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

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21
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25 **Abstract**

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

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

45

46 **NEW & NOTEWORTHY**

47 According to the optimal cue integration theory, the formation of sense of agency relies on
48 both predictive and postdictive agency cues and how they are weighted based on their
49 availability and reliability. Using a novel paradigm, we show for the first time a possible

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

53

54 **Introduction**

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

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

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

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

92 The second block (the overall performance block) was harder. Here, the motor-
93 outcome delay was either 0, 50, 100, 200, or 300 ms. (Participants were not informed about
94 the numeric values of delays. They were only told to distinguish whether the flash was
95 synchronous or asynchronous.) The feedback in this block was still associated with their
96 actual performance. The third block (the subjective block) was the hardest. Participants were
97 told to try their best to distinguish the subtle delay difference between synchronous and
98 asynchronous flashes. Participants were unaware that two deceptions were included in this

99 block. First, all trials had a delay of 100 ms, as opposed to the adaptation and overall
100 performance blocks where trials with various delays were intermixed. Second, unlike the first
101 two blocks feedback was random. (If true feedback was provided, participants could gradually
102 discover the deception that the flash always turned on with a delay.) From participants' point
103 of view (as it was confirmed by post-experiment unstructured interviews), however, trials
104 were a mix of no delay and delayed flashes and reliable feedback reflecting their actual
105 performance was provided.

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

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

124

125 **Materials and Methods**

126 **Participants.** Twenty-four healthy, right-handed students with normal or corrected-to-normal
127 vision were recruited through flyers. To reduce the occurrence of eye blinks mainly due to
128 dryness of the eye, we asked participants who normally wear contact lenses to wear their
129 glasses instead (Luck 2014). Written informed consent was obtained from all participants
130 before the study began. Four participants were excluded: One due to technical problems, one
131 for not completing the experiment, and two for incorrect responses greater than 30% in the
132 adaptation block (Figure 1). Thus, twenty participants (14 females; mean age: 22, range: 19-
133 29 years) were retained in analyses. The study was approved by the Ethics Committee of
134 Heidelberg University, and experimental procedures conformed to the Declaration of
135 Helsinki.

136 **Experimental procedure.** The primary aim of the experiment (studying sense of agency
137 under uncertainty) was kept hidden from participants and they were told that the study was
138 about synchrony detection. Participants were seated individually in a magnetically shielded
139 and darkened room at a distance of one meter from a three-color light-emitting diode (LED),
140 subtending 0.5 degree of visual angle. To cover the room background, the LED was placed at
141 the center of a matt, gray-colored plate with a width and height of 48 and 27 centimeters,
142 respectively. (Conventional LCD computer monitors typically have a screen refresh rate of
143 60-120 Hz. We used a custom LED setup with a response time of about 1 ms to minimize the
144 jitter between button release and the appearance of flash.) Throughout the experiment,
145 participants heard Gaussian white noise via headphones (EA-RTONE 3A, Aearo Corporation,
146 Indianapolis, USA) in order to superimpose the feedback clicks from button presses and
147 releases. Also, they wore two thimbles on the index and middle fingers of their right hand
148 which was placed under a covering box to minimize tactile and visual feedback from their

149 motor actions. Inside the box, there was a gaming computer mouse (Logitech G Series; report
150 rate: 1000 Hz) with which the responses were registered via its right and left buttons. (These
151 sensory blockages allowed us to ensure that participants mainly relied on the visual cues from
152 the LED to distinguish whether the flash appears synchronous or asynchronous relative to
153 their finger lift.)

154 **Experimental paradigm.** Each experimental trial began in a self-paced manner with
155 pressing and holding down the left mouse button via the right-hand index finger. Releasing
156 the button triggered a 100-ms-long blue flash light from the LED with a 0 or 300 ms of delay
157 in the adaptation block, with a 0, 50, 100, 200, or 300 ms of delay in the overall performance
158 block, and with a 100 ms of delay in the subjective block (Figure 1). In the first two blocks
159 (i.e., the adaptation block and the overall performance block), trials with a 0 ms of delay were
160 50% of the trials, and all trials were randomly intermixed. After flash offset, participants were
161 given up to 2000 ms to respond, reporting whether the flash was perceived as synchronous
162 (PS) or perceived as asynchronous (PA) relative to button release, using the right-hand index
163 and middle fingers, respectively. Finger mapping was counterbalanced across subjects. After
164 response, there was a randomly varying interval of 300, 400, 500, or 600 ms with a uniform
165 distribution before a 100-ms-long visual feedback stimulus appeared. In the first two blocks,
166 true feedback was provided, meaning feedback reflected actual performance, whereas in the
167 subjective block random feedback was presented, meaning feedback was not associated with
168 actual performance. Random feedback was either confirmatory or refutatory, with equal
169 probability. Confirmatory feedback denotes that the feedback approved the participant's
170 response correctness, although it could be an incorrect response. In contrast, refutatory
171 feedback rejected the participant's response correctness, even though it could be a correct
172 response. (It should be noted that participants were not aware of the randomness of feedback
173 in the subjective block. From participants' point of view as confirmed by post-experiment

174 unstructured interviews, feedback was reliable in all blocks, reflecting their actual
175 performance.) The color mapping for feedback stimulus was fixed within a participant but
176 switched across participants from magenta for correct and confirmatory feedback, and yellow
177 for incorrect and refutatory feedback and vice versa. (This color switch across participants
178 ensured that the potential observed effects are not contaminated by properties related the color
179 of the feedback flash. Although the brightness of the colors was adjusted to be the same, this
180 color switch further ruled out the effect of potential subtle brightness differences.) There were
181 200 trials each in the adaptation and overall performance blocks, and 400 trials in the
182 subjective block. These 800 trials built the first session of the experiment. Testing subsamples
183 of the subjective block with the same number of trials equal to that of the adaptation block did
184 not change the observed findings. Before the first session began, participants were
185 familiarized with the experimental task by performing 50 trials similar to those of the
186 adaptation block.

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

194 The reward pattern was similar in both sessions. In the first two blocks, participants
195 were rewarded 1 euro cent for each correct response. In the subjective block, an amount was
196 given suggesting that they responded correctly between 60 and 70% of trials. The exact
197 amount was randomly chosen for each participant and they were informed about their total
198 win after each block. Participants were naïve about the facts that all trials of the subjective

199 block had a constant delay of 100 ms relative to their motor action, and that the feedback was
200 not reflecting their performance level. After data collection phase ended, they were informed
201 via email about the manipulation in the subjective block. The reason we varied their reward
202 randomly (rather than keeping it fixed) in the subjective block was to increase the notion that
203 the feedback in the subjective block still reflected participants' actual performance. The
204 reason we chose the reward rate to be between 60 and 70% (rather than 50%) was to indicate
205 participants that their performance is still better than chance and as a result they will be more
206 motivated to perform the task attentively.

207 **EEG recordings.** The electroencephalogram (EEG) was recorded from 60 Ag/AgCl
208 electrodes by a QuickAmp amplifier (Brain Products GmbH, Germany) at a sampling rate of
209 2000 Hz and with a 560-Hz anti-aliasing filter. Electrodes were mounted on an electrode cap
210 (EasyCap, FMS, Germany) according to the head size with equidistant electrode positions.
211 Electrodes were named after the equivalent positions in the international 10/20 system. Small
212 position deviations are marked with the symbol ' (e.g., CP2'). A common average reference
213 was used online and later for data analysis. A ground electrode was placed on the right
214 shoulder. Electrode impedances were kept below 5 k Ω (Kappenman and Luck 2010). Four
215 additional electrodes were used to record the electrooculogram (EOG). Vertical eye
216 movements and eye blinks were monitored by two electrodes located about 1 cm above and
217 below the left eye. Horizontal eye movements were monitored with 2 electrodes located on
218 the lateral canthi of the left and the right eyes.

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

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

226 For motor-locked ERP analysis with respect to the response type (PS or PA), data
227 were segmented from -250 to +300 ms relative to button release. Trials with missed responses
228 were discarded (< 1% of trials). Baseline correction was applied from -250 to -60 ms relative
229 to button release. (Choosing an appropriate baseline is important for electrophysiological
230 studies (Keil et al. 2014). The choice may particularly become problematic if the time from
231 which differential neural activities across experimental conditions or groups begin is not clear
232 (Haggard 2008), as is the case in the study of readiness potential (Jo et al. 2014). This
233 ambiguity can potentially affect the observed differences between groups and conditions. We
234 alternatively tested another baseline (-250 to +100 ms relative to button release) as well. The
235 new baseline did not significantly affect our results.) Artefact rejection criteria were:
236 Maximum allowed voltage: 100 μV ; minimum allowed voltage: -100 μV ; maximum allowed
237 voltage step: 80 $\mu\text{V}/\text{ms}$; lowest allowed activity within 50-ms intervals: 0.5 μV . Even if only
238 one EEG channel was contaminated, all channels for that trial were rejected. The mean
239 percentage of retained trials was 94% (SD = 7.4%). ERPs were calculated by averaging all
240 retained trials of each participant separately for perceived as synchronous (PS) trials (i.e.,
241 trials in which participants responded that there was no delay between button release and flash
242 onset) and perceived as asynchronous (PA) trials (i.e., trials in which participants responded
243 that there was a delay between button release and flash onset). The averages for these two
244 conditions were then grand-averaged across participants. Electrode sites and the time window
245 of the present work were defined based on using a collapsed localizer (Luck and Gaspelin
246 2017). Using a collapsed localizer was appropriate for the current study as due to the novelty
247 of the paradigm the timing and location of the effects could not be specified by the previous
248 research. The average ERPs in the PS and PA conditions in the overall performance and

249 subjective blocks were pooled together and visually inspected to identify in which time range
250 and electrode sites the largest activities were observed. These parameters were used later to
251 compare the PS and PA conditions.

252 A group of seven neighboring channels over the right hemisphere included: FC2',
253 FC4', FC6', C4, CP2', CP4', and CP6' (Figure 3e). The measurement window was between -
254 60 and 96 ms relative to button release. To further investigate the difference between PS
255 versus PA conditions and to see if the difference between them began prior to motor action,
256 the time window was divided into three sub-windows from -60 to -4 ms (i.e., prior to motor
257 onset), 0 to 48 ms, and 52 to 96 ms (i.e., prior to flash onset), relative to the button release.
258 (Due to a sampling rate of 250 Hz, there was a 4-ms distance between sub-windows.) The
259 mean voltage amplitude at the selected channels for each of the chosen time windows was
260 used as a measure of the brain's electrical activity (Luck 2014). Topographic visualizations
261 were generated using EEGLAB (Delorme and Makeig 2004).

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

270 For response-locked ERP analysis, data were segmented from -640 to +300 ms
271 relative to response onset of a trial. As there was no unambiguous time interval for choosing
272 the baseline, the mean amplitude of the period between -640 and 0 ms was employed (Luck
273 and Hillyard 1990). (The average reaction time in the subjective block was 640 ms and was

274 chosen as the start time of segments. The time interval following response onset was not
275 analyzed and is shown in figures only for visualization purposes. Using another baseline (-640
276 to -400 relative to response onset) did not significantly affect our results.) Artefact rejection
277 criteria were similar to those described in motor-locked ERP analysis. The mean percentage
278 of retained trials was 95% (SD = 7.3%). ERPs were calculated by averaging the retained trials
279 for each participant separately in PS and PA trials. The averages for these two conditions
280 were then grand-averaged across participants. Choosing the electrode sites and time windows
281 were based on using a collapsed localizer (Luck and Gaspelin 2017). A cluster of six
282 neighboring channels over the right frontal cortex involved: AFz, AF4', Fz, F2', F6', and
283 FC4' (Figure 4e). Two measurement windows were between -400 and -300 ms and between -
284 148 and -52 ms relative to response onset.

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

298 collapsed channels in the -400 to -300 ms time window, and separately in the -148 to -52 ms
299 time window. The Bonferroni correction was used to compensate for multiple comparisons.

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

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

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

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

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

331

332 **Results**

333 We first needed to define a latency at which participants experienced the maximum level of
334 uncertainty about judging the motor-outcome temporal interval. Using trials in which the
335 latency of a light flash was altered from 0 to 300 ms following a motor event (i.e., button
336 release; the overall performance block, Figure 1), we showed that at 100-ms delay duration,
337 an approximately equal proportion of trials was perceived as synchronous (PS; mean \pm
338 standard error of the mean: $56.62 \pm 2.66\%$) and perceived as asynchronous (PA; $43.38 \pm$
339 2.66% , Figure 2). This delay was also shown previously in humans and rats to be close to the
340 point at which synchrony detection is most uncertain (Schmitgen 2017).

341 We then tested participants in trials using only the 100-ms latency described above.
342 We changed the type of feedback from actual (i.e., reflecting actual performance of
343 participants) received in the overall performance block to random (with 50% chance for being
344 PS or PA) in the subjective block. Random feedback helped that participants will not realize
345 that all trials in the subjective block have a delay. Participants were not aware of the
346 randomness of feedback. There were no significant differences between hold times in correct

347 and incorrect responses in trials with a 100 ms of delay in the overall performance block, and
348 between PS and PA responses in the subjective block (Supplemental Figure 1
349 [<https://doi.org/10.6084/m9.figshare.13227851.v1>]). The lack of significant differences in the
350 motor behavior of the participants suggested that perceived sense of agency was not
351 influenced by prior trial performance. It also removed a major electrophysiological confound
352 as the speed of voluntary action affects the onset and magnitude of the readiness potential
353 (RP; also known as Bereitschaftspotential) (Shibasaki and Hallett 2006). Like the overall
354 performance block in the subjective block, an approximately equal proportion of trials was
355 perceived as synchronous ($56.80 \pm 1.41\%$) and perceived as asynchronous ($43.20 \pm 1.41\%$).

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

365 To investigate the origin of sense of agency under high motor-outcome temporal
366 uncertainty (i.e., absence of reliable sensory cues as it was the case in the subjective block),
367 we compared event-related potentials (ERPs) prior to motor action in PS and PA conditions.
368 Magnitude of the electrophysiological signal between -60 to -4 ms from button release in the
369 PS trials was significantly larger than in the PA trials ($0.050 \pm 0.079 \mu\text{V}$ vs. -0.112 ± 0.072
370 μV , $t(19) = 2.643$, Bonferroni-corrected $p = 0.048$, Cohen's $d = 0.48$, Figure 3b). This pre-
371 motor signal difference was paired with differences in ERP immediately prior to light flash

372 onset. Between 52 and 96 ms after button release a significant larger ERP amplitude in the PS
373 condition ($0.048 \pm 0.090 \mu\text{V}$) was seen compared to that for the PA condition (-0.138 ± 0.071
374 μV , $t(19) = 4.178$, Bonferroni-corrected $p = 0.001$, $d = 0.51$). The scalp topographic maps for
375 each sub-window are provided in Figure 3d, and the dipole source modeling indicating the
376 signal differences within the -60 to -4 ms time window (prior to motor action) correlated with
377 activity in the inferior parietal lobule (IPL) in Figure 3f.

378 May these pre-motor correlates of agency have reflected memory of prior trial
379 performance (for example, via habituation (Dommett et al. 2005; Thompson and Spencer
380 1966)) rather than being directly agency-related? To assess this, we stratified trials in the
381 subjective block according to the response type (PS or PA) and the feedback type
382 (confirmatory or refutatory) of an immediately preceding trial, rather than the response type
383 of a trial itself. This stratification resulted to four conditions with trials that an immediately
384 preceding trial had a (a) PS response and confirmatory feedback; (b) PS response and
385 refutatory feedback; (c) PA response and confirmatory feedback; and (d) PA response and
386 refutatory feedback. Repeated-measures analysis of variance (ANOVA) with Bonferroni
387 correction for pairwise comparisons was used to examine condition differences prior to and
388 following motor action. Importantly, there were no significant differences between either of
389 the conditions in either of the time intervals, indicating that the subjective performance was
390 not influenced significantly by the previous trial (for example via habituation) in the
391 subjective block. Statistics are provided in Table S1.

392 To further assess whether the prediction signal was sensitive to contextual difficulty of
393 synchrony judgement, we investigated the overall performance block. Here, the 100-ms
394 latency trials were intermixed with shorter and longer latencies to more easily relate
395 performance to feedback. Thus, the participants' agency decisions were positively reinforced.
396 In these conditions no significant difference was seen between pre-motor activity (-60 to -4

397 ms prior to motor action) in PS ($-0.060 \pm 0.090 \mu\text{V}$) and PA ($-0.061 \pm 0.156 \mu\text{V}$) trials, $t(19)$
398 $= 0.006$, $p = 0.995$, $d < 0.01$, Figure 3a, c. On the other hand, repeated-measures ANOVA
399 revealed that the interaction between block (overall performance or subjective) and judgment
400 (PS or PA) was significant, $F(1, 19) = 4.55$, $p = 0.046$. These data suggested that the
401 prediction signal diminished in the overall performance block (compared to the subjective
402 block) as a function of reduced uncertainty. Statistics are provided in Supplemental Table 2
403 (<https://doi.org/10.6084/m9.figshare.13227851.v1>).

404 We then tested how this pre-motor prediction signal in the IPL influenced the
405 participants' response (PS or PA). Two decision point-locked distinct differences over the
406 right frontal cortex were observed (Figure 4b) in ERPs during the subjective block. The
407 earlier activity occurred within -400 to -300 ms relative to response onset (amplitudes of
408 $0.007 \pm 0.056 \mu\text{V}$, PS vs. $-0.135 \pm 0.056 \mu\text{V}$, PA) and the difference between PS and PA
409 conditions was statistically significant, $t(19) = 3.176$, $p = 0.010$, $d = 0.57$. The later activity
410 arose within -148 to -52 ms relative to response onset, and there was also a statistically
411 significant difference between PS ($-0.137 \pm 0.100 \mu\text{V}$) and PA ($0.044 \pm 0.092 \mu\text{V}$) conditions,
412 $t(19) = -2.821$, $p = 0.021$, $d = 0.42$. Dipole modeling revealed that the origin of the observed
413 activity is in the right superior temporal gyrus (STG; Figure 4f). Repeated-measures
414 ANOVAs revealed that the interaction between block (overall performance or subjective) and
415 judgment (PS or PA) was significant for the -400 to -300 ms pre-response, $F(1, 19) = 5.07$, p
416 $= 0.036$, and for the -148 to -58 ms, $F(1, 19) = 4.81$, $p = 0.041$, time windows, suggesting that
417 the PS and PA difference was significantly greater in the subjective than overall performance
418 block.

419 These pre-decision ERP events were strongly correlated with the prediction signal in
420 the subjective block. Pre-motor prediction signal (Figure 3b), difference between PS and PA
421 outcomes, was significantly related to pre-decision ERP differences occurring -400 to -300

422 ms relative to response (Figure 4b), $r = -0.560$, $p = 0.010$, see Figure 5. In addition, under
423 overall performance condition, where no prediction signal was seen (Figure 3a), no pre-
424 response correlate in the ERP was seen either (Figure 4a). However, no such correlation was
425 seen for the later (-148 to -52 ms) pre-decision ERP differences, $r = 0.318$, $p = 0.172$.

426 At an intra-participant level, single-trial ERP analysis revealed interesting findings. A
427 t -test of z-transformed correlation coefficients for the pre-motor and pre-response (-400 to -
428 300 ms) activities revealed that a mean $r = 0.15$ was significantly different from zero $t(20) =$
429 8.15 , $p < 0.001$. A positive correlation was observed in all 20 participants. Also, for the pre-
430 motor and pre-response (-148 to -52 ms) activities a mean $r = 0.11$ was significantly different
431 from zero, $t(20) = 6.13$, $p < 0.001$. A positive correlation was observed in 19 out of 20
432 participants. See Figure 6 for more details. These results suggested that the amplitude of the
433 pre-response activity scaled with the amplitude of the pre-motor activity at an intra-individual
434 level, and a prediction signal prior to motor action influenced whether the flash was perceived
435 as synchronous or as asynchronous.

436

437 **Discussion**

438 Our study sheds light on how uncertainty about the timing of the subsequent sensory
439 outcomes of a voluntary action activates a predictive mechanism prior to motor action and
440 generates a prediction about the timing of an upcoming sensory event. Under low temporal
441 uncertainty about outcomes of a voluntary action, however, this signal was vanished. Prior to
442 response (i.e., choosing whether a flash of light turned on immediately or with a delay with
443 respect to motor action), there was a significant difference between two conditions (PS and
444 PA) only in the experimental context with high (the subjective block), but not low (the overall
445 performance block), temporal sensory uncertainty. Additionally, single-trial analysis revealed
446 that there was a correlation between the activities prior to motor action and prior to response

447 in the high uncertainty condition, suggesting passage of information from the former to latter
448 and making this prediction available to conscious awareness likely through an insight
449 solution, colloquially known as an “Aha!” experience.

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

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

469 The current task had some advantages to increase the signal to noise ratio. By using a
470 constant delay of 100 ms between motor action and light flash in the subjective block, we
471 avoided some potential confounds. Scalp-recorded ERPs are superimposed on top of each

472 other with different weightings depending on the location and orientation of each source. By
473 having trials with identical physical characteristics including similar delay, color, and
474 brightness, we aimed to minimize the differences across conditions for the event-related
475 potentials of interest that were involved in perceiving a trial as synchronous or asynchronous.
476 Additionally, performing the current task only relied on looking at a light source in the center
477 of the screen and therefore no eye movement was required. Eye movements are a major
478 source of noise in EEG studies (Luck 2014)

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

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

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

504 The distinction between self-generated and externally generated events and their
505 sensory consequences is crucial for efficient adaptation of behavior to predictable and
506 unpredictable situations (Barrett & Simmons, 2015; Crapse & Sommer, 2008; Sawtell, 2017).
507 This self-external delineation also seems critical for the experience of agency (Blakemore,
508 Wolpert, & Frith, 1998, 2000; Haggard, 2017; Moore, 2016; Nahab et al., 2010; Nichols,
509 2011). According to optimal cue integration (Synofzik et al. 2013), agency cues are weighted
510 based on their availability and reliability. In the subjective block, the motor-outcome delay
511 was available yet highly unreliable as uncertainty about synchrony judgement was close to
512 maximum (Figure 2). In the absence of reliable external sensory cues, it was expected that
513 internal predictive cues gain a higher weight to establish agency. The observed signal prior to
514 motor action (Figure 3) is speculated to be a signature of an internal predictive mechanism
515 originating from the right inferior parietal lobule (Figure 3).

516 This region has been shown to be involved in the formation of sense of agency
517 (Chambon et al. 2015; Chambon et al. 2012; Farrer et al. 2003; Farrer and Frith 2002; Koreki
518 et al. 2019; Yomogida et al. 2010) , and more likely involved in sense of external-agency
519 rather than sense of self-agency (Seghezzi et al. 2019; Sperduti et al. 2011). This signal was

520 absent in the overall performance block where motor-outcome delay uncertainty was low, so
521 the delay could be used as a more reliable agency cue.

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

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

545 between PS and PA conditions tended to have a lower pre-response amplitude difference
546 between PS and PA conditions.

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

561

562 **Conclusion**

563 In summary, we propose that the observed prediction signal prior to motor action, which is
564 reported here for the first time, is highly likely to be involved in neural mechanisms
565 underlying the IB effect (Haggard et al. 2002). It remains an open question whether the
566 prediction signal observed in the subjective block of this study has a stochastic origin
567 (Schurger et al. 2012) or is triggered by earlier neuronal processes of certain function. Using
568 stimuli of other modalities (e.g., auditory tones) will reveal to what extent the effect is
569 modality-independent and how sense of agency integrity is preserved across multimodal

570 sensory inputs. We propose that this new experimental task provides a powerful tool to
571 investigate sense of agency in healthy and agency-disrupted (Fletcher and Frith 2008; Moore
572 and Fletcher 2012) conditions (e.g., in individuals with psychotic disorders such as
573 schizophrenia) as well as, with some modifications, in animal models (Sigurdsson et al.
574 2010). Given uncertainty in sense of agency, prediction is a critical factor in determining the
575 nature of sensory consequences of a voluntary motor action and this appears to involve
576 activity across a right parietal-temporal axis.

577

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581 scientifically reasonable request. The authors declare no conflict of interest.

582

583 **Figure legends**

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

589

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

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

595

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

609

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

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

623

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

632

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

640

641

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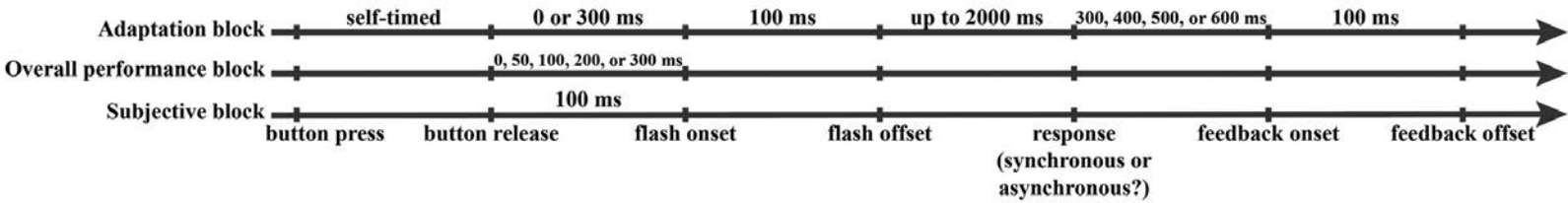
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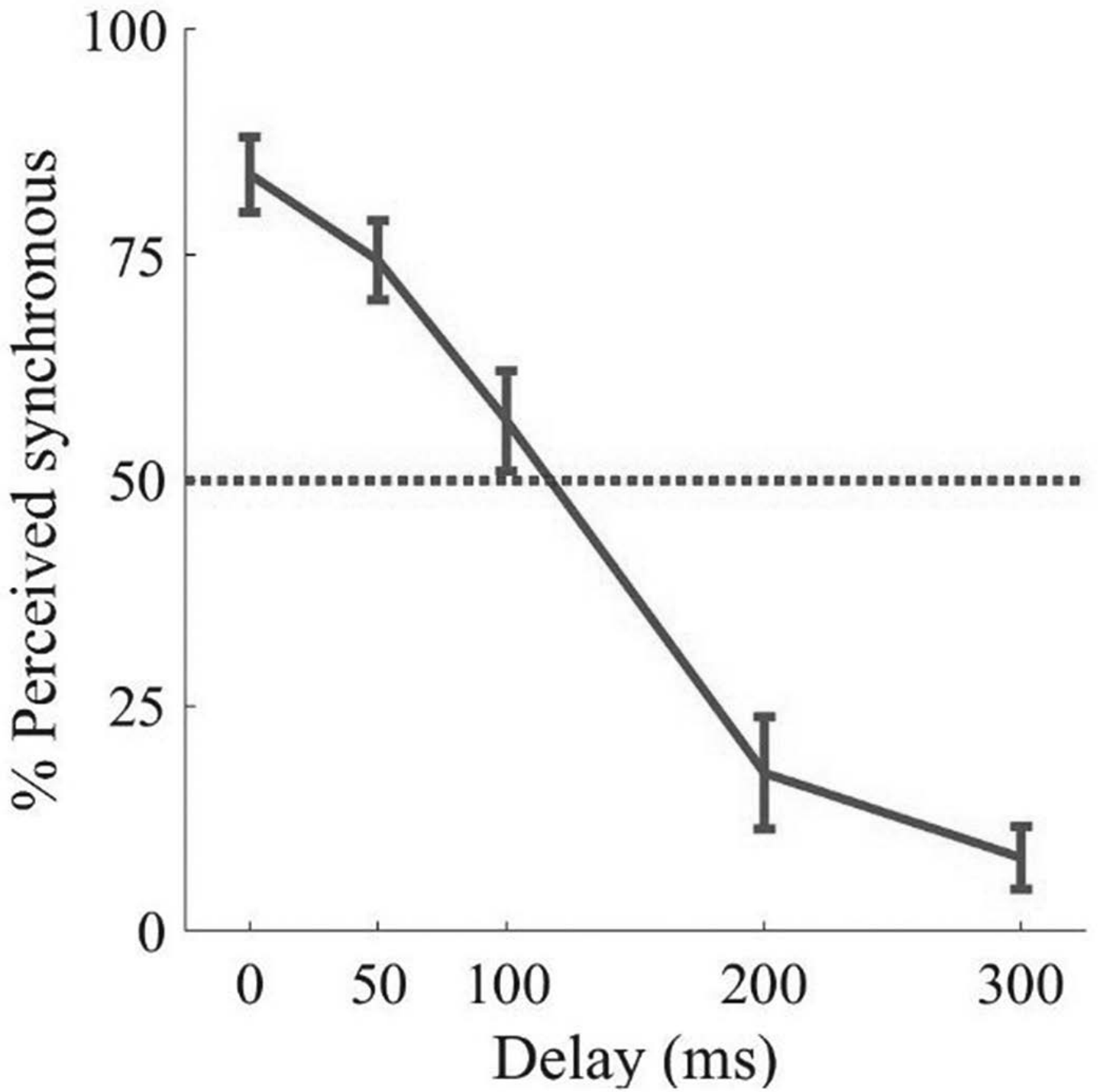
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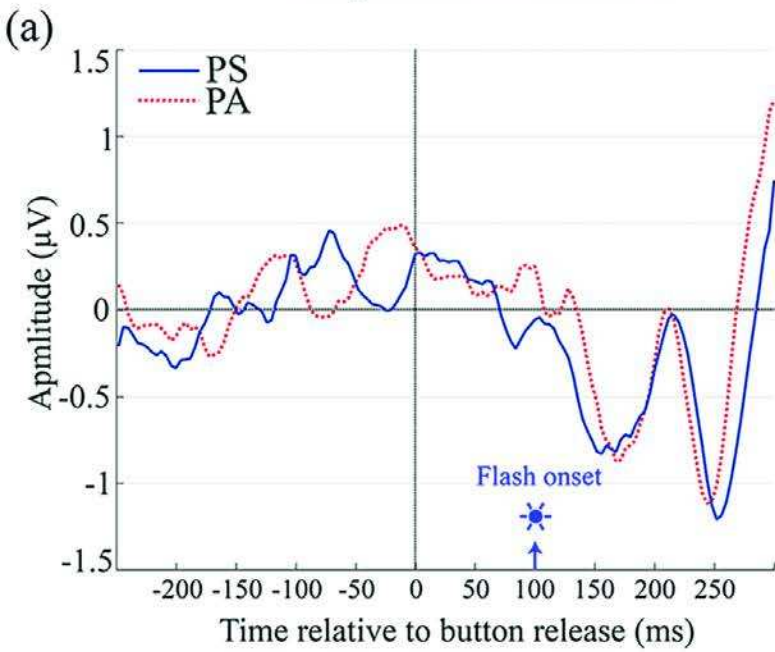
751



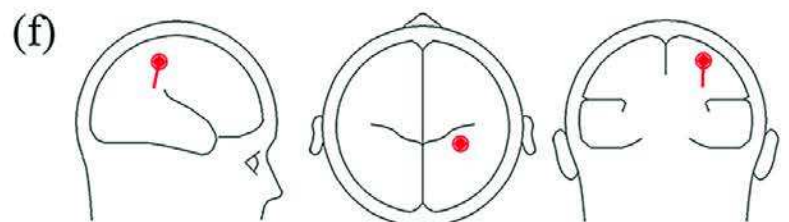
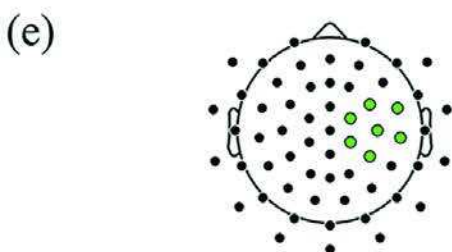
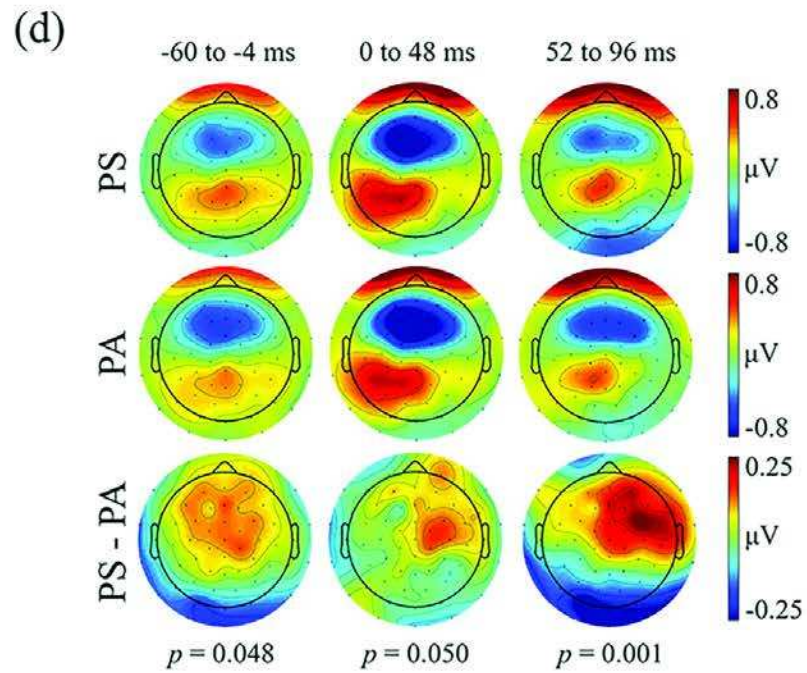
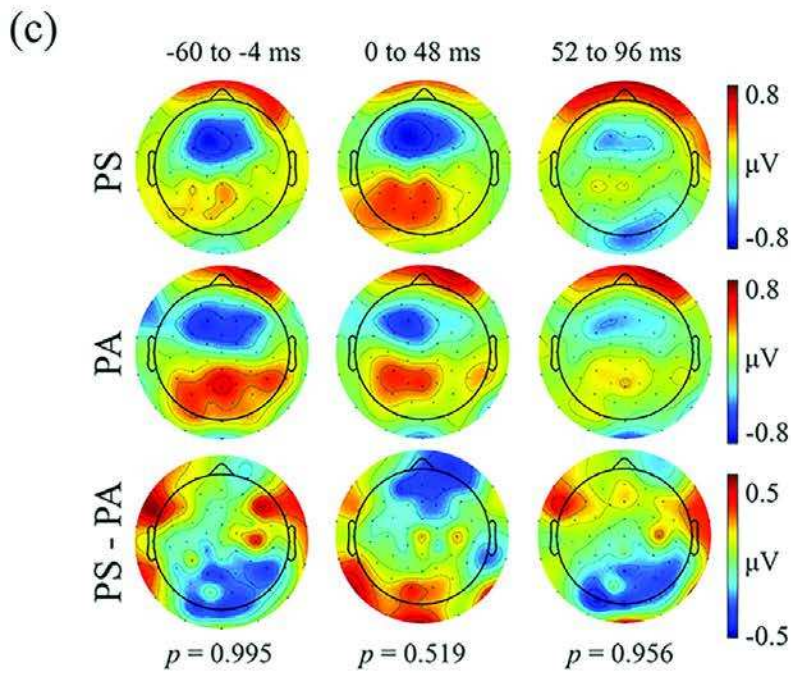
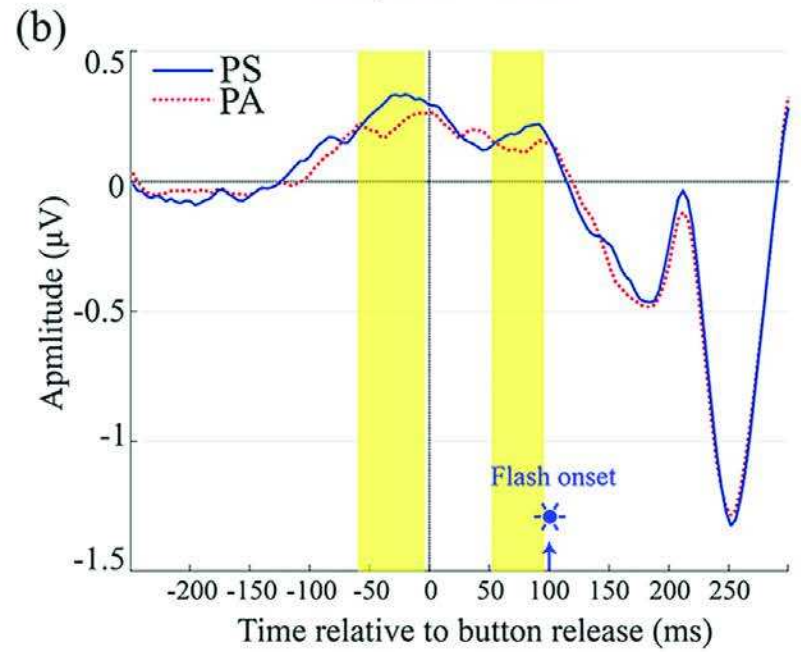


Motor-locked ERP analysis

Overall performance block



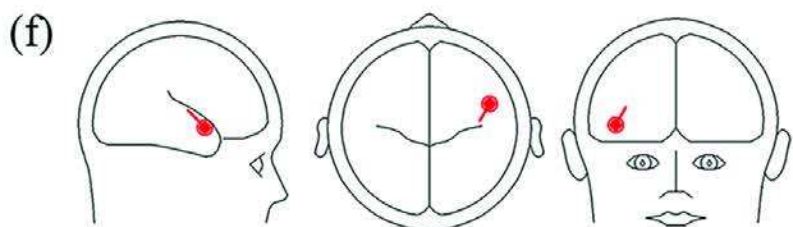
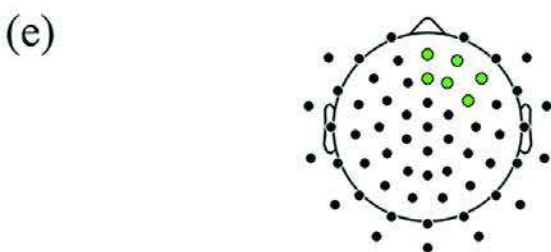
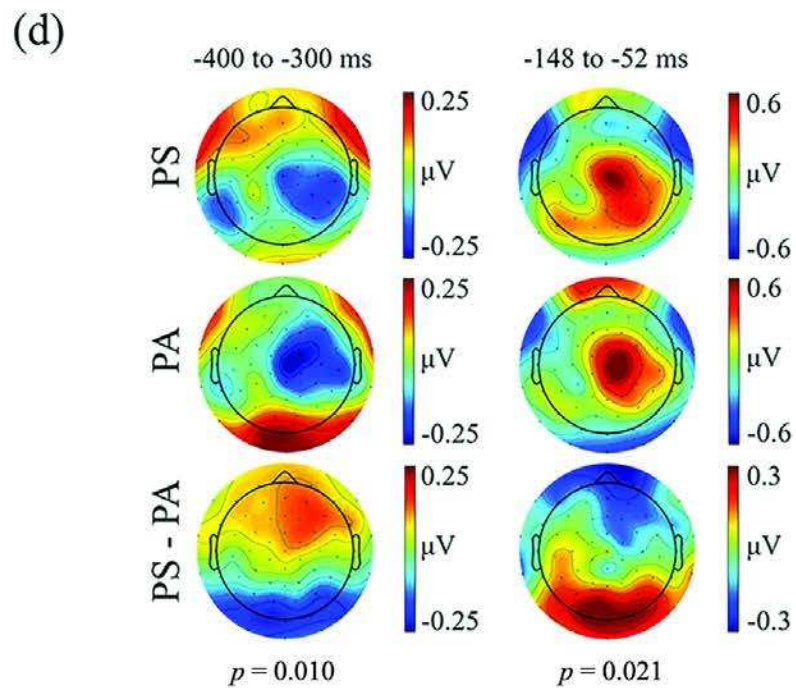
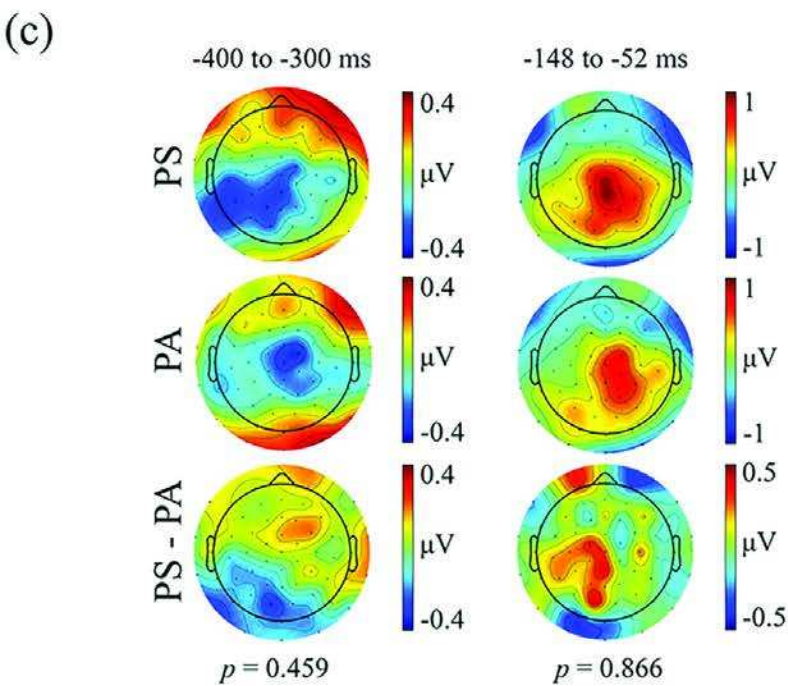
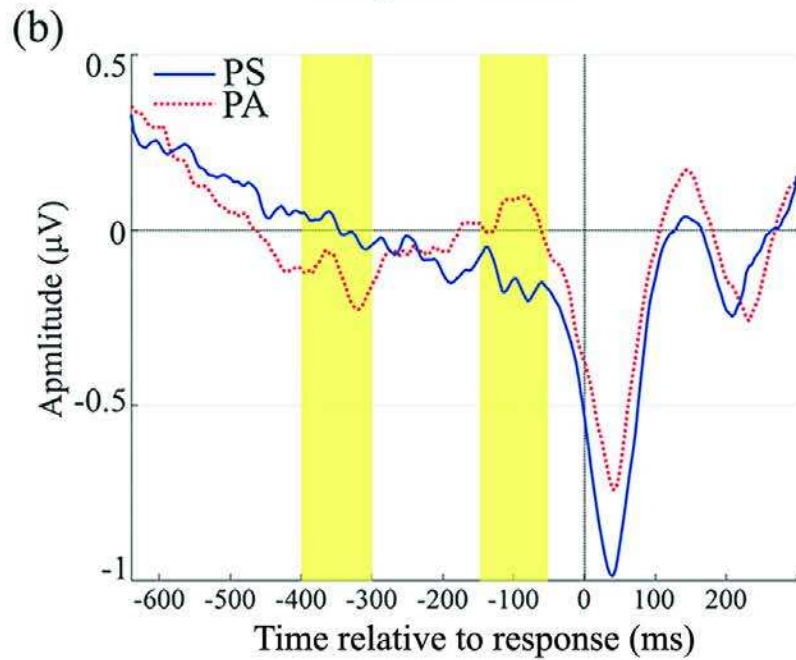
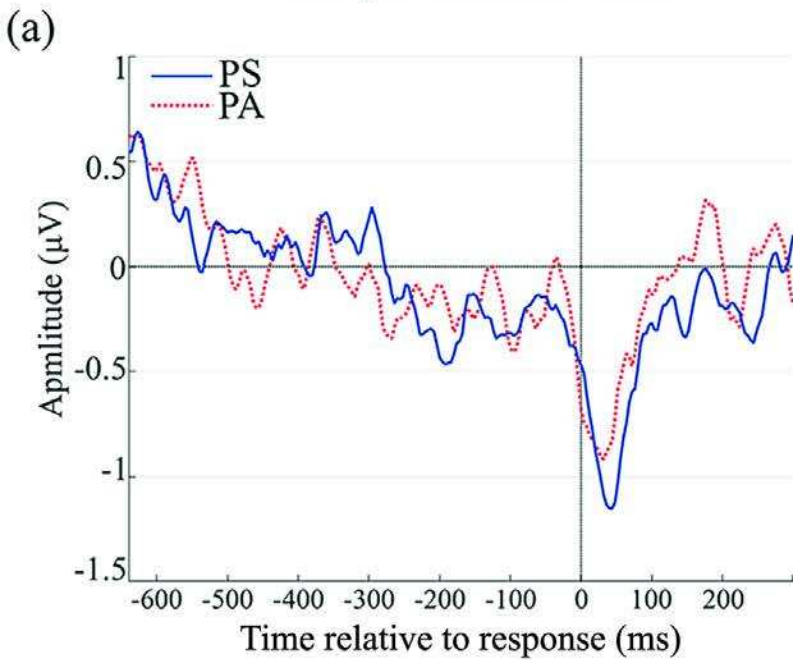
Subjective block

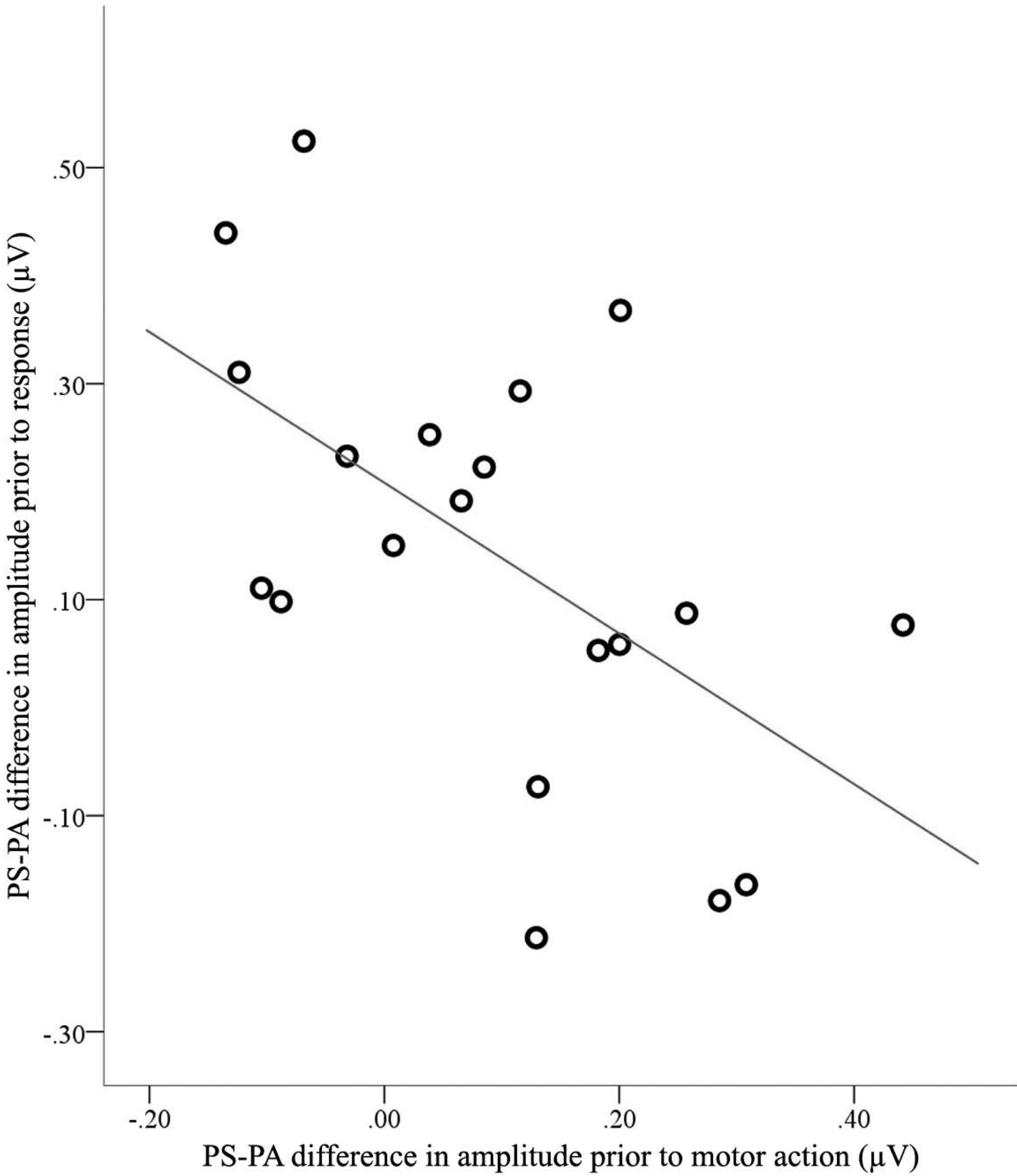


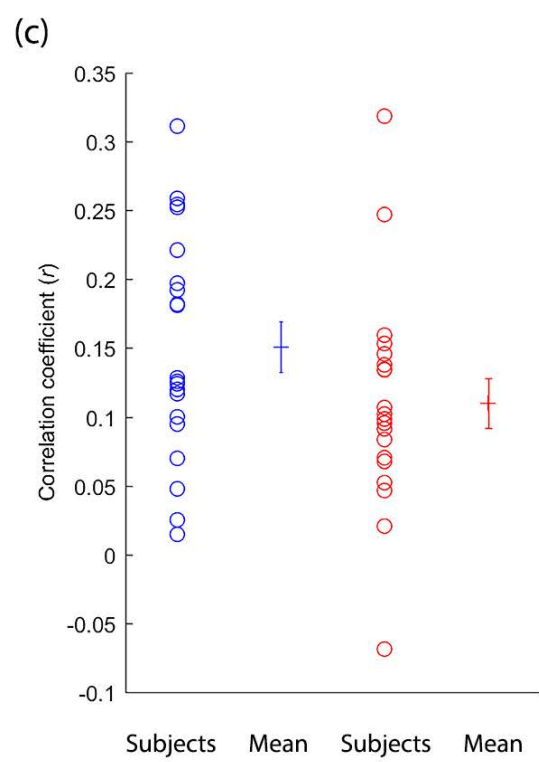
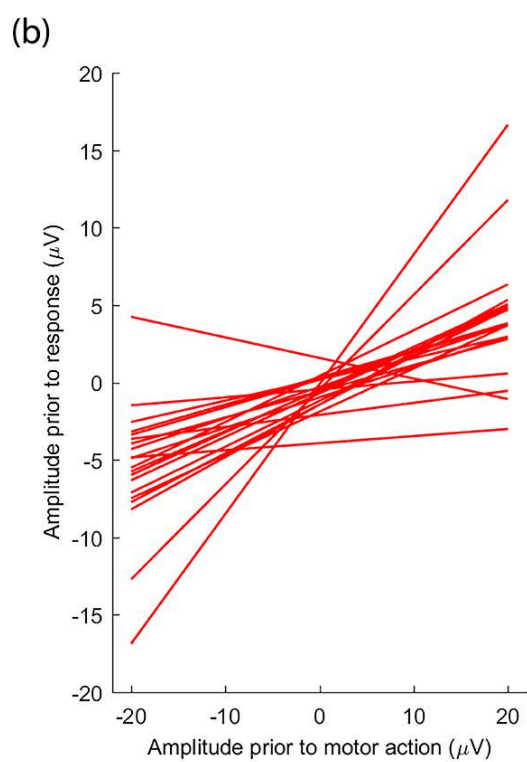
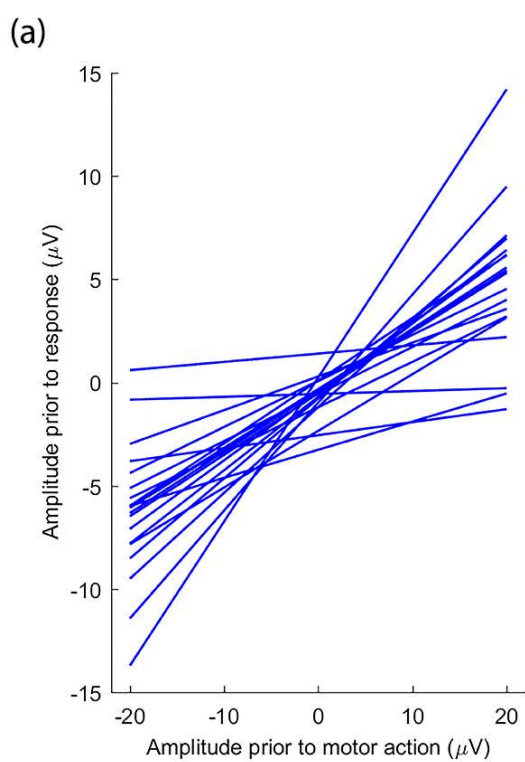
Response-locked ERP analysis

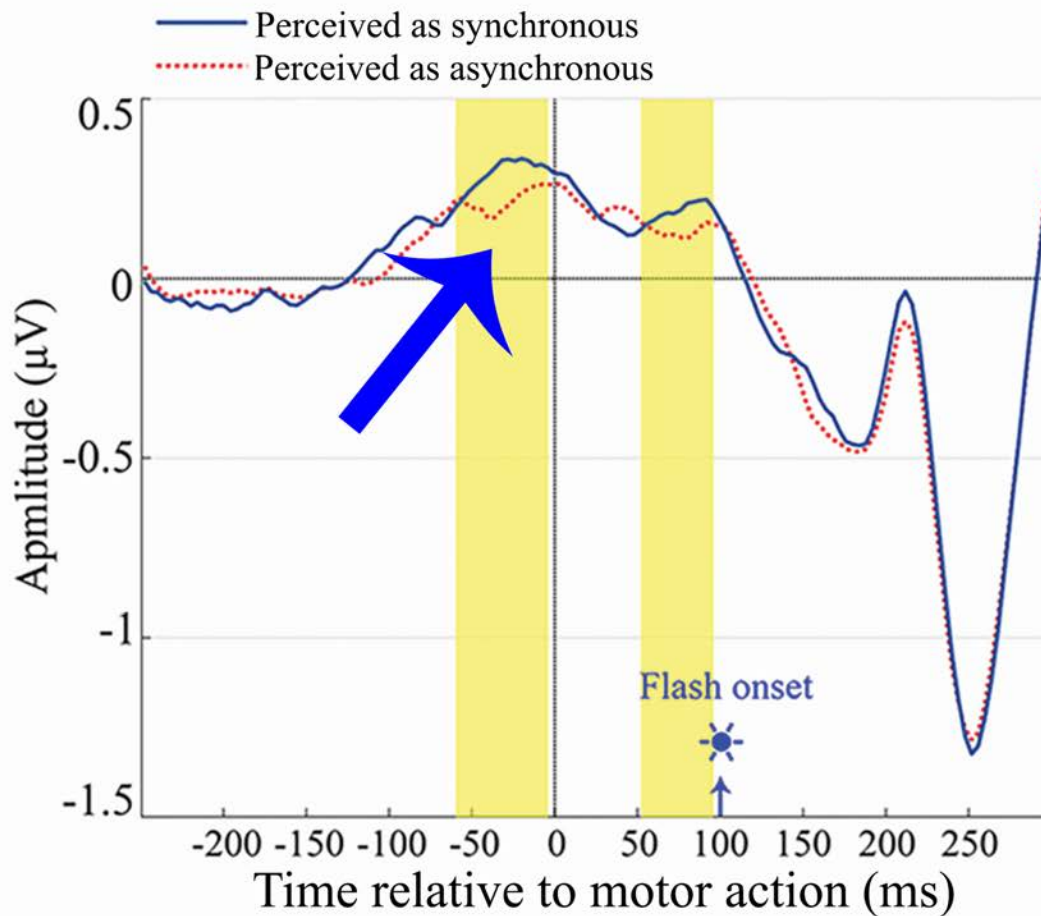
Overall performance block

Subjective block









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.