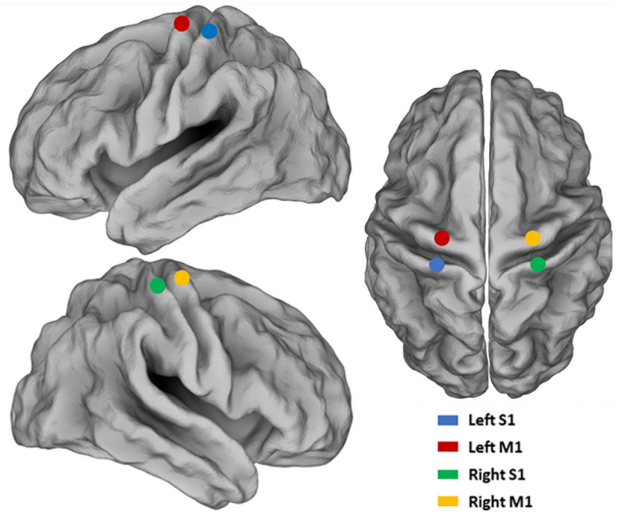

FIGURE 1 Regions of interest for the ERD/ERS analysis. Left M1: left primary motor cortex (MNI coordinates: [−37; −21; 58]); left S1: left primary somatosensory cortex (MNI coordinates [−39; −27; 60]); right M1: right primary motor cortex (MNI coordinates: [37; −21; 58]); right S1: right primary somatosensory cortex (MNI coordinates [39; −27; 60]). Coordinates are shown as [x; y; z].

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3 | RESULTS

3.1 | ERP analysis

Analysis of ERP data (see Figure 2) showed that all data were normally distributed and respected the sphericity assumption.

Regarding the effect of mirror-reflected copies of EBL stimuli, the MIRROR effect resulted to be nonsignificant ($F<1$; $p=.547$), as well as the interaction MIRROR*CHANNEL ($F<1$; $p=.807$). The only significant effect was found for CHANNEL ($F(3, 96)=5.946$, $p<.01$, $p\eta^2=0.157$) where post hoc analysis showed no differences between C3 and C4 ($p=.135$), while a significant lower amplitude was found between C3 and Fc3 ($p=.029$), C3 and Fc4 ($p<.01$) and C4 and Fc4 ($p=.041$).

Statistical analysis on fronto-central ERPs latencies during emotional processing showed no significant effects for EMOTION, CHANNEL, and for the interaction effect EMOTION*CHANNEL (all $F<1$ and all $p>.61$).

Importantly, statistical analysis on ERP amplitudes showed significant a main effect of EMOTION ($F(1, 16)=7.568$, $p=.014$, $p\eta^2=0.321$), accounted by the larger amplitudes for neutral when compared with fearful EBL. Moreover, we found a main effect of CHANNEL ($F(3, 48)=7.764$, $p<.01$, $p\eta^2=0.327$), while the interaction EMOTION*CHANNEL was not significant ($F<1$; $p=.795$). Post hoc analysis on CHANNEL showed an overall nonsignificant difference in amplitude recorded on channel C3 ($A=-1.609\pm0.107\,\mu V$) when compared with C4 ($A=-1.436\pm0.151\,\mu V$; $p=.971$), while a significantly lower activity was recorded on C3 when compared with Fc3 ($A=-2.154\pm0.175\,\mu V$; $p<.01$) and on C4 when compared with Fc3 ($p<.01$) and Fc4 ($A=-2.077\pm0.260\,\mu V$; $p<.01$).

3.2 | ERD/ERS analysis

3.2.1 | Differences in whole-brain activity

This analysis was run to identify significant differences retrieved in whole brain activity. The differences reported in Figure 3 do not show the direction in terms of desynchronization/synchronization, which were subsequently analyzed in the ERD/ERS spatial maps (see section ROIs ERD/ERS maps).

Differences in whole-brain activity between 'Fear' and 'Neutral' conditions were analyzed in the timeframe [0 ms, 200 ms] after stimulus onset, to observe early brain activity (see Figure 3). All maps are corrected for multiple comparisons. The MNI coordinates of the cerebral areas

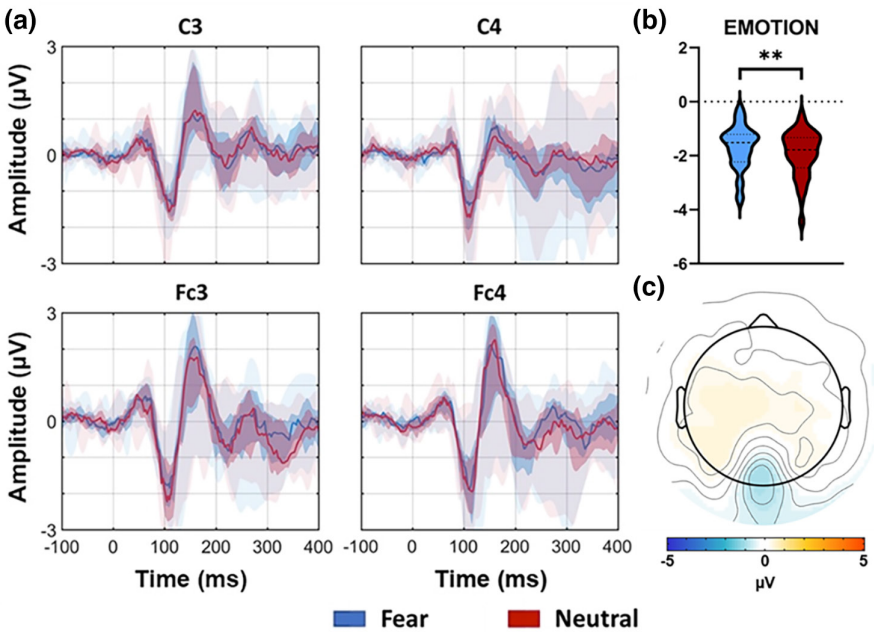

FIGURE 2 Fronto-central activity over channels C3, C4, Fc3, and Fc4. (a) The panel shows the mean amplitudes recorded over fronto-central channels in the two experimental conditions 'Fear' (blue) and 'Neutral' (red). The earliest negative component reflects the negative counterpart of the P100 in fronto-central channels. The darker shaded area represents the standard deviation, while the lighter shaded area shows the quartiles. (b) Violin plot showing the results of the statistical analysis on the main effect EMOTION (**=$p\leq.01$). (c) Voltage map displaying scalp topography differences between 'Fear' and 'Neutral' in the first 200 ms. The warmer color stands for 'Fear' < 'Neutral' while the colder color stands for 'Fear' > 'Neutral'.

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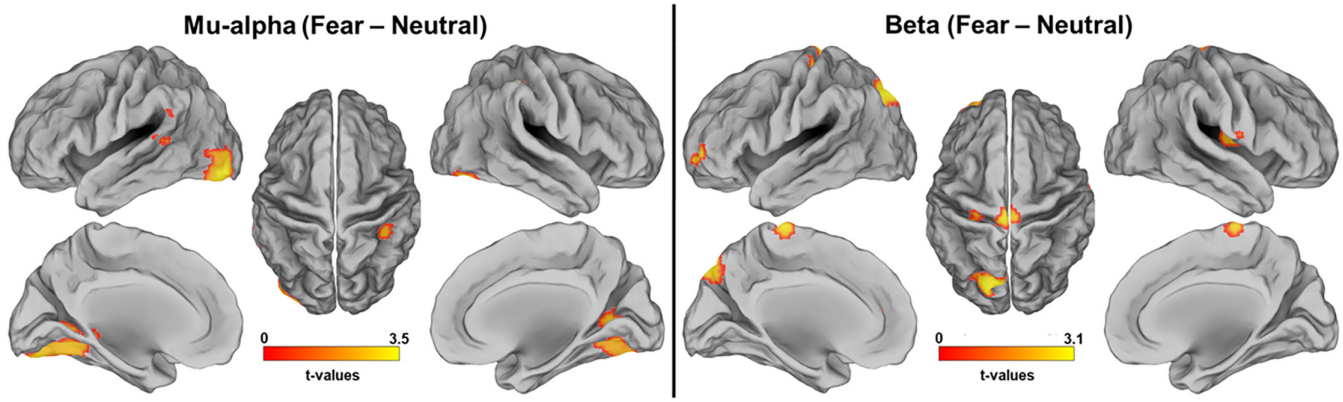

FIGURE 3 T-maps for whole-brain activity differences between 'Fear' and 'Neutral'. Brain maps depict the main differences retrieved in the mu-alpha and the beta frequency bands between the two experimental conditions. All highlighted areas represent significant differences in activity corrected for multiple comparisons. The detailed MNI coordinates of the observable areas are retrievable in Table 1. Maps were elaborated via the eLORETA method for source-space estimation (Zhao et al., 2019).

TABLE 1 Brain areas showing significant activation differences between 'Fear' and 'Neutral'.

Area	Frequency band	Side	*X*	*Y*	*Z*
Inferior occipital gyrus	mu-alpha	L	−40	−90	−12
Fusiform Gyrus	mu-alpha	L	−29	−76	−18
		R	35	−76	−18
Superior parietal lobule	mu-alpha	R	41	−37	50
Primary motor cortex (Hand)	beta	L	−32	−23	64
Primary motor cortex (Leg)	beta	L	−6	28	79
		R	5	−28	79
Primary somatosensory cortex (Hand)	beta	L	−30	−32	64
Anterior prefrontal cortex	beta	L	−33	61	2
Superior parietal Lobule	beta	L	−16	−80	48
Insula	beta	R	44	−8	48
Precuneus	beta	L	−5	−78	46

Note: The table shows all MNI coordinates of the brain areas whose differences in activity in the two investigated frequency bands resulted significantly. MNI coordinates where extrapolated via the AICHA atlas included in the MRIcroGL software (Rorden & Brett, 2000).

showing significant differences in activity between conditions are reported in Table 1. Coordinates were identified via the AICHA atlas (Joliot et al., 2015).

- In the mu-alpha band, significant differences between 'Fear' and 'Neutral were found at the level of the left occipital cortex, the fusiform gyrus (bilaterally), and in the right superior parietal lobule. No significant differences in activity between conditions were retrieved in the sensorimotor areas, specifically in the four ROI object of this study (i.e., lM1, lS1, rM1, rS1).
- Regarding the beta band, significant differences between conditions were found in the left posterior parietal cortex (PPC) and the precuneus, as well as in the left anterior prefrontal cortex. Most importantly, significant differences between 'Fear' and 'Neutral' EBL were found in the selected ROIs. More specifically, differences were found in the lM1 and the lS1, while in the right hemisphere, significant differences are observable in M1.

3.3 | ROIs ERD/ERS maps

Time-frequency analysis (ERD/ERS) was performed in the following ROIs selected a priori: lM1, rM1, lS1, and rS1. The results of the group analysis on the ERD/ERS spatial

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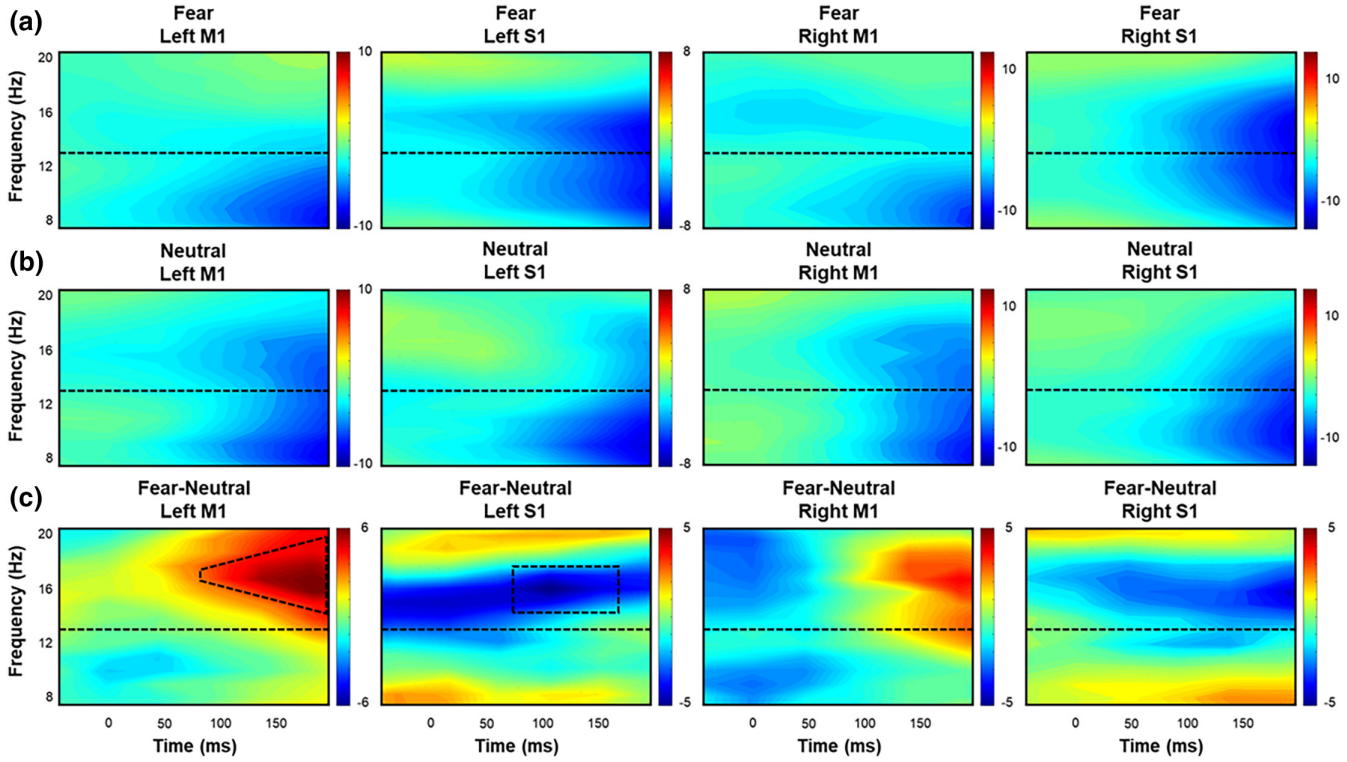

FIGURE 4 ROIs maps for ERD/ERS analysis. Rows (a) and (b) show the ERD/ERS maps of the experimental conditions ('Fear' and 'Neutral' respectively), while row (c) shows the map for the difference between conditions. The dashed line separates the mu-alpha band (below the dashed line) from the beta band (above the dashed line). Significant differences are enclosed in the dotted lines observable in the first two maps from the left in row (c).

maps for ROIs might be observed in Figure 4. Generally, as it is possible to observe in Figure 4 (panels in rows (a) and (b)), there is a significant desynchronized activity in all ROIs for all experimental conditions.

There is a consistent mu-alpha activity which generally arises around 50 ms after stimulus onset, independently from the characteristics of the stimulus, which is prolonged all over the timeframe considered in the analysis. The lower beta band, on the other hand, similarly shows an early activity onset (~50 ms after stimulus onset) and a comparable duration, but in the left and right M1, it does show desynchronized activity only in the 'Neutral' and not in the 'Fear' condition.

No significant differences were retrieved in the mu-alpha band in any conditions (see Figure 4, row (c), below the dashed line). On the other hand, for the beta band, the spatial maps 'Fear-Neutral' depicting the differences between conditions show a significantly higher desynchronization for 'Neutral' compared with 'Fear' in the left M1 (Figure 4, row (c), first map – the dotted area above the dashed line), while the opposite trend can be observed in the left S1 where a higher desynchronization is retrieved for 'Fear' (Figure 4, row (c), second map – dotted area above the dashed line). No significant differences resulted in the right hemisphere in the ROIs taken into consideration for this study in all frequency bands, but the same trend is observable in the comparison between M1 and S1 (i.e., higher activation for 'Neutral' in rM1 and higher activation for 'Fear' in rS1).

4 | DISCUSSION

This study aimed to test whether observation of EBL was able to modulate cortical activity in sensorimotor areas, specifically ERPs and cortical oscillations in the mu-alpha and lower beta frequency bands, at short latencies (around 100 ms after the onset of the EBL stimulus). We built on our previous TMS findings that sensorimotor integration, as tested in M1 using the SAI protocol, is modulated during the processing of static images depicting fear EBL, already at 120 ms from the stimulus onset (Botta et al., 2022). Based on current knowledge of the neurophysiological cortico-cortical mechanism underlying the SAI effect (Turco et al., 2018), and the increasing recognition of a key role of primary sensorimotor areas in the perception of others' actions and emotions (Adolphs et al., 2000; Bufalari et al., 2007; Gazzola et al., 2012; Keysers et al., 2010; Paracampo et al., 2017; Pitcher et al., 2008), we hypothesized that modulation of sensorimotor integration during observation of fear EBL was driven by increased activity in S1 – reflecting increased sensory vigilance – and an

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inhibitory effect on M1 excitability – reflecting a freezing response to potentially threatening signals. Therefore, using hd-EEG coupled with source activity estimation, here, we investigated the early temporal dynamics and spatial distribution of sensorimotor response to observed fear EBL and neutral body movements.

The main findings of our study allow us to clarify the neurophysiological underpinnings of early reactivity to fear EBL and neutral body movements: (i) ERP analysis showed reduced amplitude in fronto-central channels for 'Fear' EBL stimuli compared with 'Neutral' stimuli in the explored early time window (80–150 ms); (ii) source-space estimation showed significant differences between 'Fear' and 'Neutral' EBL processing mainly retrievable in sensorimotor areas in the lower beta band; (iii) ERD/ERS analysis showed increased beta-ERD in S1 and reduced beta-ERD in M1 for 'Fear' EBL compared with 'Neutral' EBL stimuli.

Emotional and motor information are inherently intertwined in the expression, and consequently perception, of EBL. In the present study, we used a validated database using static pictures with comparable amounts of emotional and motor information in the 'Neutral' and 'Fear' conditions as consistently reported in prior works (e.g., Borgomaneri et al., 2012, 2015c, 2017). Moreover, we also controlled the visual stimuli for RGB values, perceived luminance, contrast and image complexity so to rule out any possible confounder (for details see Appendix S1). Therefore, by contrasting 'Neutral' and 'Fear' EBL pictures, we could assess whether early EEG activity was influenced by the emotional features of the observed body posture or merely reflected the mapping of motor features of the movement (i.e., motor resonance), independently of the underlying emotional features.

Related to ERP analysis, our results showed an overall lower amplitude in fronto-central channels (i.e., C3, C4, Fc3, Fc4) for fearful EBL compared with neutral EBL and no differences in terms of latencies in the time window of the P100. This result is consistent with what was observed by van Heijnsbergen and colleagues who, while studying the vertex positive potential (i.e., an ERP component retrievable in fronto-central areas of the brain at ~170 ms from stimulus onset) recorded a negative deflection around the first 100 ms from stimulus onset that was not further investigated or explained because considered to be not relevant for the aim of their study (van Heijnsbergen et al., 2007). Furthermore, in previous studies, ERP source analyses revealed early activity (120–150 ms) in the pre- and postcentral cortex, typically associated with action processing (Hauk et al., 2004; Hoenig et al., 2008; Kiefer, 2001, 2005). Moreover, Sim et al demonstrated that early activity in central areas at about 120 ms from the onset of a picture of an affordable object was modulated by the content (congruent vs incongruent) of a priming movie showing hands acting with the object being erased (Kiefer et al., 2011; Sim et al., 2015). The action-priming effect was significant over the fronto-central scalp: ERPs were more negative in the congruent than in the incongruent condition (Kiefer et al., 2011; Sim et al., 2015).

Our results also showed modulation of early ERPs in relation to the emotional content of EBL; the amplitude of the negative sensorimotor counterpart of the P100 was smaller in central and fronto-central channels for 'Fear' compared with 'Neutral' EBL stimuli. Because the fronto-central early negative component has been shown to be mainly linked to action-processing processes and the amount of motor information depicted in the used stimuli was comparable (Borgomaneri et al., 2012, 2015c), it is plausible to infer that 'Fear' EBL processing exerted an effect in terms of cortical modulation, namely inhibition, resulting in reduced activity in motor areas in comparison to the one evoked by nonemotional stimuli.

Taking advantage of the hd-EEG that provides us with the possibility to gain information on the sources of the neural oscillations with an optimal temporal resolution and an improved spatial resolution relative to standard EEG (Michel & Murray, 2012), we conducted a source-space estimation analysis to localize, at early latencies, the neural areas with significant differences in activity in mu-alpha and beta bands between 'Neutral' and 'Fear' EBL. To this end, we used a validated analysis workflow for performing source localization from hd-EEG data. This workflow was capable of detecting multiple brain networks that are spatially similar to those obtained from fMRI data (Liu et al., 2017; Zhao et al., 2019). Source-space estimation analysis on whole brain activity showed that at early latencies significant differences were detectable between 'Fear' and 'Neutral' EBL processing in sensorimotor areas only in the beta band. Indeed, in the mu-alpha band, significant differences between 'Fear' and 'Neutral were detectable mainly in the posterior cortex implicated in visual processing and attention (de Echegaray & Moratti, 2021) and particularly at the level of the left inferior occipital gyrus, the fusiform gyrus and the right posterior parietal lobe (areas compatible with the findings showed in (Meeren et al., 2016).

Going further, ERS/ERD analysis over fronto-central ROIs showed an overall desynchronization in mu-alpha and beta bands in the four sensorimotor ROIs, consistent with what was reported in the literature as a neurophysiological marker of motor resonance during action processing (Hobson & Bishop, 2016; Schubring & Schupp, 2019; Siqi-Liu et al., 2018). Moreover, by computing the differences in frequency-band activity between the fearful and the neutral EBL processing, we found a significantly decreased activation for fearful EBL in M1 relative to neutral

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stimuli, while the opposite was found for fearful EBL, which showed significantly higher activity in S1 than neutral, even though these differences resulted only for the lower beta frequency band, hence confirming our initial hypothesis of increased early activity of somatosensory areas in response to fearful stimuli and decreased activity in M1.

We can make a hypothesis related to increased activity in S1 during fearful EBL processing, taking into account the role played by the amygdala in emotional processing and the role exerted by this subcortical structure in modulating attention and vigilance (Bertini & Làdavas, 2021). As shown by different experimental paradigms in animals (for a review see: Davis & Whalen, 2001; Whalen, 1998), the amygdala may be especially involved in increasing vigilance by lowering the neuronal threshold of widespread sensory cortical areas through the modulation of the release of acetylcholine from the basal forebrain (Bucci et al., 1998; Chiba et al., 1995). In addition, activation of cholinergic, dopaminergic, serotonergic, and noradrenergic neurons in the brainstem may have widespread influences on thalamic and sub-thalamic sensory as well as motor transmission. Furthermore, this mechanism is made stronger by the ambiguity of the stimulus proposed. It has been proposed that increased sensory vigilance is stronger during the processing of fearful faces relative to angry faces because if both provide information about the presence of a threat, the first gives less information about the source of that threat (Whalen, 1998). The same can be hypothesized for EBL processing. Indeed, as for facial expressions, the processing of EBL activates brain regions involved in perceptual and affective processes such as the superior temporal sulcus, fusiform and postcentral gyrus, the amygdala, and medial prefrontal cortex (de Gelder, 2006, 2009; Downing & Kanwisher, 2001; Peelen et al., 2010; Peelen & Downing, 2005; Ross et al., 2020). As previously mentioned, we recently showed an increased short latency afferent sensorimotor inhibition (SAI) at 120 ms after stimulus onset, observed specifically for fearful EBL (Botta et al., 2022). We hypothesized that an augmented release of acetylcholine from the basal forebrain might have been responsible for an increased SAI (Botta et al., 2022). Indeed, although it could be argued that the mechanisms underpinning SAI are still not entirely understood, the activity exerted by the pyramidal neurons in the somatosensory cortex engaged by the processing of afferent peripheral stimuli is likely to inhibit motor output by increasing the GABAergic tone in the cortex (for a review see Turco et al., 2018). Furthermore, this inhibitory intracortical network is not mediated only by GABA, but also by cholinergic activity (Di Lazzaro, Oliviero, et al., 2005; Di Lazzaro, Pilato, et al., 2005). Considering these pieces of evidence, it might be conceivable to hypothesize that the results we found for the lower beta band might be related to an increased allocation of neural resources to the processing of fearful EBL – particularly over S1.

Although previous studies have demonstrated the contribution of subcortical structures, such as the amygdala, to EBL processing (e.g., de Gelder, 2006; de Gelder et al., 2004; Hadjikhani & de Gelder, 2003), our data cannot provide support for the involvement of subcortical structures. This limitation arises from the inherent constraints of source estimation based on EEG data. The role of these structures in our results should be considered potential, but further studies are necessary to confirm the direct role of subcortical structures in modulating neural oscillations in response to EBL.

Our results related to decreased M1 activity align with previous neurophysiological research that has observed a freezing-like phenomenon in M1 early on during EBL processing. This freezing effect was characterized by decreased cortico-spinal excitability and decreased intracortical excitatory activity (Borgomaneri et al., 2015c). However, the causal relationship between these phenomena, specifically whether increased activity in S1 can downregulate M1 activity, leading to transient freezing, cannot be directly demonstrated by the present results. To provide more insights into the directionality of cortico-cortical interactions underlying EBL processing, future studies should investigate functional connectivity, addressing the issue of the relative influence of S1 on M1 during observation of EBL.

It should be noted that differences in activity were only observed in the lower beta band, and not in the mu-alpha band. No significant differences between conditions were found for the mu-alpha band and this might be related to the fact that this rhythm is mainly linked to action observation and action execution (Debnath et al., 2019; Hobson & Bishop, 2016; Pineda, 2005). Body expression pictures inevitably contain motor information, being embedded with emotional or nonemotional contents. Apparently, our results are going in the opposite direction of the (few) evidence available where it has been shown that the emotional content of EBL is associated with a higher mu-alpha suppression (i.e., a reduced power in the mu-alpha band indicating stronger desynchronization in the central brain areas) when compared with nonemotional body expressions (Schubring & Schupp, 2019; Siqi-Liu et al., 2018). This apparent contradiction might be explained by the time window used in our experiment for ERD/ERS activity. The mu-alpha suppression associated with nonemotional action observation has been shown to appear more or less at 600 ms after stimulus onset (Babiloni et al., 2002; Hobson & Bishop, 2016), while latencies of ERD response to EBL were found between 1 and 2 s after stimulus onset for point-light display stimuli (Siqi-Liu et al., 2018). As it

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may be noted, although evidence shows that EBL has an early processing (van Heijnsbergen et al., 2007) and can modulate intracortical networks at short latency (Borgomaneri et al., 2015c, 2020; Botta et al., 2022), to our knowledge no studies have ever focused their attention on early modulations of cortical oscillations during the processing of EBL. Moreover, to the best of our knowledge, no ERD/ERS studies investigating fearful EBL were performed since now, but only studies involving happiness, anger, and/or sadness (Schubring & Schupp, 2019; Siqi-Liu et al., 2018). Our results might indicate that the mu-alpha suppression at short latencies is not sensitive to emotional content but only to motor information carried out by EBL stimuli, hence resulting in a lack of differences in ERD activity between emotional and nonemotional conditions that appears only at longer latencies.

To gain a better understanding of the temporal dynamics of early mu-alpha desynchronization during observation of emotional stimuli depicting human body expressions, further studies are needed. These studies might shed light on the contribution of these brain rhythms to short-latency emotional processing. Notably, consistent evidence supports the modulation of mu-alpha rhythm during motor behavior, whether it is executed or observed, compared with beta modulation. Nevertheless, several works have demonstrated that the beta rhythm exhibits desynchronized activity in response to action observation. For instance, Babiloni et al. conducted an EEG study investigating brain rhythms in the sensorimotor areas during the observation and execution of hand actions. They found clear desynchronization (i.e., cortical activation) in the beta band in specific somatosensory, motor and premotor areas (BA1-2, BA4, and BA6) (Babiloni et al., 2016). Their results align with other studies examining neural oscillations and somatosensory-evoked potentials, such as the study by Rossi et al. where authors observed an increase of short-latency components (i.e., N30) reflecting an increased beta activity in precentral areas during observation of hand actions (Rossi et al., 2002). In conclusion, while further exploration of beta suppression/enhancement during action observation is warranted, especially using high-definition recording techniques, evidence in the literature suggests an overall modulation of beta rhythm during action observation, even at very short latencies.

5 | CONCLUSIONS

In conclusion, in the present study, we showed evidence of an early modulation of sensorimotor cortical activity and neural oscillations in the lower beta frequency range over S1 and M1, providing evidence of an early increased activation in S1 in response to fearful stimuli (possibly linked to increased sensory vigilance) and confirming the results of other neurophysiological studies showing decreased activity in M1. Furthermore, no differences were retrieved in the sensorimotor areas at short latency for the mu-alpha band, indicating that early suppression was not sensitive to emotions but only to motion. These results support the idea that fearful EBL is rapidly processed at a subcortical level and that this elaboration has an early modulatory effect on the sensorimotor system, probably related to an augmented sensory arousal in the presence of potential threats.

AUTHOR CONTRIBUTIONS

Alessandro Botta: Conceptualization; data curation; formal analysis; investigation; methodology; validation; writing – original draft; writing – review and editing. **Mingqi Zhao:** Investigation; methodology; software; writing – original draft. **Jessica Samogin:** Investigation; methodology; software; writing – original draft. **Elisa Pelosin:** Conceptualization; supervision; validation; visualization; writing – original draft; writing – review and editing. **Gaia Bonassi:** Data curation; formal analysis; investigation; writing – original draft. **Giovanna Lagravinese:** Data curation; investigation; writing – original draft; writing – review and editing. **Dante Mantini:** Conceptualization; supervision; writing – original draft; writing – review and editing. **Alessio Avenanti:** Conceptualization; writing – original draft; writing – review and editing. **Laura Avanzino:** Conceptualization; data curation; funding acquisition; methodology; resources; supervision; validation; visualization; writing – original draft; writing – review and editing.

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DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

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

Data S1. Supplemental method.

Figure S1. Panel A: Examples of the EBL pictures used in the study, from the original work by Borgomaneri et al. (2012).

Table S1. Image parameters for fearful EBL.

Table S2. Image parameters for neutral EBL.

Table S3. Statistical analysis results. All values are reported as mean ± standard deviation.

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