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Right parietotemporal activity predicts sense of agency under uncertain delays of sensory outcomes

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Abstract

Sense of agency is the experience of control over one's own action and its consequent outcomes. The perceived time between a motor action and its consequent sensory outcomes (e.g., a flash of light) is shorter for a voluntary than involuntary action, a phenomenon known as intentional binding which has been used extensively as an implicit measure of sense of agency. We developed a novel task in which participants had to respond whether a flash appeared immediately or with a delay relative to their voluntary action. We found that under high, but not low, uncertainty about the perceived time between voluntary finger movement and a subsequent flash of light, a prediction signal was generated in the right inferior parietal lobule prior to motor action. This prediction signal was linked to the emergence of a sudden insight solution (colloquially referred to as "Aha!" moment) in the right superior temporal gyrus prior to response. Single-trial event-related potential analysis revealed a reliable correlation between amplitudes of pre-motor and pre-response activities. The results suggest the existence of a predictive mechanism under high uncertainty about the timing of the sensory consequences of a voluntary motor action. The results are in line with the optimal cue integration theory of sense of agency which states that both predictive and postdictive agency cues are crucial for the formation of sense of agency and the weight of each type of cue (predictive or postdictive) depends on their availability and reliability.

Keywords: consciousness awareness, event-related potentials, sense of agency, sensorimotor integration, synchrony judgment

NEW & NOTEWORTHY

According to the optimal cue integration theory, the formation of sense of agency relies on both predictive and postdictive agency cues and how they are weighted based on their availability and reliability. Using a novel paradigm, we show for the first time a possible existence of a prediction signal prior to voluntary movement which appears when postdictive agency cues (i.e., the judgment of the time between voluntary movement and a subsequent flash) are not reliable.

Introduction

Sense of agency is the experience of control over one's own action and its consequent outcomes (Blakemore et al. 1998; 2000; Haggard 2017; Moore 2016; Nahab et al. 2010; Nichols 2011). The mechanisms underpinning sense of agency are poorly understood. One of the challenges for better understanding how this experience is constructed and brought to consciousness is to know how the brain selects, weighs, and integrates various agency cues to establish the experience of agency.

A model has been proposed that both predictive and postdictive mechanisms are involved in formation of sense of agency (Synofzik et al. 2013). Predictive processes mainly, but not exclusively, rely on internal forward models (Blakemore et al. 2002; Frith et al. 2000; Vercillo et al. 2018) in which a 'copy' of motor command will be compared with the actual results of a movement. The mismatch between the planned and actual action (i.e., prediction error) will be used to update the internal agentive model. Predictive processes can be modulated by sensorimotor and cognitive cues. On the other hand, postdictive processes act during and after a movement (Wegner 2003), and a sense of agency will be consciously felt if some agency-related criteria are met including exclusivity (e.g., I move my finger, not someone else.), priority (e.g., I know I am about to move my finger.), and consistency (i.e., I want to bend my right-hand index finger and this finger bends, not another finger.). Postdictive processes also possess both sensorimotor and cognitive (e.g., affective valence of the action outcome) elements.

Optimal integration of predictive and postdictive cues seems to be crucial for a normal experience of agency (Synofzik et al. 2009). If the reliability of either of these cues reduces due to internal (e.g., agency-disturbing disorders like schizophrenia) or external (lack of reliable sensory input) factors, the other cue type receives a higher weight (Moore et al. 2009; Synofzik et al. 2009).

In the current study, we developed a novel task to investigate whether a predictive mechanism may be involved when distinguishing between synchronous and asynchronous visual outcomes of a voluntary action becomes difficult. Participants were instructed to press and hold a button down and release it at the time of their own choosing. The task was to determine whether a flash of light turned on immediately or with a delay relative to button release. The reason we chose button release (instead of button press) as the trigger of the flash was to minimize the role of haptic feedback for estimating the time at which the motor action was executed. The first block (i.e., the adaptive block) was easy. See Figure 1 for the overview of the experimental task. The delay between the onset of motor action (finger lift) and flash was either 0 or 300 ms. Participants distinguished the trials with high response accuracy. After their response, they received feedback whether or not their delay judgment was correct. This block was designed to familiarize participants with the task and gain their trust that the feedback was reliable, meaning it reflected their actual performance.

The second block (the overall performance block) was harder. Here, the motor-outcome delay was either 0, 50, 100, 200, or 300 ms. (Participants were not informed about the numeric values of delays. They were only told to distinguish whether the flash was synchronous or asynchronous.) The feedback in this block was still associated with their actual performance. The third block (the subjective block) was the hardest. Participants were told to try their best to distinguish the subtle delay difference between synchronous and asynchronous flashes. Participants were unaware that two deceptions were included in this block. First, all trials had a delay of 100 ms, as opposed to the adaptation and overall performance blocks where trials with various delays were intermixed. Second, unlike the first two blocks feedback was random. (If true feedback was provided, participants could gradually discover the deception that the flash always turned on with a delay.) From participants' point of view (as it was confirmed by post-experiment unstructured interviews), however, trials were a mix of no delay and delayed flashes and reliable feedback reflecting their actual performance was provided.

In this study, we applied a novel approach to examine how the brain attributes agency under high subjective temporal uncertainty about outcomes of a voluntary action. The perceived motor-outcome delay was used as an implicit measure of sense of agency, as it has been extensively used in intentional binding studies (Haggard 2017; Haggard et al. 2002; Pansardi et al. 2020; Vastano et al. 2020). Particularly, we investigated how the brain resolves agency attribution under conditions in which the delay between a voluntary motor action and its sensory outcomes is not a reliable agency cue, and how this resolution may be consciously perceived. Our assumption was that (in trials with a motor-outcome delay of 100 ms) participants experience a more enhanced intentional binding in trials perceived as synchronous (PS) rather than perceived as asynchronous (PA).

Our assumption was that (in trials with a motor-outcome delay of 100 ms) participants experience a more enhanced intentional binding in trials perceived as synchronous (PS) rather than perceived as asynchronous (PA). As intentional binding is an implicit measure of sense of agency, an enhanced intentional binding can be linked to an enhanced sense of agency. Given the optimal cue integration theory, we expected that under high uncertainty about when visual outcomes of a voluntary movement appear, predictive mechanisms will contribute with a higher weight (comparted to postdictive mechanisms) to determine whether the visual outcomes are perceived as synchronous or asynchronous.

Materials and Methods

Participants. Twenty-four healthy, right-handed students with normal or corrected-to-normal vision were recruited through flyers. To reduce the occurrence of eye blinks mainly due to dryness of the eye, we asked participants who normally wear contact lenses to wear their glasses instead (Luck 2014). Written informed consent was obtained from all participants before the study began. Four participants were excluded: One due to technical problems, one for not completing the experiment, and two for incorrect responses greater than 30% in the adaptation block (Figure 1). Thus, twenty participants (14 females; mean age: 22, range: 19-29 years) were retained in analyses. The study was approved by the Ethics Committee of Heidelberg University, and experimental procedures conformed to the Declaration of Helsinki.

Experimental procedure. The primary aim of the experiment (studying sense of agency under uncertainty) was kept hidden from participants and they were told that the study was about synchrony detection. Participants were seated individually in a magnetically shielded and darkened room at a distance of one meter from a three-color light-emitting diode (LED), subtending 0.5 degree of visual angle. To cover the room background, the LED was placed at the center of a matt, gray-colored plate with a width and height of 48 and 27 centimeters, respectively. (Conventional LCD computer monitors typically have a screen refresh rate of 60-120 Hz. We used a custom LED setup with a response time of about 1 ms to minimize the jitter between button release and the appearance of flash.) Throughout the experiment, participants heard Gaussian white noise via headphones (EA-RTONE 3A, Aearo Corporation, Indianapolis, USA) in order to superimpose the feedback clicks from button presses and releases. Also, they wore two thimbles on the index and middle fingers of their right hand which was placed under a covering box to minimize tactile and visual feedback from their motor actions. Inside the box, there was a gaming computer mouse (Logitech G Series; report rate: 1000 Hz) with which the responses were registered via its right and left buttons. (These sensory blockages allowed us to ensure that participants mainly relied on the visual cues from the LED to distinguish whether the flash appears synchronous or asynchronous relative to their finger lift.)

Experimental paradigm. Each experimental trial began in a self-paced manner with pressing and holding down the left mouse button via the right-hand index finger. Releasing the button triggered a 100-ms-long blue flash light from the LED with a 0 or 300 ms of delay in the adaptation block, with a 0, 50, 100, 200, or 300 ms of delay in the overall performance block, and with a 100 ms of delay in the subjective block (Figure 1). In the first two blocks (i.e., the adaptation block and the overall performance block), trials with a 0 ms of delay were 50% of the trials, and all trials were randomly intermixed. After flash offset, participants were given up to 2000 ms to respond, reporting whether the flash was perceived as synchronous (PS) or perceived as asynchronous (PA) relative to button release, using the right-hand index and middle fingers, respectively. Finger mapping was counterbalanced across subjects. After response, there was a randomly varying interval of 300, 400, 500, or 600 ms with a uniform distribution before a 100-ms-long visual feedback stimulus appeared. In the first two blocks, true feedback was provided, meaning feedback reflected actual performance, whereas in the subjective block random feedback was presented, meaning feedback was not associated with actual performance. Random feedback was either confirmatory or refutatory, with equal probability. Confirmatory feedback denotes that the feedback approved the participant's response correctness, although it could be an incorrect response. In contrast, refutatory feedback rejected the participant's response correctness, even though it could be a correct response. (It should be noted that participants were not aware of the randomness of feedback in the subjective block. From participants' point of view as confirmed by post-experiment unstructured interviews, feedback was reliable in all blocks, reflecting their actual performance.) The color mapping for feedback stimulus was fixed within a participant but switched across participants from magenta for correct and confirmatory feedback, and yellow for incorrect and refutatory feedback and vice versa. (This color switch across participants ensured that the potential observed effects are not contaminated by properties related the color of the feedback flash. Although the brightness of the colors was adjusted to be the same, this color switch further ruled out the effect of potential subtle brightness differences.) There were 200 trials each in the adaptation and overall performance blocks, and 400 trials in the subjective block. These 800 trials built the first session of the experiment. Testing subsamples of the subjective block with the same number of trials equal to that of the adaptation block did not change the observed findings. Before the first session began, participants were familiarized with the experimental task by performing 50 trials similar to those of the adaptation block.

Approximately 5 minutes after the first session, there was a second session which was similar to the first session except for the following: finger mapping for response was counterbalanced, so, for example, if in the first session the index and middle fingers were for synchronous and asynchronous responses, respectively, in the second session the index and middle fingers were for asynchronous and synchronous responses, respectively. We used counterbalancing modulations within and across participants to ensure that the effects of response finger (and feedback color) are cancelled out.

The reward pattern was similar in both sessions. In the first two blocks, participants were rewarded 1 euro cent for each correct response. In the subjective block, an amount was given suggesting that they responded correctly between 60 and 70% of trials. The exact amount was randomly chosen for each participant and they were informed about their total win after each block. Participants were naïve about the facts that all trials of the subjective block had a constant delay of 100 ms relative to their motor action, and that the feedback was not reflecting their performance level. After data collection phase ended, they were informed via email about the manipulation in the subjective block. The reason we varied their reward randomly (rather than keeping it fixed) in the subjective block was to increase the notion that the feedback in the subjective block still reflected participants' actual performance. The reason we chose the reward rate to be between 60 and 70% (rather than 50%) was to indicate participants that their performance is still better than chance and as a result they will be more motivated to perform the task attentively.

EEG recordings. The electroencephalogram (EEG) was recorded from 60 Ag/AgCl electrodes by a QuickAmp amplifier (Brain Products GmbH, Germany) at a sampling rate of 2000 Hz and with a 560-Hz anti-aliasing filter. Electrodes were mounted on an electrode cap (EasyCap, FMS, Germany) according to the head size with equidistant electrode positions. Electrodes were named after the equivalent positions in the international 10/20 system. Small position deviations are marked with the symbol ' (e.g., CP2'). A common average reference was used online and later for data analysis. A ground electrode was placed on the right shoulder. Electrode impedances were kept below 5 kΩ (Kappenman and Luck 2010). Four additional electrodes were used to record the electrooculogram (EOG). Vertical eye movements and eye blinks were monitored by two electrodes located about 1 cm above and below the left eye. Horizontal eye movements were monitored with 2 electrodes located on the lateral canthi of the left and the right eyes.

EEG analysis. Data preprocessing was performed using BrainVision Analyzer software (version 2.1; Brain Products GmbH, Germany). The raw EEG and EOG data from the overall performance and subjective blocks were band-pass filtered between 0.01 and 100 Hz (order of 8) using a zero-phase-shift Butterworth filter, and were down-sampled to 250 Hz. Ocular artefact correction was applied using the "ICA ocular correction" function of BrainVision

Analyzer (for more details on the methodology, see (Jung et al. 2000)). The rest of the preprocessing for each ERP analysis depended on the type of ERP analysis:

For motor-locked ERP analysis with respect to the response type (PS or PA), data were segmented from -250 to +300 ms relative to button release. Trials with missed responses were discarded (< 1% of trials). Baseline correction was applied from -250 to -60 ms relative to button release. (Choosing an appropriate baseline is important for electrophysiological studies (Keil et al. 2014). The choice may particularly become problematic if the time from which differential neural activities across experimental conditions or groups begin is not clear (Haggard 2008), as is the case in the study of readiness potential (Jo et al. 2014). This ambiguity can potentially affect the observed differences between groups and conditions. We alternatively tested another baseline (-250 to +100 ms relative to button release) as well. The new baseline did not significantly affect our results.) Artefact rejection criteria were: Maximum allowed voltage: 100 μV; minimum allowed voltage: -100 μV; maximum allowed voltage step: 80 μV/ms; lowest allowed activity within 50-ms intervals: 0.5 μV. Even if only one EEG channel was contaminated, all channels for that trial were rejected. The mean percentage of retained trials was 94% (SD = 7.4%). ERPs were calculated by averaging all retained trials of each participant separately for perceived as synchronous (PS) trials (i.e., trials in which participants responded that there was no delay between button release and flash onset) and perceived as asynchronous (PA) trials (i.e., trials in which participants responded that there was a delay between button release and flash onset). The averages for these two conditions were then grand-averaged across participants. Electrode sites and the time window of the present work were defined based on using a collapsed localizer (Luck and Gaspelin 2017). Using a collapsed localizer was appropriate for the current study as due to the novelty of the paradigm the timing and location of the effects could not be specified by the previous research. The average ERPs in the PS and PA conditions in the overall performance and subjective blocks were pooled together and visually inspected to identify in which time range and electrode sites the largest activities were observed. These parameters were used later to compare the PS and PA conditions.

A group of seven neighboring channels over the right hemisphere included: FC2', FC4', FC6', C4, CP2', CP4', and CP6' (Figure 3e). The measurement window was between -60 and 96 ms relative to button release. To further investigate the difference between PS versus PA conditions and to see if the difference between them began prior to motor action, the time window was divided into three sub-windows from -60 to -4 ms (i.e., prior to motor onset), 0 to 48 ms, and 52 to 96 ms (i.e., prior to flash onset), relative to the button release. (Due to a sampling rate of 250 Hz, there was a 4-ms distance between sub-windows.) The mean voltage amplitude at the selected channels for each of the chosen time windows was used as a measure of the brain's electrical activity (Luck 2014). Topographic visualizations were generated using EEGLAB (Delorme and Makeig 2004).

For motor-locked ERP analysis with respect to the response and feedback type of an immediately preceding trial, preprocessing was similar to that of motor-locked ERP analysis with respect to the response type of a trial itself except for the following: Trials were here stratified into four conditions based on the response type (PS or PA) and the feedback type (confirmatory or refutatory) of an immediately prior trial. This analysis allowed us to further ensure that the potential differences between PS and PA trials are not an immediate influence of previous trial or of baseline error, but indeed an effect originated from predictive neural mechanisms.

For response-locked ERP analysis, data were segmented from -640 to +300 ms relative to response onset of a trial. As there was no unambiguous time interval for choosing the baseline, the mean amplitude of the period between -640 and 0 ms was employed (Luck and Hillyard 1990). (The average reaction time in the subjective block was 640 ms and was chosen as the start time of segments. The time interval following response onset was not analyzed and is shown in figures only for visualization purposes. Using another baseline (-640 to -400 relative to response onset) did not significantly affect our results.) Artefact rejection criteria were similar to those described in motor-locked ERP analysis. The mean percentage of retained trials was 95% (SD = 7.3%). ERPs were calculated by averaging the retained trials for each participant separately in PS and PA trials. The averages for these two conditions were then grand-averaged across participants. Choosing the electrode sites and time windows were based on using a collapsed localizer (Luck and Gaspelin 2017). A cluster of six neighboring channels over the right frontal cortex involved: AFz, AF4', Fz, F2', F6', and FC4' (Figure 4e). Two measurement windows were between -400 and -300 ms and between -148 and -52 ms relative to response onset.

Statistical analysis. At the behavioral level, a two-tailed paired-sample *t*-test was used to test if the hold time durations in PS and PA conditions were statistically different. The purpose of this comparison was to ensure that the electrophysiological analysis is not potentially confounded by the differential length of hold times in two conditions. At the electrophysiological level and for motor-locked ERPs stratified with respect to the response type of a trial, two-tailed paired *t*-test was performed to examine the effects of response type (PS or PA) on the amplitude of the pooled channels in the -60 to 96 ms time window. For the three sub-windows, two-tailed paired *t*-tests with Bonferroni correction for multiple comparisons was used. For motor-locked ERPs binned with respect to an immediately prior trial, repeated-measures ANOVA with Bonferroni-corrected pairwise comparisons was used to test the effect of condition type on the amplitude of each sub-window. Greenhouse-Geisser correction was applied if necessary. For response-locked ERP analysis, two-tailed paired *t*-test was employed to examine the effect of condition (PS or PA) on the amplitude of the collapsed channels in the -400 to -300 ms time window, and separately in the -148 to -52 ms time window. The Bonferroni correction was used to compensate for multiple comparisons.

To test whether the difference between the amplitude of pre-motor activities in PS and PA conditions was greater in the subjective than overall performance block, a 2 by 2 repeated-measures ANOVA with factors of judgement (PS or PA) and block (overall performance or subjective) was conducted. A significant block by judgment interaction suggests that PS and PA activity are differentially modulated in these blocks. Similarly, a separate ANOVA was used to test the pre-response activities in the -400 to -300 and in the -148 to -52 ms time windows. Only for illustrative purposes, the ERPs shown in Figure 3a, b and Figure 4a, b were smoothed using a 20-ms moving average filter.

Pearson's correlations (two-tailed) with Bonferroni correction were used to test the relationship between the PS-PA difference in the motor-locked ERP amplitude prior to motor action (-60 to -4 ms) and the response-locked ERP amplitudes prior to response (-400 to -300 ms and -148 to -52 ms).

Single-trial ERP analysis (Meadows et al. 2016) was performed in the subjective block to investigate the relationship between the pre-motor activity (-60 to -4 ms) and the pre-response activities (-400 to -300 ms and -148 to -52 ms time windows) at an intra-participant level. For each participant, a Pearson's correlation between the pre-motor and pre-response activity (-400 to -300 ms and separately for -148 to -52 ms time window) in each trial was calculated. The obtained correlation coefficient for each participant was Fisher z-transformed to normalize the distribution. A two-tailed one-sample *t*-test was used to test if the coefficients were significantly different than zero.

Dipole source localization and orientation were performed using the Brain Electrical Source Analysis software package (BESA version 7.0, Germany). In these calculations, a 4-

shell ellipsoidal head model was used to model the brain activity in the -60 to -4 ms time window for the motor-locked grand-averaged ERP difference waveform (PS minus PA), and in the -400 to -300 ms time window for the response-locked grand-averaged ERP difference waveform. An 87-mm head radius, and the scalp and skull thickness of 6 and 7 mm, respectively, were used. The regularization constant was set to 1%. No constraint on the location and orientation of dipoles was imposed. A one-dipole model was calculated for each time window. Introduction of additional dipoles did not change the location and orientation of the first dipole. BESA dipole coordinates were transformed into the standardized coordinate system of Talairach and Tournoux (Talairach and Tournoux 1988).

Results

We first needed to define a latency at which participants experienced the maximum level of uncertainty about judging the motor-outcome temporal interval. Using trials in which the latency of a light flash was altered from 0 to 300 ms following a motor event (i.e., button release; the overall performance block, Figure 1), we showed that at 100-ms delay duration, an approximately equal proportion of trials was perceived as synchronous (PS; mean ± standard error of the mean: 56.62 ± 2.66%) and perceived as asynchronous (PA; 43.38 ± 2.66%, Figure 2). This delay was also shown previously in humans and rats to be close to the point at which synchrony detection is most uncertain (Schmitgen 2017).

We then tested participants in trials using only the 100-ms latency described above. We changed the type of feedback from actual (i.e., reflecting actual performance of participants) received in the overall performance block to random (with 50% chance for being PS or PA) in the subjective block. Random feedback helped that participants will not realize that all trials in the subjective block have a delay. Participants were not aware of the randomness of feedback. There were no significant differences between hold times in correct and incorrect responses in trials with a 100 ms of delay in the overall performance block, and between PS and PA responses in the subjective block (Supplemental Figure 1 [https://doi.org/10.6084/m9.figshare.13227851.v1]). The lack of significant differences in the motor behavior of the participants suggested that perceived sense of agency was not influenced by prior trial performance. It also removed a major electrophysiological confound as the speed of voluntary action affects the onset and magnitude of the readiness potential (RP; also known as Bereitschaftspotential) (Shibasaki and Hallett 2006). Like the overall performance block in the subjective block, an approximately equal proportion of trials was perceived as synchronous (56.80 ± 1.41%) and perceived as asynchronous (43.20 ± 1.41%).

Participants reported that distinguishing between two conditions in the subjective block was very hard, but they often had a feeling that a trial must be synchronous or asynchronous. This report was obtained by post-experiment interviews in which participants were asked to tell more about their experience during the experiment and tell what strategies they used in the subjective block to judge if a trial was synchronous or asynchronous. No participant reported that the feedback in the subjective block was random, indicating that they believed that the feedback in the subjective block was reliable like the previous two blocks, and actually the harder nature of the subjective block was the reason they had a poorer performance in the subjective block, compared to the previous blocks.

To investigate the origin of sense of agency under high motor-outcome temporal uncertainty (i.e., absence of reliable sensory cues as it was the case in the subjective block), we compared event-related potentials (ERPs) prior to motor action in PS and PA conditions. Magnitude of the electrophysiological signal between -60 to -4 ms from button release in the PS trials was significantly larger than in the PA trials (0.050 ± 0.079 µV vs. -0.112 ± 0.072 µV, $t(19) = 2.643$, Bonferroni-corrected $p = 0.048$, Cohen's $d = 0.48$, Figure 3b). This pre-motor signal difference was paired with differences in ERP immediately prior to light flash onset. Between 52 and 96 ms after button release a significant larger ERP amplitude in the PS condition (0.048 ± 0.090 μV) was seen compared to that for the PA condition (-0.138 ± 0.071 μV, $t(19) = 4.178$, Bonferroni-corrected $p = 0.001$, $d = 0.51$). The scalp topographic maps for each sub-window are provided in Figure 3d, and the dipole source modeling indicating the signal differences within the -60 to -4 ms time window (prior to motor action) correlated with activity in the inferior parietal lobule (IPL) in Figure 3f.

May these pre-motor correlates of agency have reflected memory of prior trial performance (for example, via habituation (Dommett et al. 2005; Thompson and Spencer 1966)) rather than being directly agency-related? To assess this, we stratified trials in the subjective block according to the response type (PS or PA) and the feedback type (confirmatory or refutatory) of an immediately preceding trial, rather than the response type of a trial itself. This stratification resulted to four conditions with trials that an immediately preceding trial had a (a) PS response and confirmatory feedback; (b) PS response and refutatory feedback; (c) PA response and confirmatory feedback; and (d) PA response and refutatory feedback. Repeated-measures analysis of variance (ANOVA) with Bonferroni correction for pairwise comparisons was used to examine condition differences prior to and following motor action. Importantly, there were no significant differences between either of the conditions in either of the time intervals, indicating that the subjective performance was not influenced significantly by the previous trial (for example via habituation) in the subjective block. Statistics are provided in Table S1.

To further assess whether the prediction signal was sensitive to contextual difficulty of synchrony judgement, we investigated the overall performance block. Here, the 100-ms latency trials were intermixed with shorter and longer latencies to more easily relate performance to feedback. Thus, the participants' agency decisions were positively reinforced. In these conditions no significant difference was seen between pre-motor activity (-60 to -4 ms prior to motor action) in PS (-0.060 ± 0.090 μV) and PA (-0.061 ± 0.156 μV) trials, *t*(19) = 0.006, *p* = 0.995, *d* < 0.01, Figure 3a, c. On the other hand, repeated-measures ANOVA revealed that the interaction between block (overall performance or subjective) and judgment (PS or PA) was significant, F(1, 19) = 4.55, *p* = 0.046. These data suggested that the prediction signal diminished in the overall performance block (compared to the subjective block) as a function of reduced uncertainty. Statistics are provided in Supplemental Table 2 (https://doi.org/10.6084/m9.figshare.13227851.v1).

We then tested how this pre-motor prediction signal in the IPL influenced the participants' response (PS or PA). Two decision point-locked distinct differences over the right frontal cortex were observed (Figure 4b) in ERPs during the subjective block. The earlier activity occurred within -400 to -300 ms relative to response onset (amplitudes of 0.007 ± 0.056 μV, PS vs. -0.135 ± 0.056 μV, PA) and the difference between PS and PA conditions was statistically significant, *t*(19) = 3.176, *p* = 0.010, *d* = 0.57. The later activity arose within -148 to -52 ms relative to response onset, and there was also a statistically significant difference between PS (-0.137 ± 0.100 μV) and PA (0.044 ± 0.092 μV) conditions, *t*(19) = -2.821, *p* = 0.021, *d* = 0.42. Dipole modeling revealed that the origin of the observed activity is in the right superior temporal gyrus (STG; Figure 4f). Repeated-measures ANOVAs revealed that the interaction between block (overall performance or subjective) and judgment (PS or PA) was significant for the -400 to -300 ms pre-response, F(1, 19) = 5.07, *p* = 0.036, and for the -148 to -58 ms, F(1, 19) = 4.81, p = 0.041, time windows, suggesting that the PS and PA difference was significantly greater in the subjective than overall performance block.

These pre-decision ERP events were strongly correlated with the prediction signal in the subjective block. Pre-motor prediction signal (Figure 3b), difference between PS and PA outcomes, was significantly related to pre-decision ERP differences occurring -400 to -300 ms relative to response (Figure 4b), $r = -0.560$, $p = 0.010$, see Figure 5. In addition, under overall performance condition, where no prediction signal was seen (Figure 3a), no pre-response correlate in the ERP was seen either (Figure 4a). However, no such correlation was seen for the later (-148 to -52 ms) pre-decision ERP differences, $r = 0.318$, $p = 0.172$.

At an intra-participant level, single-trial ERP analysis revealed interesting findings. A *t*-test of z-transformed correlation coefficients for the pre-motor and pre-response (-400 to -300 ms) activities revealed that a mean $r = 0.15$ was significantly different from zero $t(20) = 8.15$, $p < 0.001$. A positive correlation was observed in all 20 participants. Also, for the pre-motor and pre-response (-148 to -52 ms) activities a mean $r = 0.11$ was significantly different from zero, $t(20) = 6.13$, $p < 0.001$. A positive correlation was observed in 19 out of 20 participants. See Figure 6 for more details. These results suggested that the amplitude of the pre-response activity scaled with the amplitude of the pre-motor activity at an intra-individual level, and a prediction signal prior to motor action influenced whether the flash was perceived as synchronous or as asynchronous.

Discussion

Our study sheds light on how uncertainty about the timing of the subsequent sensory outcomes of a voluntary action activates a predictive mechanism prior to motor action and generates a prediction about the timing of an upcoming sensory event. Under low temporal uncertainty about outcomes of a voluntary action, however, this signal was vanished. Prior to response (i.e., choosing whether a flash of light turned on immediately or with a delay with respect to motor action), there was a significant difference between two conditions (PS and PA) only in the experimental context with high (the subjective block), but not low (the overall performance block), temporal sensory uncertainty. Additionally, single-trial analysis revealed that there was a correlation between the activities prior to motor action and prior to response in the high uncertainty condition, suggesting passage of information from the former to latter and making this prediction available to conscious awareness likely through an insight solution, colloquially known as an “Aha!” experience.

Why did participants in the subjective block perceive some trials as synchronous and some as asynchronous, although all trials had a 100-ms motor-outcome delay? The delay was a highly unreliable sensory cue as it was close to a threshold where delay judgement had maximum uncertainty (Figure 2). According to the optimal cue integration theory (Synofzik et al. 2009; Synofzik et al. 2013) and given unreliability of the motor-outcome delay, a predictive signal (compared to sensory cues) may gain a higher weight to determine whether the upcoming event should be perceived as synchronous or asynchronous. We observed a significant amplitude difference between PS and PA trials prior to motor action (Figure 3) in the subjective block. The possibility was ruled out that this differential activity is simply a function of performance in an immediately prior trial (Supplemental Table 1 [https://doi.org/10.6084/m9.figshare.13227851.v1]). This analysis, for example, ruled out that participants tended to choose a response as PS (or PA) only because the previous trial was registered as PA (or PS).

In the overall performance block, participants experienced an easier synchrony judgment task compared to the subjective block. As the motor-outcome delay in this block was overall easier to judge and could be used as a more reliable synchrony cue, we predicted that the observed pre-motor signal in the subjective block should be reduced or vanished. Our analysis confirmed this prediction (Figure 3) as the pre-motor signal was only present in the subjective block in which motor-outcome delay had maximum sensory uncertainty.

The current task had some advantages to increase the signal to noise ratio. By using a constant delay of 100 ms between motor action and light flash in the subjective block, we avoided some potential confounds. Scalp-recorded ERPs are superimposed on top of each other with different weightings depending on the location and orientation of each source. By having trials with identical physical characteristics including similar delay, color, and brightness, we aimed to minimize the differences across conditions for the event-related potentials of interest that were involved in perceiving a trial as synchronous or synchronous. Additionally, performing the current task only relied on looking at a light source in the center of the screen and therefore no eye movement was required. Eye movements are a major source of noise in EEG studies (Luck 2014)

The perceived delay between a movement and its sensory outcomes has been extensively used as an implicit measure of sense of agency. One of the most employed paradigms for this purpose is intentional binding (IB) (Haggard, Clark, & Kalogeras, 2002; Moore & Obhi, 2012). Interestingly, it has been recently shown that IB also coincided with an explicit sense of agency on a trial-by-trial basis (Imaizumi & Tanno, 2019). Under IB, the perceived time between voluntary motor action and its sensory outcomes contracts compared to when a movement is involuntary (for instance, via a twitch evoked by applying transcranial magnetic stimulation over the motor cortex), or when sense of agency has been experienced to a lesser degree for example as a result of social exclusion (Malik and Obhi 2019).

In a conventional IB experiment, participants are asked to press a button at a time of their own choosing and await a short tone (100 ms) occurring 250 ms afterwards. Simultaneously, they are instructed to look at a computer screen in front of them and carefully watch a rotating clock hand. In one experimental block, the time at which they pressed the button is to be reported and in another experimental block the time at which they heard the tone. There are also two baseline blocks in which once no tone occurs following a motor action, and once a tone occurs without a button press being registered. By comparing these four blocks of trials, the net time compression between action and tone can be calculated.

Since the first report of IB as an implicit measure for agency (Haggard et al., 2002), several variables have been discovered as factors that may increase sense of agency (hyperagentic factors) such as rewarding outcomes like monetary gain (Takahata et al., 2012), or may decrease sense of agency (hypoagentic factors) such as fear and anger (Christensen, Di Costa, Beck, & Haggard, 2019) or acting under coercion (Caspar, Christensen, Cleeremans, & Haggard, 2016), similar to Milgram's classic experiment. In our study, we benefited from the IB effect to study how predictive agency cues may gain a higher weight as postdictive sensory cues become less reliable.

The distinction between self-generated and externally generated events and their sensory consequences is crucial for efficient adaptation of behavior to predictable and unpredictable situations (Barrett & Simmons, 2015; Crapse & Sommer, 2008; Sawtell, 2017). This self-external delineation also seems critical for the experience of agency (Blakemore, Wolpert, & Frith, 1998, 2000; Haggard, 2017; Moore, 2016; Nahab et al., 2010; Nichols, 2011). According to optimal cue integration (Synofzik et al. 2013), agency cues are weighted based on their availability and reliability. In the subjective block, the motor-outcome delay was available yet highly unreliable as uncertainty about synchrony judgement was close to maximum (Figure 2). In the absence of reliable external sensory cues, it was expected that internal predictive cues gain a higher weight to establish agency. The observed signal prior to motor action (Figure 3) is speculated to be a signature of an internal predictive mechanism originating from the right inferior parietal lobule (Figure 3).

This region has been shown to be involved in the formation of sense of agency (Chambon et al. 2015; Chambon et al. 2012; Farrer et al. 2003; Farrer and Frith 2002; Koreki et al. 2019; Yomogida et al. 2010) , and more likely involved in sense of external-agency rather than sense of self-agency (Seghezzi et al. 2019; Sperduti et al. 2011). This signal was absent in the overall performance block where motor-outcome delay uncertainty was low, so the delay could be used as a more reliable agency cue.

A more direct link between the effect of delay duration and agency attribution is provided by (Farrer et al. 2008). In their study, participants were seeing an avatar of their arm while moving a joystick. The avatar was either exactly imitating the actual arm movement or was offset by varying amount in time or space. The task was to report if the spatial or temporal dislocation of the avatar corresponded to their actual movement, or it was biased (spatially or temporally), or it was not their own, but a movement controlled by the experimenter. Results revealed that participants showed maximum uncertainty about self versus biased movements somewhere between 15-20 degrees in space and 50-150 ms in time. These results along with our findings suggest that an outcome delay duration of 100 ms is close to a cut-off where synchrony and agency judgments encounter maximum uncertainty.

The correlations shown in Figures 5 and 6 point to two distinct relationships. The intra-individual correlation between the pre-motor and pre-response signals shown in Figure 6 demonstrates that in each individual (except one subject for the -400 to -300 ms period prior to response), the increase in the activity in the right IPL corelated with the increase of the activity in the right STG. This significant positive correlation on an intra-individual level between these two brain regions (IPL and STG) suggests that the right IPL modulates the activity of the right STG when there is a high (versus low) temporal uncertainty about the outcomes of a voluntary action. As the polarity of event-related potentials depends on various factors including the cortical folding pattern (Luck 2014), no conclusions can be made at this point whether the IPL has an excitatory or inhibitory effect on the STG. In contrast, the correlation shown in Figure 5 does not provide insight about how the right IPL and STG are correlated on a trial-by-trial manner in each participant. Instead, this significant negative correlation only indicates that individuals who had a higher pre-motor amplitude difference between PS and PA conditions tended to have a lower pre-response amplitude difference between PS and PA conditions.

Dipole source modeling also showed that the origin of the differential activities between PS and PA trials prior to response was the right STG. This observed activity may be a neural correlate of an insight solution. In contract to an analytical solution where a problem is solved ‘step-by-step’, a prerequisite for an insight solution is its sudden emergence in awareness, although the culmination of a series of neural computations is likely to occur in advance unconsciously (Kounios and Beeman 2009). The right STG is suggested to be linked with the occurrence of an insight solution while solving compound-remote-associates problems (Jung-Beeman et al. 2004). In these high-level semantic tasks, for example, three words are presented (e.g., crab, pine, sauce) and participants are asked to find one word that can be appended to each of the three words and form meaningful compound words (e.g., apple can be added to crab, pine, and sauce to form crabapple, pineapple, and apple sauce). The present experimental paradigm seems to be suitable for investigating insight solutions using a novel low-level sensory task in which a ‘snap decision’ may play a role to judge if sensory events were proceeding motor action immediately or with a delay.

Conclusion

In summary, we propose that the observed prediction signal prior to motor action, which is reported here for the first time, is highly likely to be involved in neural mechanisms underlying the IB effect (Haggard et al. 2002). It remains an open question whether the prediction signal observed in the subjective block of this study has a stochastic origin (Schurger et al. 2012) or is triggered by earlier neuronal processes of certain function. Using stimuli of other modalities (e.g., auditory tones) will reveal to what extent the effect is modality-independent and how sense of agency integrity is preserved across multimodal sensory inputs. We propose that this new experimental task provides a powerful tool to investigate sense of agency in healthy and agency-disrupted (Fletcher and Frith 2008; Moore and Fletcher 2012) conditions (e.g., in individuals with psychotic disorders such as schizophrenia) as well as, with some modifications, in animal models (Sigurdsson et al. 2010). Given uncertainty in sense of agency, prediction is a critical factor in determining the nature of sensory consequences of a voluntary motor action and this appears to involve activity across a right parietal-temporal axis.

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Figure legends

Figure 1. Experimental task. Participants were asked to press down and release a button at the time of their own choosing, and to respond if a flash turned on instantaneously or with a delay relative to button release. They were not aware that in the subjective block the flash always triggered with a 100 ms of delay with respect to button release, and the feedback was random. See Materials and Methods for details.

Figure 2. Trials with a delay of 100 ms in the overall performance block had an approximately equal proportion of perceived as synchronous (PS) and perceived as asynchronous (PA) trials, providing a balanced condition where the uncertainty over the delay

of the sensory outcome of a voluntary motor action was close to maximum. $n = 20$; error bars represent mean ± s.e.m.

Figure 3. Subjectivity generates a sense of agency prediction event in parietal cortex. (**a, b**) Grand-averaged ERPs in perceived as synchronous (PS; blue) and perceived as asynchronous (PA; red) conditions at the CP4' channel in the overall performance 'a' and subjective 'b' blocks relative to button press. Yellow-highlighted areas indicate significant differences between PS and PA conditions. (**c**, **d**) Scalp topographic maps of PS, PA, and the subtraction of PA from PS at three different time windows (-60 to -4 ms, 0 to 48 ms, and 52 to 96 ms) in the overall performance 'c' and subjective 'd' blocks relative to button release. Significant *p* values are Bonferroni-corrected for multiple comparisons. (**e**) Green channels show the selected scalp channels for motor-locked data analysis. (**f**) Localization and orientation of a dipole within the time window of -60 to -4 ms with respect to button release in the inferior parietal lobule (IPL) accounting for 34% of the variance between the model and the observed scalp potentials. Introduction of additional dipoles did not change the location and orientation of this single-dipole solution.

Figure 4. Subjective prediction of agency was accompanied by pre-decision ERP changes in right superior temporal gyrus. (**a**, **b**) Grand-averaged ERPs in perceived as synchronous (PS; blue) and perceived as asynchronous (PA; red) conditions at pooled channels in the overall performance 'a' and subjective 'b' blocks relative to response onset. Yellow-highlighted areas indicate significant differences between PS and PA conditions. (**c**, **d**) Scalp topographic maps of PS, PA, and the subtraction of PA from PS at two different time windows (-400 to -300 ms and -148 to -52 ms) in the overall performance 'c' and subjective 'd' blocks relative to response onset. Significant *p* values are Bonferroni-corrected for multiple comparisons. (**e**) Green channels depict the selected channels for response-locked ERP analysis. (**f**)

Localization and orientation of a dipole within -400 to -300 ms relative to response in the superior temporal gyrus (STG) accounting for 28% of the variance between the model and the observed scalp potentials. Introduction of additional dipoles did not change the location and orientation of this single-dipole solution.

Figure 5. In subjective conditions, pre-motor prediction and pre-decision neural activities were correlated. The PS-PA difference in ERP amplitude prior to motor action (-60 to -4 ms relative to button release) was significantly correlated to the difference activity preceding response (-400 to -300 ms relative to response onset), $n = 20$, $r = -0.560$, $p = 0.010$. The observed activity (-400 to -300 ms) prior to response may be a neural signature of the sudden transition of an insight solution (aka, “Aha!” experience) (Jung-Beeman et al. 2004) from an unconscious to a conscious state, and may be the origin of the *feeling* participants had regarding the type of the trial (i.e., PS or PA).

Figure 6. Single-trial ERP analysis of the subjective block. Line of best fit for each participant (n = 20) derived from a scatter plot between amplitude of the pre-motor (-60 to -4 ms) activity and (a) amplitude of the pre-response (-400 to -300 ms) activity; and (b) amplitude of the pre-response (-148 to -52 ms) activity. (c) The blue circles show the correlation coefficients for each participant calculated for the -400 to -300 ms pre-response time window, and the red circles for the -148 to -52 ms pre-response time window. Error bars represent mean ± s.e.m.

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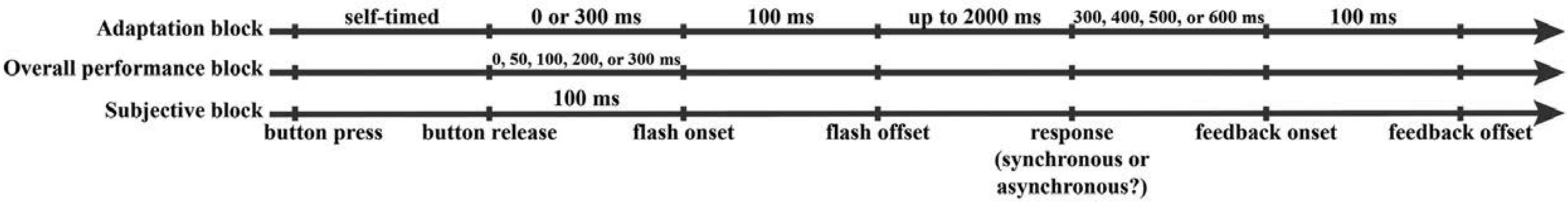
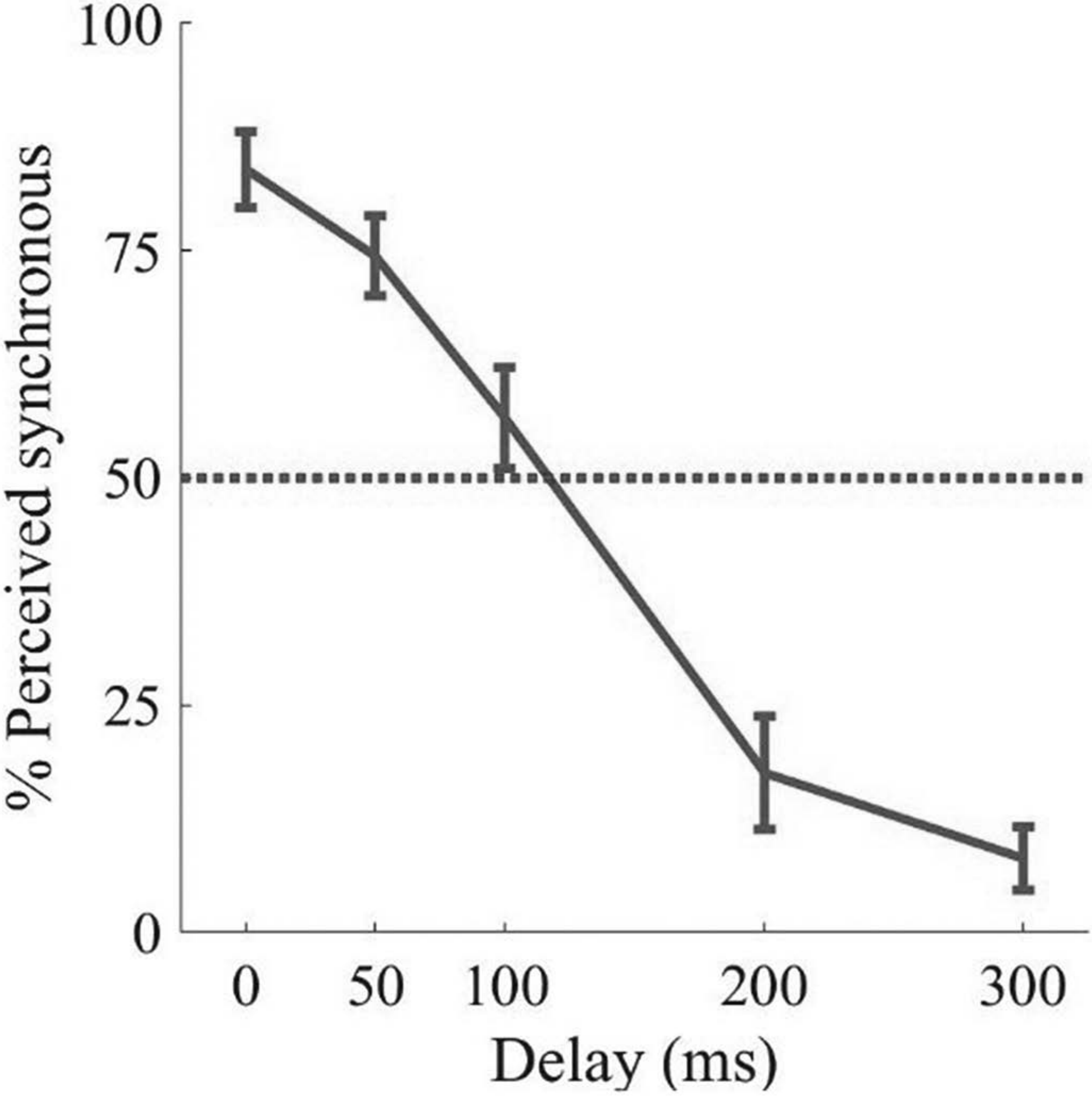
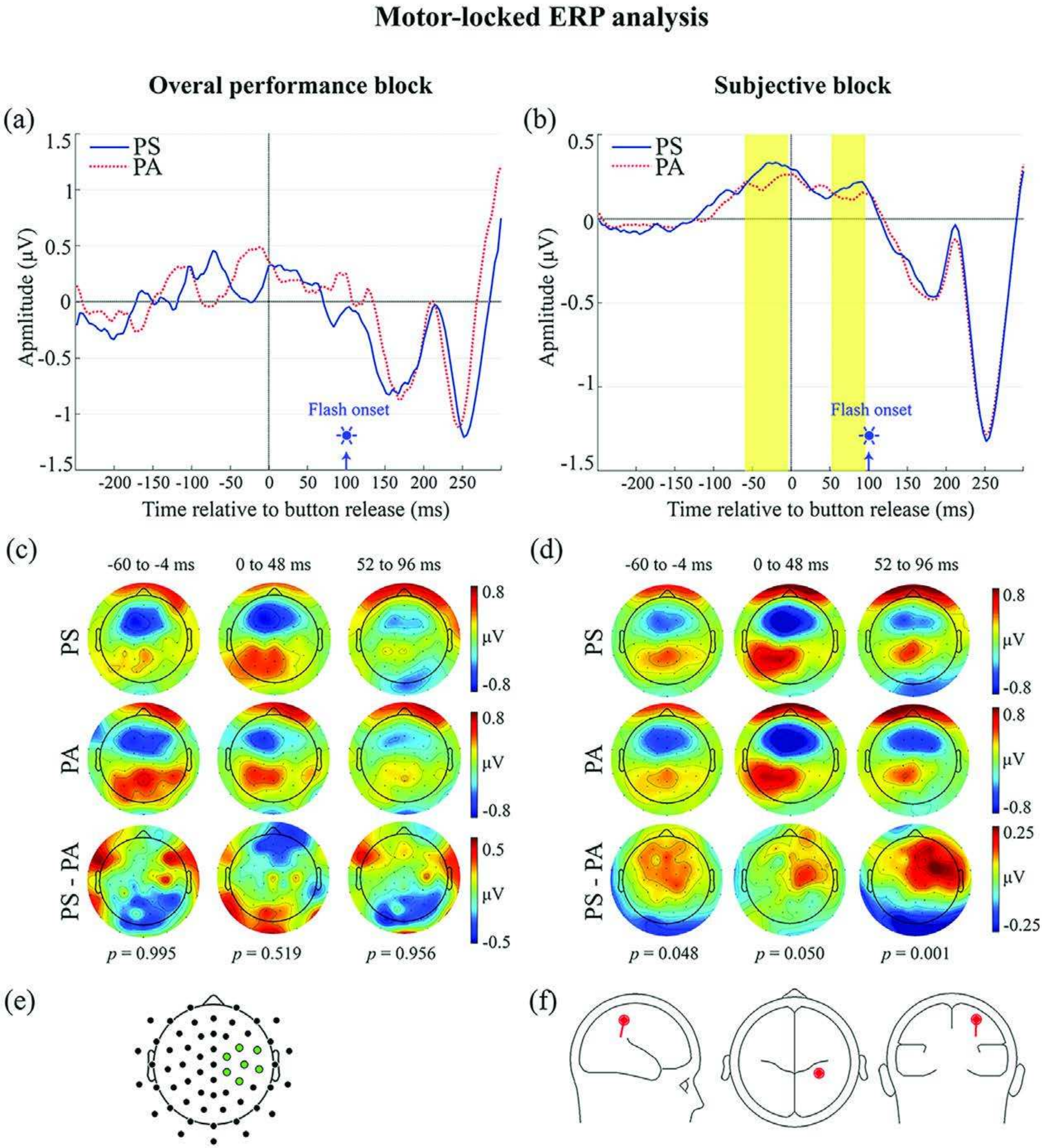
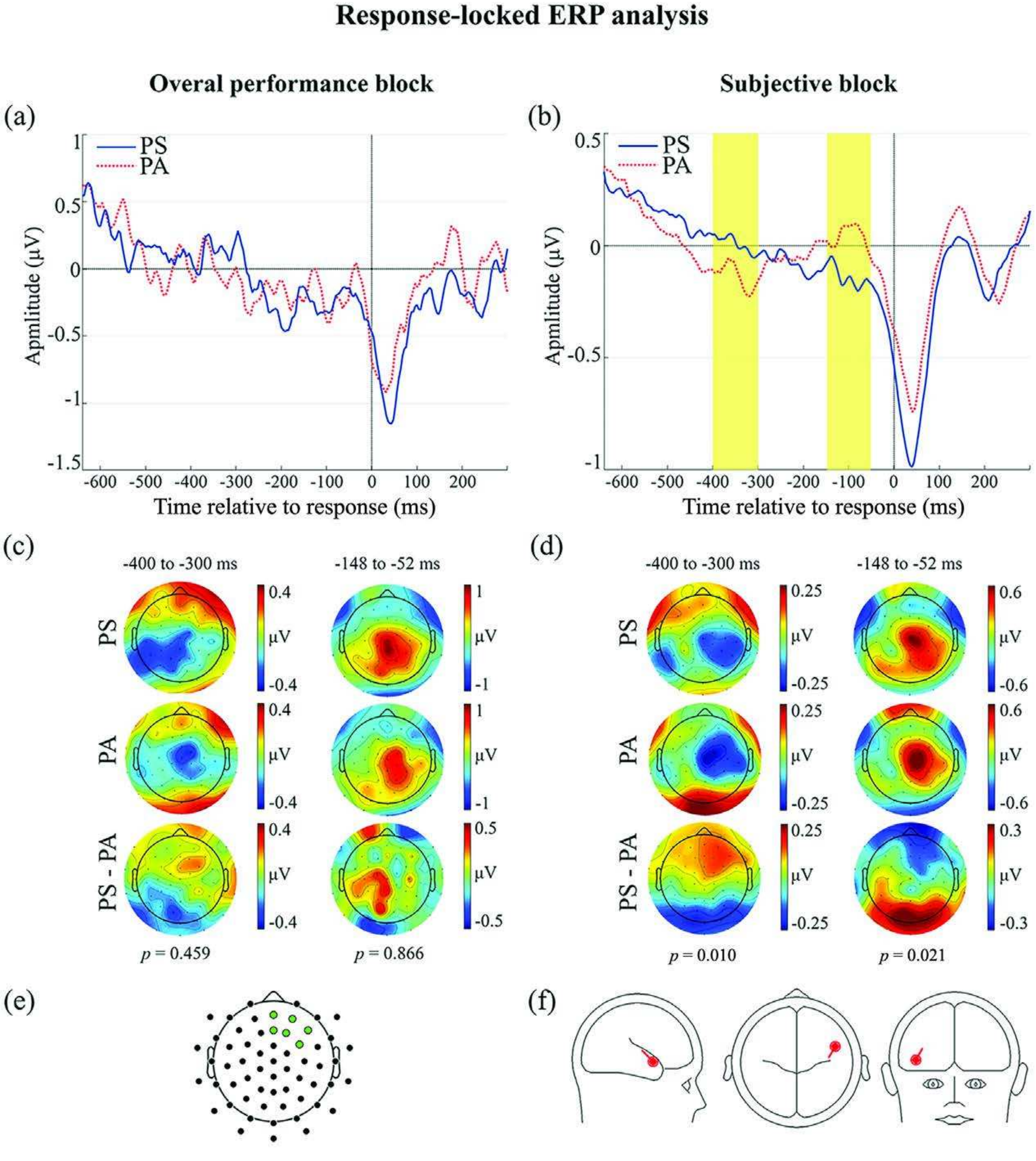
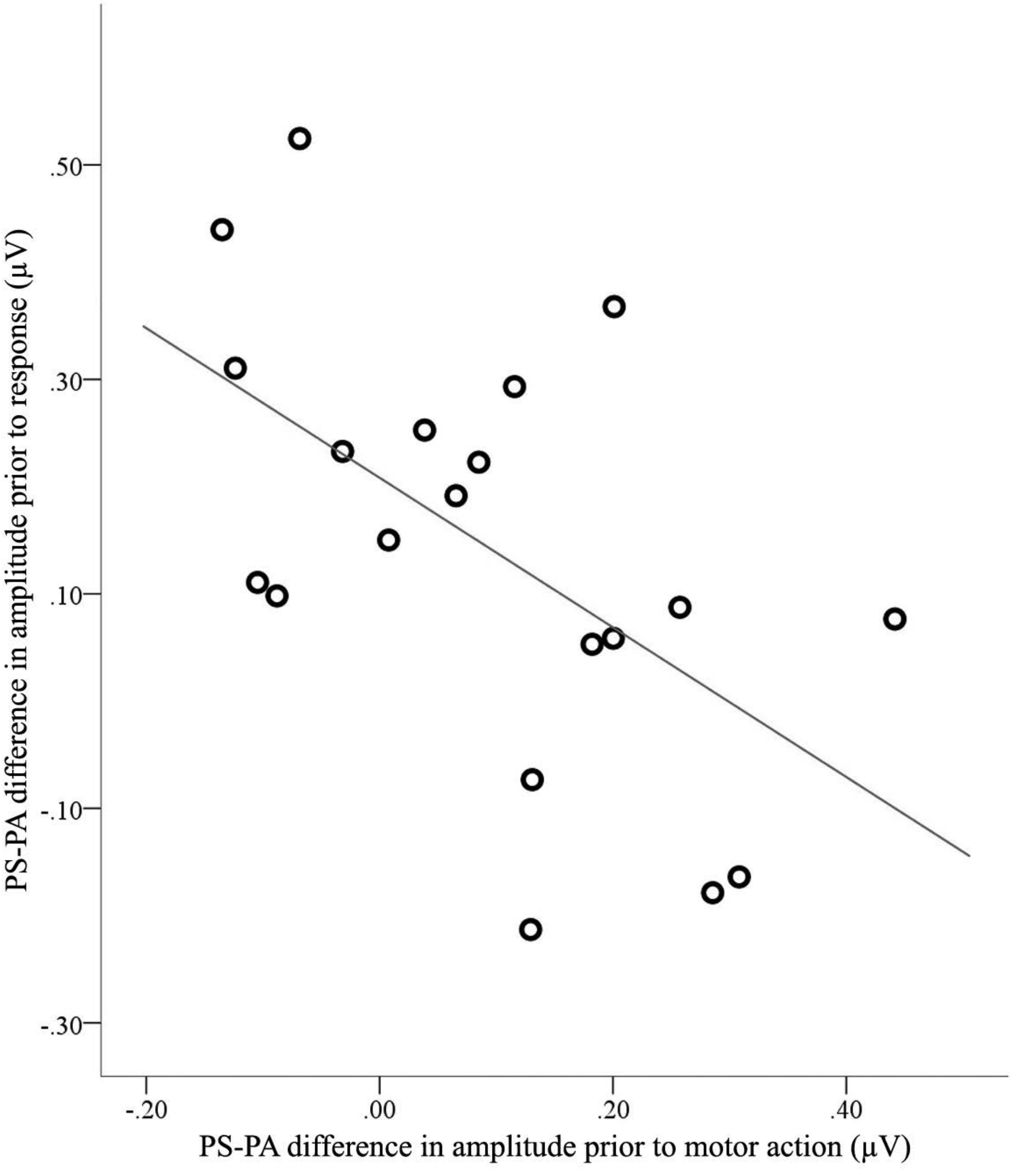

Adaptation block
Overall performance block
Subjective block
self-timed
0 or 300 ms
100 ms
up to 2000 ms
300, 400, 500, or 600 ms
100 ms
0, 50, 100, 200, or 300 ms
100 ms
button press
button release
flash onset
flash offset
response (synchronous or asynchronous?)
feedback onset
feedback offset



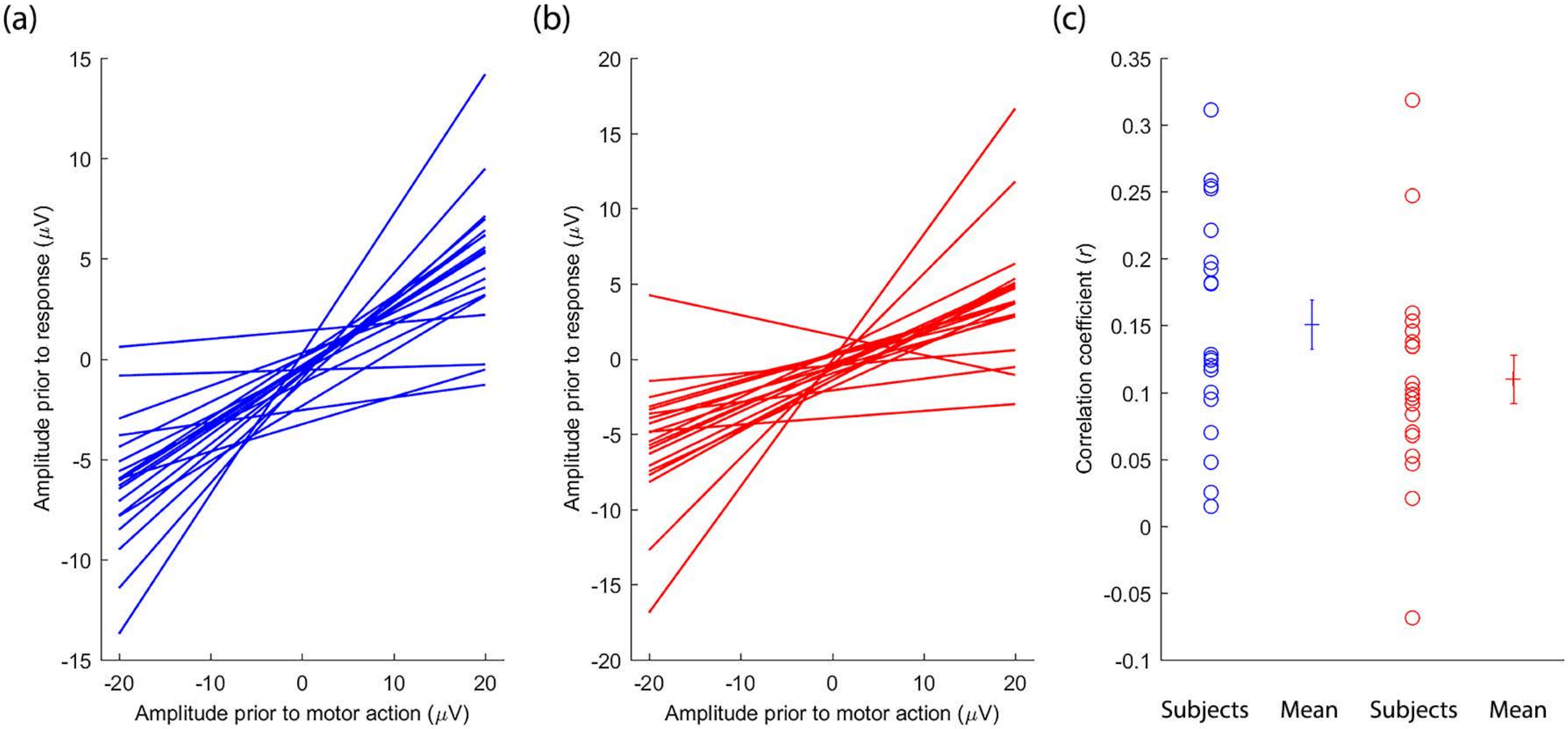
100
75
50
25
0
% Perceived synchronous
0
50
100
200
300
Delay (ms)

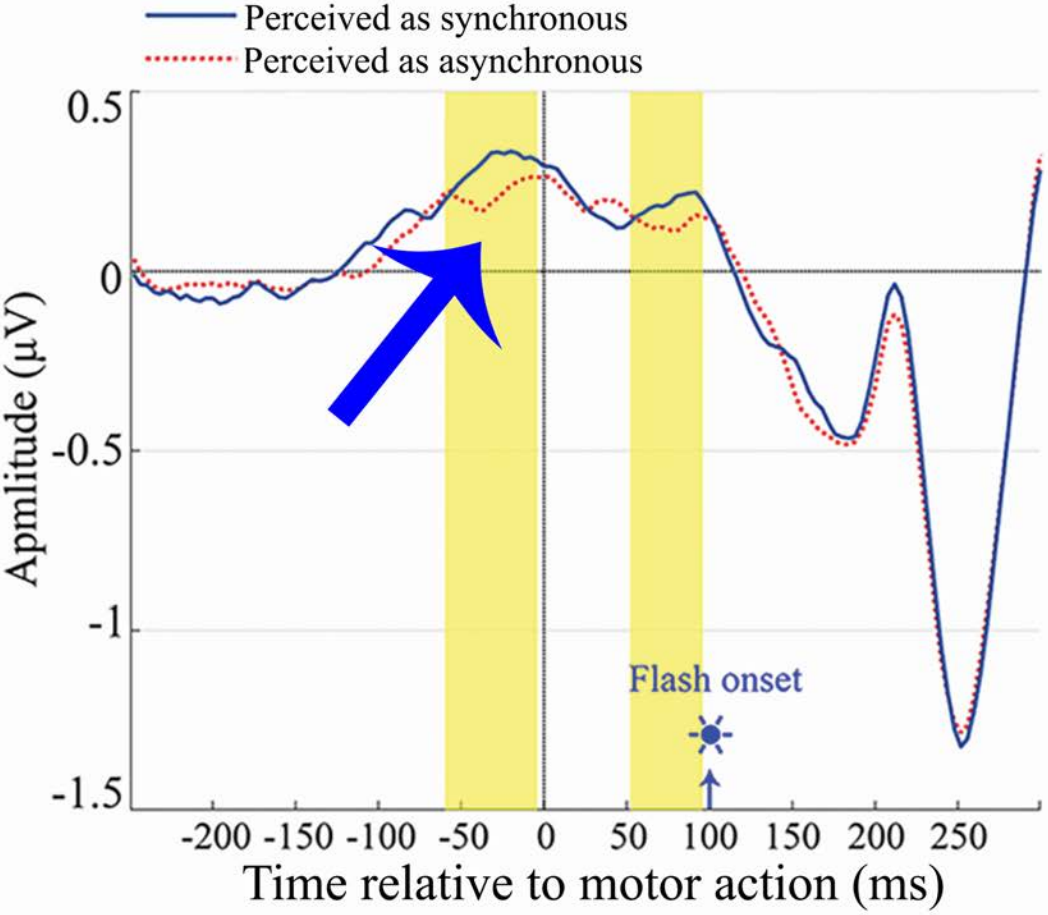

Motor-locked ERP analysis
Overal performance block
Subjective block
(a)
(b)
PS
PA
Apmlitude (μV)
1.5
1
0.5
0
-0.5
-1
-1.5
Flash onset
-200 -150 -100 -50 0 50 100 150 200 250
Time relative to button release (ms)
(c)
(d)
-60 to -4 ms
0 to 48 ms
52 to 96 ms
PS
PA
PS - PA
0.8
μV
-0.8
0.5
-0.5
0.25
-0.25
p = 0.995
p = 0.519
p = 0.956
p = 0.048
p = 0.050
p = 0.001
(e)
(f)


Response-locked ERP analysis
Overal performance block
Subjective block
(a)
(b)
PS
PA
Apmlitude (μV)
1
0.5
0
-0.5
-1
-1.5
-600
-500
-400
-300
-200
-100
0
100
200
Time relative to response (ms)
(c)
(d)
-400 to -300 ms
-148 to -52 ms
PS
PA
PS - PA
μV
0.4
-0.4
1
-1
0.5
-0.5
0.25
-0.25
0.6
-0.6
0.3
-0.3
p = 0.459
p = 0.866
p = 0.010
p = 0.021
(e)
(f)



PS-PA difference in amplitude prior to response (µV)
.50
.30
.10
-.10
-.30
-.20
.00
.20
.40
PS-PA difference in amplitude prior to motor action (µV)


(a)
(b)
(c)
Amplitude prior to response (μV)
Amplitude prior to motor action (μV)
15
10
5
0
-5
-10
-15
-20
-10
0
10
20
Amplitude prior to response (μV)
Amplitude prior to motor action (μV)
20
15
10
5
0
-5
-10
-15
-20
-20
-10
0
10
20
Correlation coefficient (r)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
Subjects
Mean
Subjects
Mean



A possible existence of a prediction signal prior to voluntary movement which appears when postdictive agency cues (i.e., the judgment of the time between voluntary movement and a subsequent flash of light) are not reliable.