When your errors make me lose or win: Event-related potentials to observed errors of cooperators and competitors

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Abstract

Monitoring one’s own errors is a fundamental ability to guide and improve behavior, with specific neural substrates in the anterior cingulate cortex (ACC). Similarly, we can monitor others’ actions and learn by observing their errors. The mirror neuron system may subserve the formation of shared representations for self-generated and observed actions, and recent research suggests that monitoring mechanisms also react to errors made by others. However, it remains unknown how these responses are modified when interpersonal context implies different goals for the actor and the observer. To investigate whether differences in social context can influence brain response to observed action errors, we manipulated competition versus cooperation between two participants taking turns in a Go/No-Go task. ERPs simultaneously recorded from both participants showed a typical negativity over frontocentral regions to self-generated errors, irrespective of interpersonal context; but early differential responses to other-generated errors only during cooperation, with sources in precuneus and medial premotor areas. Competition produced a distinct error-related negativity in ACC at later latencies. We conclude that error monitoring for others’ actions depends on their congruence with personal goals, and recruits brain systems involved in self-referential processing specifically during cooperation.

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Introduction

In team sports like football or volleyball, players do not only have to kick or hit the ball, they also have to understand or even foresee where their teammates are running or in which direction they will play the ball. In many situations of everyday life, successful interactions with other people also require a swift registration and understanding of their behavior, including when they commit errors. Indeed, there is now clear evidence that humans can represent and anticipate others' behavior in joint action (Ramnani & Miall, 2004; Sebanz, Knoblich, & Prinz, 2003). A possible neural mechanism for the coordination and monitoring of joint action could be provided by motor simulation processes that rely on the mirror neuron system (Rizzolatti, Fogassi, & Gallese, 2001). Mirror neurons are activated during own but also observed motor actions, and are therefore thought to play an important role for understanding other people's behaviors and intentions, as well as for observational learning and imitation (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 2001). Motor simulation may also underlie the monitoring of other-generated errors, since it has been suggested that similar neural processes are recruited for the detection of others' errors and one's own (Miltner, Brauer, Hecht, Trippe, & Coles, 2004; Shane, Stevens, Harenski, & Kiehl, 2008; van Schie, Mars, Coles, & Bekkering, 2004).

Although action understanding and observational learning might depend on the situational context or the relationship between the agent and the observer, very few studies have investigated the influence of social factors on the activity of the mirror neuron system (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009; Kilner, Marchant, & Frith, 2006) or on the neural representation of other-generated actions (Carp, Halenar, Quandt, Sklar, & Compton, 2009; de Bruijn, de Lange, von Cramon, & Ullsperger, 2009; de Bruijn, Miedl, & Bekkering, 2008). A recent behavioral study

(Hommel, Colzato, & van den Wildenberg, 2009) reported evidence for shared representations of action during an interactive task only when the co-actor was cooperating and friendly, but not in a competitive and hostile interpersonal setting. Other findings similarly suggest that cooperation is strongly related to self-other merging (De Cremer & Stouten, 2003), and such effect could potentially mediate the previous observations that shared action representations are enhanced by positive social relationships. However, it is unknown whether different contexts of cooperation versus competition might also affect the monitoring of action error. The aim of our study was therefore to investigate whether the neural representation of others' errors is influenced by interpersonal context, when the actor and the observer have converging or conflicting goals.

Many studies investigating brain responses to one's own errors have used EEG to record specific event-related potentials (ERPs) that are typically generated when erroneous key presses are made in choice reaction-time tasks or Go/No-Go tasks. In a typical Go/No-Go task, participants are instructed to respond to certain stimuli in "Go"-trials but to withhold their response to other, often similar stimuli ("No-Go trials"). Commission errors (or "false alarms") on No-Go-trials are known to evoke a characteristic brain response that can be recorded with EEG over frontocentral electrodes (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Coles, Meyer, & Donchin, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993): This error-related negativity (ERN or Ne) is a large negative potential peaking immediately (0-100 ms) after an erroneous motor response, and presumably reflecting an automatic detection of errors based on a comparison between the intention and execution of movement (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). The ERN/Ne is usually followed by a positive deflection (~100-300 ms), the error positivity (Pe) which is thought to denote subsequent adjustment functions (Nieuwenhuis et al., 2001). These responses are presumably generated by distinct regions in anterior cingulate cortex (ACC) (O'Connell et al., 2007; Van Veen & Carter, 2002; Vocat, Pourtois, & Vuilleumier, 2008).

Interestingly, recent studies have shown that when participants monitor errors made by another individual (e.g. the experimenter or a virtual subject), a similar ERN waveform can be recorded in the observer (oERN), with slightly later latencies (Bates, Patel, & Liddle, 2005; Miltner et al., 2004; van Schie et al., 2004). In two of the latter studies, source analysis revealed that generators of the oERN may also partly overlap with anterior cingulate areas that give rise to the ERN (Miltner et al., 2004; van Schie et al., 2004). One study also reported an observer Pe (oPe), which predicted the perceived similarity between subjects (Carp et al., 2009). These results suggest similar monitoring mechanisms for self- and other-generated errors, which might be based at least partly on the mirror neuron system and thus also subserve observational learning (van Schie et al., 2004). Correspondingly, studies using fMRI also described similar activations in medial prefrontal areas for self-generated and observed errors (de Bruijn et al., 2009; Shane et al., 2008). A critical limitation in most of these previous studies is that, in the observation condition, participants were instructed to count the errors of the observed agent, which might increase the relevance of these events and lead to target related responses partly contaminating these critical error trials. Other limitations include the use of virtual subjects or confederates in the role of observed agents, whose errors have no direct motivational relevance for the participants.

Here, we examined how brain responses to observed errors differed as a function of the social interaction between an observer and a player. Specifically, we induced a context of competition versus cooperation between two naive participants in a between-group design. EEG was recorded from sixteen pairs of volunteers, who took turns in a visual Go/No-Go task (Vocat et al., 2008) in which one of the participants (the “player”) had to press a key as fast as possible on Go-trials and to withhold response on No-Go-trials, while the other participant (the “observer”) monitored the performance of the player (see fig. 1). Three alternative predictions could be considered concerning the ERPs to observed errors in the different social contexts. 1) If error monitoring operates only on a representation of motor actions through the mirror neuron system, similar oERN and oPe should be evoked by observed errors in both the competition and cooperation contexts. 2) Instead, if monitoring operates only on abstract representations of desired goals and outcomes, congruent responses in observers should only occur for errors of cooperators; but reversed responses should be elicited in competitors, because errors made by others corresponded to a desirable outcome (wining points), whereas their success corresponded to a defeat (losing points). 3) If error monitoring operates on motor representations but more abstract goals and social relationship produce top-down influences on these representations, for instance by increasing self-other merging, then oERN and oPe amplitudes should be enhanced in cooperators and reduced in competitors.

We also asked whether any effect of the social relationship between participants on error processing would be influenced by individual factors such as empathy or aggressiveness, in keeping with the idea that early error-detection components might vary with the motivational or affective significance of errors (Hajcak & Foti, 2008).

(Please insert figure 1 about here)

Methods

Participants

Sixteen pairs of right-handed, healthy participants (total 32) with normal or corrected-to-normal vision were randomly assigned to the two experimental groups (8 males and 8 females in each group, mean age of 23.7 years in the competition and 23.4 in the cooperation group). Two additional participants had to be excluded from the analysis due to excessive movement and talking during recordings. The order of playing and observing, sitting position (left or right), and gender of the second player were counterbalanced within and kept constant between the groups. All participants gave informed consent in accordance with the ethical committee regulations of the University of Geneva and were paid 20 Swiss Francs (approximately 13 Euro) plus a bonus of up to 10 Swiss Francs depending on their individual (competition condition) or dyadic performance (cooperation condition).

Stimuli and Task

We used a slightly modified version of the No-Go task previously developed by Vocat et al. (2008). This task yields roughly equal numbers of correct responses and commission errors, with similar RTs for each, thereby allowing us to obtain reliable comparisons between hits and errors within participants, as well as between cooperation and competition. Each trial started with a black arrow, whose color changed after a random interval of 1000-2000 ms. In two third of trials (“Go-trials”), the black arrow turned green without changing its direction, and subjects had to respond as fast as possible by pressing a key with their right index finger. In the remaining trials, the arrow either turned cyan or changed direction (a sixth of trials each), requiring subjects to withhold their response (“NoGo-trials”). A black frame appeared around the arrow immediately after each key-press (correct or not) to highlight the response onset. To enforce fast responses, a time limit was initially set to 350 ms and then adapted to individual response speed during successive blocks of the task (Vocat et al., 2008). Feedback was given 1000 ms after each response, consisting of either a green dot for correct trials (fast hits on Go-trials and withheld key-press on NoGo-trials) or a red dot for incorrect or slow responses.

Across 8 successive blocks, two participants alternated their roles by either performing or observing this Go/NoGo-task (4 times each condition). Each block consisted of 60 trials and took about 5 minutes (total duration of a session ~45 minutes). To maintain sustained attention during the observation blocks and to avoid target effect on No-Go errors at the same time, observers were instructed to count silently the correct No-Go trials (i.e. successful inhibitions of the player on No-Go trials) of the player and report them to the experimenter at the end of each block. Although this instruction might lead to increased attention during observed No-Go compared to observed Go-trials, this should be similar in both experimental groups. More critically, neither correct hits nor errors *per se* were task-relevant and therefore differentially attended, unlike in previous studies that compared ERN in actors and observers (Bates et al., 2005; Miltner et al., 2004; van Schie et al., 2004).

In the competition condition, rivalry between players was induced by rewarding only the best player of a “round” (2 consecutive blocks) with an extra bonus of points (subsequently converted to Swiss Franc). In the cooperation condition, both players were rewarded as a team depending on their joint performance in a “round” (average of each participant’s results in two consecutive blocks).

Behavioral measures and questionnaires

For each participant, we calculated the median reaction times for fast hits and errors. As the distribution of reaction times across different trials of one participant are usually right-skewed (relatively few high values), medians are better suited than means in such cases. These values were submitted to repeated measures ANOVA with experimental group as between-subjects factor. Slow hits (key-presses after the time limit) were not analyzed, as they corresponded to different response latencies (unlike correct fast hits and errors that produced similar RTs). The overall performance score determining the bonus was defined as the percentage of correct fast hits plus correct No-Go trials. At the end of the experiment, participants filled three different questionnaires. The Aggression Questionnaire (TAQ) (Buss & Perry, 1992) included four subscales assessing the behavioral (physical aggression, verbal aggression), emotional (felt anger), and cognitive aspects (hostility) of aggressiveness. This scale was used because proneness to aggression could potentially influence the interpersonal relation between two participants, e.g. by enhancing competition. The Interpersonal Reactivity Index (IRI) (Davis, 1983) provides an estimate of four different dimensions of empathy: the tendency to take other’s point of view into account (‘perspective taking’), feelings of sympathy towards distressed others (‘empathic concern’), irritation and unease when confronted with emotional interpersonal situations (‘personal distress’), and the tendency to identify with the emotions and actions of fictive characters (‘fantasy subscale’). We were especially interested to investigate whether cognitive (perspective taking) or affective aspects (concern) of empathy were related to the representation of other-generated actions and errors. Additionally, we designed specific questionnaire items that provided quantitative estimates of the perceived relationship between participants (familiarity, sympathy) and allowed us to check the effects of our rivalry manipulation (competitiveness) during the experiment. This included questions about experienced happiness or discontent during errors, e.g. “During the experiment, I was happy when the other player made an error”, “During the experiment, I was happy when the other player had a correct and fast response” (see results section).

EEG Recording and Analysis

Electrophysiological data was recorded from 64 scalp electrodes in each participant simultaneously, using two Biosemi Active EEG systems. These 64 electrodes were evenly distributed over the head surface, following the extended 10-20 EEG system, and maintained with a flexible cap. Data were online high-pass filtered with 0.1 Hz and sampled at 2048 Hz. During offline processing, data was filtered with 0.5 Hz high-pass (6 dB) and corrected for eye-blinks using a standard eye blink correction algorithm, as implemented in BESA software (Berg & Scherg, 1994). Epochs from -500 to 1000 ms around own (Player condition) or other’s (Observer condition) key-presses on fast hits and commission errors were then epoched and baseline-corrected (-500-0 ms). Before averaging, trials contaminated with large and non-neurophysiological artifacts (exceeding $M = 113\mu V$, $SD = 23.5$) were removed.

Previous ERP studies have shown that the ERN component is best recorded at frontocentral electrode positions (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Holroyd & Coles, 2002; Nieuwenhuis et al., 2001). For the player condition, ERN amplitude was extracted in each participant as the minimum voltage at electrodes Fz, FCz and Cz between 0 and 100ms after response; and Pe amplitude as the maximum voltage between 100 and 300ms after response. For the observer condition, ERPs were similarly analyzed at positions Fz, FCz and Cz. Three different time-windows of interest were selected based on differential effects of experimental conditions evidenced in the grand average ERP waveforms (Figure 2B and D): the maximum voltage between 125-145 ms that characterized an early error-related negative deflection in observers (the “early oERN”); the minimum between 280-320 ms that characterized a “late oERN”; and the maximum between 320-500 ms that characterized an error-related positive deflection in observers (Carp et al., 2009; van Schie et al., 2004). The beginning of the latter time-window was chosen slightly later than in previous studies (Carp et al., 2009) in order to avoid overlap with the “late oERN” time-window.

Correlation analyses, using Pearson correlation coefficient, were also performed between amplitude differences between errors and fast hits (calculated for each subject separately) and several behavioral measures of interest (as obtained from the questionnaires). Finally, we computed the topographic distribution of the ERP effects using difference maps that were determined by subtracting the grand average amplitude for fast hits from the amplitude for errors at each electrode at the time around maximal difference (see fig. 2G).

Source Analysis

Data-driven inverse solutions were calculated on the difference waveforms (filtered 1-20 Hz) between grand average ERPs of errors and fast hits using BESA software (MEGIS software GmbH). For both the player and observer conditions, a multiple dipole approach with a 4-shell ellipsoidal head model was used. Because the player ERN was similar in both groups (see ERP results here below), we used the averaged waveform from cooperation and competition and analyzed dipole sources during a large time window covering both the ERN and the Pe components (from 0 to

250 ms), for which sources in the ACC have been previously reported (Herrmann, Römmler, Ehlis, Heidrich, & Fallgatter, 2004; O'Connell et al., 2007; Van Veen & Carter, 2002; Vocat et al., 2008). For the observer conditions, smaller time windows were used to examine each of the differential error-related components. For each source model, one initial dipole was fitted, and then another added and fitted until the explained variance reached 85 %.

Results

Behavioral results

Average median reaction times were comparable in the two experimental groups for correct responses (fast hits, 252 ms during competition and 241 ms during cooperation) as well as errors (257 ms and 256 ms respectively). An analysis of variance (ANOVA) with response condition (fast hits, errors) as within-, and group (competition, cooperation) as between-subjects factor confirmed an absence of significant effects of condition, $F(1, 30) = 3.28$, $p = .08$, group, $F < 1$, or the interaction term between these two factors, $F < 1$. The overall mean accuracy (the proportion of fast hits, slow hits and correct No-Go trials together) was also comparable in the competition (86.6%) versus cooperation groups (84.5%), $t(30) = .68$, $p = .50$. Thus, as intended by our task design, we obtained a roughly equal number of correct responses in both groups (fast hits, 53.3 trials in competition and 61.1 in cooperation, $t(30) = -1.56$, $p = .13$), as well as an equal number of slow hits (102.8 trials in competition, 93.9 in cooperation, $t(30) = 1.64$, $p = .11$) and errors (28.3 and 32.2), $t(30) = -0.66$, $p = .51$), enabling a direct comparison of the ERP data between these two groups in the absence of reliable behavioral differences.

To compare the correctness of counting during the observer blocks, the sum of divergent counts per block was calculated. It did not differ between the two groups, *t*(30) = .73, *p* = .47.

Personality questionnaires revealed no differences between experimental groups in aggressiveness, as measured by the TAQ, *t*(30) = -.38, *p* = .71, or in empathy, as measured by the IRI (Davis, 1983), *t*(30) = -1.48, *p* = .15. An additional questionnaire was also constructed to assess rivalry between participants and perceived relationship in the different experimental conditions, allowing us to verify whether our manipulation of interpersonal context was efficient. Three of these items discriminated between the competition and the cooperation group: "During the experiment, I felt happy when the other player made an error", *t*(30) = 2.44, *p* = .02 (average on a scale from 1 to 9: competition 3.3, cooperation 1.7); "During the experiment, I felt happy when the other player made a correct and fast response", *t*(30) = -2.71, *p* = .01 (competition 5.3, cooperation 7.4); and "During the experiment, my main goal was to obtain a better score than the other player", *t*(30) = 2.03, *p* = .05 (competition 6.5, cooperation 4.9). Items that aimed to measure other factors like task involvement (e.g. "During the task, I was concentrated") or friendship (e.g. "The other player and me, we are close friends") did not differ between groups. Altogether, these results verified that participants in the competition and cooperation groups showed no intrinsic personality differences, but were reliably influenced by our contextual manipulation.

Electrophysiological results

We analyzed response-locked event-related potentials (ERPs) from the player and observer at electrodes Fz, FCz, and Cz, using repeated measure ANOVAs with electrode position and response condition as within-, and experimental group as between-subject factors. Fig. 2 presents the grand average ERPs at electrode FCz, where error-related responses were most pronounced. In the player (fig. 2A and C), a classical ERN was elicited by errors, relative to fast hits. Repeated-measure ANOVA on amplitudes during the ERN time-window confirmed main effects of response condition (higher amplitudes for errors than fast hits), $F(1, 23) = 15.3$, $p < .001$, and electrode position, $F(2, 46) = 29.3$, $p < .001$. There was no main effect of group, $F < 1$. The interaction between electrode position and response condition was significant, $F(2, 46) = 5.69$, $p = .006$, as well as the interaction between group and position, $F(2, 46) = 3.36$, $p = .043$. But more importantly, there was no significant interaction between group and response, $F < 1$, and no three-way interaction between position, response, and group, $F(2, 46) = 1.34$, $p = .27$.

Similarly, for the Pe time-window, ERP amplitudes were larger following errors than fast hits, $F(1, 23) = 54.3$, $p < .001$. There was also a main effect of electrode position, $F(2, 46) = 12.5$, $p < .001$, and a significant interaction between position and response, $F(2, 46) = 11.8$, $p < .001$. Again no significant difference between the competition and cooperation conditions was found, $F < 1$; no interaction between group and response condition, $F < 1$; and no three-way interaction, $F < 1$. Thus, the monitoring of self-generated errors by the player was similar in the two interpersonal contexts.

By contrast, error-related responses in the observer were significantly modulated by interpersonal context (fig. 2B and D). Substantial differences between observed errors and observed fast hits in the grand average ERP waveforms at frontocentral electrodes occurred within two different time windows. During an early time-window of 125 to 145 ms post-response, observers in the cooperation condition showed a distinctive negativity on error trials (early “oERN”, fig. 2B) that arose on top of a larger ongoing positivity. This transient negative activity was not seen in the competition group (fig. 2D, see also difference waves in fig. 2F). The topography of this early oERN component showed a frontocentral maximum, similar to that of the player’s ERN (fig. 2G). ANOVA on the amplitudes of this component revealed a trend for the main effect of response condition, $F(1, 25) = 3.14$, $p = .089$, no group effect, $F < 1$, but most critically, the interaction between response condition and group was significant, $F(1, 25) = 9.87$, $p = .004$. There was also an effect of electrode position, $F(2, 50) = 4.12$, $p = .022$, but no interactions between position and response condition, or between position and group, $F < 1$. Planned comparison of the critical response conditions using Tukey tests showed that amplitudes differed significantly between errors and fast hits during cooperation only, $p = .008$, while there was no difference during competition, $p = .78$. The three-way-interaction between position, response and group was not significant, $F < 1$.

However, the topographical difference map at the time of this early oERN effect also showed a relative positivity at occipital electrodes (see fig. 2G), which could stem from additional differences in the N1 component of the visual evoked potential that was elicited by the “response frame” at the same latency. To exclude that the effect seen at frontocentral positions originated from the polarity reversal of this more posterior difference, we calculated a repeated measures ANOVA on the peak negativities between 140 and 160 ms at electrode PO4, where the N1 component reached its maximum amplitude. This analysis disclosed a main effect for response condition, $F(1, 25) = 10.66$, $p = .003$. There was no significant main effect for group, $F < 1$, and unlike for the oERN, no interaction effect of group x response condition, $F < 1$, confirming that differential effects observed at electrode FCz as a function of our contextual manipulation were not simply capturing differences in early visual processing within the occipital lobe. Furthermore, in both groups, N1 amplitudes were larger for observed fast hits on Go trials (mean = -4.83) than for observed errors on No-Go trials (mean = -3.53), even though the visual display was actually identical in both trial types (i.e. black frame appearing to signal the key press). This visual effect could be explained by the observer expecting a response in the Go-trials, but not in the NoGo-trials, with a probable enhancement of the neural reaction to expected events (Correa, Lupiáñez, Madrid, & Tudela, 2006; Nobre, Correa, & Coull, 2007). This result provides additional evidence for general attention and involvement of the observing participants during the task performed by their partner, in both experimental groups. Importantly, however, this modulation of the N1 did not parallel the selective effect of cooperation on the early oERN component.

In later time-windows, cooperation and competition produced two other distinct effects. From 280 to 320 ms, another relative negativity ("late oERN") arose selectively in the competition condition. Neither response condition nor group produced significant main effects, $F < 1$, but their was a main effect of electrode position, $F(2, 50) = 9.09$, $p < .001$. The interaction between position and group, $F(2, 50) = 2.00$, $p = .15$, and the interaction between position and response, $F < 1$, were not significant. By contrast, the interaction between response condition and group was again highly significant, $F(1, 25) = 23.5$, $p < .001$. The three-way interaction between electrode position, response condition and group was also significant, $F(2, 50) = 4.00$, $p = .025$. Tukey tests were performed to investigate this interaction effect in detail.

For observers in the competition condition, the commission errors of their partner produced, relative to the correct fast hits, a significantly higher negativity at all three electrode positions (Fz, FCz, Cz: all $p < .001$), peaking at 300 ms. This late oERN also showed a frontocentral topography very similar to the ERN recorded in players (fig. 2G). In the cooperation condition, an opposite pattern was seen during the same time-interval: Larger positive potentials were elicited by observation of errors than by observation of fast hits, at all electrodes Fz, FCz and Cz (all $p < .001$). This relative positivity in the cooperation group extended from 250 to 500 ms and closely resembled the oPe (Carp et al., 2009) in both latency and topography (Fig. 2G). ANOVA on the maximal positivity during the time-range of 320-500 ms (to avoid overlap with the late oERN window) revealed a main effect of response condition, $F(1, 25) = 8.16$, $p = .009$, a main effect of electrode position, $F(2, 50) = 7.80$, $p = .001$, but no main effect of group, $F < 1$. No significant interactions were found between position and group or position and response condition, but more critically, a response x group interaction, $F(1, 25) = 10.0$, $p = .004$. Accordingly, planned comparisons with Tukey tests confirmed that only in the cooperation condition, the amplitudes for observed hits and errors differed significantly, $p = .001$, whereas there was no significant difference during competition, $p = .99$. The response x group x electrode interaction was not significant, $F(2, 50) = 1.11$, $p = .34$.

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Correlations between ERP components, performance, and questionnaires

Based on the direct-matching hypothesis of mirror neurons (Gallese et al., 1996; Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti et al., 2001), one could assume a close relationship between the brain response to own and other's errors. However, across all subjects, there were no significant correlation between the mean amplitude of the player ERN and his/her early oERN, late oERN, or oPe. The same was true for correlations of the player Pe with the observer ERP components. We also hypothesized that brain responses to the observation of other's actions might be influenced by empathy and cognitive perspective taking, or conversely aggressiveness. Yet, no significant relationship was found between any error-related components and the IRI or TAQ scores.

More critically, to test whether the distinct ERP effects in the observer condition were directly linked to interpersonal context, we conducted a further correlation analysis on items from our questionnaire on perceived relationships (see methods). Across the pooled sample of all participants, the size of the negativity corresponding to the early oERN (at 135 ms) correlated significantly ($p < .05$) with four items of this questionnaire: goal to perform better than the other player ($r = .40$), happiness when the other player made a mistake ($r = .62$), joy when the other player made a correct response ($r = -.47$), and experience of discontent when the other made a correct response ($r = .54$). These items all concerned competitiveness and rivalry-related emotions during the task, which appeared to reduce the early oERN difference. Although these correlations demonstrate a direct link between oERN and the subjective experience of the participants, they might also reflect a categorical effect of our experimental manipulation (cooperation vs. competition) on both the ERPs and the questionnaire items. However, when running the correlations separately for each group, the last two effects (reduced joy and increased discontent for correct responses) were still significant in the competition group.

In contrast, the size of late oERN correlated significantly with four other items from this questionnaire, which all indexed sympathy and friendship between the two participants. These items were not different for the two experimental groups. Thus, a smaller negativity of the late oERN (at 300 ms) correlated with perceived closeness of the partner (*r* = .43), how familiar the partner was (*r* = .49), how often they saw each other (*r* = .39), and how likeable they found each other (*r* = .39). Hence, the early and late oERN each reflected distinct monitoring dimensions that were differentially sensitive to the social valence of relationships between partners. These findings indirectly support the specificity of these two distinct components in the ERPs elicited in observers and their sensitivity to social context. Finally, no specific correlation with our questionnaire items was observed for the oPE.

Source Analysis

Lastly, we performed a complementary analysis to estimate the neural generators of these ERP effects. For the player condition in both groups, a solution with two dipoles explained >95 % of variance during the period covering both the ERN and Pe (similar results were obtained by analyzing each peak separately). One dipole was located in the dorsal ACC (Talairach coordinates -0.1, 26.2, 33.6), consistent with previous studies on error monitoring (Falkenstein et al., 1991; Gehring et al., 1993; Vocat et al., 2008). A second dipole was also found in deeper medial diencephalic regions (coordinates 0.5, -16.6, -22.4).

For the observer condition, our source analysis focused on each of the three time-windows when significant differences between errors and hits were found. For the early oERN seen in the cooperation group (125-145 ms), our results revealed a solution with one dipole that was located in the left precuneus (Talairach coordinates -12.6, -48.0, 45.5) and explained 85.6 % of variance (fig. 4A). For the late oERN (280-320 ms) elicited during competition, a two dipole solution was found, explaining 87.4 % of variance (fig. 4B): A first dipole was situated in the ACC (coordinates 2.3, 18.5, 27.8), and a second one in occipital visual areas (-12.4, -88.3, 5.5). For the oPe peak difference (250-350 ms) in the cooperation group, a solution with three dipoles explained 85.1 % of variance (fig. 4C). The first dipole was located in the paracingulate/SMA (coordinates -6.2, 3.0, 53.2), the second in the left occipital lobe (-19.8, -84.3, -6.7), and the third in the right cuneus (12.9, -75.0, 31.8).

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Discussion

Our study is the first to demonstrate that errors made by others produce distinctive electrophysiological brain responses in observers that depend on the social cooperation with the actor. These results indicate that action monitoring is not only sensitive to perceived conflict with the actor's intentions, but also to conflict with the observer's own intentions and goals. For players, we found that the ERN and Pe were unaffected by changes in the rivalry context. Being in competition or in cooperation with another person, who is observing the behavior of the player, did not evidently change error monitoring processes or motivation to succeed, as far as ERP results reveal in this particular task setting. Because our experimental paradigm imposed a very strict time limit, it is likely that players had to focus on their task similarly in both conditions, irrespective of their relation to the observer. Thus, probably no attentional resources were left for the observing partner sitting next to them or for a systematic influence of the interpersonal relationship between them.

In sharp contrast, brain responses to observed errors of others were strongly influenced by the interpersonal relation of cooperation versus competition, suggesting that the monitoring of other-generated actions is significantly modulated by social context.

Effects of cooperation on early oERN and oPE

During cooperation, we found that the observer exhibited two error-related components in ERPs post-response onset, an early oERN and an oPe, similar to the results of previous studies on observation (Carp et al., 2009; Miltner et al., 2004; van Schie et al., 2004). It is noteworthy that the error representations do not seem to depend on a direct observation of the incorrect movement, because the player’s hand was not positioned in the central but rather peripheral visual field of the observer, and the latter was thus looking at the computer screen rather than at key-presses of the player. This converges with the notion that error monitoring does not operate on simple motor characteristics of actions or overt execution, but on more abstract representations of desired goals. Thus, no such differential responses to errors were seen in observers during competition, when their own goals conflicted with those of the observed actor.

Another important point is that to ensure attention to the player’s performance, we did not ask the observer to count errors made by their partner, but to track correct No-Go trials. This is unlike previous studies that required counting errors and therefore directed attention of the observer to these “target” events, which might be an important confounding factor for ERPs recorded in this condition (Carp et al., 2009; Miltner et al., 2004; van Schie et al., 2004). Thus, correct Go trials and incorrect No-Go trials were equally attended in both groups and similar to each other in that they involved a key-press with similar visual events (response frame) in both conditions.

In our study, the early oERN activity that was elicited by observed errors of cooperators arose with a rapid latency around 135 ms, but was delayed relative to the ERN elicited by one’s own errors and associated with differential neural activity in the precuneus, rather than with typical sources in ACC (as seen for the ERN of players). This finding converges with a recent fMRI study on error observation (Shane et al., 2008) in which the precuneus was also more activated for observed errors compared to observed correct responses, alongside with dorsal ACC, supplementary motor area, and paracingulate areas. The precuneus is generally thought to be involved in mental imagery and memory processes with self-referential or first-person perspective components, including body image representation and agency perception (Cavanna & Trimble, 2006). Moreover, an fMRI study on the perception of self and other agency found higher precuneus activity when subjects attributed an effect of their own actions to the action of others (Farrer & Frith, 2002). Activity in the precuneus during the early oERN could therefore reflect an early stage of error processing, and the attribution of agency to the other player, perhaps using a first-person perspective, which was specific for cooperation and did not occur during competition. Cooperation has been shown to enhance children’s attribution of other’s actions to themselves (Sommerville & Hammond, 2007), and self-other merging can enhance cooperation in social dilemma games (De Cremer & Stouten, 2003), while conversely competition is thought to strengthen the distinction between self and other(s) (Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004).

Consistent with this notion, we also found that the early oERN activity seen during cooperation was larger when observers reported less rivalry and less happiness in response to other’s errors. Hence, the early oERN and the related precuneus activity could be driven by cooperation, and possibly self-other merging, which might lead to enhanced representation of the other’s actions in a self-referential perspective in this condition, as compared with more separated self-other representations during competition. However, the results of our source analyses based on inverse solutions should be interpreted with caution. A potential limitation might ensue from the concomitant overlap with the visual component N1, which arose at a similar latency as the early oERN and could therefore influence the estimated sources during this time window, by shifting possible generators in direction of more posterior visual areas. Further neuroimaging investigation with higher anatomical resolution (such as fMRI) will be needed to confirm the role of the precuneus in error detection or action observation, and its modulation by cooperation or self-other merging.

Our results also revealed that cooperation produced another specific response to observed errors, corresponding to the oPe, which had longer latencies (from 250 to 350 ms) and a more widespread network of intracerebral generators. This ERP activity pattern had a distinctive topography resembling previous EEG results on observed errors (Carp et al., 2009) and was better explained by a network of generators including the paracingulate and medial premotor areas, as well as visual areas in occipital cortex, which altogether might further contribute to representing agency and motor action of the other in a self-relevant perspective. Remarkably, both the paracingulate and supplementary motor areas have been shown to be involved in error monitoring and conflict detection during self-generated actions (Hester, Fassbender, & Garavan, 2004; Klein et al., 2007; Ullsperger & von Cramon, 2001), and these regions might therefore be similarly recruited when observing errors during cooperation, but not during competition. This would further support the notion that cooperation enhanced a first-person perspective in the observer and activated internal representations of motor action and motor correction during observation, unlike competition.

It must be noted that the observer ERP waveforms in the cooperation condition arose on the top of a larger positivity post-response onset, which could tentatively be interpreted as a P3-like component with a shift in latency for observed errors in comparison to observed fast hits. Several studies have reported P3 components in response to Go and No-Go stimuli (e.g. de Bruijn et al., 2008) and there is also evidence for a P3 response to No-Go stimuli that are irrelevant for the participant but relevant for a partner (Sebanz, Knoblich, Prinz, & Wascher, 2006). However, it is important to underscore that in our study, the ERPs recorded in the observer conditions always represent an addition of error-related components and visual evoked components (due to the visual frame appearing around the target directly after each key-press). Thus, it is unlikely that the positive waveforms following observed responses (hits and errors) represent a true P3 component with latency shifts in the cooperative context. In addition, the peak amplitudes of this positivity arises around 150 and 220 ms respectively, which would be too early for P3. Hence, the appearance of the positive waveform is probably due to an overlap of the visual evoked N1 and P2 with the error-related components described above.

Effects of competition on late oERN

Whereas cooperators showed two distinct responses to observed errors in their partner, a very different electrophysiological pattern was seen in competitors. While the early oERN and oPE were absent, a late oERN component selectively occurred during competition, partly overlapping with the time-window of the oPe elicited in the cooperation condition. In addition, the amplitude of this late oERN was smaller for participants who reported more friendship and sympathy with the other player. The peak of this late oERN (around 300 ms) was found during the time-interval of the feedback-related negativity (FRN), a typical deflection similar to the ERN but peaking around 250-300 ms after the presentation of negative outcomes (Gehring &

Willoughby, 2002) or externally caused failures in expected outcomes (Gentsch, Ullsperger, & Ullsperger, 2009). Recent evidence suggests that the FRN may also arise in an observer (oFRN) in response to another person's gains or losses (Yu & Zhou, 2006), presumably reflecting an evaluation of outcomes based on internal criteria of the observer (Itagaki & Katayama, 2008). However, in our study, the late oERN was related to observed errors, but not to an external feedback. Furthermore, if the late oERN in our task reflected some feedback-related process, it should also be more negative for observed hits than for observed errors, because the latter is a positive outcome for a competing player. This was not the case, and it is therefore unlikely that the late oERN, despite its similar latency and topography, involved a true FRN-like (or oFRN) component.

Rather, we surmise that the late oERN may reflect the mere detection of observed errors, or unexpected events, independent of any reward value (see de Bruijn et al., 2009), with a later latency than error detection mechanisms associated with the early oERN in cooperative observers. This would be consistent with our source analysis that indicated possible neural generators in the ACC, similar to studies of the ERN (O'Connell et al., 2007; Van Veen & Carter, 2002; Vocat et al., 2008) and previous reports on error observation (Miltner et al., 2004; van Schie et al., 2004). In any case, the differences in latencies, correlation patterns, and neural sources found for early and late oERN point to the existence of two distinct processes involved in the monitoring of other-generated actions. These mechanisms might be similarly involved in the detection of other-generated errors, but with differential recruitment as a function of social context or goals, as reflected by the differential impact of cooperation and competition on the early and late oERN components. Functional imaging studies should help clarify this issue in the future.

The absence of the early oERN and oPe in the competition condition might call for additional comments. Because our study used a between-subject-design, intrinsic differences between the two samples could potentially account for distinct patterns of responses to other's errors. This is however unlikely, since we carefully matched both groups for age, sex, as well as other personal variables; and we observed no differences in average performance, reaction times, or self-reported empathy and aggressiveness. Furthermore, the ERN and Pe measured in players was similar in the competition and cooperation conditions. The two groups thus only differed on the experimentally manipulated factor of their social relationship, and accordingly, showed distinct responses to errors only during observations of their partner. A recent study by De Bruijn and colleagues (2008) suggested that the most successful players in a competitive Go/NoGo task are better able to inhibit shared representations of the action of others, when these could interfere with their own action plans (but this study did not investigate effects of cooperation). This raises the possibility that in our study, competitors could primarily focus on their task of counting correct No-Go trials and be less involved in the representation of the other's goals. There was however no difference in the correctness of the counting in both groups. Furthermore, the effect of expectancy on the visual component N1for correct hits compared to errors suggests a high level of attention during observation in both conditions.

Another alternative explanation for ERP differences between the two groups may be that observers in the cooperation condition were 'pseudo-responding' to the stimuli (e.g. silently performing the task) instead of monitoring the other. This is very unlikely, however. First, observers were clearly paying attention to the player's performance, as indicated by their high accuracy in counting correct No-Go trials (see above). Second, if the cooperating observers were simply pseudo-responding, without monitoring the other, they would presumably not produce errors in the same trials as the player, and not show different N1 amplitude to the correct response relative to unexpected errors made by the other.

Effects of social context on action representation

Taken together, our ERP results argue against the possibility that the monitoring of action errors made by others is based on shared motor representations that are not influenced by situational factors. Our results also contrast with the assumption that error-related responses might only reflect the reward value or personal relevance of the observed action. In this case, opposite effect for cooperators and competitors should be observed with an oERN to errors in cooperator, but an oERN to hits in competitors (see Itagaki & Katayama, 2008). Instead, our findings suggest a top-down influence based on social factors that can selectively enhance the recruitment of shared representations and the appraisal of observed errors during cooperation, but not in competition. We propose that the major impact of cooperation is to foster self-other merging (De Cremer & Stouten, 2003; Sommerville & Hammond, 2007), and thus create a "sense of we" during observed actions. Self-other merging could then enhance shared motor representations, by increasing activity in the mirror neuron system and monitoring from a first-person perspective. In contrast, competition between participants could entail a more self-centered perspective and greater differentiation with the other, leading to delayed error processing. This would converge with the recent findings of Hommel and colleagues (2009), who reported evidence for shared task representations (as reflected by an interactive Simon effect on reaction times) only when participants performed the task with a friendly and cooperative partner, but not with an intimidating and competitive partner.

More generally, if cooperation can enhance shared representation, whereas competition and rivalry diminish shared representation, it is plausible to predict that the mirror neuron system and the capacity of understanding others' behavior might be enhanced for in-group members, but inhibited for out-group members as well as during states of rivalry and conflicts. Such effects might have profound implications for aggressive and violent behaviors. Further research is needed to better understand the exact mechanisms of cooperative and competitive states, and their influence on shared representations and self-other relations.

In conclusion, we show that brain responses to other-generated errors are influenced by the interpersonal context, whereas processing of self-generated error is not. In a relation of cooperation, participants exhibited specific oERN and oPe components to observed errors, possibly reflecting enhanced attribution of agency and self-relevance to others' action. During competition, only a late oERN was elicited in ACC, presumably reflecting later error detection during social conflict and a reduced shared representation of the rival's intentions.

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Figure Legends

Figure 1: Experimental setup. Two participants were sitting next to each other. They alternated roles; either performed the speeded Go/No-Go task (4 blocks) or observed the other player's performance (4 other blocks, in alternation). Our experimental manipulation induced either cooperation or competition between the two participants.

Figure 2: Grand average response-locked ERP waveforms at electrode FCz and corresponding topographical maps. ERPs elicited by errors in No-Go trials and fast hits (correct Go response) are shown for each condition: (A) Player and (B) observer in the cooperation condition. (C) Player and (D) observer in the competition condition. The difference ERPs (errors – fast hits) reflecting selective neural activity elicited by errors is shown (E) for the player condition in both groups and (F) for the observer condition in both groups. (G) Topographic difference maps at the time of each error-related components, for both the cooperation and competition groups. The anterior scalp region is up.

Figure 3: ERP effects for all frontocentral electrodes (Fz first column, FCz second column, and Cz third column). The first two rows depict the mean amplitudes in the player conditions, for the ERN and Pe respectively. The last three rows show the mean amplitudes of the error-specific components in the observer condition, including the early oERN, late oERN and oPe. Note that the amplitude scale is reversed (negativity upward) corresponding to the typical ERP displays.

Figure 4: Inverse solutions for the player and observer ERP components. (A) Two sources were found for the player condition, 0-250 ms after response (combined for cooperation and competition). (B) One dipole in the precuneus was found for the early oERN in the cooperation condition, explaining 85.6 % of variance. Three dipoles in paracingulate, cuneus and inferior occipital areas explained 85.1 % of variance during the oPe in the cooperation group. (C) Two dipoles in ACC and occipital lobe explained 87.4 % of variance during the late oERN in the competition condition.

Figure 1

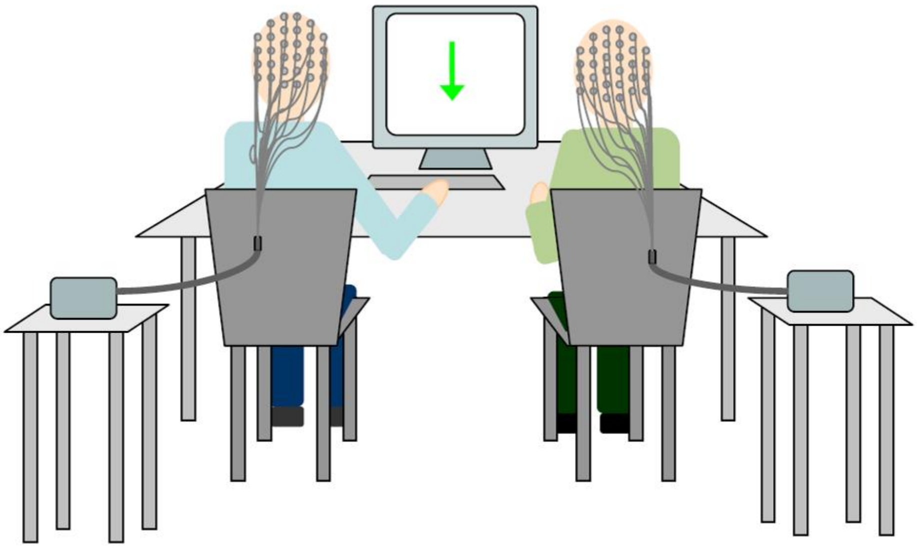
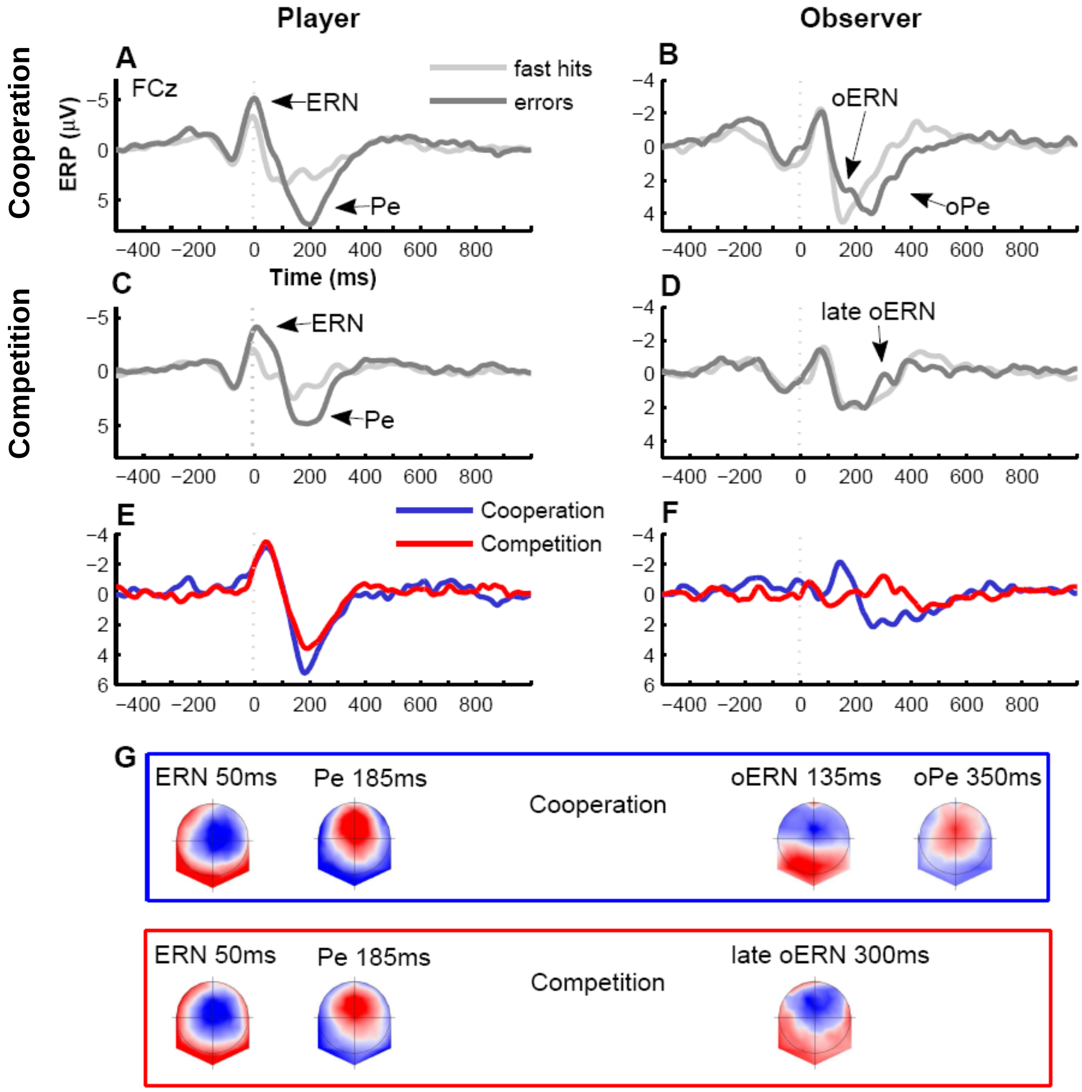


Figure 2



Player
Observer
Cooperation
Competition
A
FCz
ERP (μV)
−5
0
5
ERN
Pe
fast hits
errors
−400 −200 0 200 400 600 800
Time (ms)
B
−4
−2
0
2
4
oERN
oPe
C
D
late oERN
E
Cooperation
Competition
6
F
G
ERN 50ms
Pe 185ms
Cooperation
oERN 135ms
oPe 350ms
ERN 50ms
Pe 185ms
Competition
late oERN 300ms

Figure 3

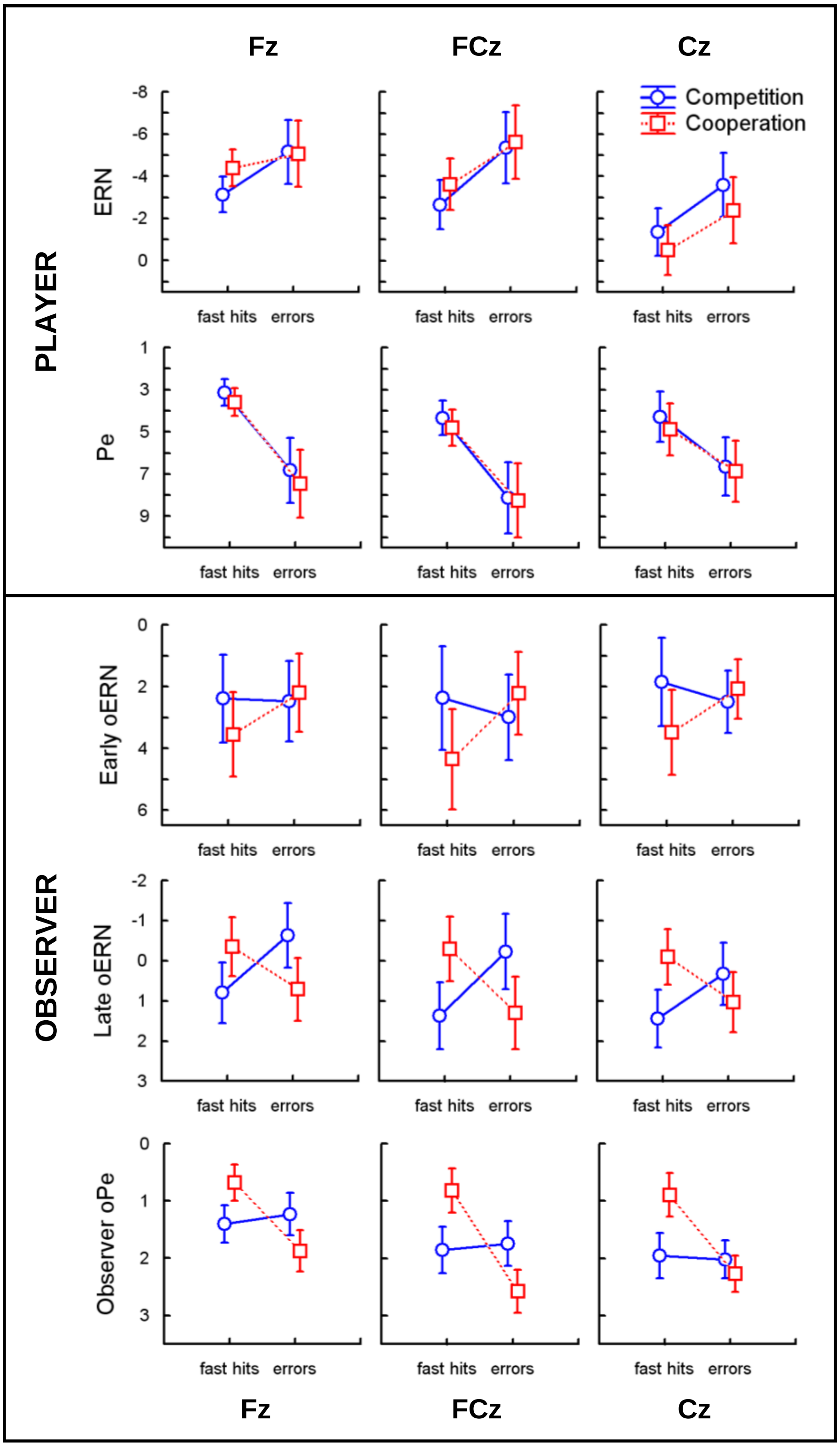
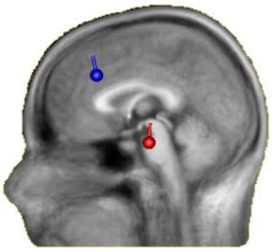
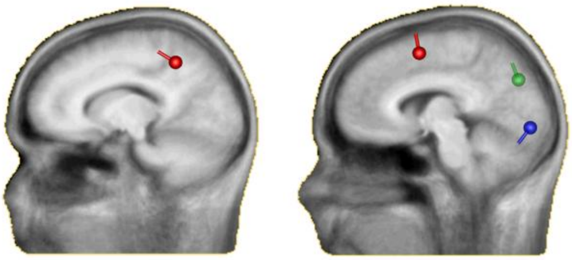

Fz
FCz
Cz
Competition
Cooperation
PLAYER
ERN
-8
-6
-4
-2
0
fast hits
errors
Pe
1
3
5
7
9
OBSERVER
Early oERN
0
2
4
6
Late oERN
-2
-1
0
1
2
3
Observer oPe
0
1
2
3
Fz
FCz
Cz

Figure 4

A) Player 0-250ms (ERN and Pe)



B) Observer Cooperation



oERN (125-145 ms) oPe (250-350 ms)

C) Observer Competition

late oERN (280-320ms)