

RESEARCH ARTICLE | *Higher Neural Functions and Behavior*

Error, rather than its probability, elicits specific electrocortical signatures:
a combined EEG-immersive virtual reality study of action observation

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¹*Social Cognitive Neuroscience Laboratory, Department of Psychology, Sapienza University of Rome, Italy;* ²*Fondazione Santa Lucia, Institute for Research and Health Care, Rome, Italy;* and ³*Centre for Studies and Research in Cognitive Neuroscience and Department of Psychology, University of Bologna, Campus Cesena, Italy*

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Pezzetta R, Nicolardi V, Tidoni E, Aglioti SM. Error, rather than its probability, elicits specific electrocortical signatures: a combined EEG-immersive virtual reality study of action observation. *J Neurophysiol* 120: 1107–1118, 2018. First published June 6, 2018; doi: 10.1152/jn.00130.2018.—Detecting errors in one's own actions, and in the actions of others, is a crucial ability for adaptable and flexible behavior. Studies show that specific EEG signatures underpin the monitoring of observed erroneous actions (error-related negativity, error positivity, mid-frontal theta oscillations). However, the majority of studies on action observation used sequences of trials where erroneous actions were less frequent than correct actions. Therefore, it was not possible to disentangle whether the activation of the performance monitoring system was due to an error, as a violation of the intended goal, or to a surprise/novelty effect, associated with a rare and unexpected event. Combining EEG and immersive virtual reality (IVR-CAVE system), we recorded the neural signal of 25 young adults who observed, in first-person perspective, simple reach-to-grasp actions performed by an avatar aiming for a glass. Importantly, the proportion of erroneous actions was higher than correct actions. Results showed that the observation of erroneous actions elicits the typical electrocortical signatures of error monitoring, and therefore the violation of the action goal is still perceived as a salient event. The observation of correct actions elicited stronger alpha suppression. This confirmed the role of the alpha-frequency band in the general orienting response to novel and infrequent stimuli. Our data provide novel evidence that an observed goal error (the action slip) triggers the activity of the performance-monitoring system even when erroneous actions, which are, typically, relevant events, occur more often than correct actions and thus are not salient because of their rarity.

NEW & NOTEWORTHY Activation of the performance-monitoring system (PMS) is typically investigated when errors in a sequence are comparatively rare. However, whether the PMS is activated by errors per se or by their infrequency is not known. Combining EEG-virtual reality techniques, we found that observing frequent (70%) action errors performed by avatars elicits electrocortical error signatures suggesting that deviation from the prediction of how learned actions should correctly deploy, rather than its frequency, is coded in the PMS.

action observation; error; event probability; theta; virtual reality

INTRODUCTION

Detecting errors in one's own actions, and in the actions of others, is a crucial ability for flexible behavioral interactions with objects and people (Avenanti et al. 2007; Cavanagh and Frank 2014; de Bruijn et al. 2011; Navarro-Cebrian et al. 2016; Panasiti et al. 2017; Ullsperger et al. 2014a). Studies in humans (Hajcak et al. 2005; Luu et al. 2004) and nonhuman primates (Tsujimoto et al. 2006) have shown that the monitoring of erroneous actions triggers specific EEG signatures that index neural activity in a network centered on the middle-frontal regions of the brain (Cohen 2011; Ridderinkhof et al. 2004). Crucially, performance-monitoring signatures are elicited by committed and observed errors, which suggests the presence of a fundamental, adaptive mechanism that detects the deviation of an action from the predicted goal (Joch et al. 2017; Ozkan and Pezzetta 2018; van Schie et al. 2004). This mechanism is particularly relevant in sports (Abreu et al. 2012; Aglioti et al. 2008; Makris and Urgesi 2015; Proverbio et al. 2012; van Pelt et al. 2016) and music performances (Candidi et al. 2014; Panasiti et al. 2016), two domains that require fast detection of salient information.

In the time domain, two event-related potentials (ERPs) have been extensively linked to error monitoring, namely, error-related negativity (ERN) and error positivity (Pe). The ERN is a negative deflection peaking around 80 ms after an error is committed (Luck and Kappenman 2011). The Pe is a sustained positive deflection that typically follows the ERN, with a diffuse distribution but with maximal amplitude over the central-parietal region of the scalp (Shalgi et al. 2009; Wessel 2012). The Pe has many overlapping features with the widely known P300 (Overbeek et al. 2005; Ridderinkhof et al. 2009). In addition to the morphology and the scalp distribution, both components are elicited in response to task-significant stimuli (e.g., low-probability targets) (Gehring et al. 2012; Overbeek et al. 2005; Polich 2007). However, the Pe has an additional property in that it reflects the motivational significance of a salient performance error (Ridderinkhof et al. 2009). In fact, whereas the ERN is believed to reflect an initial and automatic brain response to an error, the Pe likely reflects higher levels of error processing, such as error awareness, reorientation of the attention, behavioral adaptation, or context updating (Nieuwenhuis et al. 2001; Ridderinkhof et al. 2009). The ERN and the Pe appear to be two mechanisms that might be independent

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(Di Gregorio et al. 2016) and that characterize the complex performance monitoring system.

In the time-frequency domain, error monitoring has been primarily associated with mid-frontal theta oscillations (4–8 Hz) that appear to increase when an error is committed (Cavanagh and Frank 2014; Cavanagh et al. 2012; Cohen 2011). Although a study suggested that ERN and theta activity are functionally linked and that the former may originate, at least partially, from the phase-locking of the latter (Luu et al. 2004), recent data simulations contradict this idea (Yeung et al. 2007). Another frequency band engaged in the general response to infrequent and novel stimuli, a property that often characterizes errors, is the alpha activity. The decreased power in this frequency band (generally 8–12 Hz) is often linked to the physiological reaction to novelty and the orientation effect toward salient conditions. This modulation of power in alpha activity has been found mainly in the middle-central (Pavone et al. 2016; Wang et al. 2015) and middle-posterior electrodes/sensors (Carp and Compton 2009; Mazaheri et al. 2009; van Driel et al. 2012).

Whereas the original EEG characterization of the error-monitoring system has been studied in relation to performed errors (Falkenstein et al. 1991; Gehring et al. 1993), subsequent studies also indicate that the detection of errors in the actions of others is indexed by specific electrocortical signatures, as well (Bates et al. 2005; Miltner et al. 2004; Panasiti et al. 2016; van Schie et al. 2004). In particular, studies report that the so-called observed ERN (oERN) and observed error positivity (oPe) have a topographic distribution and neural localization similar to the ERN and Pe, respectively. However, the observation-related error-monitoring components exhibit smaller amplitude and delayed latency with respect to the execution-related components (Koban and Pourtois 2014; Koban et al. 2010; van Schie et al. 2004). The link between markers of error execution and observation in the time-frequency domain is less clear, because only a limited number of studies have investigated the modulation of oscillatory activity during vicarious error processing (Conejero et al. 2018; Pavone et al. 2016; Spinelli et al. 2018; Wang et al. 2015). In both error-execution and error-observation literature, error-related potentials and frontal midline theta activity have been associated with error significance (Maier and Steinhauser 2016; Nieuwenhuis et al. 2007), cognitive control (Cavanagh and Frank 2014; Cavanagh et al. 2009; Corbetta and Shulman 2002; Wokke et al. 2017), reinforcement learning (Holroyd and Coles 2002; Holroyd et al. 2006; Volpato et al. 2016), and rule violation (Arrighi et al. 2016; Krigolson and Holroyd 2006; Tzur and Berger 2007). Although certain studies suggest that error-related signatures are sensitive to outcome significance (van Driel et al. 2012; Wang et al. 2015), outcome-prediction accounts support valence-free interpretations. According to those accounts, error-related cortical responses are modulated by the likelihood of occurrence and its link with unexpectedness (Garofalo et al. 2017; Notebaert et al. 2009; Núñez Castellar et al. 2010; Oliveira et al. 2007; Wessel et al. 2014). Thus a wrong prediction (Alexander and Brown 2011; Donnarumma et al. 2017; Hajihosseini and Holroyd 2013; Kilner et al. 2007), rather than the significance of the event itself (Maier and Steinhauser 2016; Maier et al. 2012), may account for the triggering of error-related signatures.

To date, most research on action execution and observation has relied on tasks where error trials were the most infrequent events (Bates et al. 2005; Conejero et al. 2018; Miltner et al. 2004; Pavone et al. 2016; van Schie et al. 2004). This type of design makes it impossible to discern whether ERN amplitude and theta power are modulated by the goal violation or by the fact that the error is a rare event in a series.

It is worth noting that error observation studies in which the same number of correct and erroneous actions were used did not find an oERN (de Bruijn et al. 2007; Panasiti et al. 2016) or found contrasting results (de Bruijn and von Rhein 2012; Kobza and Bellebaum 2013; Padrao et al. 2016; Wang et al. 2015). Also, most of the previous studies were based on a speed-response choice task (Koelewijn et al. 2008; van Schie et al. 2004), and observed action errors were coded with respect to sequential frame pictures (de Bruijn et al. 2007) and thus considered as all-or-nothing events. In a minority of studies focused on continuous motor actions (Bekkering et al. 2009; Meyer et al. 2016), no analyses on error signals were provided. However, in the circumstances of daily life, actions and action errors occur along a continuum, because the environment requires us to constantly monitor and detect crucial information, often in the absence of explicit feedback about the instant at which the error is coded.

To deal with such issues, we designed an EEG-immersive virtual reality task in which healthy participants observed an avatar performing successful (correct) or ineffective (erroneous) reach-to-grasp actions involving a glass. At variance with Pavone et al. (2016) and Spinelli et al. (2018), we reversed the proportion of erroneous trials. This meant that erroneous actions were the most frequent event (70% of cases) and that a successful grasp was rarely observed (30% of cases). This difference allowed us to disentangle the contribution error per se, rather than its rarity, in modulating the activity of the human performance monitoring system, and specifically in detecting errors in the continuous actions of a virtual agent. Finding greater ERN amplitude and greater oscillatory activity in theta after an erroneous action would suggest that these electrical events signal the detection of an error (as a divergent event compared with the intended goal) independently from its frequency. By contrast, finding increased ERN and theta power after correct actions would suggest that these electrical correlates code for rare, and thus less expected events. On the basis of the possible link between rare stimuli and alpha modulation, we predicted stronger parietal-occipital alpha suppression in the correct, less frequent outcome.

MATERIALS AND METHODS

Participants

Twenty-five participants (one left-handed) took part in the experiment. They had normal or corrected-to-normal visual acuity and reported no history of neurological or psychiatric diseases. All participants were naive as to the purposes of the experiment, signed the written informed consent, and received a compensation of €7.5 per hour. The experimental protocol was approved by the local Ethics Committee at the Fondazione Santa Lucia Research Hospital (Rome, Italy) and was conducted in accordance with the ethical standards of the Declaration of Helsinki. Data from two participants were discarded because of technical reasons; therefore, EEG analyses were conducted on a total sample of 23 participants (14 women; age:

25.22 ± 3.02 yr, mean ± SD). The appropriateness of our sample sizes was established using G*Power software (Faul et al. 2007), which indicated that 20 participants would be required to detect a medium effect with a power of 0.8 at an alpha of 0.05. Our study counts a final sample of 23 participants (see *Experimental Procedure*).

Apparatus, Stimuli, and Procedure

Participants sat in a cave automatic virtual environment (CAVE) with projectors directed to four walls of a room-sized cube (3 m × 3 m × 2.5 m; Cruz-Neira et al. 1993). The virtual scenario consisted of a basic room with a table. At the center of the table, a yellow parallelepipedon was located with a blue glass on top of it. Participants observed one avatar in first-person perspective (1PP; see Fig. 1) seated on a chair in front of a table with its arms resting on the table. The glass was placed in the avatar's peripersonal space at a distance of ~50 cm (Costantini et al. 2011). The avatar and the scenarios were created by means of Autodesk Maya 2011 and 3D Studio Max 2011, respectively. The kinematics of the avatar were implemented by HALCA library (Gillies and Spanlang 2010), and the experiment was performed in an immersive three-dimensional (3D) virtual environment with a real-size avatar drawn on a 1:1 scale and rendered in XVR 2.1 (Huang et al. 2013; Tecchia et al. 2014). Participants wore Nvidia stereo glasses in which 3D virtual images were alternately displayed on both eyes with a refresh rate of 60 Hz. Moreover, these stereo glasses were interfaced with an Intersense 900 ultrasonic system (Thales Visionix) and constantly tracked the head position during the experiment.

Experimental Procedure

Before the beginning of the experiment, participants underwent a familiarization phase with the experimental setup, as well as a calibration phase within the virtual environment, which consisted of adapting the size of the virtual body to the real one. After this phase, a brief practice session (8 trials, 4 correct and 4 erroneous) occurred. Each participant was informed that the goal of the avatar's movements was to reach and grasp the glass on the table and that the action might

or might not be successful. The total number of trials per participant was 100, 70 of which were incorrect and 30 of which were correct. This is the same number of trials used in Pavone et al. (2016) but with the inverse proportion (70 correct and 30 incorrect). The total duration of our experiment was ~20 min. Participants were not informed about the probability of the different action outcome.

At the onset of each trial, a sound signaled the beginning of the action. During the trial, participants observed the movement of the avatar's right arm in 1PP. The kinematics of the movement were identical for the first 700 ms in both conditions and began to diverge in the last 300 ms. The trajectory deviation led to either a successful or unsuccessful grasp. The deviation from the to-be-grasped object was identical in all the erroneous trials (Fig. 1). The sequence of correct and incorrect trials was randomized. After the end of the action, the avatar's arm rested for 1,000 ms (±50 ms) before a black screen appeared. During the intertrial interval (ITI), three different situations could occur: 1) in 10% of the trials, participants had to answer a catch question ("Did the arm take the glass?" (yes/no answer)); 2) in 40% of the trials, an empty black screen was presented; and 3) in 50% of the trials, participants had to provide ratings concerning the sense of embodiment. When the first and third cases occurred, the black screen lasted until a vocal response was given, whereas when the second case occurred, the experimenter pressed a key to start the next trial, producing a variable ITI (mean duration: ~4,000 ms).

To measure their sense of embodiment, participants were asked to verbally rate two questions on a visual analog scale (VAS) from 0 to 100. One question was about their sense of ownership ("To what extent did you feel the arm was yours?"; 0 = no ownership to 100 = maximal ownership; Slater et al. 2010), and the other question was about their sense of agency ("How much did you feel in control of the arm?"; 0 = no control to 100 = maximal control; Fusaro et al. 2016; Tieri et al. 2015a, 2015b; Villa et al. 2018). The two questions were always presented together and in a randomized order. A total of 819 embodiment ratings for erroneous trials, and 351 embodiment ratings for correct trials, were collected across the whole sample, with each embodiment rating including the two questions on ownership and agency (2 participant ratings were missing due to technical issues

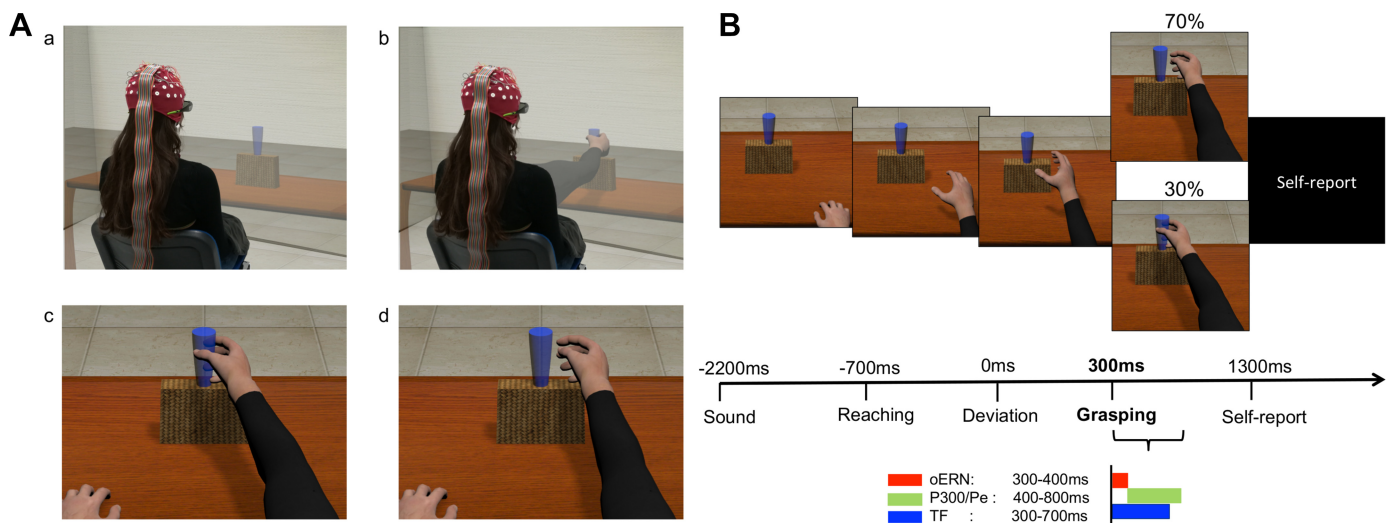


Fig. 1. A: example of the experimental paradigm and setup. *Top* images show the participant in the 3-dimensional (3D) rendering of the virtual scenario (cave automatic virtual environment, CAVE), during which projectors are directed to the 4 walls of a room-sized cube; the participant observes a static situation before the beginning of the trial (a) and at the end of an action (b). *Bottom* images represent a snapshot from inside the CAVE. The participant is immersed in the virtual scenario. In first-person perspective, using 3D visualization glasses, the participant observes a real-size avatar's arm, perceived as attached to the shoulder during a correct (c) and an erroneous (d) grasping. B: timeline of a single trial. The avatar's action lasted 1,000 ms: the reaching phase was equal for both types of movements and lasted 700 ms; the deviation phase in which the avatar's arm-path deviation could occur and define an erroneous or correct action lasted 300 ms. The onset of the avatar's limb-path deviation is set at 0 ms; the end of the avatar's action occurs at 300 ms. The main EEG analyses (reported at *bottom*) have been conducted with intervals of interest chosen a priori. oERN, observed error-related negativity; P300/Pe, error positivity; TF, window of time-frequency analysis.

during the saving of data and therefore were not included; 21 participants responded to the VAS in 50% of trials, and 4 responded to it in 30% of trials).

Statistical analyses were done using R software (R Core Team 2014). ERPs and time-frequency time series analyses were made using the *erpR* package (Arcara and Petrova 2014). All ANOVAs were performed using the *ez* package (Lawrence 2013). Analyses were performed using repeated-measures ANOVA, and Greenhouse-Geisser correction for nonsphericity was applied when appropriate. By estimating the effect size relative to the ANOVA test, we report the partial eta squared (η_p^2). Spearman correlations were executed, and Bonferroni corrections for multiple comparisons were applied when necessary. Practice trials were excluded from the analyses.

EEG Recording and Preprocessing Analysis

EEG signals were recorded using a Neuroscan SynAmps RT amplifier system and 60 scalp electrodes embedded in a fabric cap (Electro-Cap International), arranged according to the international 10–10 system.¹ Horizontal electro-oculogram was recorded bipolarly from electrodes placed on the outer canthi of each eye. EEG signal was recorded continuously in alternating current mode with a band-pass filter (0.05–200 Hz) and sampling rates of 1,000 Hz. Impedances were kept under 5 k Ω . All electrodes were physically referenced to an electrode placed on the right earlobe and re-referenced offline to the average of both earlobe electrodes. Offline, raw data were low-pass filtered with a 40-Hz filter (finite impulse response filter, transition 40–42 Hz, stopband attenuation 60 dB). For ERP analyses, an additional bandpass filter (0.5–30 Hz) was applied on the continuous raw signal. Independent component analysis (ICA; Jung et al. 2000) was performed on the continuous EEG signal while components that were clearly related to blinks and ocular artifacts were removed (on average, 3.4 ICA components; range 2–5). EEG signal was then downsampled to 500 Hz and epoched in wide windows of 3-s length, from –1.5 to +1.5 s to avoid edge artifacts induced by the following wavelet convolution. Epochs were time-locked to the onset of the avatar's arm-path deviation, (i.e., 700 ms from the beginning of the movement, as in Spinelli et al. 2018). All epochs were baseline corrected to the 200 ms preceding the avatar's arm-path deviation (i.e., when the limb movements were identical in correct and incorrect conditions; Pavone et al. 2016, Spinelli et al. 2018). The offset of the avatar's movement occurred 300 ms after the avatar's limb deviation began. Each epoch was then visually inspected for artifacts to manually remove residual eye blinks or epochs exceeding –100/+100- μ V amplitude. A total of 1,524 erroneous trials and 665 correct trials were analyzed for both ERPs and time-frequency analyses (~96% of total collected trials). Because the correct and incorrect actions had different occurrence rates (70% vs 30%), we selected the trials from the incorrect condition to keep the number of trials equal in the two conditions and avoid spurious effects due to the different signal-to-noise ratios (Cohen 2014; Luck 2005). Therefore, for each participant, trials from the incorrect condition were selected with a built-in Brainstorm function that selects a subset of trials.² The main findings, with the total amount of incorrect trials, are reported in RESULTS, *EEG Analyses on All the Incorrect Trials*. Bad channels were replaced using the spherical splines method only when necessary (4 channels were interpolated in only 1 subject; Perrin et

al. 1989). Analyses were performed using the Brainstorm toolbox (free open source for MEG/EEG analysis, <https://neuroimage.usc.edu/brainstorm/>; Tadel et al. 2011) and customized MATLAB routines (Cohen 2014).

Analysis in the Time Domain: Action Observation-Related ERPs

In line with the literature, oERN and oPe/P300 were respectively analyzed on FCz and Pz electrodes, where they reached their maximum amplitude. The oERN was analyzed in the 100-ms time window following the end of the avatar's action (300–400 ms) at FCz electrode. The oPe/P300 were measured in a preselected time window between 400 and 800 ms at the parietal sites (Pz), in line with previous results (Pavone et al. 2016). All ERPs analyses were based on mean amplitude (Luck 2005). Widely recognized in error literature, the ERN can be hidden from the massive contribution of error positivity components that propagate from parietal to frontal areas and that mask some of the frontal components (Luck 2005). For visualization purposes, we minimized overlap between different components (Fig. 2A) by computing the difference waves in which the average number of correct trials is subtracted from the average number of erroneous trials (Fischer et al. 2017; Koban et al. 2010; Maier and Steinhauser 2016).

Analysis in the Time-Frequency Domain

For the time-frequency analysis, we used a complex Morlet transformation to compute time-frequency decomposition. A mother wavelet with central frequency of 1 Hz and 3 s of time resolution (full width half maximum, FWHM) was designed as in Brainstorm software (Tadel et al. 2011). The other wavelets were computed from this mother wavelet and ranged from 1 to 30 Hz, with 0.5-Hz linear frequency steps. To normalize each signal and frequency bin separately with respect to a baseline, we computed the relative power change (in %) over the time-frequency decomposition as

$$F = \frac{S(t, f) - S_{\text{base}}(t, f)}{S_{\text{base}}(t, f)} \times 100,$$

where $S(t, f)$ is the signal spectrum at a certain given interval of time (t) and frequency (f), and $S_{\text{base}}(t, f)$ represents the signal power of the reference signal used as baseline. To avoid edge effects, the power values from –250 to –50 ms, a window in which the avatar's movement was identical in erroneous and correct conditions, was used as the baseline interval. Positive and negative values index a decrease or an increase in synchrony of the recorded neuronal population (Pfurtscheller and Lopes da Silva 1999) with respect to a given reference interval, where equal neural activity is expected between conditions. In our case, a relative power increase/decrease represents a modulation of power compared with the mean power activity during the baseline.

As in Pavone et al. (2016), the main analyses were computed on FCz electrode, focusing on theta (4–8 Hz), alpha (8–12 Hz), and beta (13–30 Hz) bands, and in the preselected time interval from 300 to 700 ms (i.e., in time windows of 400 ms from the end of the avatar's action). On theta frequency, we also performed the analyses on POz electrode to rule out the possibility of a more general, rather than a mainly frontal, effect (Pavone et al. 2016). Further exploratory analyses were also performed. To check whether the participants consciously perceived the error before the end of the action, we analyzed theta activity in the time range of action divergence before the outcome appeared (0–300 ms). It is widely held that evoked oscillations reflect a phase-locked activity to the stimulus in the time-frequency activity. To investigate whether the reported theta effect is a different representation of the oERN in the time domain, we performed an additional analysis in which we removed the evoked

¹ The EEG was recorded from the following channels: Fp1, Fpz, Fp2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, AF7, POz, AF8, PO4, PO8, O1, Oz, O2, FT7, and FT8.

² In Brainstorm, this is accomplished with the process "File Select Subset-Uniformly distributed." This selection is based on the following MATLAB command: [round (linspace (1, Number_of_erroneous_trials, n_30_selected_trials))].

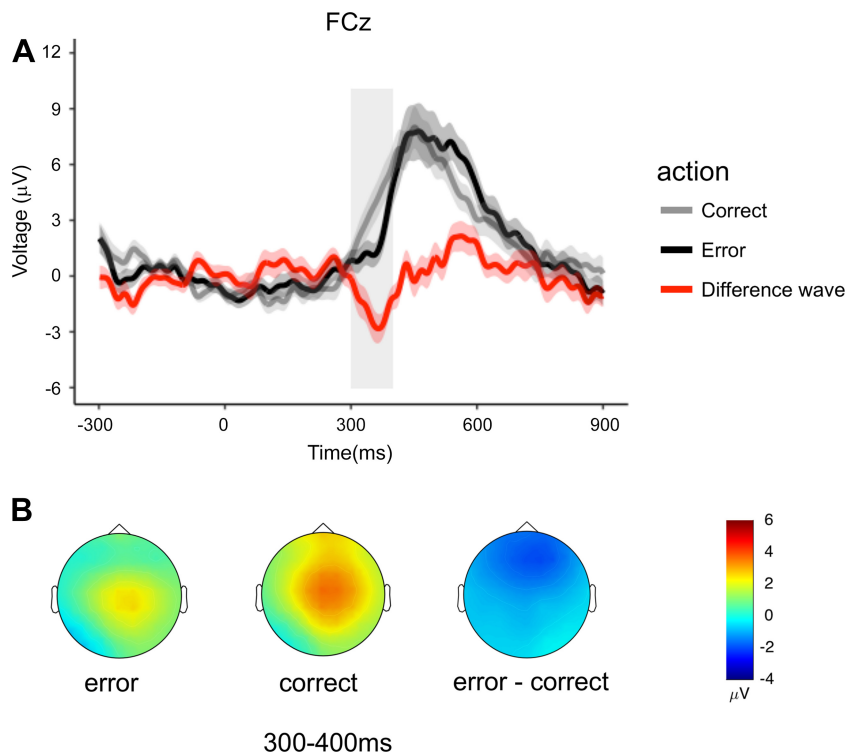


Fig. 2. Electrophysiological results in the time domain for each condition (70% erroneous actions, 30% correct actions). *A*: grand average waveforms of observed error-related negativity (oERN) at FCz electrode, over an interval of interest (300–400 ms) chosen a priori. The onset of the avatar's limb-path deviation is at 0 ms; the end of the avatar's action occurs at 300 ms. Shading denotes SE. The gray rectangle highlights the time window considered for statistical analysis. For representation purposes, we computed the difference wave on FCz, showing the negative amplitude of the oERN. *B*: topographical voltage distribution for erroneous, correct, and erroneous minus correct action condition.

response from each trial before computing the time-frequency decomposition for both experimental conditions.

RESULTS

Time Domain Analysis

oERN. Analyses on oERN revealed a main effect of condition [$F_{(1,22)} = 6.77$; $P = 0.016$, $\eta_p^2 = 0.24$], with erroneous actions showing less positive values than correct actions [mean value in erroneous condition ($M_{\text{ERR}} = 1.76 \mu\text{V}$); mean value in correct condition ($M_{\text{CORR}} = 3.54 \mu\text{V}$; Fig. 2A)]. The topographical distribution shows the typical frontocentral negativity (Fig. 2B).

oPe. Analyses on oPe revealed that the main effect of correctness between the two conditions was not significant [$F_{(1,22)} = 0.25$; $P = 0.62$, $\eta_p^2 = 0.01$; $M_{\text{ERR}} = 5.48 \mu\text{V}$; $M_{\text{CORR}} = 5.22 \mu\text{V}$; Fig. 3A]. Figure 3B shows the typical topographical distribution of oPe over centroparietal recording sites for both correct and erroneous actions.

Time-Frequency Results

Theta (4–8 Hz). ANOVA on the electrode and time interval of interest showed a significant effect of condition [$F_{(22,1)} = 18.35$; $P < 0.005$, $\eta_p^2 = 0.45$] with higher theta power activity for observation of erroneous actions compared with correct actions ($M_{\text{ERR}} = 7.18$; $M_{\text{CORR}} = -8.11$; Figs. 4 and 5). A middle-frontal cluster (FCz, FC1, FC2, Fz, F1, F2) revealed a wide frontal distribution [$F_{(22,1)} = 17.48$; $P < 0.05$, $\eta_p^2 = 0.44$], confirming the greater theta activity in the erroneous rather than correct actions ($M_{\text{ERR}} = 8.33$; $M_{\text{CORR}} = -6.44$). The same ANOVA on POz showed no significant difference concerning the accuracy of the grasp [$F_{(22,1)} = 3.34$; $P = 0.08$, $\eta_p^2 = 0.13$]. The time interval between the zero onset and the end of the avatar's movement (0–300 ms) showed no

significant difference [$F_{(22,1)} = 1.98$; $P = 0.17$, $\eta_p^2 = 0.08$]. With the removed evoked activity, the analysis of the theta activity showed a significant effect of condition [$F_{(22,1)} = 17.15$; $P < 0.005$, $\eta_p^2 = 0.44$]: higher theta power activity was found for observation of erroneous actions compared with correct actions.

Alpha (8–12 Hz). ANOVA on FCz in the time interval 300–700 ms showed a main significant effect of condition [$F_{(22,1)} = 11.08$; $P < 0.005$, $\eta_p^2 = 0.34$]. This effect was associated with increased alpha power for erroneous actions and decreased alpha power for correct actions ($M_{\text{ERR}} = 5.36$; $M_{\text{CORR}} = -12.92$) (Fig. 4). Analyses on POz revealed a consistent alpha suppression [$F_{(22,1)} = 10.09$; $P < 0.005$, $\eta_p^2 = 0.31$] in the posterior electrode during the correct rather than the erroneous actions ($M_{\text{ERR}} = -3.48$; $M_{\text{CORR}} = -23.70$; Fig. 5).

Beta (12–30 Hz). No significant main effects or interactions were found for this band [$F_{(22,1)} = 0.47$; $P = 0.50$, $\eta_p^2 = 0.02$].

Embodiment Ratings and Relation with EEG Signals

Preliminary application of the Shapiro-Wilk test showed that embodiment ratings were not normally distributed, and therefore a nonparametric analysis, including the Friedman test, for within-group comparison was used. To explore the link between sense of embodiment and electrocortical indexes of error processing, Spearman correlations between embodiment ratings and error signatures (theta and oERN) were conducted across subjects.

A significant difference in the avatar's grasp accuracy (correct vs. erroneous) in terms of sense of ownership [$\chi^2(1) = 21$, $P < 0.05$] and agency [$\chi^2(1) = 21$, $P < 0.05$] was found (Fig. 6). As expected, there was a greater sense of embodiment in the correct actions (ownership: 0.59 ± 0.20 ; agency: 0.48 ± 0.21)

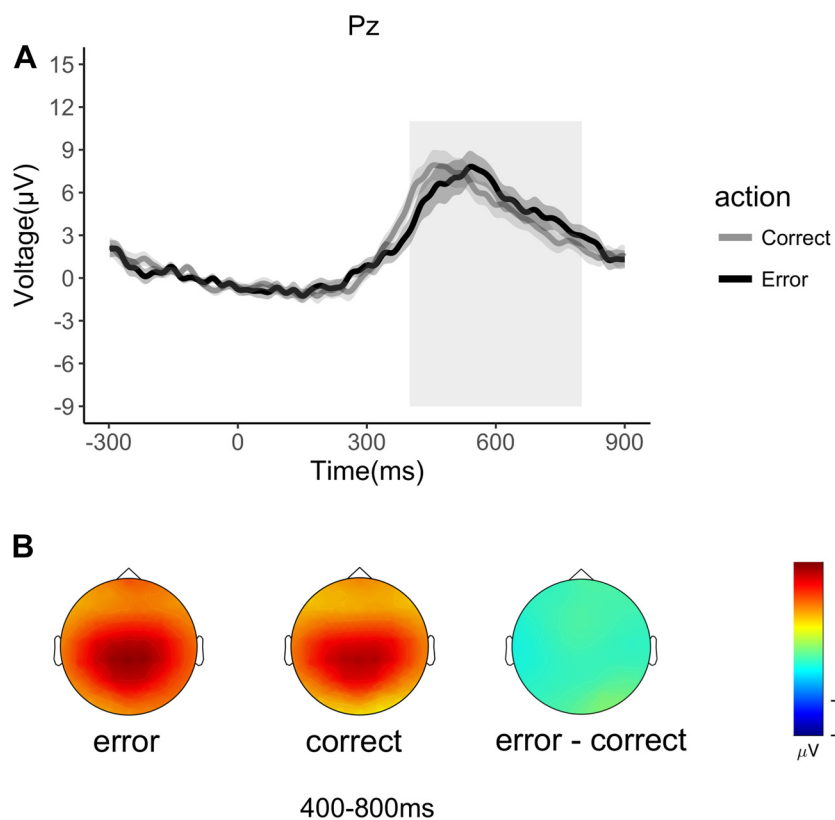


Fig. 3. Electrophysiological results in the time domain for each condition (70% erroneous actions, 30% correct actions). *A*: grand average waveforms of observed error positivity (oPe) at Pz electrode on an interval of interest (400–800 ms) chosen a priori. The onset of the avatar's limb-path deviation is at 0 ms; the end of the avatar's action occurs at 300 ms. Shading denotes SE. The gray rectangle highlights the time window considered for statistical analysis. *B*: topographical voltage distribution for erroneous, correct, and erroneous minus action condition.

compared with erroneous actions (ownership: 0.52 ± 0.20 ; agency: 0.41 ± 0.20). The correlation analysis between theta power (range 300–700 ms on FCz) and embodiment ratings revealed no significant association. Further analyses showed a negative correlation between the oERN and the sense of embodiment. In particular, the negative correlation between the oERN and the sense of embodiment was accounted for by the sense of agency ($r = -0.50$, $P = 0.02$); i.e., greater negative values of the oERN were associated with a stronger sense of agency in the erroneous actions. The sense of ownership showed a trend ($r = -0.42$, $P = 0.06$) in the same direction.

EEG Analyses on All the Incorrect Trials

Analyses on the total amount of erroneous trials confirmed the results obtained with the subselection of trials. To give a holistic overview, we report main results on the time interval of interest (300–700 ms). Analyses on the theta range on FCz revealed a significant difference between the two conditions [$F(22,1) = 11.41$; $P < 0.005$, $\eta_p^2 = 0.34$], with greater theta power activity in the erroneous actions compared with correct ones ($M_{ERR} = 5.68$; $M_{CORR} = -8.11$). Similarly, analyses on the alpha range on FCz revealed a significant difference [$F(22,1) = 8.31$; $P < 0.008$, $\eta_p^2 = 0.27$], with greater alpha power activity in the erroneous actions compared with correct ones [$M_{ERR} = -0.47$; $M_{CORR} = -12.93$]; a significant difference for alpha range between conditions was also found on POz [$F(22,1) = 11.34$; $P < 0.005$, $\eta_p^2 = 0.34$]. As in the main analysis, no significant difference was found in the beta range on FCz [$F(22,1) = 0.037$; $P = 0.84$, $\eta_p^2 = 0$]. Analyses for the time interval during trajectory divergence (0–300 ms) are also reported. In terms of theta on FCz, no significant difference was found [$F(22,1) = 1.60$; $P = 0.21$, $\eta_p^2 = 0.07$]. In the time

domain, analyses on FCz for the oERN confirm the significant difference between conditions [$F(22,1) = 8.16$; $P = 0.009$, $\eta_p^2 = 0.27$]. Analyses on Pz for the late positivity confirm no significant difference between conditions [$F(22,1) = 0.02$; $P = 0.90$, $\eta_p^2 = 0$].

DISCUSSION

To investigate whether the activation of the performance-monitoring system is triggered by the goal violation inherently linked to erroneous events or by the surprise/novelty associated to its frequency of occurrence, we designed a study in which participants observed erroneous as well as correct actions performed by a virtual agent. The percentage of erroneous (70%) vs. correct actions (30%) was opposite to what is typically used in studies with similar paradigms (Pavone et al. 2016; Spinelli et al. 2018). This manipulation allowed us to test whether the electrocortical activity associated with the observation of infrequent erroneous actions was also present when the observation of erroneous actions occurred more frequently than correct ones. We found that activity in the performance monitoring system (as indexed by oERN and theta power; Figs. 2 and 5) was specific to observed errors despite the fact that they were the most frequent event in the series. Interestingly, posterior alpha activity was instead sensitive to the frequency of occurrence of a stimulus.

Event-Related Responses to Observed Action Error

Although ERN and Pe are typically associated to performed errors (Ullsperger et al. 2014b), markers of observed errors (called oERN and oPE) have been reported previously (Koban and Pourtois 2014; van Schie et al. 2004). These studies reveal

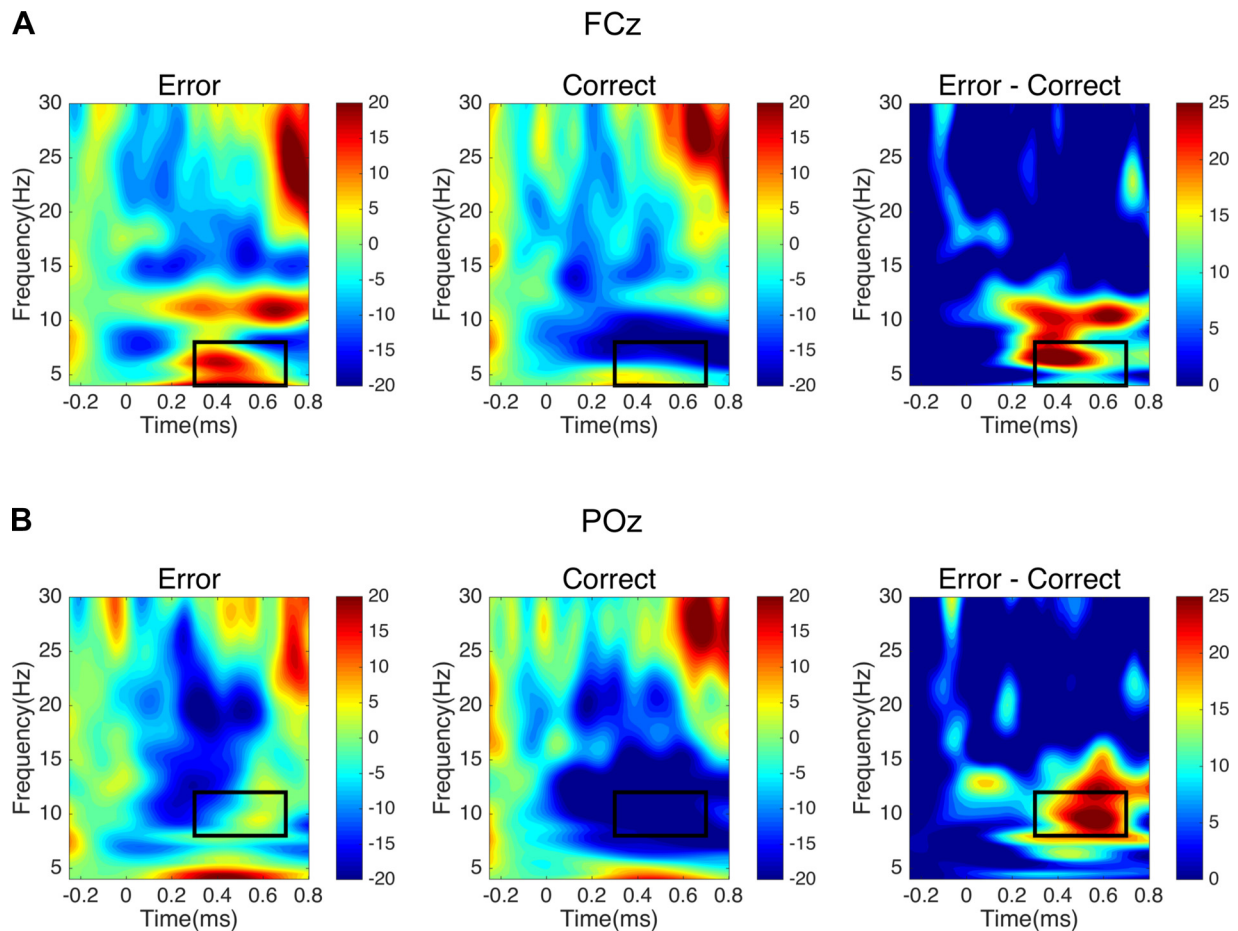


Fig. 4. Time-frequency representation of relative power change (in %) with respect to the baseline for erroneous, correct, and difference (error minus correct) conditions. The onset of the avatar's limb-path deviation is at 0 ms; the end of the avatar's action occurs at 300 ms. Black rectangles indicate the a priori chosen window of interest between 300 and 700 ms. *A*: erroneous, correct, and difference plots at FCz electrode in the selected interval (300–700 ms) for the theta band (4–8 Hz). *B*: erroneous, correct, and difference plots at POz electrode in the selected interval (300–700 ms) for the alpha band (8–12 Hz). Black rectangles indicate the values that have been submitted to statistical analyses.

that our performance-monitoring system is called into play when observing the actions of others.

A novel result of our investigation was that the oERN is not only elicited with the observation of an occasional slip in the action of an avatar (Pavone et al. 2016; Spinelli et al. 2018), but also when an erroneous grasp is the most frequent event in a series (Maier and Steinhauser 2016). Furthermore, we found a negative correlation between oERN and the feeling of agency, i.e., a greater feeling to control the virtual arm was associated with greater oERN amplitude in response to observed motor errors. These results partially mirror previous studies that found a higher feeling of embodiment associated with greater cortical response to errors (Padrao et al. 2016; Pavone et al. 2016; Spinelli et al. 2018). That being said, the relation between the sense of embodiment and brain activity is still unclear and necessitates further investigation.

Positive parietal deflections were found for both erroneous and correct actions. This result may seem somewhat counterintuitive but merits further discussion. Positive-going error-related parietal components have been reported in previous error-commission studies (Koban et al. 2010; Overbeek et al. 2005; Ridderinkhof et al. 2009). Interestingly, we found an oPe value similar to the one reported in action observation studies in which erroneous trials were

less frequent than correct trials (Pavone et al. 2016). In our study, the positivity found in the infrequent correct trials may represent a P300, which has been traditionally associated with task-relevant, novel, and rare events (Overbeek et al. 2005). The oPe has been associated with P300 and errors (Koban and Pourtois 2014; Nieuwenhuis et al. 2001; Shalgi et al. 2009). Both oPe and P300 have been further classified into an earlier frontocentral component (early oPe and P3a, respectively), associated with the orientation of attention, and a later centroparietal component (late oPe and P3b, respectively), associated with the conscious recognition of the event (Debener et al. 2005; Overbeek et al. 2005; Ullsperger et al. 2014a).

That both erroneous and correct grasping actions elicit a parietal positive-going deflection (Fig. 3) suggests that both events might be perceived as salient and meaningful (Wessel et al. 2014; Wu and Zhou 2009), on the one hand, because it represents a violation of the default expectation of goal achievement, and on the other hand, because of its rarity in the sequence. This is in line with the context-updating hypothesis (Donchin and Coles 1988), according to which positive parietal deflection reflects the conscious and active updating of the mental model on contextual information. Similarly, this aligns with the notion that the late positivity

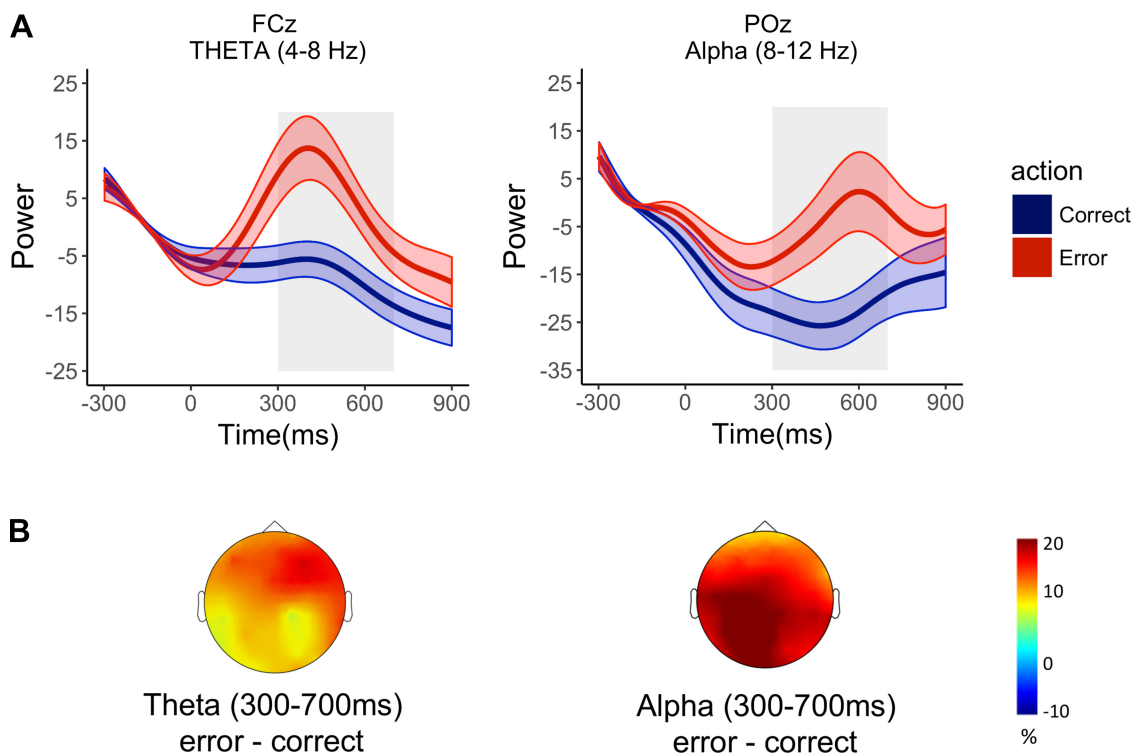


Fig. 5. *A*: time series representation of theta power (4–8 Hz) in FCz electrode (*left*) and of alpha power (8–12 Hz) in POz electrode (*right*) plotted for the correct and erroneous action observation conditions. The onset of the avatar’s limb-path deviation is at 0 ms; the end of the avatar’s action occurs at 300 ms. Shading denotes SE. Gray rectangles highlight the time window considered for statistical analysis. *B*: topographical distribution of the event-related synchronization and desynchronization from baseline of theta (*left*) and alpha (*right*) averaged in the time window of interest (300–700 ms).

reflects the accumulated subjective evidence collected from internal and external information (Wessel et al. 2011; Fischer and Ullsperger 2013; Ullsperger et al. 2014a). The fact that oPe was not significantly different from correct actions may also suggest that adaptation after an error, as well as post-error strategies, were not needed in our task where participants were unable to actively engage in the action (van Gaal et al. 2010). Future studies are needed to better understand the functional role of positive parietal deflections.

Cortical Oscillations of Observed Action Error

Theta and alpha modulations are considered to be the oscillatory bands involved in action monitoring and error detection (Cavanagh et al. 2009; van Driel et al. 2012). Most studies have investigated cortical activity during action execution (Hajihosseini and Holroyd 2013; Mas-herrero and Marco-Pallarés 2014; Oliveira et al. 2007). Much less is known about the modulation of these frequency bands during action observation, as well as the impact of outcome



Fig. 6. Subjective reports of embodiment in correct and erroneous action observation conditions. Y-axes represent embodiment ratings along a 1–100 point visual analog scale (VAS). Participants answered two questions: one concerning sense of ownership (“To what extent did you feel the arm was yours?”; 0 = no ownership to 100 = maximal ownership) and one concerning sense of agency (“How much did you feel in control of the arm?” 0 = no control to 100 = maximal control). The order of the questions was randomized. Black diamonds in the violin plots represent the mean value; gray lines connect individual subject observations (i.e., gray points) between the two conditions. The scatterplot (rightmost panel) is a representation of the correlation between observed error-related negativity (oERN) and sense of agency.

expectancy and valence on the cortical response to observed errors.

Another novel finding of our study is that theta oscillations are not necessarily associated with rare and less expected events (Jessup et al. 2010; Oliveira et al. 2007), but rather with the violation of the intended goal and the significant value of an event. It is worth noting that previous studies on error monitoring show a theta response associated with errors that were always less frequent than correct actions (Janssen et al. 2016; Padrao et al. 2016; Pavone et al. 2016; Tzur and Berger 2007). Our data suggest that a simple motor plan (e.g., the grasp of an object on a table) is deeply encoded in our daily routine. Therefore, a violation of the plan might be a relevant and significant event that elicits a strong theta response (Figs. 4 and 5).

It is also worth noting that motivationally significant errors (e.g., great monetary loss) produce enhanced theta activity (Foti et al. 2015) and larger ERN amplitude (Hajcak et al. 2005; Maier and Steinhauser 2016) with respect to less motivationally significant errors (e.g., small monetary loss). Interestingly, this effect is found independently from the frequency of bad and good outcomes. In our case, the violation of the avatar's goal of grasping the glass, and not the money loss, can be considered the significant event that modulates the response of the performance monitoring system.

On a technical note, it has been argued that ERN and theta could reflect different ways of displaying the same result. Specifically, others have claimed that the theta response associated with errors could be the consequence of the mathematical transformation performed on the ERN during time-frequency analysis (Luu et al. 2004; Trujillo and Allen 2007). However, it is possible to partially exclude this explanation by removing the phase-locked activity, namely, the ERPs activity (including the ERN), from the signal before computing the time-frequency analysis (Moreau et al. 2017; Sauseng et al. 2007). We applied this procedure and found differences between error trials and correct trials, with increasing theta power in the first compared with the latter condition. This result rules out the possibility that ERN and theta are merely a different representation of the same process. Interestingly, theta power increase after the erroneous actions was greater than the effect elicited by the same actions in the time domain (note that differences concerning oERN were found, but with a smaller effect size). This might be explained by the different sensitivity of time and time-frequency analyses in detecting non-phase-locked activity. We believe that time-frequency analyses, which could capture both phase and non-phase-locked activity, are particularly indicated to analyze the reactivity to the observation of continuous actions.

We found a parieto-occipital alpha power increase in the correct (rare) but not erroneous (frequent) actions. Although Pavone et al. (2016) found an opposite result of higher alpha desynchronization in the erroneous (rare) but not correct (frequent) actions, our result coalign with the idea that alpha desynchronization reflects the degree to which task-relevant events, as in our case natural grasping movements, recruit attentional resources (Klimesch 2012). A similar result was found in an experiment by Wang et al. (2015) during which participants observed correct responses made by others in a speed-response task where correct responses rarely occurred. Taken together, the data seem to confirm the role of alpha-

frequency band in the general orienting response to stimuli and reorientation of attention (Clayton et al. 2015; van Driel et al. 2012). The alpha synchronization we found on the frontal electrodes with observation of erroneous actions merits future discussion. Although we do not have a clear explanation for this result, we speculate that the alpha increase may be related to particular error types (Pavone et al. 2016; van Driel et al. 2012), to a transient disengagement from the task during the intertrial interval (Carp and Compton 2009), or to active internal processing of information (Benedek et al. 2014; Sauseng et al. 2005).

Overall, given the EEG results found in this study, we cannot rule out the possibility that similar modulations can be obtained with a traditional setup (i.e., observation of movies). Although only a direct 3D vs. 2D comparison may offer a straightforward response, several considerations merit further discussion. First, the virtual body was previously calibrated and adapted to the participants body size within our immersive virtual reality setup. This created the illusion of owning the virtual body. Thus our participants not only observed the virtual action from a first-person perspective, but they also observed a real-size moving body located in the very same spatial position of the participant. Our previous studies demonstrate that 1) virtual first-person perspective is sufficient to embody the avatar without external boosting (e.g., visuotactile stimulation, as in the case of virtual hand illusion; Tieri et al. 2015a), and 2) experiencing a higher sense of embodiment elicited greater theta power in response to errors (Pavone et al. 2016). Moreover, studies that directly compared brain activity in 2D vs. 3D scenarios found that the 3D scenario required a general allocation of greater resources for cognitive control compared with 2D presentations (Slobounov et al. 2015; Vecchiato et al. 2015). Finally, all the events in our experimental paradigm occurred in a 3D real-size peripersonal space, an environment that may produce an enriched source of affordance toward the object (Costantini et al. 2010, 2011; Pezzulo and Cisek 2016) and thus maximize the salience of action errors.

Conclusions

By combining EEG and immersive virtual reality, we have been able to demonstrate that increased ERN amplitude and theta oscillatory power are associated with first-person observation of an error in the action of a virtual agent even when the error occurrence is highly probable and thus less unexpected. Therefore, our data suggest that, given its relevance (Maier and Steinhauser 2016), an observed error (as a mismatch between the intended goal and the actual outcome), and not its frequency of occurrence, triggers the activity of the performance-monitoring system. Contrarily, we found that alpha power decrease was associated with the infrequency of a stimulus, independent of the outcome. Our results represent an important step toward understanding the involvement of middle-frontal and parietal regions during the observation of familiar erroneous and correct motor actions.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

R.P. and S.M.A. conceived and design the research; R.P., V.N., E.T., performed experiments; R.P. analyzed data; R.P., V.N., E.T., S.M.A. interpreted results of experiments; R.P. prepared figures; R.P. and S.M.A. drafted manuscript; R.P., V.N., E.T., S.M.A. edited and revised manuscript; R.P., V.N., E.T., S.M.A. approved final version of manuscript.

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