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Violating body movement semantics: Neural signatures of self-generated and external-generated errors

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ABSTRACT

How do we recognize ourselves as the agents of our actions? Do we use the same error detection mechanisms to monitor self-generated vs. externally imposed actions? Using event-related brain potentials (ERPs), we identified two different error-monitoring loops involved in providing a coherent sense of the agency of our actions. In the first ERP experiment, the participants were embodied in a virtual body (avatar) while performing an error-prone fast reaction time task. Crucially, in certain trials, participants were deceived regarding their own actions, i.e., the avatar movement did not match the participant's movement. Self-generated real errors and false (avatar) errors showed very different ERP signatures and with different processing latencies: while real errors showed a classical frontal-central error-related negativity (Ne/ERN), peaking 100 ms after error commission, false errors elicited a larger and delayed parietal negative component (at about 350–400 ms). The violation of the sense of agency elicited by false avatar errors showed a strong similarity to ERP signatures related to semantic or conceptual violations (N400 component). In a follow-up ERP control experiment, a subset of the same participants merely acted as observers of the avatar correct and error movements. This experimental situation did not elicit the N400 component associated with agency violation. Thus, the results show a clear neural dissociation between internal and external error-monitoring loops responsible for distinguishing our self-generated errors from those imposed externally, opening new avenues for the study of the mental processes underlying the integration of internal and sensory feedback information while being actors of our own actions.

1. Introduction

Humans can be successfully embodied in a surrogate body, either of an avatar (Slater et al., 2010; Banakou et al., 2013) or a robot (Kishore et al., 2014), opening a number of interesting scientific questions. For example, are we able to clearly discriminate whether the origin of an action is due to the intention of the human participant or the surrogate itself? Furthermore, to what extent is our brain able to distinguish self- vs. externally generated erroneous actions which may undermine one's natural sense of agency? Here, we shed light on this issue describing different neurophysiological signatures associated to both types of erroneous actions (self-generated vs. externally imposed errors) in a scenario with embodiment in a full virtual surrogate body.

In normal circumstances, when our ongoing actions and the predicted sensory consequences of these actions (feedback) are coherent, we experience the sensation of agency with respect to our actions ("this action is mine"), and we are typically not even aware of such considerations (Pacherie, 2001; Gallagher, 2005). However, in the case where there is a conflict between the predicted consequences of our actions and their actual consequences (Slachevsky et al., 2001; Haggard and Chambon, 2012), we might detect an agency violation through an error detection mechanism (referred to here as external error-monitoring loop—*E-eml*). This mechanism might be constantly checking whether the final sensory feedback is coherent with expected sensory consequences of our actions, created using an internal (*efference*) copy of our motor commands. These sensory feedback estimations during movement may rely strongly on previous representations of the body in terms of limb position, movement, or posture which normally give us a naturally sense of being the agents of our actions (Giummarra et al., 2008). In the case of a mismatch

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in this comparison between expected and actual sensory feedback outcomes, a disruption of the sensation of agency might be elicited (Synofzik et al., 2008).

While this *E-eml* might be constantly checking the congruency between our external and internal worlds, a concurrent internal and rapid error detection mechanism evaluates whether our ongoing motor plans are correct, implementing very fast corrective actions in order to prevent and abort the production of erroneous responses. Several models have proposed that an internal forward signal – *efference copy* – is used to generate constant predictions of the consequences of our actions which are used to compute error deviations from the expected goal even before the action has been completed (Holst and Mittelstaedt, 1950; Wolpert and Miall, 1996; Jeannerod, 2006; Crapse and Sommer, 2008). This *internal error-monitoring loop* (*I-eml*) has been associated with the *error-related negativity* or *error negativity* (Ne/ERN), an event-related potential (ERP) component appearing approximately 60 ms after the commission of a real error (Falkenstein et al., 1990, 1991; Gehring et al., 1993; Rodriguez-Fornells et al., 2002; Holroyd et al., 2005) and elicited in the anterior cingulate cortex (Ullsperger and von Cramon, 2001; Holroyd et al., 2004; Marco-Pallarés et al., 2008).

Even though these two error detection mechanisms – *E-eml* and *I-eml* – rely on similar representations (both rely on the efference copy), the computations that each performs involve access to different types of feedback information. The main aim of the present research was to functionally dissociate the neurophysiological mechanisms underlying the external and the internal EML. To accomplish this goal we performed two ERP experiments. In Experiment 1, we recorded for first time ERPs in healthy participants embodied in a virtual body (Slater et al., 2010) while they carried out an error-prone reaction time task (Rodriguez-Fornells et al., 2002) in a fully immersive virtual environment (IVE) (see Fig. 1a and Movie 1 in Supplementary Material). Critically, on a few occasions, participants' correct responses were falsified by an "erroneous" movement of their embodied avatar (i.e., avatar errors), which perturbed their sense of agency. ERP signals related to self-generated errors and avatar errors were then compared. While the elicitation of the ERN component was expected for self-generated errors (as a reflection of the *I-eml*), no specific prediction was made regarding externally generated (virtual body) errors. Experiment 2 was carried out in order to rule out the possibility that the ERP effects observed in Experiment 1 for external-generated errors could have been due to the mere observation of a virtual human performing a wrong action rather than the output of the external-error-monitoring loop (*E-eml*).

2. Materials and methods

2.1. Participants

Eighteen neurologically healthy right-handed volunteers from the Faculty of Psychology at the University of Barcelona participated in the first experiment (Experiment 1) (6 men; mean age, 26 ± 7 years). Two weeks after the participation in the main experiment, nine participants (3 men; mean age, 25 ± 8 years) agreed to return to the lab to participate in a control experiment (Experiment 2). All gave written informed consent according to the declaration of Helsinki and were paid for their participation. The ethical committee from the University of Barcelona gave approval to the project (Institutional Review Board IRB 00003099).

2.2. Apparatus

Participants were fitted with a stereo NVIS nVisor SX111 head-mounted display (HMD). This has dual SXGA displays with 76°H × 64°V degrees field of view (FOV) per eye, totaling a wide field of view 102° horizontal and 60° vertical, with a resolution of 1280 × 1024 per eye displayed at 60Hz. Head tracking was performed by a 6-degrees of freedom (DOF) Intersense IS-900 device.

A gender-matched virtual body (or avatar) was displayed from a first person perspective (1PP) with respect to the virtual body's eyes, so that it visually substituted the real body of the participant (see Fig. 1; see also Movie 1 at the Supplementary Material). The position of the participants' real hand was tracked using an optical infrared system (12 camera OptiTrack). The whole arm kinematics (hand, elbow, and shoulder positions and rotations) were computed from the hand position using inverse kinematics. Our setup supported the real-time display of the avatar with 6 DOF in the head and 4 DOF in the right arm giving the participant strong visual–motor coherence between real and virtual right-arm movements. The virtual environment was programmed in the XVR system (Tecchia et al., 2010) and the virtual character displayed through the HALCA library (Gillies and Spanlang, 2010; Spanlang et al., 2014).

2.3. Procedure

2.3.1. Experiment 1

Participants performed a standard error-prone Eriksen flanker attention task (Rodriguez-Fornells et al., 2002) and were required to

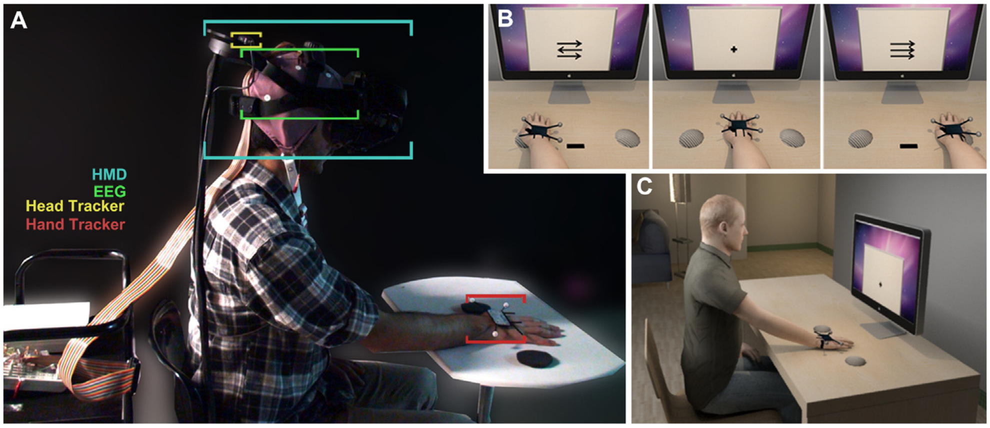

Fig. 1. Experimental design used in Experiment 1. (A) Participant in the laboratory with the head-mounted display (HMD), electroencephalography (EEG), and the head and hand tracking systems. (B) First person perspective (1PP) of the virtual arrow flanker task. Participants were instructed to perform fast movements with the right hand in the direction of the central arrow. After each movement, the hand returned to the starting position (middle panel). The virtual hand followed the tracked real hand, but in some trials the displayed virtual hand movement was incongruent (InCM) with the participants' real movements, thus generating an "false(avatar) error." Three conditions were relevant for the EEG analysis: correct responses, real errors, and false errors. (C) Gender-matched avatar of the participant in the immersive virtual environment (IVE).

respond quickly to left or right-pointing arrows (in the center of the stimulus array) in the presence of compatible or conflicting surrounding flankers (see Fig. 1b). The movements of the avatar had no noticeable delays when compared to the participant's real movements, and this strong visual–motor synchrony between avatar and participant's movements was expected to create a strong feeling of ownership (Banakou et al., 2013; Banakou and Slater, 2014; Llobera et al., 2013; Peck et al., 2013). Hence, this belongs to the category of body ownership illusions evoked by using appropriate synchronous multisensory (visual, tactile, and proprioceptive) stimulation (Lenggenhager et al., 2007; Petkova and Ehrsson, 2008; Slater et al., 2010; González-Franco et al., 2014) that can produce an illusion of ownership even over objects that are not part of the body (Botvinick and Cohen, 1998; Ehrsson et al., 2004; Longo et al., 2008).

In the virtual environment, the stimuli presentations consisted of three black arrows oriented horizontally, one central (target) and two flanker arrowheads above and below (Fig. 1b). Participants were instructed to respond both accurately and quickly to the direction of the central arrow by moving the hand to either of the two assigned buttons that were on the table. The virtual table and buttons were registered with the real table by which participants were sitting, so that there was no conflict between their tactile sensation of feeling the table and the buttons, and the visual input of seeing their virtual hand touch the table and buttons (Fig. 1). Participants were instructed to make only one response per trial and to avoid correction movements. At each trial, after the response, the hand was returned by the participants to the initial position equidistant to the two buttons.

We refer to the trials as *compatible*, when the central arrow (target) had the same direction of flankers, or *incompatible*, when target and flankers had opposite directions. The flanker incompatible condition was presented 60% (768 trials) of the times and the compatible condition 40% (512), both presented in pseudo-random order. The percentage of incompatible trials was larger in order to increase the number of erroneous responses due to the presence of incompatible flankers. The duration of each stimuli presentation was 150 ms and the interval between two successive presentations (SOA) was 1150 ms. A fixation cross was present during this interval, 1000 ms, after the disappearance of the stimulus array. Every 20 trials, participants had 5 s of pause to blink.

Experiment 1 was divided into experimental block conditions, the congruent movement (CM) condition and the incongruent movement (InCM) condition. The experiment always started with the CM block and was followed by the InCM block. In the CM condition, participants became familiar with the virtual environment and the task. In this condition, and in order to create a strong illusion of body ownership, the movements of the avatar were always the same as those executed by the participant. In this block, participants performed 160 trials in total (96 incompatible, 64 compatible trials). At the end of this CM condition, participants were required to complete the experience questionnaire (see below for a description) concerned with body ownership and agency.

After a short break, the incongruent movement (InCM) condition started. The InCM was divided into two blocks of 640 trials (approximately 15 min each separated by 10 min of rest). During the InCM blocks, in some infrequent trials, the avatar produced an unexpected hand movement (external-generated error) even though the participant had performed the correct one. Specifically, when participants moved the hand in one direction the virtual hand moved in the opposite direction, causing an external-generated error, hereafter called (false) avatar errors. The InCM trials were distributed so that they occurred randomly every 20 trials and were never the first or last trial before the pauses. The total number of InCM trials matched approximately the percentage of natural errors in the compatible flanker (approximately 5–6% of trials, 64 trials in all participants). Importantly, we avoided introducing avatar errors in the incompatible trials because in this condition, the non-compatible flankers tend to pre-activate the incorrect motor channels (resulting in more errors in the incompatible trials when compared to the compatible ones), and therefore the evaluation of the avatar error could have been unclear for the participant.

To accomplish the effect of inserting the avatar error, we made the hand move symmetrically with respect to the real hand movements (but in the opposite direction). In the InCM trials, participants did not notice anything wrong until they started moving since the virtual hand position was also at the initial position during these trials. Using the real hand position for calculating the InCM trials was very advantageous in terms of the plausibility of the symmetric virtual movement since it mirrored the real spatiotemporal movement (without noticeable delay). The crucial trials for our ERP analysis were those in which the participant *did respond in the correct direction* but the *virtual hand went into the opposite direction* thus provoking a false (avatar) error. At the end of this second block, participants were requested to complete again the experience questionnaire of body ownership and agency.

2.3.2. Experiment 2

Experiment 2 was carried out in order to rule out the possibility that the ERP effects found in Experiment 1 in the InCM condition were due to the mere observation of an avatar performing a wrong action instead of the output of the *E-eml*. The same participants from Experiment 1 were invited back to the laboratory and were again immersed in the 1PP IVE environment as in the previous experiment. However, on this occasion, we only asked the participants to observe and pay attention to the avatar performance from a 1PP and to count the number of times that the avatar was performing an erroneous action. Unknown to participants, each one saw an exact reproduction of their own session digitally recorded during the previous ERP experiment. The pre-recorded movements were first cleaned of incomplete or corrected movements by substituting these by complete movements of the same participant, i.e., participants only visualized errors or correct trials. In order to avoid covert errors of the observer, the flanker arrows were removed and only the middle arrow remained in the screen (van Schie et al., 2004; de Bruijn & von Rhein, 2012). As demonstrated in the study of Van Schie et al. (2004), observers activated the motor cortex associated with the correct response at a sub-threshold level, thus generating a representation of the appropriate response associated to the target stimuli presented. In this regard, it is important to eliminate conflicting information in the incompatible condition in order to prevent possible covert errors (incorrect pre-activation of the incorrect motor channel). Participants were also told that at the end of the observation they would be asked whether the pre-recorded performance was theirs or from another participant. The aim of these instructions was to increase their level of attention. At the end of this experiment, participants were requested to complete the questionnaire of body ownership and agency.

2.3.3. The experience questionnaire

Participants were instructed to complete a 9-item questionnaire (in Spanish) after each of the CM and InCM conditions and at the end of Experiment 2. Most questions were adapted from the study of Botvinick and Cohen (1998), and some additional questions were added in as in other body ownership related experiments (Banakou et al., 2013). The questionnaire contained a set of assertions that were scored with a 7-point Likert scale ranging from “strongly disagree” (−3) to “strongly agree” (+3). The questions were as follows, with the corresponding variable names *in italics* afterward:

Q1. It felt as if the virtual body was my body (*my body*)
Q2. I felt as if my hand was located where I saw the virtual hand to be (*collocated hand*)
Q3. It seemed as if I might have had more than one body (*more than one body*).
Q4. It seemed as if the position of the hand I was feeling came from somewhere between my own hand and the virtual hand (*dislocated hand*).
Q5. Most of the time, the movements of the virtual hand seemed to

be my movements (*my movements*).
Q6. Sometimes, I felt that the movements of the virtual hand were influencing my own movements (*influence*).
Q7. Sometimes, the virtual hand seemed to be moving by itself (*not my movements*).
Q8. It sometimes felt as if my real hand was turning 'virtual' (*my hand virtual)*.
Q9. It seems sometimes that the errors were not caused by myself (*not my errors*).

Q1 and Q3 were related to the sense of body ownership. Q2 and Q4 were related to the sense of proprioception and localization of the hand that participants experienced. Q5 and Q7 were related with visual–motor integration processes and violation of the sense of agency, important for the evaluation of the effectiveness of our experimental manipulation. Q6 was an exploratory question on motor performance to assess how the visualization of the virtual movements influenced participants' real movements. Indirectly, this question assesses also agency violation. Q8 was a filler question about which we had no expectations. Q9 was a consistency check for the task performance in each condition, evaluating whether participants were able to differentiate their own errors from the false (avatar) errors. Q9 was expected to be higher in the InCM than the CM condition. This questionnaire therefore included information about body ownership, localization, and agency (Longo et al., 2008; Kilteni et al., 2012).

2.4. Electrophysiological recording

EEG was recorded from tin electrodes mounted in an elastic cap and located at 27 standard positions (Fz, F7/8, F3/4, Fc1/2 Fc5/6, Cz, C3/4, T7/8, Cp1/2, Cp5/6, Pz, P3/4, P7/P8, Po1/2, O1/2). All scalp electrodes were referenced offline to the mean activity of the left mastoid. Vertical eye movements (electrooculogram, EOG) were monitored with electrodes located above and below the right eye. Horizontal EOG was collected from electrodes located at the outer canthus of each eye. Both vertical and horizontal EOGs were used for artifact rejection and correction. We used an approach based on blind source separation (BSS) algorithms that includes an automated independent component analysis (ICA) to isolate and remove electroocular components from the EEG data rather than rejecting artifact-contaminated trials (Joyce et al., 2004). Impedances were kept below 5 kΩ. The electrophysiological signals were filtered with band-pass of 0.1–70 Hz (half-amplitude cutoffs) and digitized at a rate of 250 Hz. Trials with amplitude of more or less than 100 μV were rejected offline.

For the behavioral and ERP analysis, only correct and error responses entered in the analysis, and all error-correction movements were excluded (see Fig. S1 for an example in Supplementary Material). In trials that immediately followed a resting period, a real error, or a false (avatar) error was discarded from the analysis. Finally, trials with reaction times shorter than 150 ms or longer than 2.5 standard deviation of the individual RT were also excluded from the behavioral and ERPs analysis.

For ERP analysis, we were interested in three specific conditions from the InCM blocks: (i) correct responses toward the target; (ii) when the avatar was introducing false avatar errors; and (iii) when participant really performed an error (self-generated real errors)." The mean number of trials that finally entered in the ERP analysis for correct responses was 785 ± 30 (mean ± SD), 119 ± 20 for real errors and 41 ± 2 false avatar errors. A previous pairwise comparison between compatible and incompatible trials showed no differences in the Ne/ERN amplitude for both type of erroneous trials and no differences also in between correct compatible and correct incompatible trials in this time window (80–120 ms after response). Thus, both compatible and incompatible trials were pooled together for the Correct Responses and Self-generated error bins.

The visual inspection of the grand average waveforms for the contrasts real errors vs. correct responses and false (avatar) errors vs. correct responses revealed two distinct negative ERP waveforms. Self-generated real errors gave rise to the standard Ne/ERN component, peaking at 80–120 ms after response onset at frontocentral locations. In turn, false errors were associated with another negative ERP component extending from 250 to 500 ms and with peak activity in the time window of ~310–360 ms post-response (hereafter referred as N400). Event-related potentials (ERPs) time locked to the onset of the response (r-ERPs) were averaged for epochs of −300 to 600 ms and with baseline set from −100 to 0 ms to the onset of the response. A low pass filter (14 Hz, half-amplitude cutoff) was applied in all computations. Mean ERP voltages were analyzed at parasagittal (F3/4, C3/4, P3/4) and midline (Fz, Cz, Pz) locations by a three-way repeated-measures ANOVA with factors *correctness* (correct, real error, false error), *anterior–posterior electrode location* (frontal, central, and parietal locations), and *lateral scalp location* (parasagittal left, midline, and parasagittal right). Time windows for statistical analyses of ERP voltages were chosen based on visual inspection of the grand average waveforms around the maximum activity for the Ne/ERN (80–120 ms) and N400 (310–360 ms). The Greenhouse–Geisser epsilon correction was applied when necessary.

For the analysis in the control Experiment 2, ERPs were response-locked averaged to the onset of the observed responses performed by the self-represented avatar and averaged for epochs of −300 to 600 ms (baseline was defined as −100 to 0 ms before the onset of the avatar response). We were specifically interested in investigating the differences between observed (avatar) correct responses and observed (avatar) error responses (see van Schie et al., 2004). Since participants were unable to distinguish real errors from avatar errors, the bin of observed avatar errors contained both type of errors. The visual inspection of the difference waveform between observed errors and observed correct responses revealed a negative waveform extending from 300 to 360 ms over frontal sensors. Mean ERP voltages on this time window (300–360 ms) were analyzed at parasagittal (F3/4, C3/4, P3/4) and midline (Fz, Cz, Pz) locations by a three-way repeated-measures ANOVA with factors *avatar correctness* (observed avatar correct response, observed avatar error response), *anterior–posterior electrode location* (frontal, central, and parietal locations), and *lateral scalp location* (parasagittal left, midline, and parasagittal right).

Finally, to inspect the impact of individual differences regarding the experience of body ownership with the avatar in error-related brain activity associated with avatar errors, we performed a correlation analysis (Pearson correlation) with the mean amplitude of the N400 component in the false avatar error (false error vs. correct amplitude difference) and the psychometric assessment of the illusion of body ownership. For the evaluation of the subjective strength of virtual body ownership, we chose the ratings obtained immediately after the fist block (CM condition), where the expected illusion is stronger (due to the congruence of all avatar and self-generated movements). We computed the difference score between Q1 and the control condition (Q3) and correlated this value with the N400 difference amplitude. The difference between Q1 and Q3 represents a normalization of the body ownership illusion, a high score on Q1, and a low score on Q3, indicating stronger body ownership illusion.

2.5. Movement analysis

The recorded hand tracker movements were analyzed offline to compute response accuracy and reaction times. This was critical to calculate the onset movement and response-locked event-related potentials (r-ERPs). In order to correctly detect the participants' responses, we used the projected position of the hand as the Euclidean distance on the axis between the two buttons. For each trial, we distinguished among four different response types: correct, error, corrected, and no response. Once the response was classified, we used the derivative of the position to assess the onset movement described as the moment just before the hand starts to move (see Fig. S1, Supplementary Material).

3. Results

3.1. Experiment 1: Error monitoring of real errors vs. false (avatar) errors

3.1.1. Assessment of the ownership and agency illusions toward the virtual body

In order to evaluate the illusion of body ownership, localization, and agency in this experimental setting, volunteers were instructed to complete a 9-item questionnaire (see Section 2) after each of these CM and InCM conditions (Botvinick and Cohen, 1998; Ehrsson et al., 2004; Longo et al., 2008). Nonparametric Wilcoxon matched pairs signed-rank tests were used to assess participants' questionnaire scores related to the experience of ownership toward the avatar during Experiment 1 (Fig. 2 shows medians and interquartile ranges).

During the CM condition (see Fig. 2), when the avatar movements corresponded to those of the real body, a strong feeling of body ownership illusion and agency was induced toward the avatar (as reflected by the scores in response to questions such as “It felt as if the virtual body was my body” (Q1) or “Most of the time, the movements of the virtual hand seemed to be my movements” (Q5)). This result is consistent with previous findings (Sanchez-Vives et al., 2010; Slater et al., 2010; Banakou et al., 2013; Llobera et al., 2013; Peck et al., 2013). Interestingly, even in the InCM condition, participants still reported a strong and stable experience of body ownership: Q1 scores (“It felt as if the virtual body was my body”) were found high in both CM and InCM conditions, with no significant difference between the two conditions ($Z = 1.519$, $p = 0.13$). Notice also that the control question that we included for body ownership (Q3, “It seemed as if I might have had more than one body”) was significantly lower than Q1 in both CM ($Z = 3.682$, $p = 0.0002$) and InCM condition ($Z = 2.489$, $p = 0.013$; the global comparison between the Q1 and the control question Q3 was significant, $Z = -4.2857$, $p < 0.0001$). The occasional divergence between real and virtual hand locations during avatar errors also had an effect on the hand localization item (Q2), and the scores for the CM were greater than for the InCM condition ($Z = 2.902$, $p = 0.004$).

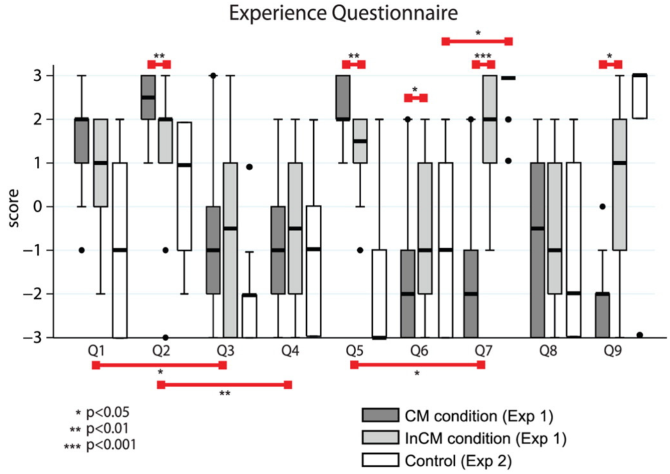

Fig. 2. Box plots showing the results of the questionnaire used to assess the feeling of ownership (embodiment) and agency at the end of the congruent movement (CM) and incongruent movement (InCM) blocs in Experiment 1 and Experiment 2 [7-point Likert scale, from “strongly disagree” (−3) to “strongly agree” (+3)]. Global illusory ownership and violation of the sense of agency of the virtual body were corroborated by the scores on relevant questionnaire items: for ownership (Q1, Q2 and Q5) and for agency (Q6, Q7, and Q9). These scores were compared with control questions (Q3 and Q4). Significant differences were observed between CM and InCM conditions, and with the control Experiment 2 (non parametric Wilcoxon signed-rank tests) in these relevant questions.

Participants' sense of agency (associated to visual–motor integration processes) were impaired or partially disrupted when avatar errors began to appear in the InCM condition as demonstrated by the scores in questions Q5, Q6, Q7, and Q9 (Fig. 2). Q5 mean scores (“The movements of the virtual hand seemed to be my movements”) were significantly higher in the CM than the InCM condition ($Z = -3.266$, $p = 0.0012$). In contrast, the control question Q7 (“Sometimes, the virtual hand seemed to be moving by itself”) scored higher in the InCM condition than the CM ($Z = 3.648$, $p = 0.0003$). In the InCM condition, Q7 was marginally greater than Q5 ($Z = -1.963$, $p = 0.05$). This result shows that the sense of agency was impaired by the introduction of avatar errors in the InCM. The InCM condition also influenced significantly more the participants' feeling about their movements (Q6) than the CM one ($Z = 1.978$, $p = 0.048$). Finally, it is worth mentioning that in the InCM condition participants were aware that the errors introduced by the avatar were not their own errors (Q9, “It seems sometimes that the errors were not caused by myself”) (for the comparison InCM vs. CM, $Z = 3.543$, $p = 0.0004$).

Overall, the CM condition induced a high level of embodiment toward the self-represented avatar (as measured by body ownership, localization, and agency) (Banakou et al., 2013; Maselli and Slater, 2013; Banakou and Slater, 2014). However, although a strong feeling of body ownership was found in the InCM, the feeling of agency was disrupted, and participants were aware that the errors introduced sporadically by the avatar were not their own errors.

3.1.2. Behavioral performance

The performance of participants during the reaction time task was as expected for this paradigm. The mean percentage of own errors produced by the participants was equal in the CM (mean + SD, 17 ± 9%) and InCM (17 ± 8%) conditions ($t(17) < 1$); thus, the inclusion of avatar errors did not have a major impact on the overall performance. As in other versions of the reaction time Erikson flanker task, our manipulation in the virtual environment revealed that participants were more accurate and faster responding to compatible trials compared to the incompatible ones: accuracy (compatible trials: 91.5 ± 6.9%; incompatible trials: 77.1 ± 10.5%, $t(17) = 11.302$, $p < 0.001$) and mean reaction time for correct responses (compatible: 259 ± 36 ms; incompatible trials: 273 ± 44 ms, $t(17) = -4.48$, $p < 0.001$). Finally, the percentage of missed trials (no response) along the experiment was very low (0.6 % ± 0.6 SD in CM block; 0.1 % ± 0.4 in the InCM condition), although being significant across conditions ($t\,(23) = 2.8$, $p < 0.009$).

We also investigated the extent to which compensatory cognitive control mechanisms were triggered after the real or the false error. As has been previously described, errors are usually followed by more accurate and slower responses (e.g., *post-error slowing* effect), which reflects control compensatory mechanisms triggered automatically after an erroneous response (Rabbitt, 2002; Marco-Pallarés et al., 2008; Logan and Crump, 2010). As expected, self-generated real errors were followed by slower correct reactions than correct responses preceded by correct trials (e.g., 270 ± 46 ms vs. 262 ± 42 ms, respectively; $t(17) = 2.7$, $p = 0.027$). Strikingly, after false (avatar) errors, there was an even slower correct reaction (post-error slowing effect, 292 ± 51 ms; comparison with correct trials, 262 ± 42 ms: $t(17) = 7.1$, $p < 0.001$). The greater post-error slowing effect after false (avatar) errors (~30 ms) compared to self-generated real errors (~8 ms) is surprising considering that the participant performed a correct action during avatar errors. This result might reflect a great impact in performance when participants detected a discrepancy between the expected (correct) output of their motor command and the observed (incorrect) movement performed by their avatar self-representation, suggesting that compensatory cognitive control mechanisms might as well be activated.

3.1.3. ERP signatures of error-monitoring for real errors vs. false (avatar) errors

ERP responses during the performance of both experimental conditions are depicted in Fig. 3a. Participants' self-generated real errors when compared to their correct responses showed the standard development of the Ne/ERN component (see *blue line* in Fig. 3a) (Gehring et al., 1993; Rodriguez-Fornells et al., 2002; Holroyd et al., 2005). This component peaked at about 100 ms immediately after the production of an error at frontocentral brain locations (see difference waveform, real error vs. correct responses, in Fig. 3b). This component was followed by a positive error component (known as the Pe) and showing a peak in between 200 and 300 ms (see difference waveform for real error condition in Fig. 3b) and in accordance to previous studies using similar paradigms (Overbeek et al., 2005; Rodriguez-Fornells et al., 2002; Krämer et al., 2007).

A repeated-measures ANOVA showed a main effect of Correctness (correct, real error, false error) ($F(2,34) = 12.9$, $p < 0.001$) as well as significant interactions: correctness per antero-posterior electrode location ($F(4,68) = 6.6$, $p < 0.005$) and correctness × anterior–posterior × lateral position ($F(4,68) = 2.6$, $p < 0.05$). The Ne/ERN component elicited for real errors was maximum at the midline frontal electrode (Fz) (see Fig. 3b). Pairwise comparisons at the Fz electrode showed that the amplitude of the Ne/ERN was significantly enlarged for real errors compared to correct responses ($t(17) = 4.6$, $p < 0.001$) and real errors when compared to false (avatar) error trials ($t(17) = 4.2$, $p < 0.001$). It is worth noting that at frontocentral locations, no clear traces of the Ne/ERN component were registered for the contrast false (avatar) errors vs. correct responses ($t(17) < 1$). The Ne/ERN component during self-generated real errors is supposed to reflect the output of the internal error-monitoring loop (*I-eml*) described in the introduction.

Surprisingly and in contrast to real errors, false (avatar) errors elicited a large negative ERP component over parietal locations, an N400 (see *green line*, Fig. 3a), developing from 250 to 500 ms and peaking at about 310–360 ms. The amplitude of this N400 was larger on false (avatar) errors when compared to real errors and correct responses as revealed by a main effect of Correctness, ($F(2,34) = 14.4$, $p < 0.001$). The N400 effect after false errors was maximal at parietal locations (see difference waveform, false errors vs. correct responses, and its topographical distribution at Fig. 3b) and somewhat lateralized to the right hemisphere (correctness × anterior–posterior: $F(4,68) = 11.8$, $p < 0.001$; correctness × anterior–posterior × Lateral locations: $F(8,136) = 2.7$, $p < 0.05$). Further, pairwise comparisons confirmed that the amplitude of the N400 at Pz electrode was enhanced in the comparisons between the false error condition and real errors ($t(17) = 4.6$, $p < 0.001$) and between false error vs. correct responses ($t(17) = 5.5$, $p < 0.001$).

Furthermore, we observed that the amplitude of N400 over parietal regions elicited by avatar errors (for the difference false error vs. correct responses) was negatively correlated with the subjective strength of virtual body ownership (computed as the difference Q1–Q3) ($r(18) = -0.6$, $p < 0.009$) (see Fig. 4).

Thus, the larger the subjective feeling of body ownership as measured by the subjective report, the stronger the amplitude of the negative parietal signal following avatar errors. This result suggest that participants who experienced stronger subjective body ownership elicited stronger N400 modulations in response to agency violations.

This result is important as it suggests a neurophysiological dissociation between the *I-eml* and *E-eml*, which is involved in the evaluation of the sense of agency of our own actions in conflicting contexts. In ERP analysis, different topographical distributions and latencies of two ERP components provide direct evidence of the necessary involvement of at least different neurophysiological mechanisms (Picton et al., 1995). In order to test more accurately whether the scalp distribution of both components differed, we carried out an additional statistical analysis considering all the 27 electrode locations registered and testing for the interaction between condition [Ne/ERN (real error minus correct response difference) − N400 (false error minus correct response difference)] × electrodes at 27 locations. A significant interaction was obtained ($F(1,17) = 5.3$, $p < 0.001$) demonstrating the implication of distinct neural sources in the generation of both ERP components associated respectively to the *I-eml* (Ne/ERN) and the *E-eml* (N400).

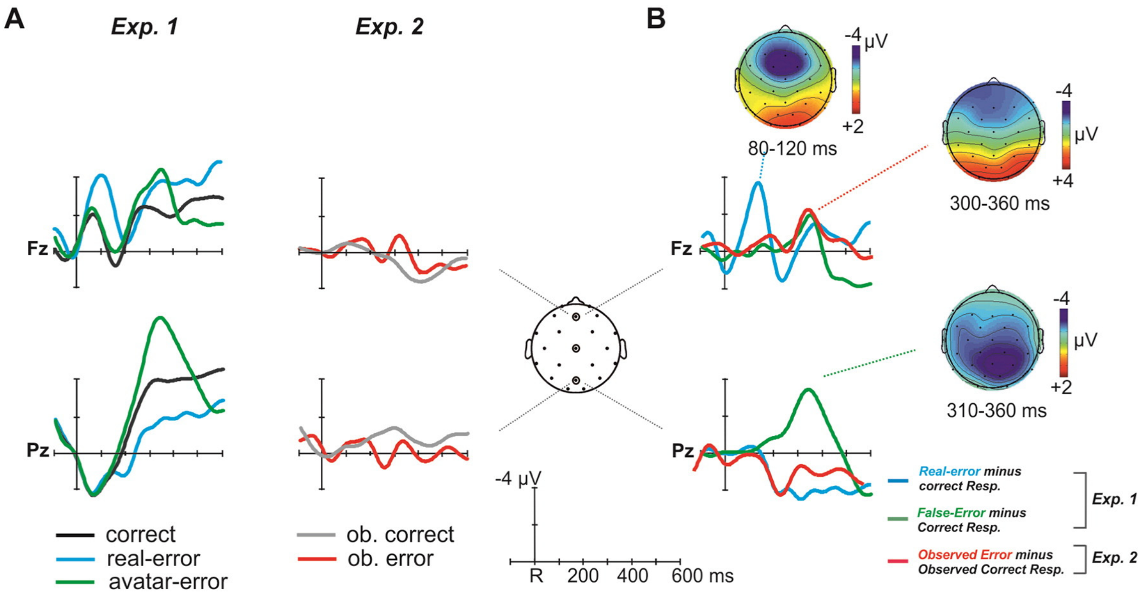

Fig. 3. ERP results of Experiment 1 (participants executing the actions in 1PP) and control Experiment 2 (participants observing actions in 1PP). (A, left panel) Response-locked grand average waveforms during Experiment 1 at frontal (Fz) and parietal (Pz) locations for Correct responses (black line), real errors (blue line), and false (avatar) errors (green line). At the right panel and for Experiment 2, we depict the grand averages for observed errors (red line) and observed correct responses (gray line) conditions. (B) Difference in waveforms and related scalp distribution maps for the contrasts real errors minus correct responses (blue line), false (avatar) errors minus correct responses (green line), and observed errors–observed correct responses (red line). Notice that while real errors showed the standard frontocentral Ne/ERN peaking at about 100 ms (blue line), false (avatar) errors (green line) yielded a slower negative parietal component (green line, at about 300–400 ms, the N400). The contrast of observed errors vs. observed correct responses (red line) revealed a delayed Ne/ERN component, at about 300–360 ms exclusively shown at frontal electrodes.

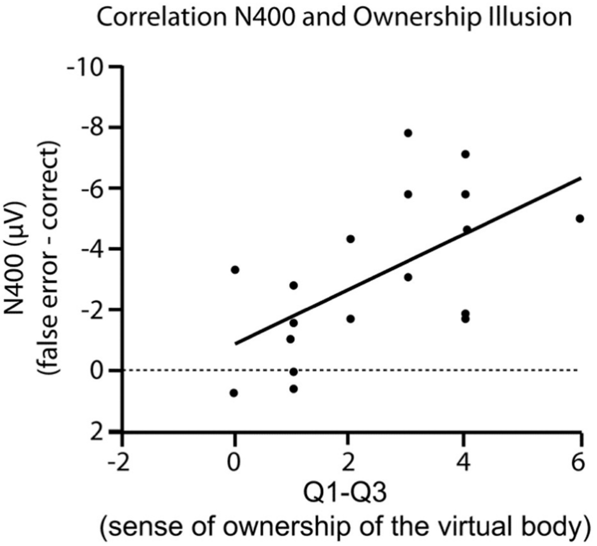

Fig. 4. Correlation between the strength of the virtual embodiment illusion (feeling of ownership) and the N400 component. The amplitude of the N400 component was computed subtracting false (avatar) errors minus correct responses in the incongruent movement (InCM) condition over a selected region of interest over parietal locations (Pz, P3, P4 electrodes). The subjective strength of virtual body ownership (embodiment) was computed as the difference Q1–Q3, where Q1 and Q3 are items of the subjective questionnaire (see Fig. 2).

3.2. Experiment 2: error monitoring of observed avatar errors

3.2.1. Assessment of the ownership and agency illusions toward the virtual body

During the control Experiment 2, participants (see Fig. 2) reported lesser subjective body ownership when comparing Q1 scores to the Experiment 1 CM condition's scores ($Z = -2.032$, $p = 0.042$). This result suggests that the absence of visual–motor synchrony disrupted the experience of body ownership. Additionally, the proprioceptive consistency of the hand localization item (Q2) was also significantly diminished in Experiment 2 when compared to the Experiment 1 CM condition ($Z = -2.687$, $p < 0.007$).

Regarding visual–motor integration (Q5), the comparison shows a reduction in the sense of agency during Experiment 2 when compared to Experiment 1 CM condition ($Z = -2.536$, $p < 0.011$). Further analysis on (Q5 vs. Q7) showed significant differences ($Z = -2.570$, $p = 0.012$), meaning that overall, participants noticed that they could not control the avatar movements, thus showing a low sense of agency.

Overall, these results are consistent with our expectations and show a low level of embodiment toward the self-represented avatar when compared to the Experiment 1 scores since the three most commonly described aspects of embodiment – body ownership, localization, and agency – had low scores during the observation control Experiment 2. This result demonstrates that the visual–motor incongruence between own actions (not moving hands, only observing) and the perception of the avatar's movements extinguished the experience of body ownership and agency which was present in Experiment 1 (as expected considering previous findings (Banakou and Slater, 2014)).

3.2.2. ERP signatures of observed avatar errors

The ERP analysis of Experiment 2, in which participants merely observed avatar erroneous actions (see Fig. 3a, *red line*), did not show the parietal N400 component observed during Experiment 1. Instead, a delayed frontal Ne/ERN-like component was elicited about 300 ms after the occurrence of the avatar's erroneous action, at the frontal electrode (see Fz electrode at Fig. 3b). Corroborating this, a significant interaction between correctness (observed correct, observed error) × anterior–posterior electrode location ($F(2,16) = 26.4$, $p < 0.001$) was observed. The present results are in agreement with previous experiments showing error-related brain activity when participants have been exposed to errors performed by other agents (i.e., observational errors), where no parietal N400 was reported (van Schie et al., 2004). This result rules out the possibility that the parietal N400 component elicited under violations on agency could be due to mere observational effects.

To ensure that the delayed frontal Ne/ERN signal following avatar error observation could be dissociated from the parietal N400 signal in the false error condition, we directly compared the amplitudes of the observational avatar Ne/ERN (from the difference waveform observed error minus observed correct Experiment2), the Ne/ERN component (real error minus correct responses, Experiment 1), and the N400 component (false error minus correct responses, Experiment 1) at the midline anterior–posterior electrode locations (Fz, Cz, and Pz) and for the 9 participants that carried out both experiments. An interaction between the ERP components (observational-Ne/ERN, false errors, real errors) × anterior–posterior location ($F(4,32) = 41.8$, $p < 0.001$) was found, showing an increased negativity of the observational avatar Ne/ERN [-2.4 ± 0.6 μV (SEM)] and the Ne/ERN (−4.7 ± 0.9 μV) at Fz location when compared with the N400 amplitude for false errors (0.1 ± 0.5 μV). Larger negativity in contrast was observed at Pz location for false errors, the N400 component (−3.8 ± 0.6 μV) (see Fig. 5 for a summary). Paired *t*-test comparisons confirmed the differences between the observational avatar Ne/ERN and the false errors N400 at Fz ($t(8) = 3.2$, $p < 0.05$) and at Pz locations, where the N400 amplitude was maximal ($t(8) = 6.8$, $p < 0.001$).

4. Discussion

In this study, two different neurophysiological signatures appeared associated to the embodied avatar errors resulting from the internal (*I-eml*)- and external-error-monitoring (*E-eml*) loops, the Ne/ERN and the N400 component, respectively. The appearance of the first

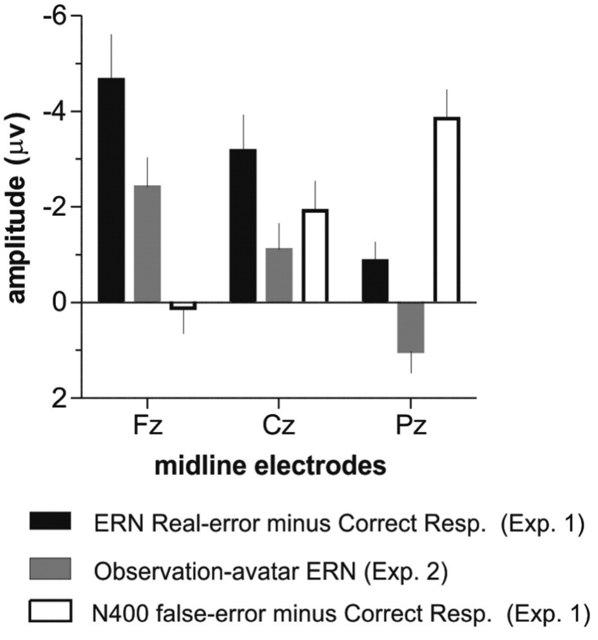

Fig. 5. Summary of the mean amplitudes of the ERP components identified (mean ± SEM): (i) Ne/ERN (difference waveform real error minus correct responses, mean amplitude 80–120 ms, black bars), (ii) delayed Ne/ERN (difference waveform observed error minus observed correct, mean amplitude 310–360 ms, gray bars), and (iii) the N400 component (difference waveform false (avatar) error minus correct responses, mean amplitude 300–360 ms, white bars). These results compared only the nine participants that participated in both experiments.

component (Ne/ERN) was expected to generalize from previous results on internal error monitoring of real body movements (Gehring et al., 1993; Rodriguez-Fornells et al., 2002; Holroyd et al., 2005) to the virtual body. Indeed, this is the first study to show the appearance of the Ne/ERN component in humans embodied in a virtual body. However, the appearance of the N400 during the false errors (avatar-induced errors) was unexpected. As mentioned earlier, our ability to recognize ourselves as agents of our own behavior depends on constantly monitoring the sensory consequences of our ongoing actions. In normal everyday circumstances, we experience an implicit and diffuse sense of coherence regarding the feeling of agency, mostly because there is a perfect congruence between the internal representations of our actions (e.g., efference copy), the sensory predictions of our actions, and the flow of resulting sensory events (multimodal reafferent feedback) (Pacherie, 2001). When a mismatch is detected between any of these internal predictions and reafferent signals, a violation of the sense of agency might be triggered. Thus, the N400 could be reflecting the output of this comparison process, which might lie at the core of the *E-eml*.

Interestingly and in agreement with this, a significant association was observed between the amplitude of the N400 component (*false* error *minus correct responses*) and the subjective feeling of body ownership (see Fig. 4). The greater the subjective feeling of body ownership, the stronger the N400 amplitude or the electrophysiological signature of agency violation. Furthermore, the timing of this comparison process (with approximately 350–400 ms delay after the error) is slower than that needed for the *I-eml* (in between 60 and 150 ms), which depends exclusively on the efference copy information. Since the *E-eml* requires the processing of different feedback information arriving at the somatosensory, visual, and auditory regions, this comparison process might not be finished until the degree of coherence is computed and a coherent multimodal representation is built.

More importantly, the parietal distribution of the N400 component converges with the results of functional neuroimaging and lesion studies in which the role of the angular gyrus in the inferior parietal cortex has been highlighted in relation to diminished feeling of agency (Farrer et al., 2008) and the comparison processes between predicted and actual consequences of ongoing actions (Sirigu et al., 2004; Desmurget et al., 2009; Chambon et al., 2013). Indeed, it has been proposed that this region might contain an internal model used for conscious monitoring of voluntary actions (Sirigu et al., 1996, 2004; Desmurget and Grafton, 2000; Farrer et al., 2008). Increased activation in this region is observed for stronger subjective feelings of non-agency reflecting the elicitation of an error signal associated to the mismatch detected between predicted and actual consequences of ongoing actions. This error signal might trigger therefore the conscious experience of perturbed sense of control or agency. Interestingly, several studies have shown that this mechanism of agency attribution is probably impaired in schizophrenia and might explain the problems associated with delusions of control, auditory hallucinatory experiences, or thought insertion (Daprati et al., 1997; Frith, 2005; Synofzik et al., 2010). Similarly, right inferior parietal cortex lesions have been associated with delusions about the patient's limb that may be perceived as an alien object, belonging to another person or causing alien hand movement (Nightingale, 1982; Leiguarda et al., 1993; Daprati et al., 1997; Assal et al., 2007). Although caution is needed in the interpretation of EEG data and the location of its neural sources, we believe that the N400 component associated in the present study to the *E-eml* could reflect an ERP component associated to this error signal generated in the inferior parietal cortex and associated to conscious error monitoring of voluntary actions.

Importantly, although no previous ERP studies have investigated the violation of the sense of agency in humans with a strong virtual embodiment illusion of an avatar body, two previous ERP studies on externally-caused errors (induced by simulated technical malfunctions), showed a similar negative ERP component as that reported here although with different onset latencies (Gentsch et al., 2009; Steinhauser and Kiesel, 2011). In the first study (Gentsch et al., 2009), errors were induced by omitting a normally occurring positive visual feedback signal that occurred nearly immediately after a correct response (with 10 ms delay). Participants knew in advance that these computer system malfunctions could happen due to unexpected technical problems. Thus, participants performed a correct response in this scenario and the expected-immediate feedback was omitted in some trials. The absence of positive feedback elicited a negativity with a similar posterior–parietal scalp distribution as the one observed in our experiment (with an earlier onset, at 250 ms) (see also Steinhauser and Kiesel, 2011). The authors used independent component analysis (ICA) and found that this delayed negativity could also be associated to a source in the medial prefrontal cortex, similar to that observed in the standard Ne/ERN for real errors.

These studies and ours converge in pointing to the existence of both error-monitoring loops (*I-eml*/*E-eml*). A similar idea of a dual-route structure for conscious and non-conscious decision making has been proposed (Del Cul et al., 2009) and applied to the detection and correction of fast human errors (Charles et al., 2013). From this perspective, two parallel routes might simultaneously accumulate evidence from the sensory input: a fast non-conscious sensory-motor route and a slower but more accurate conscious route. In making rapid decisions, the unconscious route probably dominates and responses might be triggered before the slower conscious route emits its conservative judgment. A discrepancy between the outputs emitted by these two routes could signal that an error has occurred (Coles et al., 2001) or that conflict exists between the actual and intended actions (Botvinick et al., 2001; Yeung et al., 2004). From this perspective, while the *I-eml* might be the monitoring processes implemented in the unconscious route, the *E-eml* could be associated to the computation of a slower but more accurate route for conscious monitoring predicted and actual consequences of ongoing actions. Notice that this unconscious route associated to the *I-eml* might fit well with current interpretation that the Ne/ERN component is associated to unconscious conflict or error detection mechanisms (Endrass et al., 2007; Nieuwenhuis et al., 2001; Rodriguez-Fornells et al., 2002; Wessel, 2012; Yeung et al., 2004) and that its appearance precedes the appearance of the subjective perception of error commission (which is normally delayed in time, see Rabbitt, 2002).

An intriguing question to be explored is the exact computational nature of this comparison process involved in the *E-eml*. The N400 component discovered in the present study associated to the external error monitoring resembles in terms of scalp distribution and latency the well-known N400 component associated with semantic and conceptual violations and classically associated with the activation of amodal semantic memory (McPherson and Holcomb, 1999). This component has been attributed to the violation of semantic or conceptual information (Kutas and Federmeier, 2011) (e.g., when listening to the sentence “I am going to eat a house”), and it has also been found to occur as a result of observing incorrect motor plans (e.g., inserting screwdriver versus key into a keyhole) (Bach et al., 2009). Thus, an interesting question is the extent to which the clash in the feeling of agency (“this is not my action”) reflects a violation in the process of understanding our own actions (or our own “body movement semantics”). In this sense, the comparison process underlying the ability to recognize ourselves as agents of our actions might not be too different from that carried out when comparing linguistic inputs or conceptual representations, as it might rely as well on the congruence of our own actions and the external consequences generated by these actions. Thus, observing the representation of an embodied body performing a non-planned action might be evaluated in a similar fashion as a semantic-conceptual violation. In a way, we might be somehow observing “semantic violations of our own body actions.”

In conclusion, using ERPs, we dissociated internal and external error-monitoring controllers and we unraveled the timing of both monitoring processes associated with the violation of the feeling of agency.

The results provide important evidence about how to distinguish at the neurophysiological level own- vs. externally generated errors in surrogate bodies that could be governed by remotely located participants. We believe the present results provide new neural evidence regarding the integration of internal and sensory feedback information in the build-up of a coherent sense of agency and opens new avenues for studying the mental processes underlying agency attribution in healthy and clinical populations using virtual bodies.

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