Title: Midline frontal and occipito-temporal activity during error monitoring in dyadic motor interactions.

Abbreviated title: Theta/Alpha responses to unexpected partner's actions

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Data Availability Statement: The present data and codes used for the analysis are available on GitHub (https://github.com/quentinmoreau/Cortex-2020). Please refer to the original article if substantial parts of the codes are used. Please share with the corresponding author any results and interpretations emerging from new analysis run on the current data. No part of the study procedures was pre-registered prior to the research being conducted.

Conflict of interest: The authors certify that they have no affiliation with or involvement in any organization or entity with any financial interest in the subject matter or materials discussed in this manuscript.

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Abstract

Discrepancies between sensory predictions and action outcome are at the base of error coding. However, these phenomena have mainly been studied focusing on individual performance. Here, we explored EEG responses to motor prediction errors during a human-avatar interaction and show that Theta/Alpha activity of the frontal error-monitoring system works in phase with activity of the occipito-temporal node of the action observation network. Our motor interaction paradigm required healthy individuals to synchronize their reach-to-grasp movements with those of a virtual partner in conditions that did (Interactive) or did not require (Cued) movement prediction and adaptation to the partner's actions. Crucially, in 30% of the trials the virtual partner suddenly and unpredictably changed its movement trajectory thereby violating the human participant's expectation. These changes elicited error-related neuromarkers (ERN/Pe - Theta/Alpha modulations) over fronto-central electrodes during the Interactive condition. Source localization and connectivity analyses showed that the frontal Theta/Alpha activity induced by violations of the expected interactive movements was in phase with occipito-temporal Theta/Alpha activity. These results expand current knowledge about the neural correlates of on-line interpersonal motor interactions linking the frontal error-monitoring system to visual, body motion-related, responses.

Keywords: Dyadic human-avatar interaction, Error, EEG, Theta, Alpha, action perception, Extrastriate Body Area, Lateral Occipito-temporal cortex, motor prediction.

Introduction

Interpersonal motor coordination requires dynamic and efficient encoding of others' actions and spatio-temporal synchronization between individuals (Sebanz et al., 2006; Moreau et al., 2016), thus involving several mechanisms ranging from action perception to goal prediction (Pezzulo, 2013; Panasiti et al., 2017) and motor adaptation (Era et al., 2018; 2019a). When interacting without having physical contact with a partner, coordination with the partner's on-going behaviour is supported by the integration and the prediction of visual and sensorimotor information about others' and one's own actions.

However, at times, one's visuo-motor predictions happen to be wrong. The success of adaptive social behaviours relies on the ability to detect prediction errors regarding the movements of the partner and readjust one's own movement accordingly.

At the neural level, individuals' ability to predict the fate of observed actions (Aglioti et al., 2008; Abreu et al., 2017) is thought to rely on the activity of the Action Observation Network (AON, Rizzolatti & Craighero, 2004; van Overwalle & Baetens, 2009; Molenberghs et al., 2012; Hardwick et al., 2018) comprising occipito-temporal regions responsible for visual processing of body images (Extrastriate Body Area, EBA; lateral occipito-temporal cortex, LOTC) and biological motion (Superior Temporal Sulcus, STS, Puce & Perrett, 2003; Giese & Poggio, 2003) as well as parietal (anterior Intra Parietal Sulcus, aIPS) and premotor (ventral and dorsal PreMotor, vPM, dPM) areas where the transformation of visual information into motor coordinates is thought to be computed (Keysers & Gazzola, 2014).

The current study focuses on the neural underpinnings associated to the detection of, and adaptation to, unpredicted movement's changes of a partner (i.e. prediction errors). Neural correlates of error performance have been previously investigated thoroughly using experimental paradigms such as the Flanker (Hermann et al., 2004) and Simon task (Masaki et al., 2007; Cohen, 2011). EEG studies established that detecting and evaluating our own errors generate two Event Related Potentials (ERPs) - the Error-Related Negativity (ERN; Falkenstein et al., 1991; Gehring et al., 1993) and the Positivity error (Pe; Falkenstein et al., 2000) - recorded over fronto-central and parietal electrodes (i.e. FCz and Pz), respectively. The ERN and the Pe are thought to reflect distinctive processes of the monitoring system. It has been proposed that the ERN, which originates from the anterior cingulate cortex (ACC; Carter et al., 1998; van Veen et al., 2001), underlies the detection of "high-level errors" (i.e. failure to meet a goal; Krigolson & Holroyd, 2006), conflict monitoring (Botvinick et al., 2001; Yeung et al., 2004) or action outcome predictions (Quilodran et al., 2008; Alexander & Brown, 2011) while the later and more posterior (centro-parietal) Pe is thought to reflect the detection of "low-level motor errors" (i.e. differences between real and anticipated motor commands, Krigolson & Holroyd, 2007) and is sensitive to error awareness (Endrass et al., 2005; Overbeek et al., 2005). In the time-frequency domain, EEG studies described Theta (4-7Hz) and Alpha (8-13Hz) synchronizations over fronto-central electrodes as markers of the activity of the performance monitoring system (Luu et al., 2004; Trujillo & Allen, 2007; Cavanagh et al., 2009; Cohen, 2011). In line with this, a recent study showed that inducing Theta over FCz by means of transcranial alternating current stimulation (tACS) resulted in modulation in behavioural adjustment after error execution (Fusco et al., 2018). Theta and Alpha synchronizations have also been detected during the observation of motor errors performed by an embodied avatar seen from a first-person perspective (Pavone et al., 2016; Spinelli et al., 2017; Pezzetta et al., 2018).

Crucially, observing someone else performing an error induces similar time and time-frequency EEG responses to those generated when performing an error in first person (van Schie et al., 2004; Miltner et al., 2004; Koelewijn et al., 2008; de Brujin et al., 2007). Thus, the frontal error monitoring system (including the ACC) is considered a generic error processing system which may code in similar ways errors performed by an individual and those observed in another. However, other regions may contribute to error encoding such as inferior parietal areas and insular cortices (Malfait et al., 2010; Orr & Hester, 2012; Shane et al., 2008), as well as occipito-temporal nodes of the AON (Abreu et al., 2012).

Studying error perception during an interactive scenario is central to the broader understanding of the neural correlates of motor prediction, motor control and accurate behavioural responses to unexpected movements during a joint performance. Such studies represent a challenge at a technical level (Schilbach et al., 2013; Gallotti & Frith, 2013; Moreau & Candidi, 2016, Dumas et al., 2019) and raise relevant theoretical considerations, as the definition of the error (and the related neural responses to it) needs to be framed according to the integration of one's own and other's actions and to the outcome of the interaction (i.e. success or failure of the shared goal). The latter notion bears on the problem of not knowing whether, and how, the error monitoring system dedicates resources to monitor the action that one needs to perform, the action of the partner and the outcome of the interaction. Furthermore, it is not known whether, and how, frontal error-related activity interacts with activity in the sensory systems processing relevant information for the interaction.

To deal with this issue, we studied modulations of frontal error-related neuromarkers in time and time-frequency domains during a visuo-motor interactive task in which a Virtual Avatar suddenly changes its movement trajectory, thus creating a mismatch between what the partner predicts and what he actually sees. Importantly, we also tested whether the lateral occipito-temporal cortex might respond to interactive errors based on the notion that this region may forward visual information to fronto-parietal areas and also may receive top-down information about forthcoming perceptual predictions from frontal nodes of the AON (Keysers & Gazzola, 2015; Zanon et al., 2018). According to predictive accounts of perception (Kilner et al., 2007) top-down motor predictions would filter sensory inflow and generate prediction errors in lower level, visual areas (e.g. lateral occipito-temporal cortex) thus implying that frontal error systems would work in phase with occipito-temporal visual areas.

More specifically, we explored in healthy participants what are the electrocortical signatures of adaptive behaviour to a correction during a visuo-motor interpersonal interaction (see Figure 1; Sacheli et al., 2015a; 2015b; Candidi et al., 2017). Participants were asked to reach and grasp a bottle in front of them (with an upper and a lower grasping site) and to synchronize their grasping timing with a virtual partner in two separate conditions, namely: 1) a Cued condition, requiring participants to adapt only the timing of their movements in order to synchronize their touch time with the virtual partner (participants knew in advance where they have to grasp the object) and, 2) an Interactive condition, requiring participants to adapt in time and space as they needed to coordinate their action according to the avatar's movement and the instruction received, i.e. imitate or complement the movement of the partner. Crucially, in 30% of the trials of both conditions, the Virtual Avatar performed an unexpected trajectory change along the reaching phase and grasped the other site of the bottle-shape object. In the Interactive condition, this change in the avatar's movement generated in the human participants the need to adjust their trajectory in reaction to events that diverged from what they had expected (i.e. prediction error). Furthermore, by asking participants to perform imitative or complementary (with respect to those of the virtual partner) reach-to-grasp actions, we explored whether a full match between observed and executed movements would induce any difference in the neural activity associated to the interaction. To this aim, in addition to analysing the classic fronto-central EEG markers, we performed whole-brain analysis to investigate if prediction errors in an interactive motor task would modulate the activity of regions outside the error monitoring system and supporting the visual processing of observed actions.

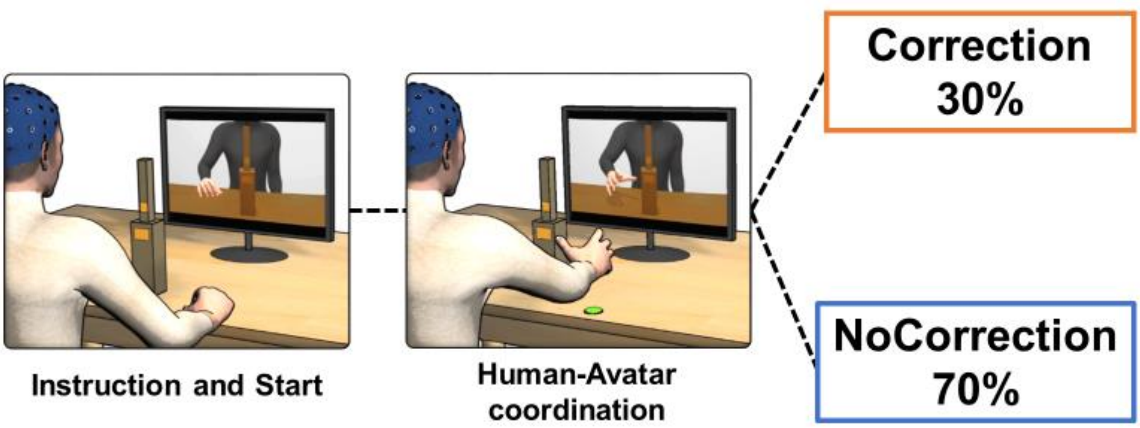

Figure 1 | *Schematic representation of the experimental set-up and percentage of Correction/NoCorrection of the virtual partner's reach to grasp trajectory.*

Material and Methods

Transparency statement

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study

Participants

22 individuals (13 females, mean age: 26.35 [19-31]; S.D. = 3.54) took part in the experiment. The sample size selection was based on previous studies targeting observed error-related EEG activity (i.e. Pavone et al., 2016; n=20; Pezzetta et al., 2018; n=25; Spinelli et al., 2018; n=22) and on a power analysis, performed with the software More Power (Campbell and Thompson, 2012). More specifically, we indicated as expected effects sizes the partial eta squared value obtained by Pezzetta and colleagues (2018) (.45). The output indicates that a 2x2 within subject design, a power of .95 and a partial eta squared of .45 (as in Pezzetta et al., 2018), requires a sample size of 18 participants. All participants were right-handed with normal or corrected-to-normal vision. Participants were naive as to the aim of the experiment at the outset and were informed of the purpose of the study only after all the experimental procedures were completed. All participants provided written informed consent and were reimbursed 7 €/h. The experimental procedures were approved by the Ethics Committee of the IRCCS Santa Lucia Foundation (Rome, Italy) and the study was performed in accordance with the 2013 Declaration of Helsinki. One participant was detected as an outlier (see below) and therefore removed from all EEG analysis.

Experimental stimuli and set-up

Participants were comfortably seated in front of a rectangular table of 120 × 75 cm and viewed a 1.024 × 768 resolution LCD monitor placed on the centre of the table at ~60 cm from their eyes.

Participants were asked to reach and grasp a bottle-shaped object (37 cm total height) constituted by two superimposed rectangles of different thickness (small, 2.7 cm; large, 6.5 cm) placed next to the centre of the working surface. To record participants' grasping time of the bottle, two pairs of touch-sensitive markers (one pair per rectangle) were placed at 15 cm and 22 cm along the vertical height of the object (see Figure 1). Before each trial, participants positioned their right hand on a starting button placed at 34 cm from the bottle-shaped object with their index finger and thumb. The tasks (see below) asked participants to grasp the bottle in synchrony with the avatar appearing on the screen in front of them. Note that the avatar's index-thumb contact times were measured trial-by-trial by a photodiode placed on the screen that sent a signal recorded by E-Prime 2 professional (version 2.0.10.242, Psychology Software Tools Inc., Pittsburgh, PA) by means of a TriggerStation (BrainTrends ltd., Italy). The photodiode was triggered by a white dot displayed on the screen (not visible to the participants) during the clip frame corresponding to the instant when the avatar grasped its virtual object.

Creation of the virtual interaction partner.

The kinematic features of the virtual partner were based on the movements of human participants performing different grasping movements during a human-human joint-grasping task, identical to the procedures described in Candidi et al. (2017) (see Tieri et al., 2015; Fusaro et al., 2019 for technical details of the Motion Capture recording). The final processed trajectories were realized and applied to a Caucasian male character by using commercial software MotionBuilder 2017 and 3DS Max 2017 (Autodesk). Since we wanted the participants to ignore facial expressions of the virtual partner, the final video stimuli contained only the upper body down from the shoulders, without the neck and head. The complete sample of clips comprised 10 different grasping movements. Half of the movements ended when the hand grasped the bottom part (that is, required power grips Figure 2, Panel A), whereas the other half of the movements ended when the hand grasped the top part of the bottle-shaped object (that is, required precision grips, Figure 2, Panel B). In 30% of the trials the grasps included an online correction, in which the avatar performed a movement correction by switching from a precision to a power grip (or vice versa) during the reaching phase. The correction-videos were created in 3DS Max by merging the initial key frames of a clip (e.g. a power grasp clip) with the last key frames of a different clip (e.g. precision grasp clip) (Figure 2, Panel C-D).

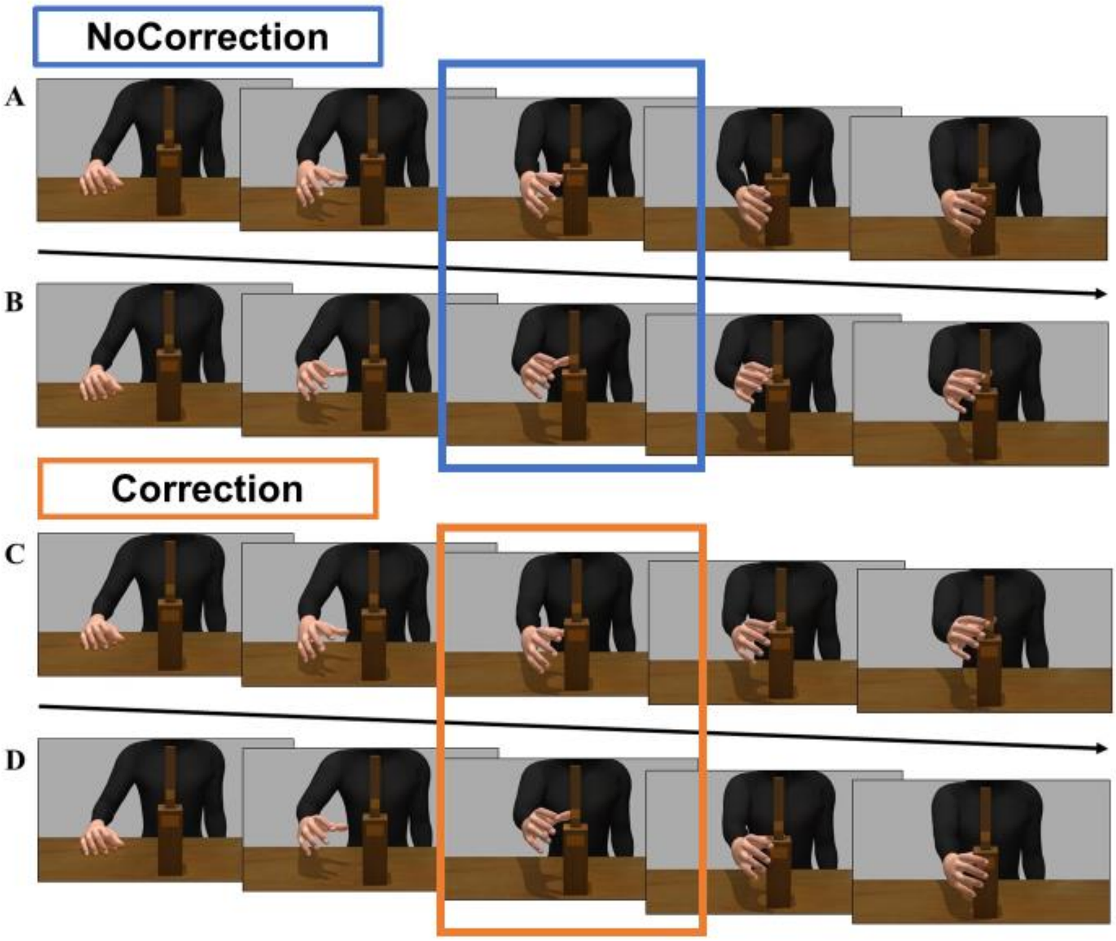

Figure 2 | *Examples of the sequence of frames for each type of virtual partner's movements: A) Power Grasp; B) Precision Grasp; C) Correction Power to Precision and D) Correction Precision to Power Grasp; The middle frame of each sequence represents the 0 time point for EEG marker in which the Avatar corrects (orange) or does not correct (blue) its behaviour.*

Experimental Task

We used an ecological and controlled human-avatar interactive task (Sacheli et al., 2015a; 2015b;

2018; Candidi et al., 2017; Era et al., 2018a; Gandolfo et al., 2019; Era et al., 2018b), which has been shown to recruit the same behavioural processes called into play during human-human interaction, namely motor adjustment and automatic imitation (Sacheli et al., 2012; 2013; Candidi et al., 2015; Curioni et al., 2017; Era et al., 2018b). Importantly, in the present task, one's own action goal cannot be achieved without considering the virtual partner's online movements and adapting to them. Participants were required to reach and grasp the bottle-shaped object placed in front of them with their right hand, as synchronously as possible with the action of the avatar (shown on the screen in front of them) in respect to its bottle-shaped object. Given the dimensions of the bottle-shaped object, grasping the lower part implied a whole-hand grasping (a power grip), whereas grasping the upper part implied a thumb-index finger precision grip (Movement Type Factor).

Participants performed the task in two different conditions (Condition Factor): (1) the "Cued Condition", where subjects received either a high pitch sound (indicating that they had to grasp the bottle in the upper part) or a low pitch sound (indicating that they had to grasp the bottle in the lower part), and (2) the "Interactive Condition", where subjects received either a sound indicating that they had to perform an imitative action (i.e. participant and virtual partner both grasping the upper or lower part of their bottle) or a sound indicating they had to perform a complementary action (i.e. if the virtual partner was grasping the lower part of its bottle, participant had to grasp the upper part of his/her bottle, and vice versa). The timeline of a trial was as follows: participants received the auditory instruction about what kind of action they should perform, followed by the presentation of a fixation cross (300ms), preceding the appearance of the Avatar on the screen; the Avatar started its movement between 200 and 600ms after a "go signal" was given and performed its action (trial duration ~2000 ms). Subjects' movement time (i.e. from the start of the movement to the reaching of the object) was on average 1248.13 ms SD = 238.3 (see Supplementary Materials for more details). The inter-trial interval depended on the time participants took to go back from the bottle to the starting position. The experimenter manually triggered the next trial as soon as participants went back to the starting position.

In the Cued Condition, participants had to predict and adapt to the avatar's movement in time (i.e. when the virtual partner is going to grasp the bottle) but not in space, since they knew in advance where they had to grasp the bottle-shaped object. In contrast, in the Interactive Condition, participants had to predict and adapt in time *and* space (i.e. when and where the virtual partner is going to grasp the bottle). It was emphasized that in all the conditions participants had to touch the bottle as synchronously as possible with the virtual partner.

The clips' frame during which the avatar started correcting its behaviour (e.g. by switching from a power to a precision grasp or vice versa, Correction Factor) was used as the 0-time-point for EEG markers. In the trials where the virtual partner did not correct its behaviour, the time 0 corresponds to the same frame where the switching would have happened in the change clip (see above, Figure 2). The average time for the Avatar to reach its bottle-shaped object after the Correction (or No-Correction frame, i.e. time 0) was on average 540 ms, SD = 0.066.

Participants performed four 100-trial blocks (2 blocks of the Cued Condition, 2 for the Interactive Condition, presented in a counterbalanced order between participants). In 30% of the trials, the virtual partner performed a correction. It is worth noting that in Correction-Cued trials, the Avatar's change of trajectory is not relevant to the participant's choice in grasping site and does not require a correction from the subject. The factor Correction/NoCorrection refers to the Avatar's behaviour, and only in Interactive-Correction trials did the participants have to change their motor behaviour based on the Avatar's correction.

Thus, each participant performed in 140 trials for Cued-NoCorrection, 140 trials for Interactive-NoCorrection, 60 trials for Cued-Correction and 60 trials for Interactive-Correction. The interaction type (Complementary/Imitative) and the movement type (Precision/Power) factors were randomized trial-by-trial and pooled together. While an unequal number of Correction (lower) and NoCorrection (higher) trials has been used in action-related error processing studies (Pavone et al., 2016), previous studies demonstrated that reversing the Correction/NoCorrection proportion of trials, or randomly selecting an equal number of trials for the two distributions does not change error-related EEG results

(Pezzetta et al., 2018). Based on this evidence, in the present study we did not randomly select an equal number of trials across conditions.

Stimuli presentation and randomization were controlled by E-Prime2 Professional software (Psychology Software Tools Inc.).

Behavioural data

We considered the Grasping Synchrony as the main behavioural measure, i.e. the absolute value of the time delay between subjects' index-thumb contact-times on their bottle and the avatar's bottle touch time (Sacheli et al., 2015a). This showed the success of human-avatar coordination. Analysis regarding other behavioural and kinematics measures are reported as Supplementary Materials.

EEG preprocessing

EEG signals were recorded and amplified using a Neuroscan SynAmps RT amplifiers system (Compumedics Limited, Melbourne, Australia). These signals were acquired from 60 tin scalp electrodes embedded in a fabric cap (Electro-Cap International, Eaton, OH), arranged according to the 10-10 system. 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. Horizontal electro-oculogram (HEOG) was recorded bipolarly from electrodes placed on the outer canthi of each eye and signals from the left earlobe were also recorded. All electrodes were physically referenced to an electrode placed on the right earlobe and were algebraically re-referenced off-line to the average of both earlobe electrodes. Impedance was kept below 5 KΩ for all electrodes for the whole duration of the experiment, amplifier hardware band-pass filter was 0.01 to 200 Hz and sampling rate was 1000 Hz. To remove the blinks and eyes saccades, EEG and horizontal electro-oculogram were processed in two separate steps. Data were then downsampled at 500 Hz before a blind source separation method was applied on continuous raw signal, using Independent Component Analysis (ICA) (Jung et al., 2000) implemented in the Matlab toolbox EEGLab_ (version 14_1_1_b running on Matlab 2010a) (Delorme & Makeig, 2004) to remove any components related to eye movements from the EEG. 59 components were generated and artifactual components (blinks and saccades) were removed based on the topography and the explained variance (components are ordered by the amount of variance they represent), data were then visually inspected after the removal of the components, to check if both blinks and saccades were no longer present (2.83 components per participants were rejected on average). The signal was then segmented into epochs of 2000 ms (-1000 ms to +1500 ms around the Avatar's Correction/NoCorrection frame) and visually inspected to control for residual eyes movements as well as muscular artifacts in Brain Vision Analyzer. Bad epochs were identified and removed from further analysis; the artifact rejection procedure led to 9.2% of the trials being rejected. The average number of trials per participants was 127.9 trials for Interactive-NoCorrection, 128.4 trials for Cued-NoCorrection, 56.5 trials for Cued-Correction and 55.5 trials for Interactive-Correction. For all EEG variables presented below, participants with a mean 2.5 SDs above or below the group mean were excluded from the analyses. According to this criterion, one participant was detected as an outlier for the Theta ERD/ERS and therefore removed from all EEG analyses, resulting in 21 kept participants for all analyses.

EEG Analysis

ERPs

Time domain analyses were performed by using the FieldTrip (version 2015-01-13) routines (Donders Institute, Nijmegen; Oostenveld et al., 2010) in Matlab2010a (The MathWorks, Inc.). The EEG time series were band-pass filtered (2 to 30 Hz) to reduce the contribution of slow potentials that masked some of the frontal components relevant to our study (Pavone et al., 2016). It is held that high-pass filters > 1 Hz may generate artefactual effects in ERPs (Tanner et al., 2015). However, we checked that grand average waveforms with and without filters maintain the same morphology

(Acunzo et al., 2012), and did not introduce distortions that may bias the estimated parameters (Widmann et al., 2015; see Supplementary Figure S4A and S4B for ERPs filtered with a 0.5 Hz high-pass filter; the figures show that even with a different type of filter with respect to what was used in Figure 4, the ERN and Pe are clearly detectable). Each epoch was baseline corrected from 200ms to 0ms before the Avatar's correction (or absence of correction). Two main components, already described in the Error-related ERP literature (i.e., ERN over FCz and Pe over Pz) were individuated. Visual inspection of the results showed the generation of an ERN component only for the Interactive-Correction and Cued-Correction trials (see Figure 4). It also appears that the ERN component peaked at different times for Interactive and Cued conditions (i.e 194 ms for Interactive-Correction and 228 ms for Cued-Correction). Therefore, we extracted the ERP mean amplitude over a time window of 100 ms around the ERNs respective latency-peaks (Spinelli et al., 2018). The Pe component was also identified for Interactive-Correction trials, peaking at 402 ms after Avatar's correction and peaking at 536 ms for Cued-Correction trials; therefore, we extracted the mean amplitude from a time window of 100ms around these two peaks. As no clear peaks has been detected for Interactive-NoCorrection and Cued-NoCorrection conditions, we extracted the mean amplitudes using the same latencies as the ones used for their respective Correction trials.

ERD/ERS – Induced Power

Time-frequency analyses were performed by using the Fieldtrip (version 2015-01-13) routines (Donders Institute, Nijmegen; Oostenveld et al., 2010) in Matlab2010a (The MathWorks, Inc.). The EEG time series were obtained by segmenting the signal into epochs of 2000 ms length and band-pass filtered (0.1 to 100 Hz). To remove the potential effects of ERPs in the time-frequency domain (including the source computation and connectivity measures), the mean evoked response was subtracted from each individual trial, therefore removing phase-locked activity, prior to the time-frequency computation (Sauseng et al., 2007). Each epoch was transformed in the frequency domain using Hanning-tapered window with a 50 ms time resolution (using the 'ft_freqanalysis' function with ‘mtmconvol’ method as implemented in FieldTrip). Estimated induced power results were displayed as event-related desynchronization/synchronization (ERD/ERS) with respect to a baseline between -500 and 0 ms (cfg.baselinetype = ‘relchange’) before the Avatar’s change. Positive and negative ERD/ERS values index synchronization and desynchronization with respect to a given reference interval (Pfurtscheller & Lopes da Silva, 1999). For each experimental condition, ERD/ERS were computed from zero (Avatar’s change) to 500 ms. We extracted ERD/ERS for the 3-13 Hz band and analysed the modulation of power over FCz (see Supplementary Materials for analysis on the Beta band). Usually, Theta and Alpha bands are reported and analysed separately. However, visual inspection (see Figure 5) and specific correlation analyses (see Supplementary Materials) do not allow us to draw a clear line between the activity of these two frequency bands. Therefore, the activity between 3-13 Hz was averaged and discussed as Theta/Alpha power.”.

Source Analysis

Beamformer analyses were performed to estimate cortical sources of the effects found at the sensor level and were accomplished using the Dynamic Imaging of Coherent Sources (DICS) approach, as implemented in Fieldtrip to account for frequency specific effects. The cross spectral density matrix was calculated at the frequency of interest (i.e. 3-13 Hz) using only non-phase locked activity (Sauseng et al., 2007). The head model used to project the estimated source was based on a standard MRI template (Holmes et al., 1998; Oostenveld et al., 2003) and the electrodes position used was based on the international standard 10-10 system. Sources activity post-trigger (0-500ms) was contrasted to source activity pre-trigger (-500 to 0 ms) and divided across the cortex according to the AAL atlas (http://www.gin.cnrs.fr/en/tools/aal/). The change in oscillatory induced power was averaged out cross participants (see Figure 6) and plotted using the Connectome Workbench provided by the Human Connectome Project (Van Essen, 2012; Seymour et al., 2017; see also the shared Matlab/Fieldtrip code “get_source_power.m” at https://github.com/neurofractal/sensory_PAC). Two Region of Interest (ROIs) present in all conditions (see Figure 6) were visually identified based on the inspection of the results: a Fronto-central ROI (AAL labels 'Supp_Motor_Area' and 'Paracentral') and aright-LOTC ROI (AAL labels 'Occipital_Inf_R' and 'Occipital_Mid').The average power for these two ROIs was extracted for analysis.

Connectivity Analysis

Based on the visual inspection and statistical results of the source analysis, in order to index functional connectivity, we focused on the two separate source estimates (namely right LOTC and Fronto-central ROI). Using the maximum power coordinates of these two sources (estimated on the subjects' grand average; [-1 8 66] for Fronto-central, [-39 -86 5] for right LOTC in the MNI system), we performed Linear Constrained Minimum Variance (LCMV) source analysis in the time domain to extract time series at the two locations of interest, creating two "virtual channels" (i.e. "Fronto-central" and "right LOTC", see Figure 7). For a description of the entire procedure, see the "MEG virtual channels and seed-based connectivity" tutorial on the Fieldtrip webpage (http://www.fieldtriptoolbox.org/workshop/chieti/virtualchannel/). Once extracted, the virtual channels were treated as normal EEG data and averaged in the time domain (see Figure 7) (Lappe et al., 2013; Baumgarten et al., 2015). In similar fashion to the computation of induced power, phase-locked activity (ERPs) was removed prior to the transformation from the time-domain to the time-frequency domain. Then, we used the complex time-frequency estimates of the two virtual channels to compute the Phase-Locking Value (PLV) between the two regions of interest (See Figure 7B) where the PLV is computed as a value between 0 and 1 that quantifies the phase consistency across multiple trials. The PLV is the absolute value of the mean phase difference between the two signals, expressed as a complex unit-length vector (as described by Lachaux et al., 1999). PLV values were baseline corrected by subtracting pre-stimulus values (time window -500 to 0 ms) to post stimulus values and Fisher's z-score transformation was applied. PLV data were extracted from 400-600ms after the Avatar's correction in frequencies between 3-13 Hz, based on visual inspection of the data.

Data handling and Statistics

Our main hypothesis concerns ERPs (ERN, Pe) and time-frequency (Theta/Alpha ERD/ERS) modulations in conditions during which participants need to: i) predict the action of their partner and proactively adapt to it (Interactive vs Cued levels of the Condition factor, see below); ii) predict and adapt to an error performed by their partner (Correction vs NoCorrection levels of the Correction factor, see below).Therefore, the analyses presented in the main text focus on these two factors. Moreover, collapsing Interaction Type (Complementary/Imitative) and Movement type (Power/Precision grasping) factors allowed us to have a higher number of trials for each condition. See Supplementary Material for analysis using all the factors.

Grasping Synchrony, ERN and Pe components, Time-frequency index (Theta/Alpha ERD/ERS) and the PLV results were analysed through separated 2 x 2, within-subject, repeated measures ANOVA, with Correction (Correction/NoCorrection) and Condition (Interactive/Cued) as within-subject factors.

Source power indexes for the 2 ROIs were analysed through a 2 x 2 x 2 repeated measures ANOVAs with ROIs (Fronto-central/right-LOTC) Correction (Correction/NoCorrection) and Condition (Interactive/Cued) as within-subject factors.

Frequentist statistical analyses (Shapiro-Wilk test for normality, General Linear Model (GLM) and Greenhouse-Geisser correction for non-sphericity when appropriate (Keselman & Rogan, 1980)) were performed with Statsoft Statistica 8 software. Post-hoc correction for multiple comparisons was made using the Bonferroni test. Violin plots have been computed using the shared Matlab function 'violin..m' (https://github.com/bastibe/Violinplot-Matlab/blob/master/Violin.m).

Results

Behavioural

Grasping Synchrony

The 2 Correction (Correction/NoCorrection) x 2 Condition (Interactive/Cued) ANOVA showed that Grasping synchrony was worse for the Correction (M = 174.10 ms, SD = 85.66) compared to the NoCorrection trials (M = 151.43 ms, SD = 51.60) ($F(1,20) = 15.53$, $p < 0.001$, $\eta p^2 = 0.43$). Grasping Synchrony was also worse for Interactive trials (M = 199.09 ms, SD = 80.99) compared to Cued ones (M = 126.43, SD = 31.60) ($F(1,20) = 29.75$, $p < 0.001$, $\eta p^2 = 0.60$). The two factors interacted significantly ($F(1,20)= 49.53$, $p < 0.001$, $\eta p^2 = 0.71$). Post-hoc tests indicated that the synchrony was worse for Interactive-Correction compared to the other conditions (all *ps* < 0.001), and for Interactive-NoCorrection compared to the Cued-Correction and Cued-NoCorrrection conditions (all *ps* < 0.001) (see Figure 3).

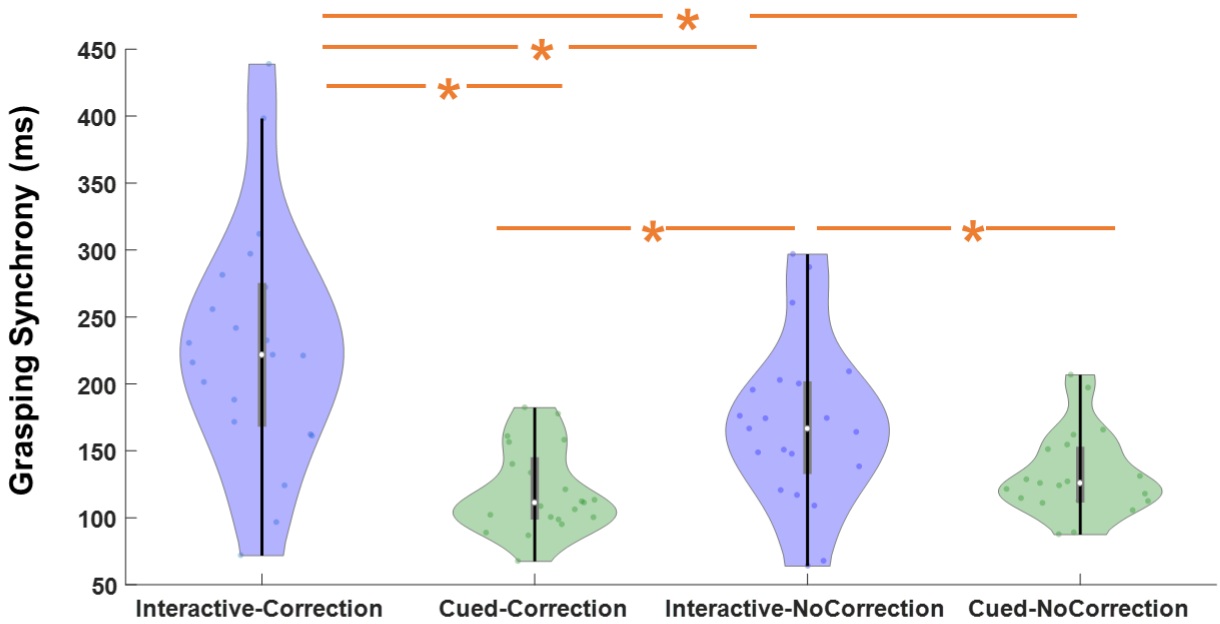

Figure 3 | *Grasping Synchrony (the absolute value of the time delay between subjects' index-thumb contact-times on their bottle and the avatar's bottle touch time). The ANOVA showed a significant interaction between Correction and Condition ($F(1,20)= 49.53$, $p < 0.001$, $\eta p^2 = 0.71$). The post-hoc test indicated that the synchrony was worse for Interactive-Correction compared to the other conditions (all ps < 0.001) and for Interactive-NoCorrection compared to the Cued-Correction and Cued-NoCorrrection conditions (all ps < 0.001). Asterisks indicate significant ($p < 0.05$) differences.*

ERPs

ERN over FCz

The 2 Correction (Correction/NoCorrection) x 2 Condition (Interactive/Cued) ANOVA showed that the ERN amplitude was larger for Correction (M = -1.47, SD = 1.55) compared to NoCorrection trials (M = 0.01, SD = 0.51) ($F(1,20) = 31.45$, $p < 0.001$, $\eta p^2 = 0.61$). ERN amplitude was also larger for the Interactive condition (M = -0.93, SD = 1.63) compared to the Cued one (M = -0.53, SD = 1.04) ($F(1,20) = 4.46$, $p = 0.47$, $\eta p^2 = 0.18$). The two factors interacted significantly ($F(1,20) = 7.82$, $p = 0.011$, $\eta p^2 = 0.28$). Post-hoc tests indicated that ERN amplitude was larger during Interactive-Correction trials than the one recorded during all the other conditions (all *ps* < 0.015) and that the ERN amplitude observed for Cued-Correction condition was larger than both Interactive-NoCorrection ($p < 0.001$) and Cued-NoCorrection ($p = 0.014$) (see Figure 4).

Pe over Pz

The 2 Correction (Correction/NoCorrection) x 2 Condition (Interactive/Cued) ANOVA showed that Pe amplitude was larger for Correction trials (M = 0.91, SD = 1.05) compared to NoCorrection ones (M = 0.04, SD = 0.43) ($F(1,20) = 25.09$, $p < 0.001$, $\eta p^2 = 0.55$) (see Figure 4).

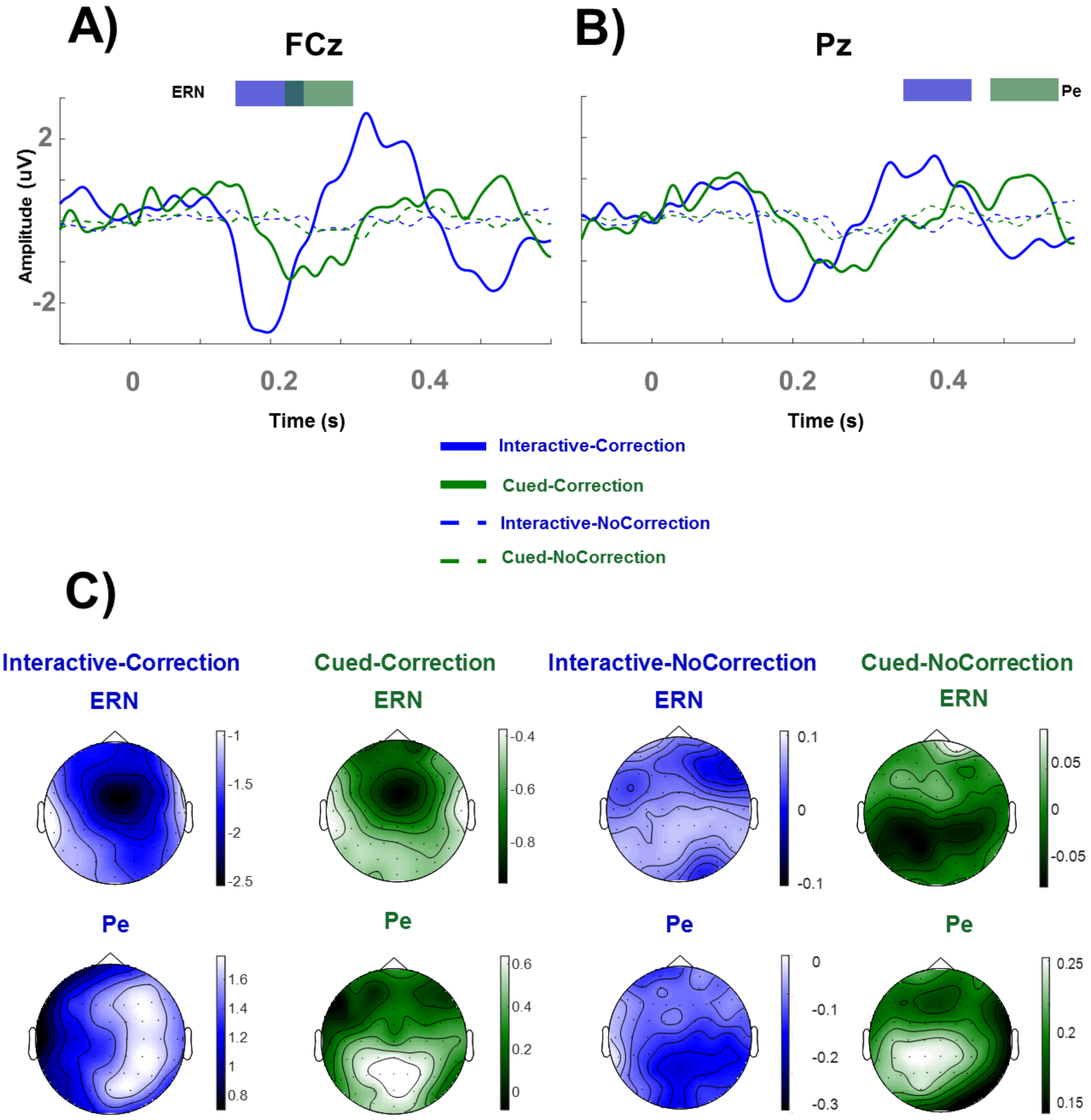

Figure 4 | *Grand averages of A) the ERN over FCz (144-244 ms for the Interactive conditions, 178-278 ms for the Cued conditions, shown in blue and green thick lines above the Amplitude panel) and B) the Pe over Pz (352-452 ms for the Interactive conditions, 486-586 ms for the Cued conditions, shown in blue and green thick lines above the Amplitude panel) components in the four different experimental conditions, C) Topographies of each components.*

Time Frequency

Theta/Alpha (3-13Hz) ERD/ERS Over FCz

The 2 Correction (Correction/NoCorrection) x 2 Condition (Interactive/Cued) ANOVA showed a main effect of Correction, with higher Theta/Alpha synchronization for Correction (M = 0.38, SD = 0.42) compared to NoCorrection trials (M = 0.16, SD = 0.24) ($F(1,20) = 22.23$, $p < 0.001$, $\eta p^2 = 0.52$). Also the factor Condition reached statistical significance as a main effect, larger Theta/Alpha synchronization during the Interactive condition (M = 0.51, SD = 0.36) compared to the Cued one (M = 0.035, SD = 0.36) ($F(1,20)= 39.51$, $p < 0.001$, $\eta p^2 = 0.66$). The two factors Correction and Condition interacted significantly ($F(1,20) = 9.66$, $p < 0.001$, $\eta p^2 = 0.33$). Post-hoc test indicated the following: 1) Theta/Alpha ERS during Interactive-Correction trials was larger than the one recorded during all the other conditions (all *ps* < 0.001); 2) Theta/Alpha ERS in Interactive-NoCorrection condition was larger than Cued-Correction ($p < 0.001$) and Cued-NoCorrection ($p < 0.001$); 3) Theta/Alpha ERS for Cued-Correction trials and Cued-NoCorrection trials did not differ ($p = 0.31$) (see Figure 5).

Previous literature has highlighted the common origin of the ERN and lower frequency synchronization (i.e. Theta; Luu et al., 2004; Trujillo & Allen, 2007). To assess this matter, we ran a correlation between the ERN mean amplitude and the Theta/Alpha ERS (see Table 1). The analysis shows no pairwise significant correlation between Theta/Alpha synchronization and ERN over FCz.

			ERN		
		Interactive-Correction	Cued-Correction	Interactive-NoCorrection	Cued-NoCorrection
Theta/ Alpha ERS	Interactive-Correction	-0.22	-0.38	-0.07	-0.05
	Cued-Correction	**-0.60**	-0.36	-0.32	-0.23
	Interactive-NoCorrection	-0.19	-0.14	0.02	0.08
	Cued-NoCorrection	-0.23	-0.02	-0.20	-0.12

Table 1 | *Correlations between Theta/Alpha ERS and ERN over FCz, bold values shows significant correlation (p < 0.05).*

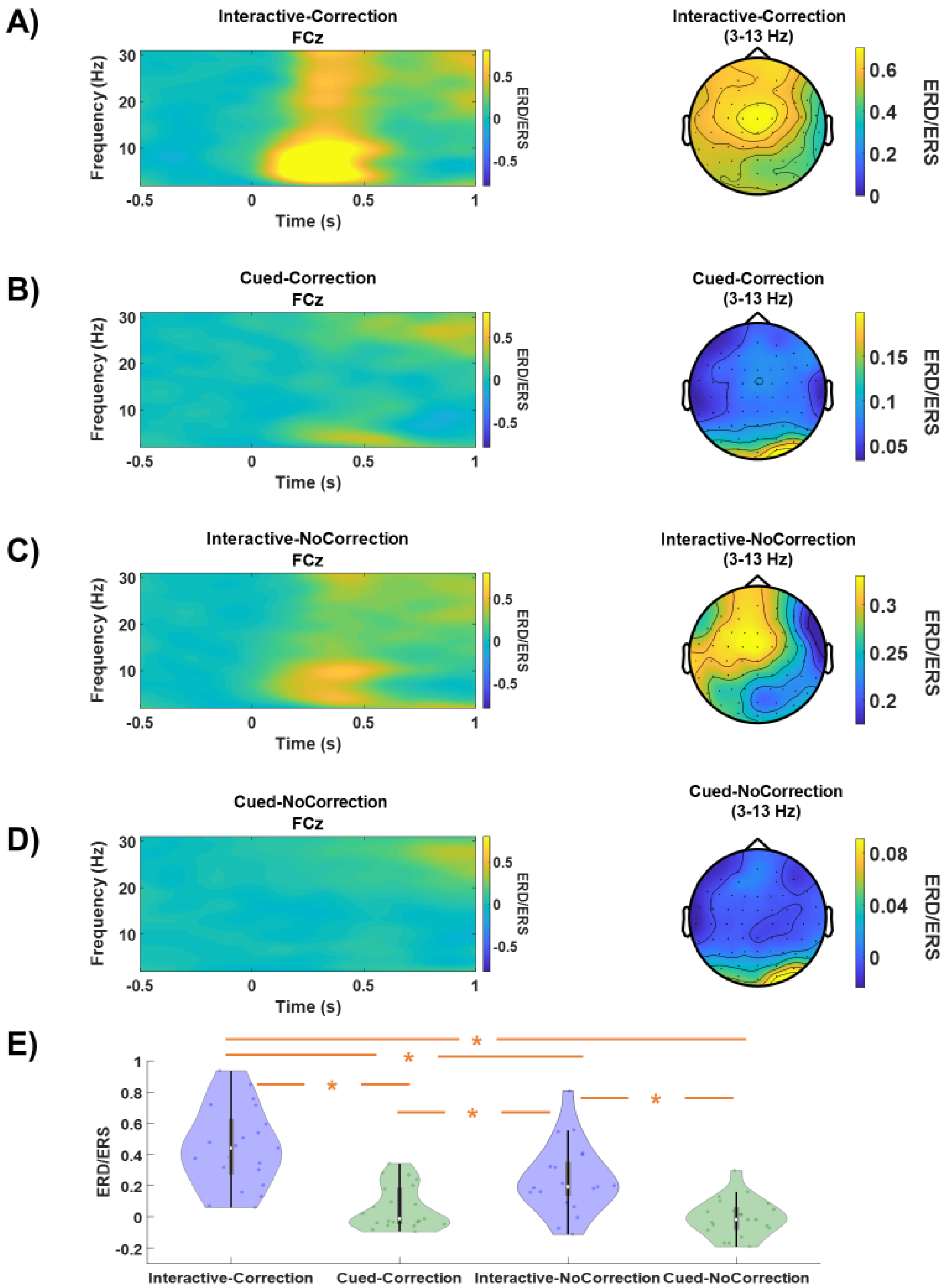

Figure 5 | *ERD/ERS plot (0-30 Hz) over FCz and Theta/Alpha (0-500 ms) topographical view in the A) Interactive-Correction condition, B) Cued-correction condition, C) Interactive-NoCorrection conditions and D) Cued-NoCorrection condition. E) shows the Theta/Alpha ERS over FCz (see text for the description of the effects).*

To sum-up, Theta/Alpha ERS is influenced by the different conditions. In details, there is stronger Theta/Alpha synchronization for Interactive-Correction trials compared to all other conditions, and stronger Theta/Alpha synchronization for Interactive-NoCorrection compared to Cued-Correction and Cued-NoCorrection trials. Frontal midline Theta is usually associated with error processing, but it has been shown that Theta power could affect nearby frequencies (i.e. Delta and Alpha; Trujillo & Allen, 2007).

Source Analysis

Two Regions of Interest (ROIs) were identified for Theta/Alpha power modulations: a fronto-central and right occipito-temporal one (i.e. right LOTC and Fronto-central ROIs) and average power for these two ROIs was extracted for analysis (see Figure 6).

ANOVA on ROIs – Theta/Alpha Source – 0-500ms post observed error

The 2 ROIs (Fronto-central/right-LOTC) x 2 Condition (Interactive/Cued) x 2 Correction (Correction/NoCorrection) ANOVA showed that all three factors reached significance. The main effect of Condition reveals more Theta/Alpha source power for Interactive (M = 0.30, SD = 0.27) compared to Cued trials (M = 0.11, SD = 0.19) ($F(1,20) = 17.66$, $p < 0.001$, $\eta p^2 = 0.47$). The main effect of Correction shows more Theta/Alpha source power for Correction (M = 0.31, SD = 0.29) compared to NoCorrection trials (M = 0.11, SD = 0.17) ($F(1,20) = 40.34$, $p < 0.001$, $\eta p^2 = 0.66$). The main effect of ROIs highlights more Theta/Alpha source power over the Fronto-central (M = 0.24, SD = 0.29) ROI compared to the right-LOTC (M = 0.17, SD = 0.20) ($F(1,20) = 5.07$, $p = 0.035$, $\eta p^2 = 0.20$). Three interactions also reached significance: 1) the interaction between Condition and Correction ($F(1,20) = 20.97$, $p < 0.001$, $\eta p^2 = 0.51$) showing that the Interactive-Correction condition showed more Theta/Alpha power than all the other conditions ($ps < 0.001$), that the Cued-NoCorrection condition generated less Theta/Alpha source power than all the other conditions ($ps < 0.001$), and that the Interactive-NoCorrection generated more Theta/Alpha power than Cued-

NoCorrection (*p*< 0.001); 2) the interaction between ROIs and Condition ($F(1,20) = 39.54$, $p < 0.001$, $\eta p^2 = 0.66$) showing that the both ROIs in the Interactive condition showed more Theta activity than both ROIs in the Cued condition (*ps* < 0.001), that within the Interactive condition, the Fronto-central ROI generated more power than the right-LOTC ($p < 0.001$) and that Frontal and r-LOTC power did not differ in the Cued condition ($p = 0.77$); 3) the interaction between ROIs and Correction ($F(1,20) = 21.14$, $p < 0.001$, $\eta p^2 = 0.51$), showing that the source power was significantly higher over the Fronto-central ROI during Correction trials compared to all other condition (*ps* < 0.001), that the right-LOTC ROI generated more power in Correction trials compared to the Fronto-central ROI in NoCorrection trials ($p < 0.001$) and to the right-LOTC ROI in NoCorrection trials ($p < 0.001$), while the Fronto-central and the right-LOTC ROIs do not differ in NoCorrection trials ($p = 1$).

In sum, the Fronto-central and the right-LOTC ROIs show a significant increase of Theta/Alpha source power during the Interactive-Correction condition compared to the other conditions (Figure 6). By using the coordinates of these two ROIs, we subsequently targeted functional connectivity between these areas.

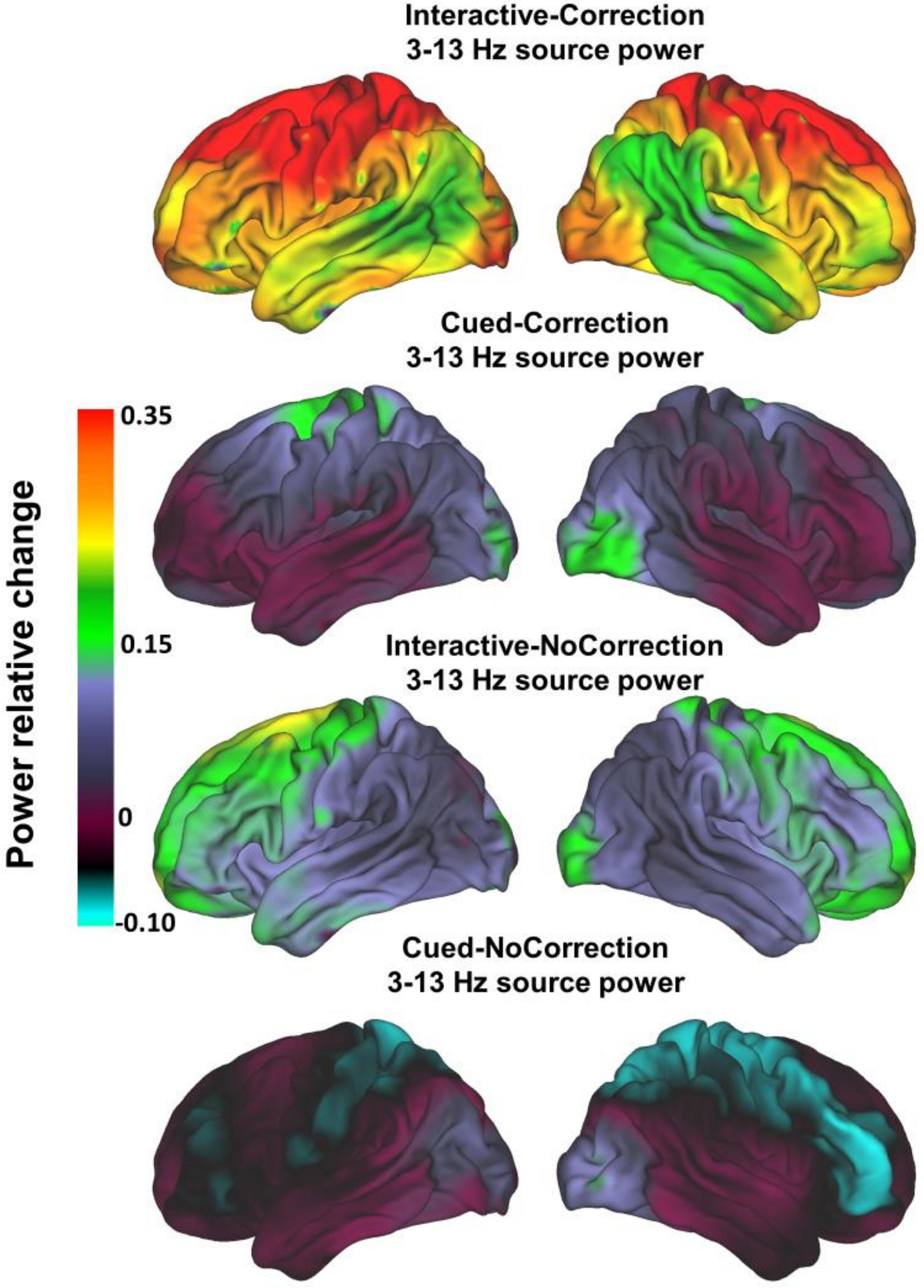

Figure 6 | *Whole brain Theta/Alpha source power.*

Fronto-central-right occipito temporal connectivity - Phase-Locking Value

The 2 Correction (Correction/NoCorrection) x 2 Condition (Interactive/Cued) ANOVA showed that the factors Correction and Condition reached statistical significance as main effects, with larger Phase Locking Value for Correction compared to NoCorrection trials ($F(1,20) = 4.56$, $p = 0.045$, $\eta p^2 = 0.18$) and larger PLV during the Interactive condition compared to the Cued one ($F(1,20) = 10.18$, $p = 0.005$ $\eta p^2 = 0.33$) (see Figure 7). Furthermore, the Correction x Condition interaction also reached significance (($F(1,20) = 5.56$, $p = 0.028$, $\eta p^2 = 0.22$). Post-hoc tests reveal that the PLV was larger for Interactive-Correction trials compared to all other conditions (*ps* < 0.004). These results suggest an increase in phase-locking between the Fronto-central ROI and the right LOTC in the 3-13 Hz frequency range during the Interactive condition, only when the Avatar corrected its movement.

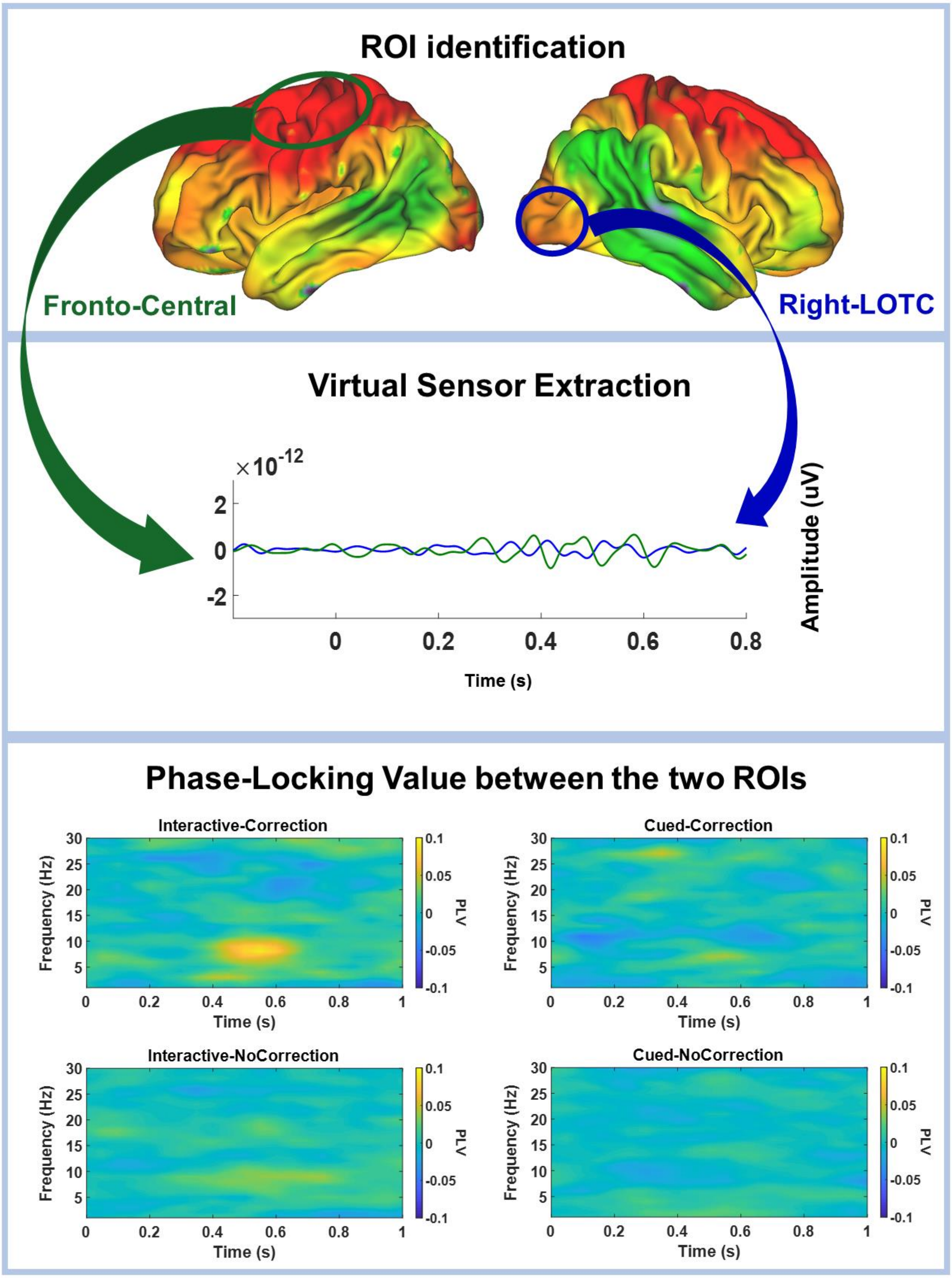

Figure 7 | *Functional connectivity between the two virtual sensors (Fronto-central and Right-LOTC).*

Discussion

In the present study we recorded EEG in participants who performed a human-avatar joint-grasping task to explore the link between visual action prediction and action monitoring systems in an interactive context where a virtual partner could perform actions that violated the motor prediction of human participants. We obtained four main results: 1) electrocortical indices of error monitoring were higher in conditions requiring the participant to predict in space and time their partner's action (Interactive condition) compared to when only coordination in time was required (Cued condition); 2) modulation of the above-mentioned indices, particularly of Theta/Alpha activity over fronto-central electrodes, was stronger in conditions where the virtual partner changed its initial action (Interactive-Correction condition) compared to when its action unfolded as predicted (Interactive-NoCorrection condition); 3) the virtual partner's correction generates an additional increase of right-occipito-temporal 3-13 Hz activity; 4) there is an increased frontal and occipito-temporal connectivity when the avatar unpredictively changed its movement and the actions of the participants depend on those of the virtual partner (Interactive-Correction condition).

Action and error monitoring during motor interactions

Studies show that similar activity is found when people perform errors (Debener et al., 2005; Gehring et al., 1993) and observe another person making an error (van Schie et al., 2004; Malfait et al., 2010; Cracco et al., 2016; Desmet & Brass, 2015). This suggests that the detection of ones' own error and of those made by others shares analogous neural mechanisms. Furthermore, individuals' motor expertise in specific action domains influences behavioural and neurophysiological responses to erroneous action observation (Aglioti et al., 2008; Abreu et al., 2012; Candidi et al., 2012; Panasiti et al., 2016; Özkan et al., 2019) suggesting that individuals' motor expertise contributes to monitoring the actions of others.

Besides the suggested overlap between the neural systems responding to observed and executed actions and errors (Zubarev et al., 2018) studies have documented a differential contribution of brain areas to the observation of errors performed by others (Shane et al., 2008; Abreu et al., 2012; Somon et al., 2019; Ninomiya, et al., 2018; Somon et al., 2017). In the present study we explored the neural responses associated to coordinating one's own movements with those of a virtual partner who could perform unexpected changes in its motor behaviour. When acting with a partner, both members need to fulfil their own motor sub-goal while aiming at coordinating each other's actions in order to achieve a common goal.

In all the experimental conditions of the present study, the individual goal is to grasp a target in synchrony with a partner which implies that the behaviour of our experimental participants is always dependent on the behaviour of the partner. Crucially, however, in the Interactive condition participants need to realize imitative or complementary interactions which can only be achieved by also taking into account the spatial/goal organization of both one's own and the avatar's behaviour. In this sense, the definition of an error in the Interactive condition pertains to linking other's action perception to own action execution. Hence, participants had to monitor visual inputs from the body of the partner to plan their own action. We suggest that the higher 3-13 Hz phase locking between frontal-error-related and occipito-temporal (i.e. visual cortices) areas in the Interactive-Correction condition may support this function. We speculate that during interactive scenarios, given the bodily nature of the visual information of our task, visual nodes of the AON (the LOTC) may support the activity of the error monitoring system to allow behavioural adaptation.

Error-related ERPs

Error-Related-Negativity is usually associated with an early detection of an unexpected outcome (compared to an internally-generated prediction) which may be represented in our study by the unpredicted Avatar's movement. The ERN over FCz reveals specific modulation of error monitoring associated with Interactive-Correction trials. The components were only visually identified in conditions where the Avatar changed its behaviour (Correction factor) (see Figure 4). Interestingly, the Avatar's changes in the Interactive condition elicited greater ERN mean amplitudes than in the Cued condition, while the Pe was only modulated by the Correction factor. This pattern of results indicates that time-dependent neural responses triggered by error detection are induced by others' errors, and that the ERN is modulated by the relevance of these errors for one's own movements during interaction.

Besides the relevance of the others' error, a recent study found that the ERN is also influenced by the magnitude of an observed error in space with greater amplitude and earlier latency for large errors compared to small ones (Spinelli et al., 2018). An imaging study complemented this error-magnitude pattern of neural responses showing that also activity in occipito-temporal cortex is sensitive to the magnitude of observed reaching deviations (Malfait et al., 2010). On the other hand, the Pe is associated with conscious perception of an error, reflecting motivational aspects and top-down cognitive control (Ridderinkhof et al., 2009). It has been shown that while the ERN is always present following error-trials, the Pe is elicited only in trials in which subjects are aware of their errors (Nieuwenhuis et al., 2001). In the present study, an unexpected correction in the Avatar's movement was implemented in both the Interactive and Cued conditions. Crucially, only in the Interactive condition participants needed to spatially predict the outcome of the partner's behaviour. Thus, the higher activation of the early error detection system (ERN) in this condition seems to be associated to the need to use information concerning the partner's movements to guide one's own movements.

Previous EEG studies have described the occurrence and modulations of ERN and Pe responses to the perception of odd events as well as of errors of a partner in turn taking interactive scenarios (Koban et al., 2010; Kato et al., 2016). Similarly, other studies have investigated the occurrence of ERN and Pe responses during interpersonal musical performance in turn taking set-ups (Maidhof et al., 2010; Huberth et al., 2018). One EEG study demonstrates that performing errors together with a partner modulates neural activity related to outcome evaluation (i.e. the Feedback-Related Negativity is larger for joint errors compared to other's ones) but has less impact on activity related to the motivation to adapt future behaviour (i.e. P3b is not modulated by own, joint or other's errors; Loehr et al., 2015). This suggests that producing a phasic error by pressing the wrong key synchronously with a partner impacts outcome evaluation response rather than generating neural responses associated to adaptive behaviour. Instead, our study characterizes error-related responses when participants need to adapt on-line to the synchronous behaviour of an interactive partner that violates a motor prediction.

Error-related responses in time-frequency domain

The time-frequency analysis on FCz reveals a greater Theta/Alpha synchronization for the Interactive-Correction condition compared to all other conditions. In the error-related literature, Theta and Alpha have both been found over fronto-central electrodes during the processing of errors (Pavone et al., 2016, Pezzetta et al., 2018). However, Trujillo and Allen (2007) have argued that activity in the lower Alpha band is due to leakage of the Theta frequency to the neighbouring bands. Interestingly, when the Avatar corrected his action the Theta/Alpha synchronization was reduced in the Cued compared to the Interactive condition suggesting a dissimilar processing of the correction in Interactive and Cued conditions. Furthermore, in the Interactive condition, Theta/Alpha activity was found even in trials when the virtual partner performed no correction. This error-related activity in the absence of error (i.e. during Interactive-NoCorrection trials) suggests that the monitoring system does not only react to unexpected actions but plays a key-role in continuously monitoring the partner's and ones' own behaviour in order to integrate the partner's behaviour when participants' actions rely on them.

Monitoring System and Error Detection

Our results in the Theta/Alpha-band indicate that goal-related and temporal coding of the observed actions might undergo different processing systems. We suggest that the violation of the predicted goal of the observed actions (Correction factor), and the need to adjust to them (Interactive condition), represent the crucial features upon which the error-related monitoring system is based. A parsimonious interpretation of this pattern of results is that the monitoring system is differentially activated by the behavioural relevance of events in the Interactive and Cued conditions. Accordingly, frontal Theta/Alpha activity is less present during the Cued condition compared to the Interactive one regardless the presence of a change in the partner behavior. In the Cued condition the subject is not engaged in monitoring the partner's action goals and likely dedicates less resources to processing the partner's behaviour. Coherently with this, our DICS analysis in the 3-13 Hz band revealed a fronto-central source estimate (Cohen, 2011; Kovacevic et al., 2012) where the Anterior Cingulate Cortex (ACC) is believed to be a key-part of the cognitive control network.

Theta/Alpha dynamics shown in the current study provide new insights on the neural underpinnings of cognitive control and action-related processing during motor interactions. Importantly, such an effect was maximal during sudden changes in the virtual partner's movement. This shows that higher uncertainty in the Interactive condition generates stronger source-located fronto-central activity.

Interpersonal motor interactions

An often-described EEG marker of engagement in interactive paradigms is the sensorimotor alpha/mu desynchronization over central sites (Tognoli et al., 2007; Dumas et al., 2010; Naeem et al., 2012; Ménoret et al., 2014; Konvalinka et al., 2014; Novembre et al., 2016). This rolandic alpha/mu band activity has been considered an index of the MNS activity since it is suppressed during both action observation and action execution (Cochin et al., 1999; Muthukumaraswamy et al., 2004; Oberman et al., 2005; Pineda, 2005). On the other hand, recent studies suggest more cautious interpretation concerning the alpha/mu modulation, and temper some of the conclusions made about the implication of the MNS in processing self and others' actions in healthy participants (Coll et al., 2017) and clinical samples - such as people with autism (Dumas et al., 2014). In our analysis, we do not find any modulation of the sensorimotor alpha/mu rhythms between conditions. However, our set-up lacks a 'solo action' control condition, usually used in previous studies as a baseline to highlight the activity of fronto-parietal areas (in the alpha-beta range) in synchronous joint actions (Naeem et al., 2012; Ménoret et al., 2014). Furthermore, the error-related activity spreads over both the theta and alpha range, therefore potentially masking co-occurrent desynchronization in the alpha/mu range. Future studies are needed to target classic fronto-parietal dynamics in adaptive contexts and in relation to error-monitoring.

Occipito-temporal activity during interactions

The Action Observation Network (AON) has been proposed as a neural substrate for action understanding (see for review Rizzolatti et al., 2014; Avenanti et al., 2013; Urgesi et al., 2014). However, recent findings associated the ability to decode an action with activity in the lateral occipito-temporal cortex (Lingnau & Downing, 2015; Tucciarelli et al., 2015). Interestingly, in addition to fronto-central Theta/Alpha activity associated with error-detection, source analysis of the present data revealed 3-13 Hz activity in the right occipito-temporal cortex locked to hand movement changes. This region is thought to play a role in the processing of body images as indicated by functional methods (Downing et al., 2001; Thierry et al., 2006), virtual lesions (Urgesi et al., 2004, 2007) and studies on brain-damaged patients (Moro et al., 2008). More recently we have shown that an occipito-temporal Theta ERS is found during the passive observation of hands and arms images (Moreau et al., 2018; Moreau et al., 2019) while Tucciarelli et al. (2015) showed that activity in the Theta band over LOTC areas distinguishes between hand pointing and grasping actions. Coherently with this, an fMRI study showed that during the observation of kinematic errors in a reaching task activity of occipito-temporal areas increases parametrically with the dimension of the observed error (Malfait et al., 2010).

Here we describe a Theta/Alpha increase when the hand of a partner deviates from its expected trajectory during an interaction. Therefore, we submit that the 3-13 Hz source activity detected over occipito-temporal area during Interactive-Correction trials is associated with processing an action after a deviation from the predicted goal was perceived in the movement of the avatar. This re-coding appears to be a necessary step to adapt to the avatar's sudden change in movement. This suggests that the increase of Theta activity over occipito-temporal regions during perception of static hand images (Moreau et al., 2018; Moreau et al., 2019) extends to the perception of dynamic hand movements in a similar (though larger) frequency band. Therefore, Theta may be an intrinsic rhythm of occipito-temporal areas that becomes enhanced when attention is deployed (Engel et al., 2001) over body-related movements, for example, when the movement of a partner is different from what was predicted. Furthermore, this region seems to be connected to other brain regions as suggested by our connectivity results (PLV), that indicate an increase of phase-locking between the occipito-temporal and the fronto-central areas in the 3-13 Hz range. This result suggests that these two regions belong to a common functional neural network recruited during behavioural adaptation in a social context.

Conclusions

We describe the EEG correlates of error detection during motor interactions with a virtual partner that performed a change in its action. We found that electrocortical markers of error processing were stronger for unpredicted actions; particularly in the Interactive condition during which goal-related and temporal predictions of the partner's actions are required. Moreover, the source estimates of the 3-13 Hz activity show the recruitment of fronto-central and occipito-temporal regions, indicating their potential role in processing and integrating visual and motor information during social interactions. Taken together, these findings suggest a connection between the fronto-central performance monitoring system and occipito-temporal visuo-motor processes and hint at a role for occipito-temporal areas a role in social motor adaptation.

Fundings

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Supplementary Material

Behavioural data

We considered the following as behavioural measures: 1) Grasping Synchrony, i.e. the absolute value of the time delay between subjects' index–thumb contact-times on their bottle and the avatar's reaching time; 2) Accuracy, that is the number of movements executed correctly (according to the instructions); 3) Reaction Times (RTs), i.e. time from the go-signal to the release of the start button; 4) Movement Times (MTs), i.e. time interval between participants releasing the start button and their index-thumb touching the bottle.

Motion Kinematics data

Motion tracking was continuously recorded during the experimental blocks. During off-line analyses, the participants' start button-hand-release times and index-thumb-bottle contact times were used to subdivide the kinematics recordings with the aim of analysing only the reach-to-grasp phase (from start button hand-release to index-thumb contact-times). To obtain specific information on the reaching component of the movement, we analysed wrist trajectory as indexed by the maximum peak of wrist height on the vertical plane (Maximum Wrist Height). To obtain specific information on the grasping component of the movement, we analysed maximum grip aperture (Maximum Grip Aperture, i.e., the maximum peak of index-thumb 3D Euclidean distance). We excluded from the analyses (behavioural, kinematics and EEG) trials in which participants 1) missed the touch-sensitive sensors and thus no response was recorded, 2) released the start button before the go instruction or 3) did not comply with the complementary/imitative instructions.

Behavioural and kinematic values that fell 2.5 SDs above or below each individual mean for each experimental condition were considered as outliers and excluded from the analyses. We calculated the individual mean value in each condition for each of these behavioural and kinematics measures. The obtained values were entered in different within-subject ANOVAs (see below). We used non-parametric tests concerning the Accuracy measures. Kinematics, Accuracy, MTs and RTs results are presented below.

Additional Analyses and Results

Behavioural, kinematics and EEG (Grasping Synchrony , Reaction Times, Movement Times, Maximum Wrist Height, Maximum Grip Aperture, Theta/Alpha and Beta over FCz) data were analysed through repeated measures ANOVAs; with Correction (Correction, NoCorrection), Condition (Interactive, Cued), Interaction Type (Complementary, Imitative), Movement Type (Precision, Power) as within subject factors. Accuracy was analysed by means of non-parametric tests.

Behavioural and Kinematics results

Accuracy

A Friedman ANOVA revealed significant cross-condition differences (Chi Sqr. (N = 21, df = 15) = 48.90, $p < 0.001$). Follow-up Wilcoxon Matched Pairs Tests between Correction and NoCorrection conditions showed that Correction condition was never more difficult (i.e. less accurate) than NoCorrection condition. (all *ps* > 0.02, corrected *p* threshold = 0.05/8 = 0.006).

Grasping Synchrony

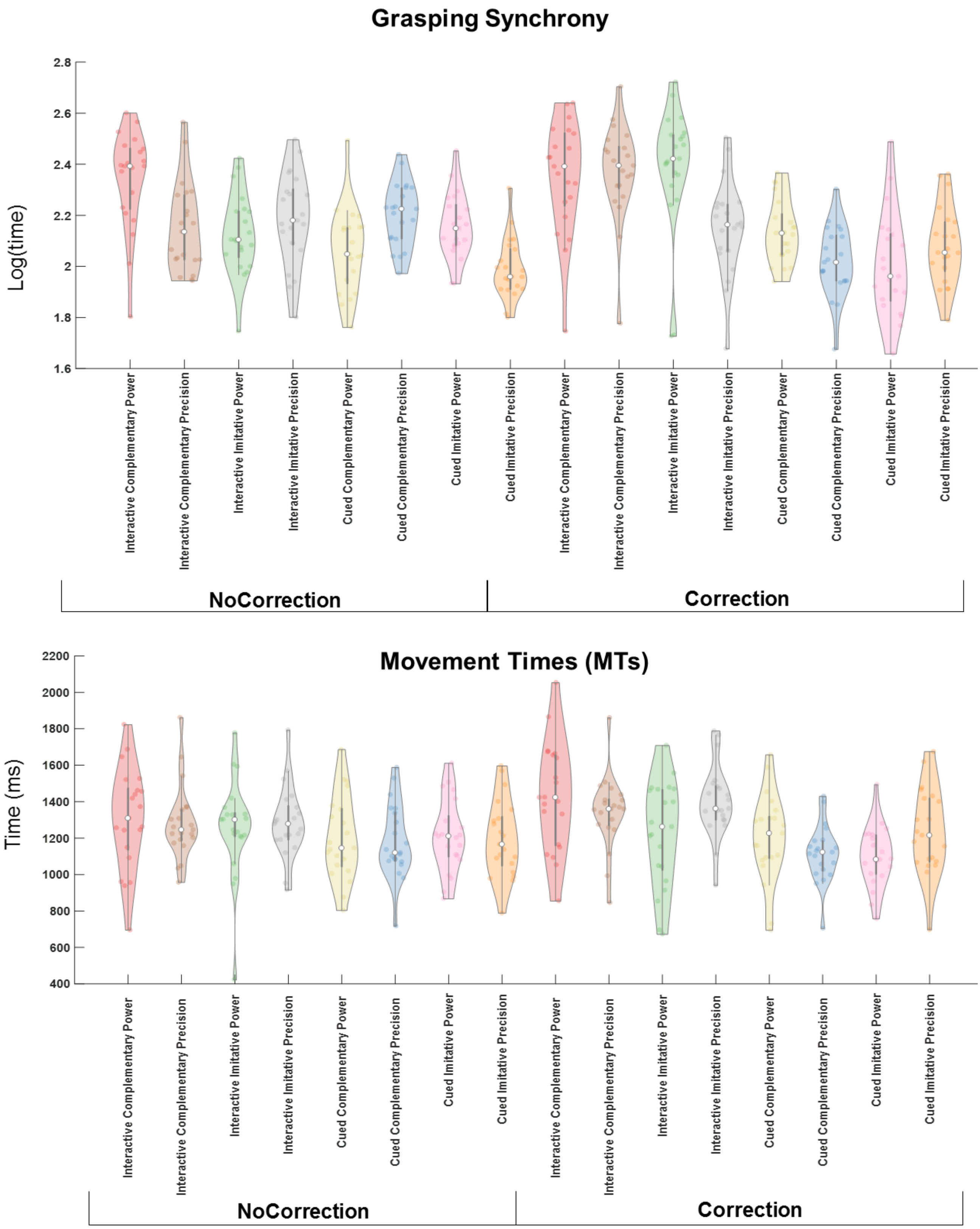
Because of violations of normality assumptions, Grasping Synchrony data were transformed, using logarithmic (log10) transformation.

The ANOVA on Grasping Synchrony showed: a significant Correction x Condition x Interaction Type x Movement Type interaction ($F(1, 20) = 56.74$, $p < 0.001$, $\eta p^2 = 0.74$), which explained all other significant Main effects and lower level interactions (see Figure S1). Post-hoc tests showed that participants were less synchronous when performing Complementary compared to Imitative movements during power grasping in the Interactive Condition, when the Avatar did not correct its movement trajectory ($p = 0.02$) and when performing NoCorrection-Complementary-Power grasping during the Interactive compared to the Cued condition ($p = 0.001$). Grasping Synchrony decreased during NoCorrection-Cued-Complementary compared to NoCorrection-Imitative-Imitative grips ($p = 0.027$). Moreover, performance decreased during Correction compared to NoCorrection trials in the Interactive condition, when performing Imitative movements through Power grips ($p = 0.002$). Grasping synchrony was worse in Correction trials, during Interactive interactions, when performing Complementary compared to Imitative Precision grips ($p = 0.018$). Furthermore, participants were less synchronous in Correction trials, when performing Interactive interactions involving Imitative movements with Precision compared to Power grips ($p = 0.001$). Moreover, synchrony decreased during Correction trials in the Interactive compared to the Cued condition, when performing Complementary movements through Precision and Power grips ($p < 0.001$; $p = 0.08$). Synchrony also decreased during Correction trials in the Interactive Imitative Power compared to Precision grips ($p = 0.007$). Finally, synchrony was worse in Correction trials, when performing Interactive compared to Cued interactions, during Imitative power grips ($p < 0.001$).

Movement Times (MTs)

The ANOVA on Movement Times showed a significant main effect of Condition ($F(1, 20) = 15.44$, $p < 0.001$, $\eta p^2 = 0.44$), indicating that coordinating in the Interactive condition resulted in slower movement times compared to the Cued condition (see Figure S1). The ANOVA also showed a significant Condition x Correction interaction ($F(1,20) = 18.36$, $p < 0.001$, $\eta p^2 = 0.48$). Post-hoc tests showed movement times were slower in Interactive compared to Cued conditions (all *p*s < 0.001) and in Interactive condition during Correction compared to NoCorrection trials ($p = 0.004$). Moreover, the ANOVA showed a significant Condition x Interaction Type interaction ($F(1,20) = 7.5$, $p = 0.013$, $\eta p^2 = 0.27$). Post-hoc tests showed movement times were slower in Interactive compared to Cued conditions (all *p*s < 0.001) and in Interactive condition during Complementary compared to Imitative movements ($p = 0.028$). The ANOVA on Movement Times also showed a significant Interaction

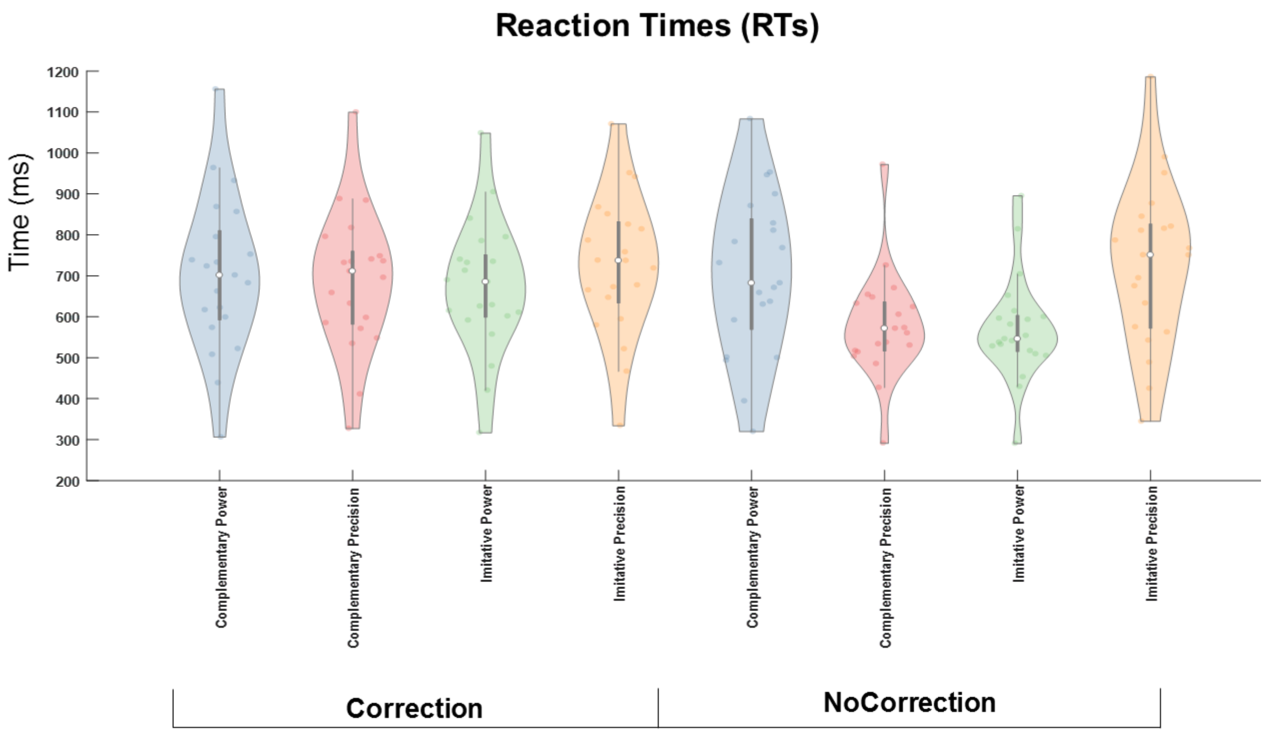
Type x Movement Type interactions ($F(1,20) = 20.68$, $p < 0.001$, $\eta p^2 = 0.5$), explained by the higher order Correction x Interaction Type x Movement Type interaction ($F(1,20) = 19.5$, $p < 0.001$ $\eta p^2 = 0.49$)). Post-hoc tests showed movement times were slower during Correction trials, when performing Complementary movements by means of Power compared to Precision grips ($p = 0.056$) and during Correction trials, when performing Complementary compared to Imitative movements by means of Power grips ($p < 0.001$). Moreover, post-hoc tests showed slower movements times during Correction trials, when performing Imitative compared to Complementary movements by means of Precision grips ($p = 0.037$). Finally, post-hoc tests showed slower movements times during Correction trials, when performing Imitative precision compared to power grips ($p < 0.001$).



Supplementary Figure S1. Grasping Synchrony Movement Times data across all factors. See text for detailed results.

Reaction Times (RTs)

The ANOVA on Reaction Times showed: a significant Correction x Interaction Type x Movement Type interaction (F(1, 20) = 37.078, *p* < 0.001, ηp² = 0.65), which explained all the other significant Main effects and lower level interactions. Post- hoc tests showed that participants were faster to start moving during Correction trials, when performing Complementary actions through Power grips, and during Correction trials, when performing Imitative actions through Precision grips, compared to all the other conditions (all *ps* < 0.001).



Supplementary Figure S2. Reaction Times data illustrating the Correction x Interaction Type x Movement Type interaction (F(1, 20) = 37.078, *p* < 0.001, ηp² = 0.65), see text for post-hoc results.

Maximum Grip Aperture (MaxAp)

The ANOVA on Maximum Grip Aperture showed a significant Correction x Condition x Movement Type interaction (F(1, 20) = 133.69, *p* < 0.001, ηp² = 0.87), which explained all the other significant

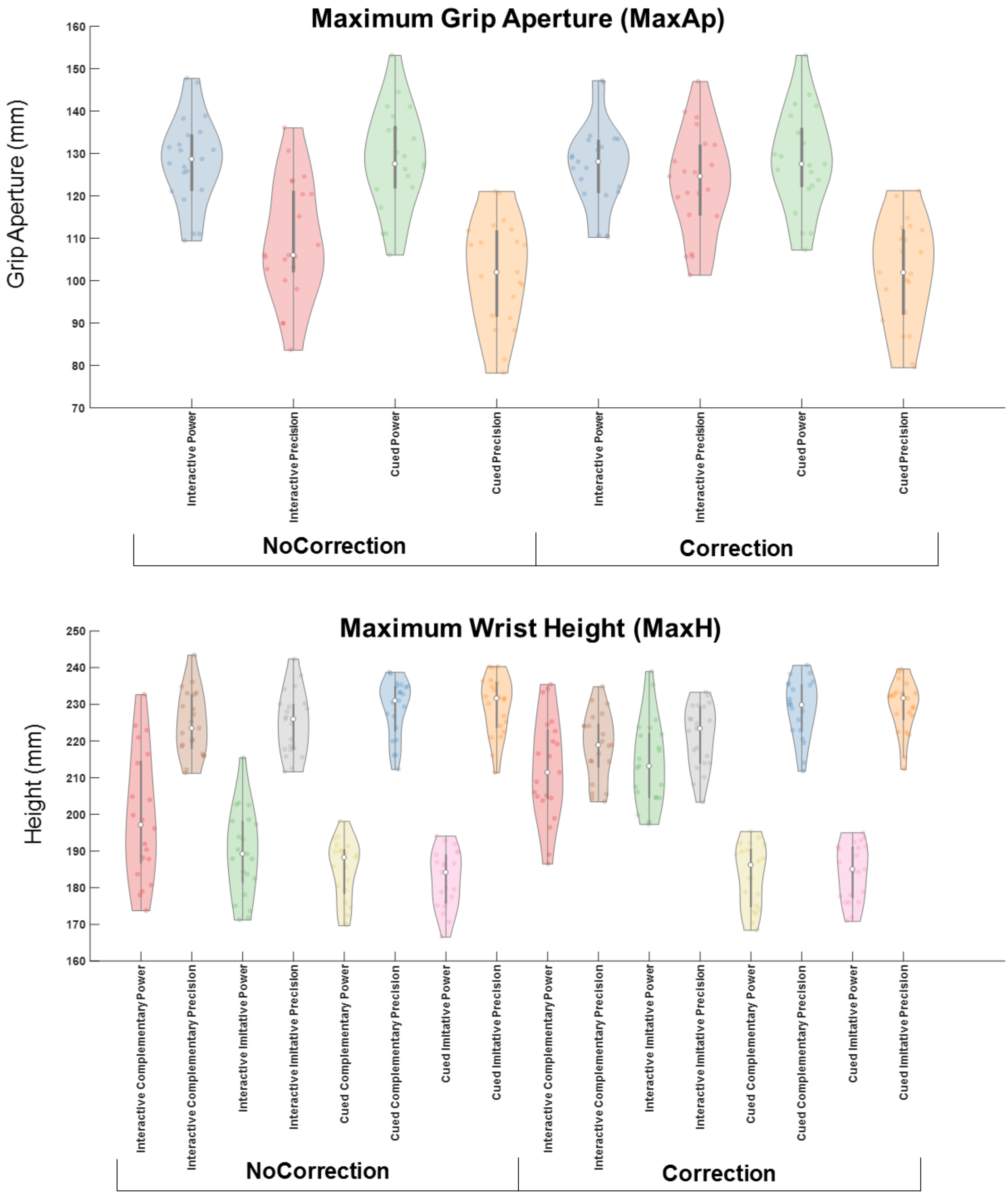
Main effects and lower level interactions. Post-hoc tests showed larger maximum grip aperture during Power compared to Precision Grips (all *p*s < 0.001) and larger maximum grip aperture during Interactive compared to Cued interactions (all ps < 0.001), but not during NoCorrection and Correction trials, in Interactive compared to Cued interactions, by means of Power Grips ($p = 1$; $p = 0.93$). Moreover, maximum grip aperture was larger during Correction compared to NoCorrection during Interactive condition by means of Precision grip ($p < 0.001$).

Maximum Wrist Height (MaxH)

The ANOVA on Maximum Wrist Height showed a significant Correction x Condition x Interaction Type interaction ($F(1,20) = 15.52$, $p < 0.001$, $\eta p^2 = 0.44$). Post-hoc tests indicated that maximum wrist height was higher during Interactive compared to Cued conditions (all *p*s < 0.001), except during Imitative NoCorrection ($p = 1$), moreover, post-hoc tests showed higher maximum wrist height during Interactive Complementary compared to Imitative NoCorrection ($p < 0.001$). Maximum wrist height was also higher during Correction compared to NoCorrections trials in Interactive conditions (all ps < 0.01). The ANOVA on Maximum Wrist Height also showed a significant Correction x Condition x Movement Type interaction ($F(1,20) = 124.13$, $p < 0.001$, $\eta p^2 = 0.86$). Post-hoc tests indicated that maximum wrist height was different during Interactive compared to Cued conditions (all *p*s < 0.01), during Precision compared to Power Grips (all *p*s < 0.001) and that maximum wrist height was different during Correction compared to NoCorrection trials only during Interactive conditions (all *p*s < 0.004). The ANOVA on Maximum Wrist Height showed a significant Correction x Interaction Type x Movement Type interaction ($F(1,20) = 9.87$, $p = 0.005$, $\eta p^2 = 0.33$). Post-hoc tests indicated that maximum wrist height was higher during Correction compared to NoCorrection trials (all *p*s < 0.001) only during power grips. Moreover, post-hoc tests indicated that maximum wrist height was higher during Complementary compared to Imitative trials ($p < 0.001$) during NoCorrection power grips and maximum wrist height was higher during Precision compared to Power Grips (all *p*s < 0.001).

Interestingly, the ANOVA on Maximum Wrist Height showed a significant Condition x Interaction Type x Movement Type interaction ($F(1,20) = 10.95$, $p = 0.003$, $\eta p^2 = 0.35$). Post-hoc tests indicated that when performing power grips maximum wrist height was higher during complementary compared to imitative movements during the Interactive condition ($p < 0.001$) but not during the Cued one ($p = 1$). These significant interactions explained all the other significant Main effects and lower level interactions

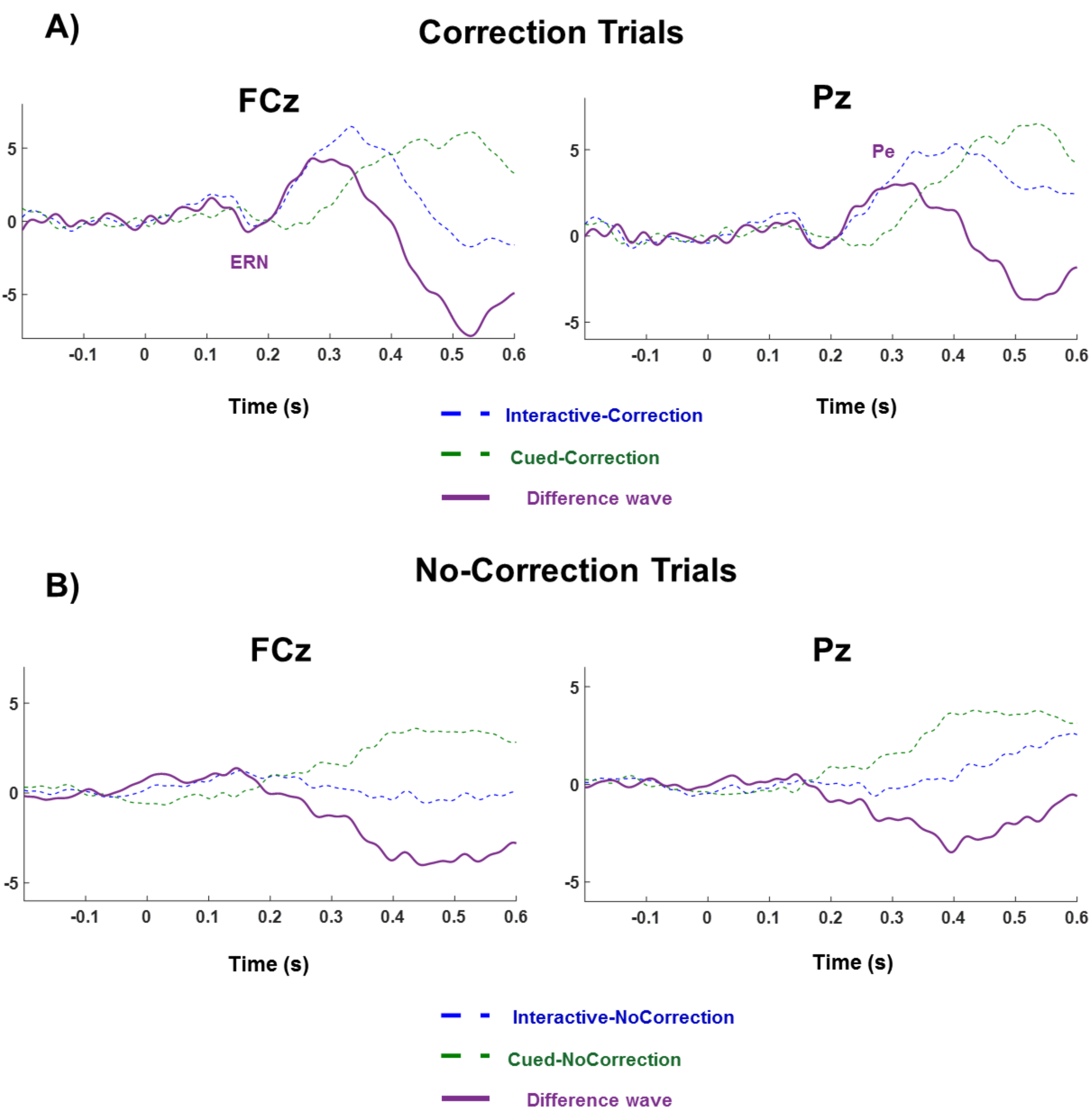
This result highlights the presence of visuo-motor interference between self-executed actions and those observed in the partner as an index of automatic imitation. These results mirror previous studies (Sacheli et al., 2012; 2013; 2015a; 2015b; Candidi et al., 2015; Curioni et al., 2017), only in the condition during which predictions about the partner's movements are needed. Visuo-motor interference effects were present only when performing power grips on the lower part of the bottle as, when performing precision grips on the upper part of the bottle, the maximum wrist height is always reached when touching the bottle – thus impossible to modulate.



Supplementary Figure S3. Maximum Grip Aperture illustrating the Correction x Condition x Movement Type interaction ($F(1, 20) = 133.69$, $p < 0.001$, $\eta p^2 = 0.87$) and Maximum Wrist Height data across all factors. See text for more details.

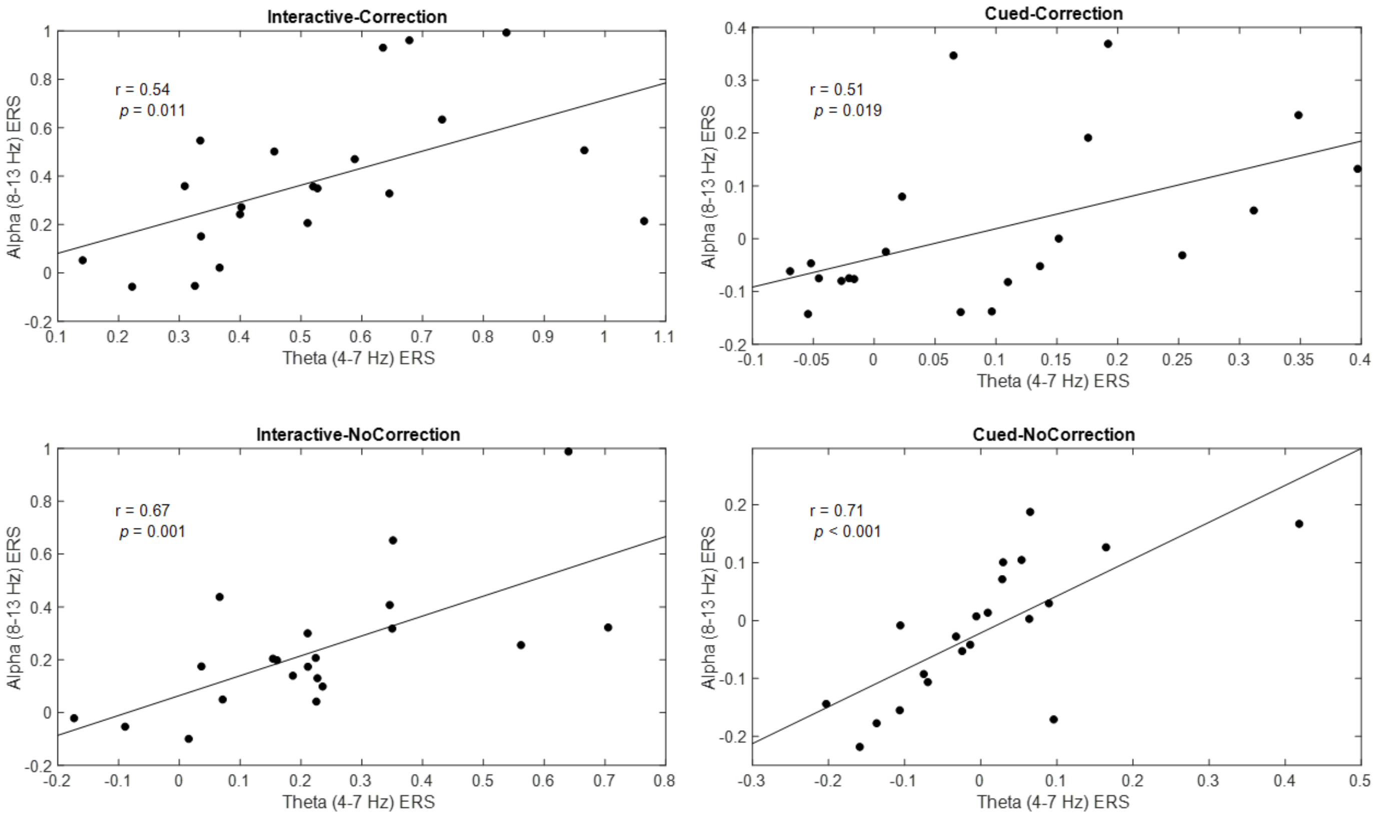
EEG Analysis

ERPs filtered at 0.5-30 Hz



Supplementary Figure S4 |. *ERN-Pe components filtered at 0.5 Hz for A) Correction trials and B) No-correction trials. Dotted lines represent the ERPs for each condition, plain line shows the difference wave between Interactive-Correction and Cued-Correction (S1A) and Interactive NoCorrection and Cued-NoCorrection conditions (S1B).*

Correlation of Theta (4-7 Hz) and Alpha (8-13 Hz) activity



Supplementary Figure S5. *Correlations between Theta and Alpha ERS. The significant correlations across all conditions and the visual inspection of the patterns of results (See Figure 5 of the main text) lead to analyse the EEG data in the main results in a broader 3-13 Hz band.*

Theta/Alpha over FCz

The 2 Correction (Correction/NoCorrection) x 2 Condition (Interactive/Cued) x 2 Interaction type (Imitative/Complementary) x 2 Movement type (Precision/Power) ANOVA showed that the factors Correction, Condition and Movement type reached statistical significance as main effects, with larger Theta/Alpha synchronization for Correction compared to NoCorrection trials ($F(1, 20) = 29.68$, $p < 0.001$, $\eta p^2 = 0.59$), larger Theta/Alpha synchronization during the Interactive condition compared to the Cued one ($F(1,20)= 39.49$, $p < 0.001$, $\eta p^2 = 0.66$) and larger Theta/Alpha synchronization for

Power grasps than Precision grasps ($F(1,20) = 8.36$, $p = 0.009$, $\eta p^2 = 0.30$). The interaction between Correction and Condition reached statistical significance ($F(1,20) = 9.12$, $p = 0.006$, $\eta p^2 = 0.31$). Post-hoc test indicated the following: 1) Theta/Alpha ERS during Interactive-Correction trials was larger than the one recorded during all the other conditions (all *ps* < 0.001); 2) Theta/Alpha ERS in Interactive-NoCorrection condition was larger than Cued-Correction ($p < 0.001$) and Cued-NoCorrection ($p < 0.001$); 3) Theta/Alpha ERS for Cued-Correction trials and Cued-NoCorrection trials did not differ ($p = 0.07$). The interaction between Correction, Condition and Interaction type also reached statistical significance ($F(1,20) = 4.49$, $p = 0.046$, $\eta p^2 = 0.18$), with no additional effects than the ones described above: post-hoc showed no significant pairwise differences involving Imitative and Complementary factors (*ps* >0.59). Finally, the interaction between Condition, Interaction type and Movement type reached significance ($F(1,20) = 4.70$, $p = 0.042$, $\eta p^2 = 0.19$). However, post-hoc tests only reveal that Interactive trials showed more Theta/Alpha synchronization than Cued ones (*ps* < 0.001), with no difference involving Interaction type (*ps* > 0.18) or Movement type (*ps* > 0.71).

Interestingly, we detect a main effect of Movement type, with higher Theta/Alpha activity for Power grasp compared to Precision ones. Previous results showed that the neural basis of Precision and Power grips show little overlap and can be considered as two separate actions (Ehrsson et al., 2000). Here, the main effect of Movement Type does not significantly interact with the factors on which the current study principally focused (i.e. Correction and Condition), limiting our interpretation.

Beta over FCz

The ANOVA on Beta synchronization over FCz showed a significant main effect of Correction $F(1, 20) = 21.09$, $p < 0.001$, $\eta p^2 = 0.51$) indicating a greater Beta for Correction trials and a main effect of Condition ($F(1, 20) = 22.12$, $p < 0.001$, $\eta p^2 = 0.52$) indicating a greater Beta for the Interactive interaction. The ANOVA also revealed a Correction x Condition interaction ($F(1, 20) = 4.42$, $p = 0.048$, $\eta p^2 = 0.18$). Post hoc tests indicated a larger Beta for Correction trials in the Interactive condition compared to the other conditions (*ps* < 0.001), and a larger Beta for NoCorrection trials in the Interactive condition compared to Cued ones in both Correction ($p = 0.02$) and NoCorrection ($p < 0.001$).

A greater Beta synchronization for Correction during the Interactive condition might be linked to the so-called Beta rebound, associated with the degree of error in a movement (Tan et al., 2014).

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