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1 Neural substrates of body ownership and 2 agency during voluntary movement 3

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9 Abstract

10 Body ownership and the sense of agency are two central aspects of bodily self-consciousness. While
11 multiple neuroimaging studies have investigated the neural correlates of body ownership and agency
12 separately, few studies have investigated the relationship between these two aspects during
13 voluntary movement when such experiences naturally combine. By eliciting the moving rubber hand
14 illusion with active or passive finger movements during functional magnetic resonance imaging, we
15 isolated activations reflecting the sense of body ownership and agency, respectively, as well as their
16 interaction, and assessed their overlap and anatomical segregation. We found that perceived hand
17 ownership was associated with activity in premotor, posterior parietal and cerebellar regions,
18 whereas the sense of agency over the hand's movements was related to activity in the dorsal
19 premotor cortex and superior temporal cortex. Moreover, one section of the dorsal premotor cortex
20 showed overlapping activity for ownership and agency, and somatosensory cortical activity reflected
21 the interaction of ownership and agency with higher activity when both agency and ownership were
22 experienced. We further found that activations previously attributed to agency in the left insular
23 cortex and right temporoparietal junction reflected the synchrony or asynchrony of visuo-
24 proprioceptive stimuli rather than agency. Collectively, these results reveal the neural bases of
25 agency and ownership during voluntary movement. Although the neural representations of these
26 two experiences are largely distinct, there are interactions and functional neuroanatomical overlap
27 during their combination, which has bearing on theories on bodily self-consciousness.

28 Introduction

29 When you raise your arm, you automatically experience that it was you who caused the arm to lift
30 and that the moving arm is your own. These two experiences blend so naturally during everyday
31 voluntary behavior that we rarely think of them as distinct. However, in philosophy, cognitive
32 science, and cognitive neuroscience, there is a long tradition of studying the sense of being in control
33 of and causing bodily action through volition, i.e., the *sense of agency* (Haggard, 2017; Jeannerod,
34 2003), and the immediate perceptual experience of limbs and body parts as one's own, i.e., the *sense*
35 of *body ownership* (Ehrsson, 2020; Petkova & Ehrsson, 2010), as distinct processes. Body ownership
36 and agency are both considered to be fundamental aspects of self-consciousness and critical for
37 defining what it means to be a conscious embodied agent distinct from the environment. However,
38 most previous studies have focused on these two experiences in isolation using different
39 experimental paradigms, so little is known about how they combine during voluntary movement.

40 Body ownership is considered to depend on the integration of visual, somatosensory and other
41 sensory bodily signals into coherent multisensory percepts of the own body through mechanisms of
42 multisensory integration (Blanke et al., 2015; Ehrsson, 2020; Ehrsson et al., 2004; Samad et al., 2015),
43 whereas agency relates to the association between voluntary action and outcome and has been
44 linked to the match between the expected sensory consequences of movement and their sensory
45 feedback (Frith et al., 2000a) and the experience of volition during voluntary movement (Haggard,
46 2017). Previous functional magnetic resonance imaging (fMRI) studies have identified brain areas
47 associated with the sense of body ownership and sense of agency, where body ownership is
48 associated with activity in a set of premotor-parieto-cerebellar regions (Ehrsson et al., 2004, 2005;
49 Gentile et al., 2015; Guterstam et al., 2013; Limanowski & Blankenburg, 2016) and agency related to
50 activations in the right inferior parietal cortex, temporoparietal junction, presupplementary motor
51 area (pre-SMA), insula (Chambon et al., 2013; David et al., 2008; Farrer et al., 2003; Farrer & Frith,
52 2002; Schnell et al., 2007; Yomogida et al., 2010), superior temporal gyrus (STG) (Nahab et al., 2011;
53 Uhlmann et al., 2020) and left primary sensorimotor cortex (Sperduti et al., 2011). However, agency
54 studies have focused on agency over external sensory events that occur as a consequence of bodily
55 movement rather than agency experienced directly over one's moving limbs, and body ownership
56 studies have not investigated movement (but see Tsakiris et al. 2010). Therefore, the precise
57 functional neuroanatomical relationship between ownership and agency during simple voluntary
58 movement remains unclear.

59 Here, we used the rubber hand illusion (RHI) (Botvinick & Cohen, 1998) elicited by finger movements
60 – the moving RHI (Kalckert & Ehrsson, 2012) – to investigate the neural bases of body ownership and
61 agency within a single fMRI paradigm. To elicit this bodily illusion, the participants perform a
62 repetitive finger movement with their hidden index finger while they observe a rubber hand placed
63 in full view making the corresponding finger movements. After a few synchronous movements, the
64 participants start to experience the moving rubber hand as their own and that they are directly
65 controlling its movements voluntarily (Kalckert & Ehrsson, 2012, 2014). By manipulating the relative
66 timing of the real and rubber hand finger movements (synchrony or asynchrony), the type of
67 movement (active or passive), and the spatial-anatomical orientation of the rubber hand with
68 respect to the real hand (congruent or incongruent), the sense of body ownership and agency can be
69 individually manipulated (Kalckert & Ehrsson, 2012). Thus, we implemented a 2x2x2 factorial within-
70 subjects experimental design with these three factors to identify active neuronal populations that
71 reflect body ownership, agency and their potential interaction. We hypothesized that ownership and
72 agency should be associated with activity in different neural circuits in line with previous studies but
73 also that their combination should be associated with overlapping and stronger activation in certain
74 frontoparietal regions due to the integration of the two sensations.

75 Materials and Methods

76 Participants

77 Thirty healthy volunteers were recruited for the experiment. One of the participants cancelled their
78 participation last minute, and thus, 29 participants who completed the experiment (15 males, 14
79 females, mean age 28 ± 5). The number of participants recruited was based on previous similar
80 studies on body illusions (Preston & Ehrsson, 2016) as well as another fMRI study with a similar 2x2x2
81 factorial design and eight conditions in a block design (Kiltenny & Ehrsson, 2020). All the participants
82 were right-handed, which was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971).
83 The participants had normal or corrected-to-normal vision and had no history of neurological or
84 psychiatric illness. Informed consent was obtained prior to the experiment. The experiment was

85 conducted according to the Declaration of Helsinki and was approved by the Swedish Ethical Review
86 Authority.

87 **Moving rubber hand illusion setup**

88 The moving rubber hand illusion setup in its original design is a vertical setup in which the
89 participants' real hand is placed under a small table over which the rubber hand is placed (Kalckert &
90 Ehrsson, 2012). The illusion also works in other spatial arrangements as long as the rubber hand is
91 presented close to the real hand within peri-hand space (approx. within a 30-40 cm distance); we
92 took this into consideration when redesigning the setup for the current fMRI study. The vertical
93 setup did not fit inside the constrained space of the modern General Electric (GE) 3T magnetic
94 resonance (MR) scanner we used, so a horizontal version of the moving rubber hand illusion setup
95 had to be designed. Importantly, the setup had to be able to rapidly switch between active and
96 passive movements of the participant's index finger, as well as between synchronous and
97 asynchronous movements of the participants' index finger and the index finger of the rubber hand.
98 To achieve this, a new mechanical design consisting of two levers, two supports and a plastic pin was
99 developed (Fig. 1, Panels A-D). By removing the plastic pin connecting the levers, the movements of
100 the participants' index finger could be decoupled from the movements of the index finger of the
101 rubber hand. By having the experimenter push the lever beneath the index finger up, the fingers
102 could be passively moved. The "rubber hand" used in our experiment was in fact a wooden hand
103 with flexible joints (HAY design brand, 31 cm model; similar to (Kalckert & Ehrsson, 2012)). All joints
104 of the wooden hand except the metacarpophalangeal (MCP) joint of the index finger were fixated
105 with glue, thus only permitting movement in the MCP joint. The rubber hand was covered with a gray
106 nitrile glove, occluding the fact that it was a wooden hand and giving it the impression of being more
107 humanoid.

108 **Procedures**

109 The participant lay comfortably in a supine position on the MR scanner bed wearing earplugs and
110 headphones over the earplugs to protect the participant's hearing from scanner noise while allowing
111 them to hear the instructions through headphones. The participant's head was tilted approximately
112 30 degrees using a custom-made wooden wedge under the head coil along with foam pads inside the
113 head coil. The tilting of the head allowed the participants to see through the openings on the head
114 coil and view their body from a natural (first-person) perspective. With the participant in a supine
115 position, a small custom-made table was placed over their abdomen (fixed to the scanner bed). The
116 participant's right hand was placed on the right side of this table, and the rubber hand was placed on
117 the left side of this table, with the index finger of the rubber hand placed 15 cm to the left of the
118 index finger of the participant's real hand (Fig. 1, Panel A). The participant's real right arm and hand
119 were occluded by taping a dark cloth to the table and then to the roof of the MR scanner bore, thus
120 completely hiding the participants' real hand from sight (Fig. 1, Panel A). The participant's right elbow
121 was supported with a pillow to have the participants lay comfortably and not have to strain or
122 actively maintain their arm in the required position but make it possible for them to have the arm in
123 a relaxed posture. The rubber hand and the participant's real hand were placed parallel to each
124 other, with the same rotations of approximately 20 degrees counterclockwise from the participants'
125 perspective, which gave the impression of the rubber hand originating from the insertion of the
126 participants' real arm into the torso. The participants' right index finger was placed inside a small
127 plastic ring that was connected to a rod that in turn was connected to a lever below the table (Fig. 1).
128 The index finger of the rubber hand was placed in an identical plastic ring and in turn connected via a
129 separate rod to a second lever under the table. This setup allowed us to manipulate the synchrony of
130 the movements between the rubber hand and the real hand by coupling (synchrony) or decoupling

131 (i.e., removing the plastic pin connecting the two levers) the rubber hand from the participant's hand
132 (Fig. 1B-E). This decoupling allowed the index finger of the rubber hand and the participant's hand to
133 move independently, and thus, the experimenter could move the index finger of the rubber hand
134 with a delay of approximately 0.5 seconds by pressing the lever under the rubber hand up
135 (asynchrony). Furthermore, it allowed us to manipulate whether the movement was active or passive
136 by either having the participants lift their index finger up actively or having the experimenter push
137 the index finger of the participant up by pressing the lever. Finally, this setup allowed us to
138 manipulate the anatomical orientation of the rubber hand by either having the rubber hand placed in
139 an anatomically congruent position, giving the impression of it being continuous with the body, or
140 having the rubber hand rotated 180 degrees to an anatomically incongruent position (Ehrsson et al.,
141 2004).

142 Throughout the experiment, the participants were asked to maintain fixation on the rubber hand.
143 The participants received verbal instructions through headphones, which consisted of two
144 prerecorded 1-second-long audio clips of either "tap finger" or "relax". During the active conditions,
145 the participants were asked to perform a tapping motion with their right index finger. The tapping
146 motion was performed by extending and then flexing the metacarpophalangeal joint while keeping
147 the proximal and distal interphalangeal joints static, in other words, tapping with a straight finger (as
148 in Kalckert & Ehrsson, 2012). In the active conditions, the tapping was self-paced, and the
149 participants had to produce a regular rhythm of taps at approximately 1 Hz without the support of a
150 metronome or other external cues. The participants were trained to produce tapping movements at
151 a regular speed (brief taps with short pauses between each tap) and tap gently (i.e., not forcefully
152 press the surface). Before the scan started, the participants were trained to produce the required
153 tapping movements in a practice trial that lasted a few minutes. In this practice trial, the participants
154 listened to a 1-Hz metronome while tapping their right index finger in the moving rubber hand
155 illusion condition and were then asked to continue tapping without the metronome. Self-paced
156 tapping was used to ensure internally generated movement rather than "externally triggered"
157 movement (Passingham, 1993), thereby avoiding potential interactions between external cue
158 processing and agency. Participants were also trained to generate the tapping movement with a
159 certain amplitude (3 cm; see further below). If the participants failed to maintain a reasonably
160 consistent tapping frequency or amplitude, they received feedback from the experimenter and
161 performed one more practice trial until the participants were consistent and reliable in their tapping
162 frequency and amplitude throughout the trial. In the passive conditions, the participants were
163 relaxing their index finger, and the experimenter generated the movements as described above. In
164 these passive conditions, the experimenter matched the frequency of the participant's self-paced
165 movements in the preceding active condition. To ensure that the amplitude of each tap that the
166 experimenter produced was consistent, the experimenter was guided by a measuring stick taped to
167 the table that showed the 3 cm movement amplitude target (see further below). In all conditions, the
168 experimenter was hidden from sight of the participant by standing on the left side of the scanner
169 bore behind the cloth that also occluded the view of the participants' real hand (Fig. 1A). The
170 experimenter received continuous instructions about the onset and end of the conditions through
171 headphones as well as through text on a screen that displayed the next condition (the screen was
172 placed in the control room and facing scanner through the glass window of the control room so that
173 it could be seen from the location of the experimenter inside the scanner room).

174 **Movement registration and optical sensor**

175 Underneath the index finger of the participant, approximately 3 millimeters proximal to the hole that
176 the rod connected to the plastic ring passed through, there was another small hole (2 mm in
177 diameter). In this smaller hole, a fiber optic cable attached to an optical sensor (Omron E3X-HD11,

178 Omron Industrial Automation, Osaka, Japan) was placed, which was able to register when the
179 participant's index finger was lifted off the table and when it returned to the table during the tapping
180 movements. The optical sensor registered the luminance from the fiberoptic cable with preset
181 thresholds so that it recorded dichotomic on/off data (finger on or lifted off) with a sampling
182 frequency of 100 Hz and saved this to a text file. This allowed us to record the frequency of taps, the
183 duration of each tap and the total number of taps in each participant and in each condition. As
184 described above, the experimenter had a measuring stick taped to the table and could visually
185 inspect that the participant's taps reached the same amplitude of approximately 3 centimeters,
186 ensuring that the amplitude of the taps was consistent across conditions.

187 **Design**

188 To test the hypothesis that the sense of agency and the sense of body ownership have different
189 neural substrates and identify possible neural interactions when the two co-occur, we opted for a full
190 factorial design with 2x2x2 conditions, with the factors movement type (active/passive), timing
191 (synchronous/asynchronous), and orientation (congruent/incongruent) (Fig. 2, Panel A), giving rise to
192 eight unique conditions (Fig. 2, Panel B). The rationale behind this design is that it allows for
193 independent manipulation of body ownership and agency by manipulating only three experimental
194 parameters in otherwise equivalent conditions, made possible by the fact that illusory body
195 ownership and agency in the moving rubber hand illusion follow different perceptual-cognitive rules.

196 Illusory body ownership depends on multisensory temporal and spatial congruence rules so that
197 when visual and somatosensory information is matching, the brain will combine these sensory signals
198 and illusory hand ownership is experienced, but when the incongruence between visual and
199 somatosensory information is too great, these signals will be segregated, and illusory ownership will
200 not be evoked (Blanke et al., 2015; Chancel, Ehrsson, et al., 2022; Ehrsson, 2012; Fang et al., 2019;
201 Ismail & Shimada, 2016; Samad et al., 2015). Thus, synchronously seen finger movements of the
202 rubber hand and corresponding felt movements of the real hand elicit illusory hand ownership when
203 the rubber hand is presented in the same spatial orientation as the participant's hidden real hand
204 (congruent), whereas asynchrony with a 0.5-s delay (Ismail & Shimada, 2016) or presenting the
205 rubber hand in an incongruent orientation, rotated 180 degrees with respect to the real hand
206 (Kalckert & Ehrsson, 2012; Ide, 2013; Ehrsson et al 2004), breaks the body ownership illusion. Active
207 or passive movements can both be used to trigger the moving rubber hand illusion, so the factor
208 movement type does not determine the sense of body ownership (Kalckert & Ehrsson, 2012). Thus,
209 illusory body ownership corresponds to the interaction of the factors of timing and orientation in our
210 2x2x2 factorial design, elicited in the two conditions with synchronous visuo-somatic sensory
211 feedback and congruent rubber hand orientation ($A_{MS_T}C_O$ and $P_{MS_T}C_O$; Figure 2B).

212 Agency relates to another pair of factors in our design, namely, movement type and timing. Active
213 movement is required for a sense of agency because active movement production is associated with
214 volition, a prerequisite for agency (Haggard, 2017). Agency also requires a match between the
215 expected sensory feedback from active movements and the actual sensory feedback (Frith et al.,
216 2000b). Thus, synchronously seen rubber hand movements and felt active movements of the real
217 hand evoke a sense of agency over the rubber hand, whereas asynchrony or passive movements
218 break the agency experience (Kalckert & Ehrsson, 2012). The orientation of the rubber hand does not
219 matter, and one can experience agency over the rubber hand's finger movement when the rubber
220 hand is presented in a spatially incongruent orientation (Kalckert & Ehrsson, 2012). Thus, agency is
221 captured by the interaction of movement type and timing in our design and will be experienced in
222 the two conditions with active and synchronous movements ($A_{MS_T}C_O$ and $A_{MS_T}I_O$; Figure 2B).

223 Thus, combined with fMRI, the 2x2x2 factorial design allowed us to isolate neural correlates of the
224 sense of agency and the sense of body ownership (as the two-way interactions) while controlling for
225 basic effects related to differences between active and passive movements, visuo-somatosensory
226 and visuo-motor synchrony, and visual impressions from observing the rubber hand in different
227 orientations (captured by the three main effects) and to examine possible (three-way) interaction
228 between body ownership and agency when combined in the active moving RHI condition ($A_M S_T C_O$).
229 Since the two two-way interactions defining ownership and agency are orthogonal in this design, we
230 can also examine their overlap in activation by using a conjunction analysis. Thus, we reasoned that
231 this experimental design would be ideal for addressing the questions we were interested in.

232 Behavioral experiment

233 Prior to the fMRI experiment, all subjects participated in a behavioral experiment. The rationale was
234 fourfold: 1) we wanted to verify that the behavioral paradigm worked as expected for the purpose of
235 the fMRI design; 2) we wanted to quantify ownership and agency using the extensive questionnaires
236 that have been used in previous studies and that are unpractical to use during the scan sessions; 2)
237 since the current eight conditions have never been tested in a single within-subjects design before
238 (Kalckert and Ehrsson 2012 tested the various conditions we use in separate experiments), we also
239 wanted to test for a possible interaction between ownership and agency; and 4) we wanted to
240 register how rapidly the moving RHI was induced in this group of participants exposed to the current
241 paradigm to take this into account in the later fMRI analysis.

242 Thus, in this behavioral experiment, the participants were tested with the identical moving rubber
243 hand illusion setup that would be used in the MR scanner but laying on a bed in our behavioral
244 testing lab instead. The position of the participants' limbs, head and body was the same as during the
245 MR scans. The participants had all eight conditions repeated once and received a 16-statement
246 questionnaire at the end of each condition that probed the illusory experience of the sense of body
247 ownership and the sense of agency (Table 1; based on Kalckert & Ehrsson, 2012). Control questions
248 probing suggestibility and task compliance were also included. The questionnaire was rated on a 7-
249 point Likert scale ranging from (-3) to (+3), with (-3) corresponding to "completely disagree", (+3)
250 corresponding to "completely agree", and (0) corresponding to "neither agree nor disagree". The
251 stimulation period for each condition was 45 seconds. When all conditions had been tested, six more
252 trials, three with the active/synchronous/congruent ($A_M S_T C_O$) condition and three with the
253 passive/synchronous/congruent ($P_M S_T C_O$) condition, were conducted. In these additional trials of the
254 $A_M S_T C_O$ and $P_M S_T C_O$ conditions, the illusion was induced in the same manner, but this time, the
255 participants were instructed to verbally indicate when they started to experience that the "rubber
256 hand was their hand" (corresponding to the fourth statement in the ownership questionnaire, Table
257 1; (Ehrsson et al., 2004)). This yielded average "illusion onset time" measurements for each
258 participant in both the $A_M S_T C_O$ and $P_M S_T C_O$ conditions (Extended Data Table 3-1). These time
259 individual intervals ($A_M S_T C_O$ range 0-30 s, mean 11.5 ± 8.2 s, $P_M S_T C_O$ range 0-30.2, mean 12.26 ± 9.1 s,
260 nonsignificant difference between onset time in $A_M S_T C_O$ and $P_M S_T C_O$, $W=127.00$, $p=0.346$, rank-
261 biserial Correlation -0.218) were then used to define the start of the illusion conditions of interest in
262 the fMRI analyses (see below). This allowed us to focus our analysis on the periods when the moving
263 rubber hand illusion had been elicited (Ehrsson et al., 2004). The periods before the illusion onset
264 times were modeled as conditions of no interest and not used in the statistical contrasts.

265 fMRI experiment

266 The fMRI experiment was designed as a block design given the efficiency of this design type (Friston
267 et al., 1999). The experiment was divided into four runs, where two runs were collected with the
268 rubber hand in the congruent position and two runs with the rubber hand in the incongruent

269 position. The separation of the congruent and incongruent trials in separate runs was done because
270 it took approximately a minute to properly reorient the rubber hand, which made it unfeasible to do
271 within a run. The order of the runs was randomized. Each block (epoch) contained a stimulation
272 period of 45 seconds followed by a 5-second resting baseline before the next condition. Each run
273 contained four repetitions of each of the four conditions in said run, totaling 8 blocks per condition
274 per participant. Every four blocks, there was a 30-second block of a rest baseline condition in which
275 the participants looked at the rubber hand without performing or observing any movement (Fig. 3).

276 fMRI data acquisition

277 The experiment was conducted using a 3 Tesla GE MR750 scanner equipped with an 8-channel head
278 coil. T2*-weighted gradient echo EPIs with BOLD contrast were used as an index of brain activity
279 (Logothetis, 2003; Logothetis et al., 2001). Each functional volume consisted of 43 continuous slices
280 with a slice thickness of 3 mm and an interslice space of 0.5 mm. The field of view (FOV) was defined
281 as a matrix with dimensions of 72x72 (3x3 mm in plane resolution, TE=30 ms), thus ensuring
282 coverage of the whole brain. One volume was collected every 2.048 s (TR=2048 ms), and a total of
283 1812 functional volumes were collected for each participant, divided into 4 runs of 453 volumes
284 each. A high-resolution structural image was collected for each participant at the end of the
285 experiment (3D MPRAGE sequence, 1x1x1 mm voxel size, FOV 240 x 240 mm, 180 slices, TR=6404
286 ms, TE=2808 ms, flip angle = 12°).

287 Statistical analysis

288 Questionnaire data

289 The data from the behavioral pretest experiment were tested for normality using Shapiro–Wilks
290 test. If the data deviated from normality, the results were analyzed using the nonparametric
291 Wilcoxon signed rank test. The questionnaire data from the pretesting were analyzed using JASP
292 (version 0.11.1, 2019, University of Amsterdam, The Netherlands). For each participant, the
293 subjective ratings from the four statements probing ownership were averaged into an ownership
294 score, the four agency statements into an agency score, and the control statements were similarly
295 averaged into an ownership control score and agency control score (Kalckert & Ehrsson, 2012). For
296 each condition, a sense of body ownership or agency was defined as a mean ownership or agency
297 score of >0. To test for body ownership or agency within a condition and control for unspecific
298 suggestibility effects, the ownership score was compared statistically to the ownership control score
299 and the agency score to the agency control score, respectively. To compare body ownership and
300 agency between conditions, an ownership index and agency index were calculated. The indices were
301 defined as the difference between the ownership score and the ownership control score (ownership
302 index) and between the agency score and agency control score (agency index), respectively
303 (Abdulkarim & Ehrsson, 2016).

304 Movement sensor data

305 The data from the optical sensor were analyzed using MATLAB (version 2018b, statistical toolbox,
306 Mathworks, Massachusetts, USA). The optical sensor was not available for the first 10 participants
307 (still under development due to unexpected delay), which is why we only included data from the
308 optical sensor from 19 participants. The number of taps from each trial was extracted for participants
309 10-29. The frequency of taps was calculated by dividing the number of taps by each condition's total
310 time. The number of taps as well as the frequency of taps was then averaged across participants for
311 each condition. The statistical analysis focused on testing for main effects of synchrony, active or
312 passive movements and congruent or incongruent rubber hand orientation in terms of the frequency
313 of taps in line with the fMRI design.

314 fMRI data preprocessing, modeling and statistical inference
315 The fMRI data from all participants were analyzed using Statistical Parametric Mapping 12 (SPM12;
316 Wellcome Trust Center for Neuroimaging, University College London, UK). Before the functional
317 imaging data underwent the preprocessing steps, all functional and anatomical images were rotated
318 back to the standard position, which they deviated from due to the forward head tilt inside the
319 scanner coil. After that, the preprocessing steps included motion correction, slice timing correction,
320 coregistration, and normalization (to the Montreal Neurological Institute (MNI) standard brain). The
321 functional images were resampled to a resolution of 2x2x2 mm, and spatial smoothing was applied
322 using a 6-mm FWHM Gaussian kernel. The statistical analysis was performed by fitting a general
323 linear model (GLM) to the data for each participant. The hemodynamic response function was
324 convolved with boxcar regressors for each condition of interest. Linear contrasts were defined at the
325 individual level and exported to the second level random effects analysis. Importantly, we modeled
326 the first period in each condition as a condition of no interest, based on the time it took for each
327 individual participant to experience the illusion in the behavioral pretest (see above), and the periods
328 from illusion onset to the end of each condition as the condition of interest used in our main analyses
329 (in line with (Ehrsson et al., 2004; Guterstam et al., 2013). For the A_MS_TC_O and P_MS_TC_O conditions, we
330 used their corresponding rubber hand illusion onset times, whereas for all other conditions (that did
331 not trigger the rubber hand illusion), we used the average of the A_MS_TC_O and P_MS_TC_O times.
332 For the main contrasts, we had anatomical hypotheses regarding which regions we expected to be
333 activated during experiences of body ownership and agency based on the previous fMRI literature
334 (see introduction); therefore, in these regions, we report the results that are statistically significant at
335 a threshold of p<0.05 after small volume correction (familywise error correction; "FWE"). However,
336 since earlier ownership studies used brushstrokes or similar tactile stimulation applied to relaxed
337 hands instead of finger movements, we anticipated that the exact location of peaks associated with
338 the rubber hand illusion could change within the hypothesized frontal, parietal, and subcortical
339 regions. Therefore, the volumes of interest used in the small volume correction were centered on
340 peak coordinates obtained from a "localizer" study where we used the same 3T MR scanner and
341 fMRI scanning protocol as in the main experiment to identify the locations of active candidate areas
342 during the moving rubber hand illusion. In brief, the localizer study included 27 participants looking
343 at and controlling the index finger movement of a robotic hand wearing a plastic glove identical in
344 shape and size to the rubber hand used in our current experiment. This robotic "rubber hand" was
345 placed in view of the participant on a supporting table in a very similar arrangement to the one used
346 in the current study. When the participant moved his or her index finger, the rubber hand moved its
347 index finger in the same way and synchronously, triggering the moving rubber hand illusion (verified
348 with illusion questionnaire ratings that were affirmative in most participants; data not shown). In the
349 localizer study, we contrasted this illusion condition (corresponding to the A_MS_TC_O condition in the
350 present study) to a resting baseline condition where the participants were just looking at the rubber
351 hand without performing or observing any movement. Peaks from this localizer contrast were then
352 used to define the coordinates in MNI space for the spheres (10 mm in radius) in the small volume
353 corrections (Extended Data Table 12-2 for list of all peaks used from this localizer study to define the
354 volumes of interest). For the intraparietal cortex – a region often associated with the RHI and illusory
355 hand ownership in the previous fMRI literature – we added peaks from (Ehrsson et al., 2004) since no
356 activations were detected in the localizer contrast in this region. Similarly, for the left insular cortex
357 and right angular gyrus in the temporoparietal junction (TPJ) region – two areas often associated
358 with different aspects of agency in the previous literature – we used coordinates from classic
359 neuroimaging agency studies (Farrer et al., 2003; Farrer & Frith, 2002) to define peaks for small
360 volume correction in these regions. In the rest of the brain, i.e., outside the regions related to our a

361 priori defined anatomical hypotheses, we corrected for the number of comparisons in the whole
362 brain space using a test of false discovery rate (FDR) set at $p<0.05$. All our statistical inferences and
363 main findings are based on results that survive multiple comparison correction based on these two
364 approaches, which collectively balances type 1 and type 2 errors and hypothesis-driven and
365 explorative approaches.

366 Some activations that did not survive correction for multiple comparisons are still mentioned in the
367 text or shown in figures as part of the statistical parametric maps produced by SPM12 (based on a
368 threshold of $p<0.005$ uncorrected). We report these for purely descriptive purposes (Gentile et al.,
369 2013; Preston & Ehrsson, 2016) and always clearly identify these as not reaching our significance
370 criterion. We report these nonsignificant activations mainly for five reasons: (i) false-negatives and
371 limited sensitivity is a concern in fMRI studies, so being overly conservative might conceal potentially
372 interesting results; (ii) we want to report the activation maps in a transparent fashion and not only
373 describe those regions that were part of our hypothesis; (iii) activation peaks that did not survive
374 correction for multiple comparison can still be used to define anatomical hypotheses for future fMRI
375 studies; and (iv) the reporting of the entire activation maps including nonsignificant activation can
376 provide information about the anatomical specificity of these latter effects (i.e., single active brain
377 area or widespread effects in many regions); (v) nonsignificant peaks can be used in future imaging
378 meta-analysis where it is often important to have data from the whole brain (and not only a few
379 peaks that survive multiple comparisons correction). As mentioned, all main conclusions in the
380 manuscript are based on activations that are significant (in one case, almost significant) after
381 correction for multiple comparisons, i.e., $p<0.05$ after FWE correction.

382 The visualization of the results is performed by overlaying the peaks on a 3D rendering of a standard
383 MNI brain using Surf Ice (<https://www.nitrc.org/projects/surface/>) as well as on sections from the
384 average anatomical image for all participants. The anatomical localizations of the activations were
385 based on macroanatomical landmarks (sulci and gyri) using the terminology from the Duvernoy and
386 Parratte brain atlas (Duvernoy, 1999). For peaks in the cerebellum, we used the SUIT toolbox for
387 anatomical localization based on a probabilistic atlas of the cerebellum (Diedrichsen et al., 2009,
388 2011). All coordinates for the activation peaks are given in MNI space. Contrast estimates for each
389 significant peak were extracted using MATLAB (version 2018b) and presented in bar charts together
390 with the corresponding standard errors (SEs) for purely descriptive purposes. In line with the SPM
391 approach, we make no further statistical analyses on these bar chart plots, but all conclusions and
392 statistical inferences are based on significant (two-way and three-way) interaction contrasts in line
393 with our factorial design.

394 **Planned fMRI analyses**

395 To identify regions that display BOLD responses that reflect the sense of body ownership or the sense
396 of agency, we defined linear contrasts that corresponded to the two-way interactions that captured
397 ownership and agency in our factorial design (ownership: interaction timing x orientation; agency:
398 interaction timing x movement type). In other words, we subtracted the control conditions where no
399 illusory experience in question was present (or strongly suppressed) from the experimental condition
400 in which they were present. Thus, for the sense of body ownership, we defined the contrast
401 $[(P_M S_T C_O - P_M A_T C_O) - (P_M S_T I_O - P_M A_T I_O)] + [(A_M S_T C_O - A_M A_T C_O) - (A_M S_T I_O - A_M A_T I_O)]$, including both the active
402 and passive conditions. This contrast corresponds to the interaction between the factors synchrony
403 (of the movements) and congruency (between the orientation of the rubber hand with the
404 participant's real hand) since we know asynchronous movements and anatomical incongruity to
405 disrupt the sense of ownership of the rubber hand in the moving rubber hand illusion (Kalckert &
406 Ehrsson, 2012). Similarly, for the sense of agency, we defined the contrast $[(A_M S_T C_O - P_M S_T C_O) -$

407 $(A_M A_T C_0 - P_M A_T C_0) + [(A_M S_{T0} - P_M S_{T0}) - (A_M A_{T0} - P_M A_{T0})]$, including both the congruent and incongruent
408 conditions. This contrast is the interaction between the two factors of timing (synchronous or
409 asynchronous) and type of movement (active or passive) because we know that both the sense of
410 volition associated with active movements and the match between expected and actual sensory
411 feedback from the movements are required for a sense of agency to develop (Haggard, 2017); hence,
412 both asynchronous movements and passive movements should abolish the sense of agency of the
413 rubber hand. Note that these key contrasts are balanced and fully matched in terms of the
414 magnitude of visual and somatosensory stimulation related to the observed and felt movements, as
415 well as the frequency and amplitude of finger taps (Extended Data Table 13-1), and thus isolate the
416 neural activities related to ownership and agency in which we are interested.

417 A further strength of this design is that the two interaction contrasts that operationalize ownership
418 and agency are orthogonal (i.e., independent), which means that we can also test for active voxels
419 that are significantly active in both contrasts by using a conjunction analysis. Thus, this conjunction
420 analysis identifies active areas that show increases in activity that reflect both ownership and agency.

421 Finally, the current 2x2x2 factorial design allows us to investigate the interaction between the sense
422 of body ownership and the sense of agency. To this end, we defined a linear contrast that was
423 composed of a three-way interaction between the three factors in the factorial design, namely,
424 movement type, synchrony and orientation of the fake hand, congruent or incongruent with the real
425 hand. This contrast $[(A_M S_T C_0 - P_M S_T C_0) - (A_M A_T C_0 - P_M A_T C_0)] - [(A_M S_{T0} - P_M S_{T0}) - (A_M A_{T0} - P_M A_{T0})]$ identifies
426 a neural response that specifically reflects the combination of body ownership and agency when
427 voluntary moving one's body. This can reflect a stronger sense of ownership during active
428 movements or differences in agency over an own body part (the rubber hand during the rubber hand
429 illusion) compared to agency over an external object (the rubber hand in the incongruent orientation
430 that does not feel like part of one's body).

431 Post hoc fMRI connectivity analyses
432 Task-related connectivity was assessed by performing a psychophysiological interaction (PPI)
433 analysis. The PPI indices task or contrast specific changes in the connectivity between two brain
434 regions. A significant PPI indicates that the correlation of the brain activity in the two regions
435 (measured as the change in the slope of their linear regression curve) changes significantly with the
436 experimental or psychological context (Friston et al., 1997). To follow up on the regional results (see
437 below), we decided to conduct a post hoc PPI analysis for purely descriptive purposes. We placed a
438 seed voxel in the postcentral gyrus contralateral to the stimulated hand. The seed was selected
439 based on activity in this region that was elucidated during the three-way interaction contrast
440 described above. The seed was defined for each participant as a 10-mm sphere around the group
441 level activation in the postcentral gyrus. From this, the time series of activity (first eigenvariate) was
442 extracted and entered into the PPI analysis with the contrast weights from the three-way interaction.
443 The PPI regressors created at the individual level were analyzed at the group level using one-sample
444 t-tests.

445 Post hoc descriptive correlation analysis of ownership contrast and questionnaire ratings.
446 In a post hoc complementary approach, we explore a possible relationship between the subjective
447 ratings of ownership as rated by the individual participants in the questionnaires in the behavioral
448 experiment (before the fMRI) and the contrast that describes the ownership-related activation.
449 Unlike agency, which can be experienced by everybody, the feeling of ownership in the rubber hand
450 illusion is vividly experienced in approximately 60-80% of participants (Ehrsson et al., 2005; Kalckert
451 & Ehrsson, 2014; Lloyd, 2007), making it possible to probe how individual differences in illusion
452 strength relate to brain activation. Previous studies have shown such a relationship in the premotor

453 cortex (Ehrsson et al., 2004, 2005; Gentile et al., 2013). To this end, we conducted analyses of the
454 fMRI data combined with a behavioral covariate. For each participant, we calculated “behavioral
455 contrast” (analogous to the defined contrasts in the fMRI analyses; $[(P_M S_T C_0 - P_M A_T C_0) - (P_M S_T I_0 -$
456 $P_M A_T I_0)] + [(A_M S_T C_0 - A_M A_T C_0) - (A_M S_T I_0 - A_M A_T I_0)]$) of the ownership ratings from all eight conditions and
457 entered this as a covariate in the GLM in the second level analysis together with the contrast images
458 reflecting the ownership contrast. This analysis allowed us to examine whether stronger subjective
459 ownership in the synchronous and congruent conditions ($A_M S_T C_0$ and $P_M S_T C_0$ compared to the other
460 conditions) correlated with stronger BOLD signals specifically in the ownership contrast.

461 Post hoc conjunction analysis across ownership and agency contrasts

462 To investigate which brain regions showed overlapping activation in both the ownership and agency
463 contrasts, we conducted a conjunction by performing a one-way ANOVA at the second level analysis
464 and entering the two different first level contrasts as the groups in the one-way ANOVA. The
465 contrasts are then specified for the two groups ([0 1] and [1 0]) and both contrasts are selected and
466 displayed as a conjunction at the second level.

467 **Results**

468 **Behavioral experiment**

469 The results from the behavioral pretest experiment replicated the main findings from the original
470 moving rubber hand illusion paper and confirmed that our behavioral paradigm worked as expected
471 (Kalckert & Ehrsson, 2012) but in a full 2x2x2 factorial within-subject design. The results confirmed
472 that the sense of body ownership and sense of agency can be dissociated behaviorally, as we had
473 expected (Fig. 4, Panel A). In the $A_M S_T C_0$ conditions, the participants experienced both a sense of
474 body ownership and agency of the rubber hand, i.e., the mean rating scores of these two sensations
475 were both positive, meaning that, on average, the participants affirmed both these experiences in
476 the classic moving RHI condition with active finger movements. Furthermore, in the $P_M S_T C_0$
477 condition, the classic moving RHI condition with passive finger movements, the participants
478 experienced a sense of body ownership (positive rating score) of the rubber hand but denied
479 experiencing a sense of agency (negative mean agency score). Finally, in the $A_M S_T I_0$ condition, the
480 participants experience a sense of agency over the rubber hand but no sense of body ownership
481 (positive and negative agency rating scores, respectively). In the control conditions, the participants
482 did not report sensing body ownership or agency, and the mean ownership and agency scores were
483 negative (Fig. 4, Panel A).

484 We then compared the ownership to the ownership control ratings and found significantly higher
485 ratings of the ownership statements compared to the control statements in the $A_M S_T C_0$ condition
486 ($W=349$, $p<0.001$, rank-biserial correlation 0.989) and $P_M S_T C_0$ condition ($W=314$, $p<0.001$, rank-
487 biserial correlation 0.932). The same analysis for the sense of agency showed significantly higher
488 ratings of the agency statements compared to the agency control statements in the $A_M S_T C_0$ condition
489 ($W=351$, $p<0.001$, rank-biserial correlation 1.00) and $A_M S_T I_0$ condition ($W=351$, $p<0.001$, rank-biserial
490 correlation 1.00). The individual ratings for each statement and condition are given in Extended Data
491 Table 4-1.

492 We then directly tested the hypothesis that the sense of body ownership depended on synchronous
493 visuo-somatosensory feedback when moving the finger as well as spatial congruency between the
494 orientations of the rubber hand and the participants’ real hand (Botvinick & Cohen, 1998; Ehrsson,
495 2012; Guterstam, Larsson, et al., 2019; Tsakiris, 2010). To this end, we analyzed the ownership
496 indices (the difference between the ownership score and ownership control score to control for
497 unspecific cognitive effects, e.g., suggestibility; (Ehrsson et al., 2022)) in a 2x2x2 ANOVA (see Fig. 4,

498 Panel B for ownership and agency indices across the eight conditions). The factors *movement type*
499 (*active/passive*), *timing* of movements (*synchronous/asynchronous*), and *orientation* of the rubber
500 hand (*congruent/incongruent*) were entered in the analysis. The results showed a significant main
501 effect of movement ($F=6.63$, df 29, 1, $p=0.016$, $\eta^2=0.012$), a significant main effect of timing
502 ($F=41.276$, df 29, 1, $p<0.001$, $\eta^2=0.216$), and a significant main effect of orientation ($F=17.645$, df 29,
503 1, $p<0.001$, $\eta^2=0.091$). Importantly, the interaction between timing and orientation was significant
504 ($F=31.933$, df 29, 1, $p<0.001$, $\eta^2=0.109$), in line with the spatial and temporal multisensory rules of
505 illusory rubber hand ownership (Kalckert and Ehrsson 2012) and our operationalization of ownership
506 in the fMRI factorial experimental design. There was no significant interaction between timing and
507 movement type ($F=0.894$, df 29, 1, $p=0.353$, $\eta^2=0.002$). However, the interaction between movement
508 type and orientation was also significant ($F=5.982$, df 29, 1, $p=0.022$, $\eta^2=0.008$), which suggests
509 higher ownership ratings during the active finger movements when the rubber hand was in a
510 spatially congruent orientation. Moreover, there was a significant three-way interaction between
511 timing, movement type and orientation ($F=6.421$, df 29, 1, $p=0.018$, $\eta^2=0.013$). This three-way
512 interaction suggests enhanced ownership of the rubber hand in the active synchronous congruent
513 condition when participants experience both ownership and agency over the moving rubber hand
514 compared to the passive synchronous congruent condition when people only experience illusory
515 ownership and thus provides behavioral support for examining the interaction of ownership and
516 agency in our factorial fMRI design. In line with this, post hoc pairwise comparisons between the
517 A_{MS_TCo} and P_{MS_TCo} conditions in terms of ownership index ($t=3.155$, df=29, $p=0.004$, Cohen's
518 $d=0.607$) and ownership scores ($t=2.413$, df=29, $p=0.023$, Cohen's $d=0.464$) further revealed
519 significant differences in both cases. This is an interesting behavioral finding that suggests that active
520 finger movements provide a stronger cue for body ownership than passive finger movements, which
521 has a bearing on an ongoing debate in the behavioral literature on whether body ownership and
522 agency interact in the moving rubber hand illusion or if they are completely independent (Dummer et
523 al., 2009; Hara et al., 2022; Kalckert & Ehrsson, 2012, 2014, 2017; Riemer et al., 2013; Tsakiris et al.,
524 2010; Walsh et al., 2011)

525 We hypothesized that the sense of agency is dependent on synchronous visuomotor feedback, i.e.,
526 the match between predicted sensory consequences of the active movement and sensory feedback,
527 as well as on participants actively moving the index finger, i.e., voluntarily generating the movements
528 (Kalckert & Ehrsson, 2012, 2014). To this end, we analyzed the agency indices (the difference
529 between the agency scores and the agency control scores to control for suggestibility effects) in a
530 2x2x2 ANOVA. The three factors of movement type (*active/passive*), timing
531 (*synchronous/asynchronous*), and orientation (*congruent/incongruent*) were entered in the analysis
532 (Fig. 4, Panel B). As expected, the results showed a significant main effect of movement type
533 ($F=42.244$, df 29, 1, $p<0.001$, $\eta^2=0.207$) and a significant main effect of timing ($F=107.572$, df 29, 1,
534 $p<0.001$, $\eta^2=0.255$), which suggests that both active movements and synchronous seen and felt
535 movement enhanced agency ratings. There was no main effect of orientation ($F=0.021$, df 29, 1,
536 $p=0.886$, $\eta^2=0.00002$), indicating that the orientation of the rubber hand did not influence agency.
537 Importantly, the interaction between synchrony and movement type was significant ($F=36.751$, df
538 29, 1, $p<0.001$, $\eta^2=0.132$), in line with the hypothesis and our operationalization of agency as this
539 two-way interaction in our fMRI design. The interaction between movement type and orientation
540 was not significant ($F=0.406$, df 29, 1, $p=0.530$, $\eta^2=0.0005$), nor was the interaction between
541 synchrony and orientation ($F=0.379$, df 29, 1, $p=0.251$, $\eta^2=0.001$). The three-way interaction between
542 synchrony, movement type and orientation was also nonsignificant ($F=1.560$, df 29, 1, $p=0.223$,
543 $\eta^2=0.002$). These latter results are consistent with the hypothesis that agency does not depend on
544 the orientation of the rubber hand and that agency can be operationalized as an interaction between

545 movement type and temporal congruence, only arising for active movements with synchronous
546 visual feedback. Overall, the questionnaire results from our behavioral experiment confirmed that
547 our selective manipulation of ownership and agency in the moving rubber hand illusion worked as
548 expected and in line with established multisensory and cognitive constraints and provided behavioral
549 support for examining the interaction of ownership and agency in the fMRI data (see below).

550

551

552

553 fMRI

554 The sense of body ownership is associated with activity in multisensory frontal and parietal
555 regions as well as cerebellar regions.

556 To identify activations associated with the sense of ownership of the rubber hand in both the active
557 and passive conditions, we used the contrast $[(P_{MS}C_0 - P_{MA}C_0) - (P_{MS}I_0 - P_{MA}I_0)] + [(A_{MS}C_0 -$
558 $A_{MA}C_0) - (A_{MS}I_0 - A_{MA}I_0)]$. In line with our hypothesis, this contrast revealed significant activation
559 peaks in the left premotor cortex, posterior parietal cortex and cerebellum ($p < 0.05$ FWE corrected
560 for multiple comparisons; Fig. 5; Table 2). The premotor activations were located in the precentral
561 gyrus at a location that corresponds to the dorsal premotor cortex (PMd; -34, -10, 64; $p < 0.05$, FWE
562 corrected; Fig. 5), and parietal lobe activations were observed in the supramarginal gyrus (SMG; -60,
563 -48, 38; $p < 0.05$, FWE corrected; Fig. 5). Activation peaks were also observed in the primary motor
564 cortex (precentral gyrus) and the primary somatosensory cortex (postcentral gyrus) at sites that
565 corresponded very well to peaks identified in the localizer experiment (see above). However, since
566 no a priori hypotheses existed for these regions and they did not survive correction for multiple
567 comparisons at the whole-brain level, they are reported with their uncorrected p values. We also
568 observed activity in the intraparietal cortex ($p < 0.001$ uncorrected) but more posteriorly than we had
569 predicted based on previous work. In the subcortical structures, we observed significant activity in
570 the crus 1 (lobule VIIa; 40, -74, -34) and vermis (lobule VIIa; 4, -68, -46) of the cerebellum ($p < 0.05$,
571 FWE corrected; Fig. 5). Finally, we observed a large active cluster in the left dorsolateral prefrontal
572 cortex (Figure 5, Panel A; $p < 0.001$ uncorrected)). No clusters survived correction for multiple
573 comparisons at the whole-brain level (FDR corrected). Further statistical details on the anatomical
574 locations in MNI space of the abovementioned peaks are shown in Fig. 5 and Table 2.

575 Correlation between subjective ownership ratings and ownership contrast

576 In a complementary descriptive approach, we followed up on the above ownership-interaction
577 contrast by examining whether those BOLD effects also correlated with the subjective ratings in the
578 ownership statements. To this end, we performed a multiple regression analysis using the ownership
579 ratings from each participant to search for voxels whose parameter estimates could be predicted
580 from the behavioral contrast (see methods). We identified four such regions whose parameter
581 estimates were significantly correlated with the behavioral contrast (Fig. 6). The activity in the left
582 premotor cortex (PMd; -24, -12, 70; $p < 0.05$, Fig. 6) and cerebellum was significant after FWE
583 correction (Cerebellum; -26, -46, -26; $p < 0.05$, Fig. 6), whereas the activity in the postcentral gyrus
584 and postcentral sulcus was not ($p < 0.001$, uncorrected; Fig. 6).

585 The sense of agency is associated with activity in the left precentral and postcentral gyrus as
586 well as right superior temporal gyrus.

587 We then examined activations that reflect the sense of agency, that is, increases in activity
588 dependent on actively generated movements as well as synchronous sensory feedback from the

589 moving limb irrespective of whether the hand was experienced as part of one's body. To this end, we
590 used the contrast $[(A_M S_T C_0 - P_M S_T C_0) - (A_M A_T C_0 - P_M A_T C_0)] + [(A_M S_I O - P_M S_I O) - (A_M A_I O - P_M A_I O)]$, which
591 represents agency across the congruent and incongruent conditions. In line with our hypotheses, we
592 observed a significant activation peak in the left premotor cortex (-38, -8, 62; $p < 0.05$, FWE corrected;
593 Fig. 7; Table 2) and an activation in the right superior temporal gyrus that almost reached significance
594 (58, -24, 12; $p = 0.051$, FWE corrected; Fig. 7; Table 2). This cluster is the second largest ($k=347$) in this
595 contrast (the largest one being the left superior temporal gyrus), and its location is very close to the
596 peak from the localizer experiment around which the small volume correction was made, which is
597 why we chose to report it despite the p value of 0.051. We also observed increases in activity in the
598 intraparietal cortex bilaterally as well as the left superior temporal gyrus and left postcentral gyrus
599 ($p < 0.001$, uncorrected), but these activations did not survive correction for multiple comparisons and
600 are thus only mentioned for descriptive purposes.

601 **Conjunction analysis: agency and ownership overlap in the precentral gyrus (PMd)**

602 To test for areas that showed increases in activity reflecting both ownership and agency, we used a
603 conjunction analysis with the two two-way interaction contrasts described above for ownership and
604 agency (Friston et al., 1999) (Fig. 8, Panel A). The analysis revealed a significant activation peak in the
605 precentral gyrus (PMd, -38, -8, 62, $p < 0.05$ FWE corrected; Fig. 8, Panel A).

606 **Interaction between ownership and agency** revealed activation in the somatosensory cortex
607 To test for interaction between ownership and agency, we used the contrast $[(A_M S_T C_0 - P_M S_T C_0) -$
608 $(A_M A_T C_0 - P_M A_T C_0)] - [(A_M S_I O - P_M S_I O) - (A_M A_I O - P_M A_I O)]$. This corresponds to the three-way interaction
609 between movement type (active/passive), timing (synchronous/asynchronous) and rubber hand
610 orientation (congruent/incongruent) and thus reveals neural responses unique to the combination of
611 ownership and agency in the moving rubber hand illusion condition ($A_M S_T C_0$). The results show
612 significant activation in the left primary sensorimotor cortex with a significant peak of activation
613 located in the postcentral gyrus at the level of the hand representations (-38, -28, 52; $p < 0.05$, FWE
614 corrected; Fig. 9) and three further peaks in the postcentral gyrus that did not survive corrections for
615 multiple comparisons ($p < 0.005$) (Fig. 9; Table 2).

616 We should clarify here that the somatosensory activation under discussion can probably not be
617 explained by somatosensory attenuation (Kilteni & Ehrsson, 2017, 2020; Zeller et al., 2014) or gating
618 (Angel & Malenka, 1982; Kilteni & Ehrsson, 2022; Post et al., 1994; Voudouris et al., 2019) because
619 we observed an increase in activity, not a reduction. Moreover, we controlled the amplitude of the
620 movements, and there were no significant differences in movement frequency between conditions
621 (see below; Fig. 13). Therefore, it is unlikely that low-level differences in motor output or
622 somatosensory feedback confounded our S1 findings. We also think it is implausible that differences
623 in tap force between the active and passive movements could explain our results because
624 participants were trained to apply gentle taps and the experimenter reproduced such gentle taps in
625 the passive condition; furthermore, the effects of passive movements are matched in the three-way
626 interaction contrast (as well as in the agency and ownership interaction contrasts).

627 Next, we examined the opposite direction of the three-way interaction contrast of movement type,
628 movement type, synchrony, and orientation $[(A_M S_T C_0 - P_M S_T C_0) - (A_M A_T C_0 - P_M A_T C_0)] - [(A_M S_I O - P_M S_I O) -$
629 $(A_M A_I O - P_M A_I O)]$. This contrast only revealed one activation in the left middle occipital gyrus and one
630 smaller activation in the right middle occipital gyrus (Fig. 10; Table 2), but neither of these activations
631 survived correction for multiple comparisons.

632 Psycho-physiological interaction analysis of functional connectivity
633 Our results reported above revealed activation in the postcentral gyrus (S1) associated with the
634 combined experience of illusory ownership and agency (three-way interaction). This made us curious
635 if there could be changes in functional connectivity between S1 and other brain areas that could help
636 us understand this finding further. Thus, in a post hoc exploratory PPI analysis of the functional
637 connectivity in the three-way interaction of the factors timing, movement type and orientation, we
638 investigated the task-specific connectivity changes between the section of the postcentral gyrus
639 under discussion (-38-28 52) and the rest of the brain. We found that the sense of ownership in the
640 presence of a sense of agency increased the functional coupling between the left primary sensory
641 cortex and the ipsilateral supplementary motor area (SMA; -2, -6, 64; $t=3.56$, $p=0.001$ uncorrected)
642 (Fig. 8, Panel B). In the rest of the brain, no active clusters were observed apart from one in
643 cerebellum (R VIIb; 28 -68 -46; $t=3.51$, $p=0.001$, uncorrected).

644
645 Activations in the insular cortex and right temporoparietal cortex reflect visuo-proprioceptive
646 synchrony and asynchrony, respectively
647 In the previous literature, it has been suggested that the right angular gyrus located in the
648 temporoparietal region is involved in the loss of agency when there is a mismatch between the
649 expected sensory consequences of self-generated movement and the sensory feedback (Farrer et al.,
650 2003; Farrer & Frith, 2002; Tsakiris et al., 2010). Furthermore, it has been reported that the insular
651 cortex shows increases in activation when people experience agency (Farrer et al., 2003; Farrer &
652 Frith, 2002). However, in our main planned contrasts reported above, we did not find any changes in
653 activation in these two regions, even at the level of uncorrected p values ($p<0.005$). To examine this
654 apparent inconsistency further, we looked at the main effect of synchrony
655 $[(A_M S_T C_O + A_M S_T I_O + P_M S_T C_O + P_M S_T I_O) - (A_M A_T C_O + A_M A_T I_O + P_M A_T C_O + P_M A_T I_O)]$ and main effect of asynchrony
656 contrasts $[(A_M A_T C_O + P_M A_T C_O + A_M A_T I_O + P_M A_T I_O) - (A_M S_T C_O + P_M S_T C_O + P_M S_T I_O + A_M S_T I_O)]$, i.e., areas that show
657 greater activation when visual feedback and finger movements are synchronous or asynchronous
658 irrespective of the senses of ownership or agency (i.e., across active and passive movements and
659 across anatomically congruent or incongruent hand orientations). Interestingly, we found a large and
660 significant activation ($t=3.66$, $p=0.022$, FWE-corrected) located in the right angular gyrus of the TPJ
661 region (50, -50, 32) that reflected the asynchronous relation between movement and visual feedback
662 (main effect of asynchrony; Fig. 11; Panel A). In contrast, synchrony of finger movements and visual
663 feedback of the model hand's finger movement (main effect of synchrony) was associated with
664 significant activation ($t= 3.71$, $p=0.020$, FWE-corrected) of the left insular cortex (-38, -2, 10; Fig. 11;
665 Panel B). Thus, rather than reflecting the sense of agency or the loss of agency by mismatching
666 sensory feedback, our results suggest that the insular cortex and right temporoparietal cortex are
667 involved in the basic detection of synchronous or asynchronous multimodal stimuli.

668 Activation in the supplementary motor cortex reflects the main effect of active vs. passive
669 movements
670 Another area suggested to be involved in agency in previous fMRI studies, including agency in the
671 moving RHI (Tsakiris et al. 2010), is the supplementary motor area (SMA). However, this area did not
672 show any agency-related activity in our agency contrast described above, not even at $p<0.005$
673 uncorrected. However, when we examined the main effect of movement type, contrasting all active
674 versus all passive movement conditions in the current design, we observed significant activation of
675 the SMA ($A_M S_T C_O + A_M A_T C_O + A_M S_T I_O + A_M A_T I_O$) - ($P_M S_T C_O + P_M A_T C_O + P_M S_T I_O + P_M A_T I_O$) (Fig. 12). This region
676 seems to be important for generating movements voluntarily, thereby indicating its role movement
677 planning, programming and volition more generally (Fried et al., 1991; Makoshi et al., 2011; Roland

678 et al., 1980). However, we found no evidence for specific involvement in the sense of agency of the
679 moving rubber hand.

680 When we looked for areas showing greater activity in the passive movement conditions than in the
681 active ones, we found a large activation in the medial prefrontal cortex in a region associated with
682 default mode activity (Buckner et al., 2008; Raichle et al., 2001; Tacikowski et al., 2017),
683 autobiographical episodic memory (Baddeley et al., 2001; Bergouignan et al., 2014; Svoboda et al.,
684 2006), and self-related information processing (Qin & Northoff, 2011; Tacikowski et al., 2017). The
685 most straightforward interpretation is that since participants did not have an active task in this
686 condition (they just relaxed their hand and the experimenter generated the finger movements), the
687 activity was higher in the default mode, thus explaining the relatively higher activity in this medial
688 prefrontal region compared to the active movement conditions when the participant had a task to
689 move their finger repeatedly. This activation also corresponds well to similar activity observed in the
690 passive finger movement condition in the study of Tsakiris et al. 2010, which these authors attributed
691 to ownership (Fig. 12).

692 Controlling for the number and frequency of taps in the different conditions

693 Using the optical sensor placed under the index finger of the participants, the number of taps as well
694 as frequency of taps for each condition could be analyzed. The analysis was performed on the time
695 periods included in the fMRI analysis (i.e., excluding the time before illusion onset and corresponding
696 time periods for conditions without illusion). A one-way ANOVA revealed no significant differences
697 across conditions for the frequency of taps (mean: 1.53 Hz; $F=0.636$, $df=7$, $p=0.725$). (Fig. 13).
698 Moreover, when the frequencies of taps were analyzed using the same 2x2x2 design as the fMRI
699 experiment we found no significant main effect of movement type ($F=2.519$, $df=19, 1$, $p=0.129$,
700 $\eta^2=0.014$), no significant main effect of timing ($F=2.353$, $df=19, 1$, $p=0.142$, $\eta^2=0.007$), no significant
701 main effect of orientation ($F=2.390$, $df=19, 1$, $p=0.139$, $\eta^2=0.041$), and no significant interactions
702 (Movement type x Timing: $F=0.928$, $df=19, 1$, $p=0.348$, $\eta^2=0.008$; Movement type x Orientation:
703 $F=0.152$, $df=19, 1$, $p=0.701$, $\eta^2<0.001$; Orientation x Timing: $F=2.215$, $df=19, 1$, $p=0.152$, $\eta^2=0.006$;
704 Movement type x Timing x Orientation: $F=0.430$, $df=19, 1$, $p=0.520$, $\eta^2=0.003$).

705 Discussion

706 This study has three main novel findings. First, the neural substrates of ownership and agency were
707 largely distinct, with body ownership associated with increases in activity in the premotor cortex,
708 posterior parietal and cerebellar regions and the sense of agency related to increased activity in the
709 superior temporal cortex and dorsal premotor cortex. Second, one active section of the dorsal
710 premotor cortex was associated with both agency and body ownership, indicating a cortical site
711 where ownership and agency information may be combined. Third, there was an interaction
712 between body ownership and agency in the somatosensory cortex so that its activity was higher
713 when participants experienced both sensations. This was accompanied by higher ownership ratings,
714 suggesting an agency-induced ownership enhancement of somatosensory cortical activity specific for
715 voluntary movement. Collectively, these findings extend our knowledge of the neural basis of body
716 ownership and agency and reveal their functional interaction and the relative neuroanatomical
717 overlap and segregation during simple movement, which advances our understanding of how bodily
718 self-consciousness is implemented in the human brain.

- 719 The sense of body ownership during movement: integration of spatiotemporally
720 congruent visuo-proprioceptive signals in premotor-parietal- cerebellar regions
721 The present study extends the previous neuroimaging literature on the neural basis of body
722 ownership (Brozzoli et al., 2012; Chancel, Iriye, et al., 2022; Ehrsson, 2007; Ehrsson et al., 2004;
723 Gentile et al., 2013; Guterstam, Collins, et al., 2019; Guterstam et al., 2013; Limanowski &
724 Blankenburg, 2016; Petkova et al., 2011; Preston & Ehrsson, 2016) into such experience arising from
725 the sensory feedback of movement. The sense of ownership of the moving rubber hand was
726 associated with significant activations in the left premotor cortex (precentral gyrus), posterior
727 parietal cortex (left supramarginal gyrus) and right lateral cerebellum. These activations probably
728 reflect the integration of spatially and temporally congruent visual information from the moving
729 rubber hand and kinesthetic-proprioceptive information from the hidden real hand because the
730 neural response was specifically related to the conditions when the rubber hand was placed in an
731 anatomically congruent condition and the seen and felt movements synchronous, i.e., when the
732 visual and kinesthetic-proprioceptive information obeyed the temporal and spatial rules of body
733 ownership (Blanke et al., 2015; Chancel, Ehrsson, et al., 2022; Ehrsson, 2012; Kalckert & Ehrsson,
734 2012; Samad et al., 2015), controlling for agency effects and effects related to active versus passive
735 movement.
- 736 The difference between visuo-kinesthetic integration, which was studied herein, and visuo-tactile
737 integration, which was investigated in previous RHI studies, can probably explain the differences in
738 precise localization of the activation peaks in the premotor cortex compared to previous studies (e.g.,
739 (Ehrsson et al., 2004)). Although activations have been seen in both ventral and dorsal aspects of the
740 premotor cortex in previous RHI studies (Gentile et al., 2013; Guterstam, Collins, et al., 2019), the
741 most consistent activations tend to have been located in the ventral premotor cortex (Ehrsson et al.,
742 2004; Gentile et al., 2013; Grivaz et al., 2017; Guterstam, Collins, et al., 2019; Guterstam et al., 2013;
743 Limanowski & Blankenburg, 2016). The dorsal premotor cortex is active during passive hand and arm
744 movements (Zhavoronkova et al., 2017), finger tapping (Bengtsson et al., 2009; Ullén et al., 2003),
745 and illusory hand and arm movements triggered by muscle tendon vibration (Naito et al., 1999,
746 2005), consistent with a role in multisensory representation of the upper limb in space. The current
747 activation in the supramarginal gyrus ($p<0.05$ corrected) is consistent with earlier body ownership
748 illusion studies based on visoutactile stimulation (Gentile et al., 2011, 2013; Petkova et al., 2011), and
749 the current intraparietal cortex activation is located in a section of this sulcus associated with
750 multisensory integration in perihand space (Brozzoli et al., 2011; Lloyd et al., 2003; Makin et al.,
751 2007) and illusory hand ownership (Chancel et al. 2022a). We also observed activity in the ipsilateral
752 lateral cerebellum in line with previous fMRI studies on various versions of the rubber hand illusion
753 based on visoutactile stimulation (Ehrsson et al., 2004, 2005; Guterstam et al., 2013) and limb-
754 movement illusions (Ehrsson et al., 2005; Hagura et al., 2009). Importantly, the current findings
755 extend the previous literature on body ownership and body representation by demonstrating a role
756 for these premotor-parietal-cerebellar regions in the sense of limb ownership during movement.
- 757 The sense of agency in one's own bodily movement: premotor and superior temporal
758 cortex
759 We could isolate activity in the dorsal premotor cortex and superior temporal cortex reflecting
760 agency over limb movement while controlling for unspecific effects related to multisensory
761 synchrony- asynchrony detection, active versus passive movement, and body ownership. The dorsal
762 premotor area has been reported in previous studies on the sense of agency over sensory events
763 caused by voluntary movement (David et al., 2008; Haggard, 2017; Nahab et al., 2011; Sperduti et al.,
764 2011; Yomogida et al., 2010), so our finding extends this to agency over perceived own bodily

765 movement. The dorsal premotor cortex is anatomically connected to and receives input from the
766 dorsolateral prefrontal cortex regarding intentions and the initiation of voluntary action in the
767 context of an overall action plan (Abe & Hanakawa, 2009; Koechlin et al., 2003; Passingham, 1993;
768 Yamagata et al., 2012) and receives multisensory input from the posterior parietal cortex regarding
769 one's own body as well as external sensory events; the dorsal premotor area can also influence
770 movement execution in M1 and receive feedback from this area through direct cortico-cortical
771 connections (Dum et al., 2002; Porter & Lemon, 1995). The dorsal premotor cortex is thus in an
772 excellent position, anatomically and physiologically, to play a central role in the sense of agency by
773 integrating and comparing signals related to voluntary motor commands and sensory feedback,
774 consistent with our findings.

775 Interestingly, the section of the dorsal premotor cortex associated with agency also showed body
776 ownership-related activity, as revealed in our conjunction analysis. This finding suggests that the
777 neural bases of body ownership and agency are not completely distinct (Tsakiris et al., 2010), and at
778 least one cortical area is involved in both processes. Different neuronal populations within the dorsal
779 premotor cortex could implement the formation of a coherent multisensory representation of the
780 hand in space (ownership) and generation of voluntary motor commands and the matching of those
781 commands' outcomes with the sensory feedback and predictions (agency), or the same neuronal
782 population within this area may implement both these mechanisms (which could be tested in future
783 studies with BOLD adaptation or multivoxel pattern analysis). Our findings suggest a more intimate
784 relationship of the representations of body ownership and agency in the premotor cortex than
785 commonly assumed and indicate that more attention should be devoted to this region in future
786 studies on the neural mechanisms of agency of bodily action.

787 Previous neuroimaging studies have suggested that the superior temporal cortex plays a role in the
788 sense of agency, but they reported that activation in the superior temporal gyrus reflected the *loss* of
789 agency when controlling a virtual limb (Nahab et al., 2011; Uhlmann et al., 2020). However, these
790 studies did not control for multisensory synchrony-asynchrony, the visual appearance (and identity)
791 of the hand, or body ownership. In contrast, we found a relative activity *increase* that reflected
792 *gaining* agency of the moving rubber hand, although all experimental conditions were deactivated
793 compared to the resting baseline. The current activation peak is located more ventral and anterior to
794 the deactivations in previous studies (Nahab et al., 2011; Uhlmann et al., 2020), making direct
795 comparisons difficult. Although the precise functional role of the superior temporal cortex in agency
796 is unclear, this region has been associated with action observation (Kilintari et al., 2014), visual
797 processing of biological motion (Saygin, 2007), and perception of causality between sensory events
798 (Blakemore et al., 2001), which collectively points toward a function of supporting the (visual)
799 perception of causality relationships between the seen finger movement and the executed finger
800 action, which presumably is an important component of the agency experience.

801 **Interaction of body ownership and agency in the somatosensory cortex**

802 Our analysis revealed somatosensory activity that was uniquely related to the situation when both
803 ownership and agency were experienced over the moving rubber hand (interaction between
804 ownership and agency). In principle, this activity could reflect a change in body ownership caused by
805 agency or a change in agency caused by ownership. We think the former is more likely because the
806 behavioral data showed a significant corresponding interaction effect in the questionnaire hand-
807 ownership ratings but not in the agency ratings. Thus, the somatosensory activity may be related to a
808 change in the somatic feeling of the rubber hand illusion when this illusion is produced by
809 visuomotor-kinesthetic correlations during active movements as opposed to visuokinesthetic
810 correlations during passive movements. Motor commands and efferent signals can influence limb

811 movement sensations (Gandevia et al., 2006; Walsh et al., 2010), and thus, we theorize that
812 information related to the active motor command signals made the ownership experience more vivid
813 by boosting kinesthetic sensations from the rubber hand's finger movements. Such motor command
814 signals could originate from premotor areas and influence the somatosensory cortex via cortico-
815 cortical connections, which is supported by the finding of increased functional connectivity between
816 the SMA and S1 in the active synchronous congruent condition when both ownership and agency
817 were experienced (Fig. 8). Alternatively, agency might influence the multisensory integration process
818 that determines body ownership by facilitating combination over segregation by influencing the prior
819 probability of a common cause (Chancel, Ehrsson, et al., 2022; Samad et al., 2015), although it
820 remains unclear how this would lead to enhanced S1 activation rather than increased premotor or
821 posterior parietal activity. The somatosensory activity might also reflect a special component of
822 agency over one's bodily movements – “bodily agency” – perhaps reflecting differences between
823 own-movement-related somatosensory predictions and predictions about external (e.g., visual)
824 events that are indirectly caused by voluntary action (Frith et al. 2000a). According to this view,
825 somatosensory activity would reflect somatosensory predictions during bodily agency, whereas
826 visual cortical activity would reflect visual predictions associated with ‘external agency’ over the
827 nonowned (rotated) rubber hand (Fig. 10). Regardless of the underlying mechanism and
828 conceptualization as neural changes related to agency modulation of body ownership or bodily
829 agency, our finding links somatosensory activity to the combination of ownership and agency during
830 voluntary limb movement.

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840

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1111 **Figure 1.** A. Depicts a montage of what the participants would see lying inside the MR scanner. The white
 1112 semiopaque field illustrates the dark cloth used to cover the participant's real right hand from view. The
 1113 participant's hand and the rubber hand are seen resting on a small table. The index finger of the rubber hand as
 1114 well as the participant's hand is placed inside a plastic ring, which is connected to the two most lateral vertical
 1115 rods seen in Panels B-E. Panels B-E illustrate the levers of the moving rubber hand illusion setup under the table
 1116 that moved the index finger of the participant and the rubber hand. In B, the levers are in a relaxed position
 1117 with the index finger of the rubber hand and the participant's hand resting on the table. In C, both the
 1118 participant's index finger and the index finger of the rubber hand are lifted off the table. The two levers are
 1119 connected to each other through a pin. In this configuration, the participants could lift their index finger, which
 1120 would simultaneously lift the index finger of the rubber hand (active synchronous conditions), or the
 1121 experimenter could push the index finger of the participant up by pressing on the rod underneath the
 1122 participants' index finger (as seen in the image; passive synchronous condition). In D & E, the two fingers have
 1123 been decoupled by removing the pin holding the two levers together. In this configuration, the index finger of
 1124 the rubber hand and the participant's hand could be moved independently by the experimenter; delayed
 1125 movements (approx. 0.5 s) of the rubber hand's index in the asynchronous conditions (active and passive
 1126 asynchronous conditions).

1127 **Figure 2.** A Schematic illustration of the design matrix for the 2x2x2 factorial giving rise to eight unique
 1128 conditions. B All eight unique conditions and their acronyms used in this paper. Each letter indicates the
 1129 movement type (active or passive), the timing of the movements (synchronous or asynchronous) and the
 1130 orientation of the rubber hand relative to the participant's hand (congruent or incongruent) and is followed by a
 1131 subscripted letter indicating which factor the letter belongs to (M=movement type, T=timing, O=orientation).

1132 **Figure 3.** Schematic illustration of the fMRI block design. Each stimulus block consisted of one of the eight
 1133 conditions with 45 seconds of continuous finger tapping, either actively or passively. Between each block, there
 1134 was a five-second rest baseline. After every four blocks, there was a longer 30-second rest condition. Four of the
 1135 eight conditions were repeated four times in each run since the congruent and incongruent conditions were split
 1136 into separate runs. The participants received auditory instructions at the beginning and end of each block that
 1137 consisted of a 1-second-long prerecorded voice saying, "tap finger" or "relax".

1138 **Figure 4.** A. The results from the behavioral experiment. These results show a double dissociation between the
 1139 sense of body ownership and sense of agency in our full factorial design. The A_MS_TC_O condition displayed high
 1140 ratings for both sense of body ownership and sense of agency. The P_MS_TC_O condition showed high ownership
 1141 ratings and low agency ratings, whereas the A_MS_TI_O condition showed high agency ratings and low ownership
 1142 ratings. Bars represent mean ratings, and error bars indicate the SEM. B. Ownership and agency indices
 1143 calculated by subtracting the pooled ownership and agency control ratings from the pooled ownership and
 1144 agency ratings, respectively. Bars indicate the means, and error bars indicate the SEM.

1145 **Figure 5.** A. Overview of the brain regions that display activation reflecting the sense of body ownership over
 1146 the rubber hand defined by the contrast $[(P_M S_T C_O - P_M A_T C_O) + (A_M S_T C_O - A_M A_T C_O) - (A_M S_T I_O -$
 1147 $A_M A_T I_O)]$. For display purposes only, the activations are projected onto a three-dimensional render of a standard
 1148 brain with a threshold of $p < 0.005$ (uncorrected for multiple comparisons, $k \geq 5$). RH/LH, right/left hemisphere.
 1149 Occ, occipital view. CS, central sulcus. B. Bar charts displaying the parameter estimates (a.u.) and SEs for the
 1150 major peaks of activation. The coordinates are given in MNI space. The peaks are displayed in representative
 1151 sections indicated by a dotted white circle on an activation map ($p < 0.005$ uncorrected for display purposes).
 1152 L/R, left/right. PrCG, precentral gyrus. PoCG, postcentral gyrus. SMG, supramarginal gyrus. IPS, intraparietal
 1153 sulcus. Asterisks indicate activation peaks that survive small volume correction (* $p < 0.05$ corrected, ** $p < 0.01$);
 1154 the peaks without an asterisk did not survive small volume correction and are reported in Table 2 with their
 1155 uncorrected p value. All peaks from the contrast are reported in Extended Data Table 5-1. Condition key: first
 1156 letter A or P (active or passive) subscript M (movement), second letter S or A (synchronous or asynchronous)
 1157 subscript T (timing), third letter C or I (congruent or incongruent) subscript O (orientation).

1158 **Figure 6.** Correlation between behavioral ownership ratings (x-axis) and parameter estimates (y-axis, a.u.) in
 1159 the left precentral sulcus (PrCS, -24, -12, 70), left postcentral gyrus (PoCG, -24, -40, 68), left postcentral sulcus
 1160 (PoCS, -22, -38, 70) and left cerebellum (-26, -46, -26). Pearson's r and p values are given in each respective

1161 correlation plot. The peaks are displayed as activation maps ($p<0.005$, uncorrected) on representative sections
 1162 of an average anatomical section and indicated with a dotted white line.

1163 **Figure 7. A.** Overview of the brain regions that display activation reflecting the sense of agency defined by the
 1164 contrast $[(A_M S_T C_0 - P_M S_T C_0) - (A_M A_T C_0 - P_M A_T C_0)] + [(A_M S_T I_0 - P_M S_T I_0) - (A_M A_T I_0 - P_M A_T I_0)]$. For display purposes only,
 1165 the activations are projected onto a three-dimensional render of a standard brain with a threshold of $p<0.005$
 1166 (uncorrected for multiple comparisons, $k \geq 5$). RH/LH, right/left hemisphere. STS, superior temporal sulcus. CS,
 1167 central sulcus. **B.** Bar charts displaying the parameter estimates (a.u.) and SEs for the major peaks of activation.
 1168 The coordinates are given in MNI space. The peaks are displayed in representative sections indicated by a
 1169 dotted white circle on an activation map ($p<0.005$ uncorrected for display purposes). L/R, left/right. STG,
 1170 superior temporal gyrus. PrCG, precentral gyrus. PoCG, postcentral gyrus. IPS, intraparietal sulcus. * indicates
 1171 activation peaks that survive small volume correction ($p<0.05$ corrected); the peaks without an asterisk did not
 1172 survive small volume correction and are reported in Table 2 with their uncorrected p value. All peaks from the
 1173 contrast are reported in Extended Data Table 7-1.

1174 **Figure 8. A.** Conjunction analysis between the agency contrast and ownership contrast revealed overlapping
 1175 activation in the left precentral gyrus (PMd). The significant activation peak ($p<0.05$ corrected) is displayed as
 1176 an activation map ($p<0.005$, uncorrected) and indicated with a dotted white line. **B.** PPI analysis of regions
 1177 displaying increased connectivity with the seed region in the left postcentral gyrus (-38 -28 52). The left
 1178 supplementary motor area (SMA) displays a task-specific increase in connectivity with the left postcentral gyrus
 1179 (SMA; $t=3.56$, $p=0.001$ uncorrected). The peak is displayed as part of an activation map ($p<0.005$, uncorrected)
 1180 and indicated with a dotted white line. The activation maps are presented on representative sagittal and
 1181 coronal sections of a mean anatomical MRI image made up of all participants' structural brain scans.

1182 **Figure 9. A.** Overview of the brain regions that display activation reflecting increased activation related to
 1183 agency of bodily objects compared to external objects defined by the contrast $[(A_M S_T C_0 - P_M S_T C_0) - (A_M A_T C_0 -$
 1184 $P_M A_T C_0)] - [(A_M S_T I_0 - P_M S_T I_0) - (A_M A_T I_0 - P_M A_T I_0)]$. For display purposes only, the activations are projected onto a
 1185 three-dimensional render of a standard brain with a threshold of $p<0.005$ (uncorrected for multiple
 1186 comparisons, $k \geq 5$). RH/LH, right/left hemisphere. IPS, intraparietal sulcus. PoCS, postcentral sulcus. CS, central
 1187 sulcus. **B.** Bar charts displaying the parameter estimates (a.u.) and SEs for the major peaks of activation. The
 1188 coordinates are given in MNI space. The peaks are displayed in representative sections indicated by a dotted
 1189 white circle on an activation map ($p<0.005$ uncorrected for display purposes). L/R, left/right. PoCG, postcentral
 1190 gyrus. * indicates activation peaks that survive small volume correction ($p<0.05$ corrected); the peaks without
 1191 an asterisk did not survive small volume correction and are reported in Table 2 with their uncorrected p value.
 1192 All peaks from the contrast are reported in Extended Data Table 9-1. Condition key: first letter A or P (active or
 1193 passive) subscript M (movement), second letter S or A (synchronous or asynchronous) subscript T (timing), third
 1194 letter C or I (congruent or incongruent) subscript O (orientation).

1195 **Figure 10.** To investigate which brain regions are associated with the sense of agency of external objects as
 1196 opposed to bodily objects, we defined a contrast that was the inverse of the three-way interaction $[(A_M S_T C_0 -$
 1197 $P_M S_T C_0) - (A_M A_T C_0 - P_M A_T C_0)] - [(A_M S_T I_0 - P_M S_T I_0) - (A_M A_T I_0 - P_M A_T I_0)]$. The results show activation in the left middle
 1198 occipital gyrus ($p<0.001$ uncorrected; did not survive correction for multiple comparisons) and right middle
 1199 occipital gyrus ($p=0.002$, uncorrected). The coordinates are given in MNI space. L/R, left/right. MOG, middle
 1200 occipital gyrus. The peak is displayed in a representative section and indicated by a dotted white circle on an
 1201 activation map ($p<0.005$, uncorrected for display purposes, $k \geq 5$). The bar chart represents the parameter
 1202 estimates (a.u.) for the peak.

1203 **Figure 11. A.** Activation in the right angular gyrus represented by the main effect of asynchrony
 1204 $(A_M A_T C_0 + P_M A_T C_0 + A_M A_T I_0 + P_M A_T I_0) - (A_M S_T C_0 + P_M S_T C_0 + P_M S_T I_0 + A_M S_T I_0)$. **B.** Activation in the left insular cortex
 1205 represented by the main effect of synchrony $(A_M S_T C_0 + P_M S_T C_0 + P_M S_T I_0 + A_M S_T I_0) -$
 1206 $(A_M A_T C_0 + P_M A_T C_0 + A_M A_T I_0 + P_M A_T I_0)$. The coordinates are given in MNI space. The peak is displayed in a
 1207 representative section and indicated by a dotted white circle on an activation map ($p<0.005$ uncorrected for
 1208 display purposes).

1209 **Figure 12.** Main effect of movement type (active or passive). Using the contrast
 1210 $(A_M S_I C_O + A_M A_I C_O + A_M S_I l_O + A_M A_I l_O) - (P_M S_I C_O + P_M A_I C_O + P_M S_I l_O + P_M A_I l_O)$, we compared all active movement
 1211 conditions to all passive conditions (irrespective of ownership or agency) (yellow-red color scale for activation,
 1212 top row). Active movement was associated with significant activations in the left supplementary motor area (-4,
 1213 -4, 58; $t=4.98$, $p<0.001$ uncorrected), left precentral gyrus (PMD; -42, -10, 60; $t=7.82$, $p<0.001$, FDR corrected,
 1214 not shown), left precentral gyrus (M1; -40, -18, 56; $t=9.20$, $p<0.001$, FDR corrected, not shown), right cerebellum
 1215 (lobule VI; 20, -50, -24; $t=9.23$, $p<0.001$, FDR corrected, not shown), left thalamus (-14, -22, 4; $t=5.90$, $p=0.026$,
 1216 FDR corrected, not shown), and right angular gyrus (34, -50, 24; $t=5.79$, $p=0.033$, FDR corrected, not shown). We also compared all passive movement conditions to all active movement conditions,
 1217 $(P_M S_I C_O + P_M A_I C_O + P_M S_I l_O + P_M A_I l_O) - (A_M S_I C_O + A_M A_I C_O + A_M S_I l_O + A_M A_I l_O)$. Passive movements were associated with a
 1218 relative increase in neural activity compared to active movements in the bilateral medial frontal cortex (only
 1219 right shown in section; 10, 44, -2; $t=5.8$, $p<0.001$ uncorrected; left medial frontal cortex; -6, 46, -2; $t=5.18$,
 1220 $p<0.001$; blue-green color scale for activation). The peaks are displayed in a representative section and
 1221 indicated by a dotted white circle on an activation map ($p<0.005$ uncorrected for display purposes). All peaks
 1222 from the contrast are reported in Extended Data Table 12-1. RH, right hemisphere. LH, left hemisphere. SFG=
 1223 superior frontal gyrus, MFG= medial frontal gyrus.
 1224

1225 **Figure 13.** The number and frequency of taps across conditions. The bars represent the mean number and
 1226 frequency of taps for all conditions for the period excluding the illusion onset times (see methods). Error
 1227 bars indicate the SEMs. The analysis of the frequencies of taps revealed no significant main effects and no
 1228 significant interactions, and there were no differences in frequencies across conditions. The exact values
 1229 for each condition are given in Extended Data Table 13-1.

1230 **Table 1.** The statements used in the questionnaire experiment conducted before the fMRI study (the “behavioral
 1231 pretest”). Each statement was rated once per condition. The statements were rated on a 7-point Likert scale
 1232 ranging from (-3) to (3). There were four statements assessing the sense of body ownership and the sense of
 1233 agency, as well as four control statements for both the sense of body ownership and the sense of agency.

1234 **Table 2.** Activation peaks for the main contrasts. **A.** The sense of body ownership in the moving rubber hand
 1235 illusion expressed as the interaction between synchrony and orientational congruency between the participant’s
 1236 real hand and the rubber hand, defined as the contrast $[(P_M S_I C_O - P_M A_I C_O) - (P_M S_I l_O - P_M A_I l_O)] + [(A_M S_I C_O - A_M A_I C_O) -$
 1237 $(A_M S_I l_O - A_M A_I l_O)]$ **B.** The sense of agency expressed as the interaction between synchrony and movement type
 1238 (active/passive), defined as the contrast $[(A_M S_I C_O - P_M S_I C_O) - (A_M A_I C_O - P_M A_I C_O)] + [(A_M S_I l_O - P_M S_I l_O) -$
 1239 $(A_M A_I l_O - P_M A_I l_O)]$. **C.** The three-way interaction between synchrony, movement type (active/passive) and orientation,
 1240 representing the areas that demonstrate increased activity when experiencing agency over bodily objects as
 1241 opposed to external objects, defined as the contrast $[(A_M S_I C_O - P_M S_I C_O) - (A_M A_I C_O - P_M A_I C_O)] - [(A_M S_I l_O - P_M S_I l_O) -$
 1242 $(A_M A_I l_O - P_M A_I l_O)]$. **D.** The inverse of the three-way interaction between synchrony, movement type
 1243 (active/passive) and orientation, representing the areas that demonstrate increased activity when experiencing
 1244 agency over external objects as opposed to bodily objects, defined as the contrast $[(A_M S_I C_O - P_M S_I C_O) - (A_M A_I C_O -$
 1245 $P_M A_I C_O)] - [(A_M S_I l_O - P_M S_I l_O) - (A_M A_I l_O - P_M A_I l_O)]$. PrCG= precentral gyrus, PoCG= postcentral gyrus, SMG=
 1246 supramarginal gyrus, ITG= inferior temporal gyrus, dlFPC= dorsolateral prefrontal cortex, mPFC= medial
 1247 prefrontal cortex, IPS= intraparietal sulcus, IOG= inferior occipital gyrus, STG= superior temporal gyrus, MOG=
 1248 middle occipital gyrus. * indicates activation peaks that survive small volume correction (FWE correction, $p<0.05$
 1249 corrected); + indicates an activation peak in the agency contrast that almost reached statistical significance
 1250 after small volume correction (FWE correction); the peaks without an asterisk did not survive small volume
 1251 correction and are reported with their uncorrected p value.

1252

A



B



C

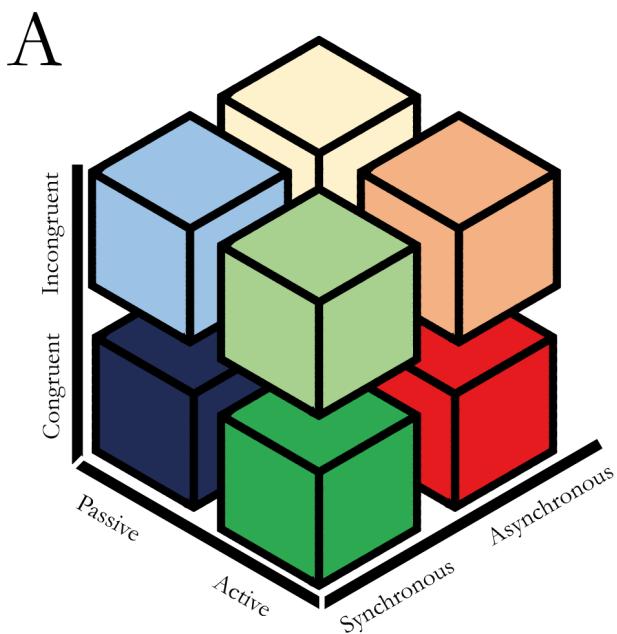


D



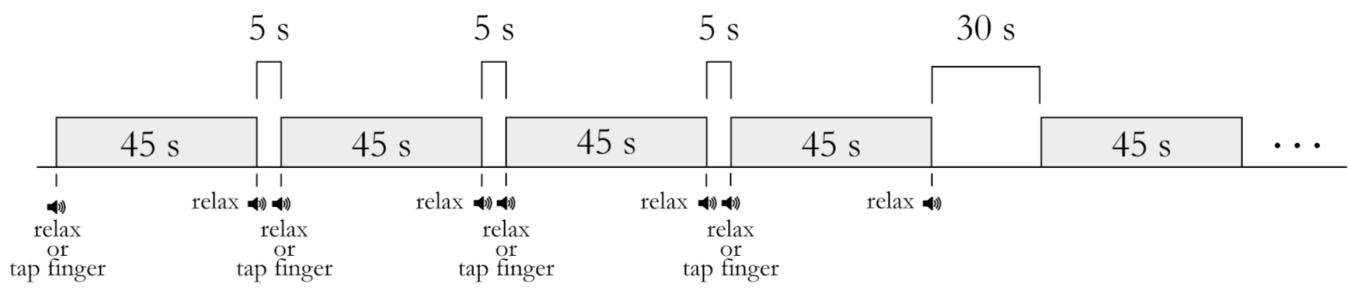
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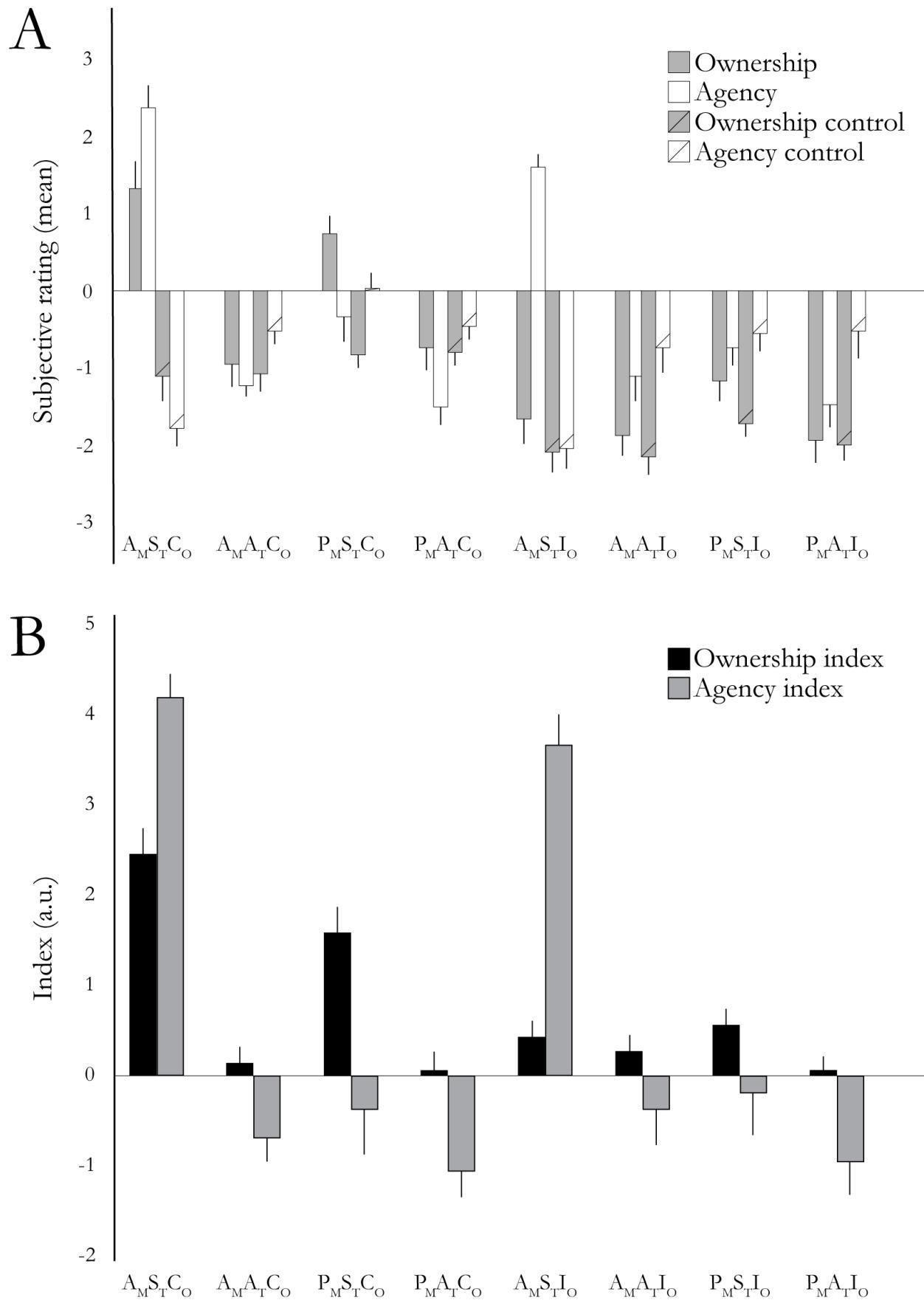


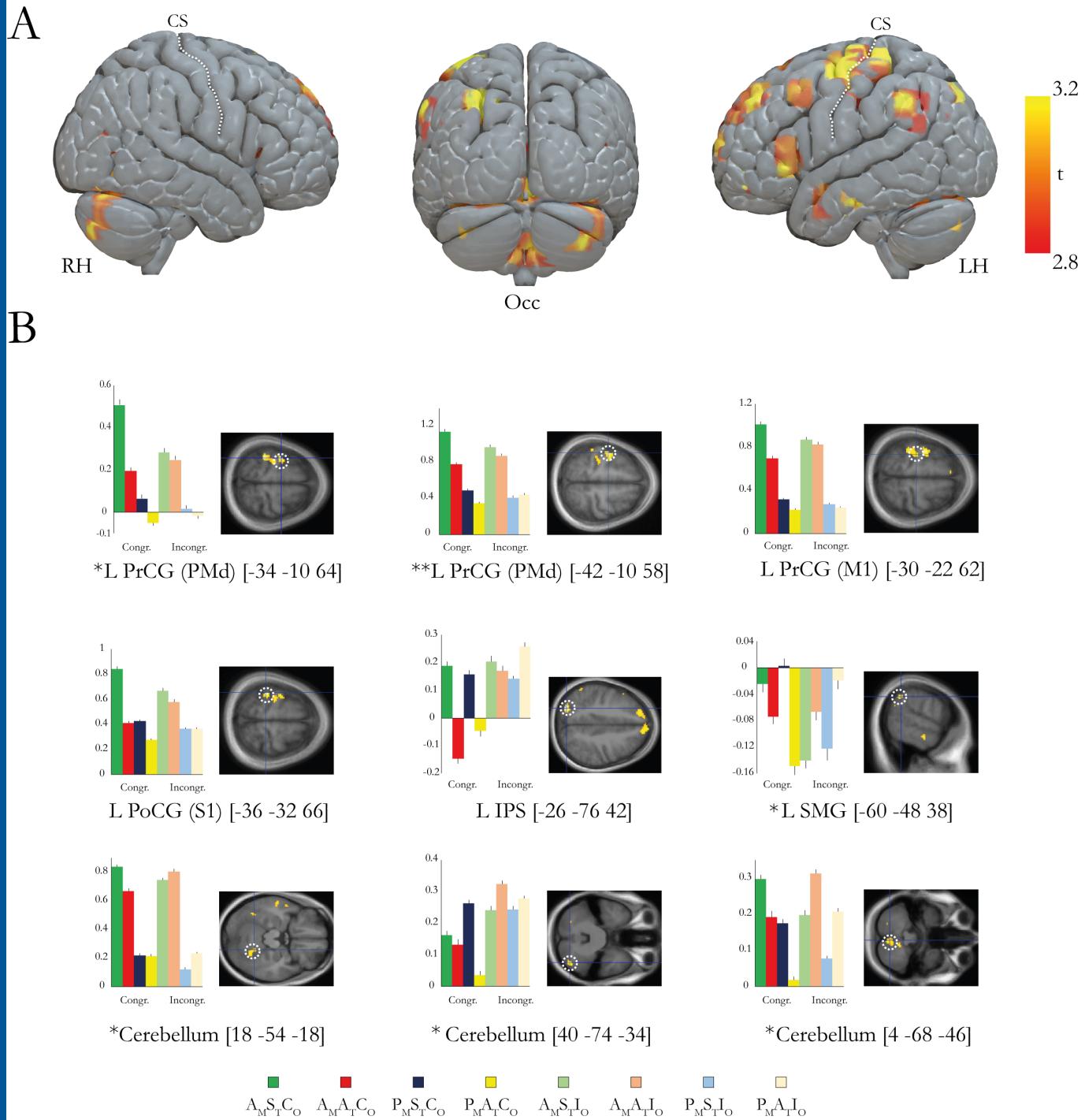


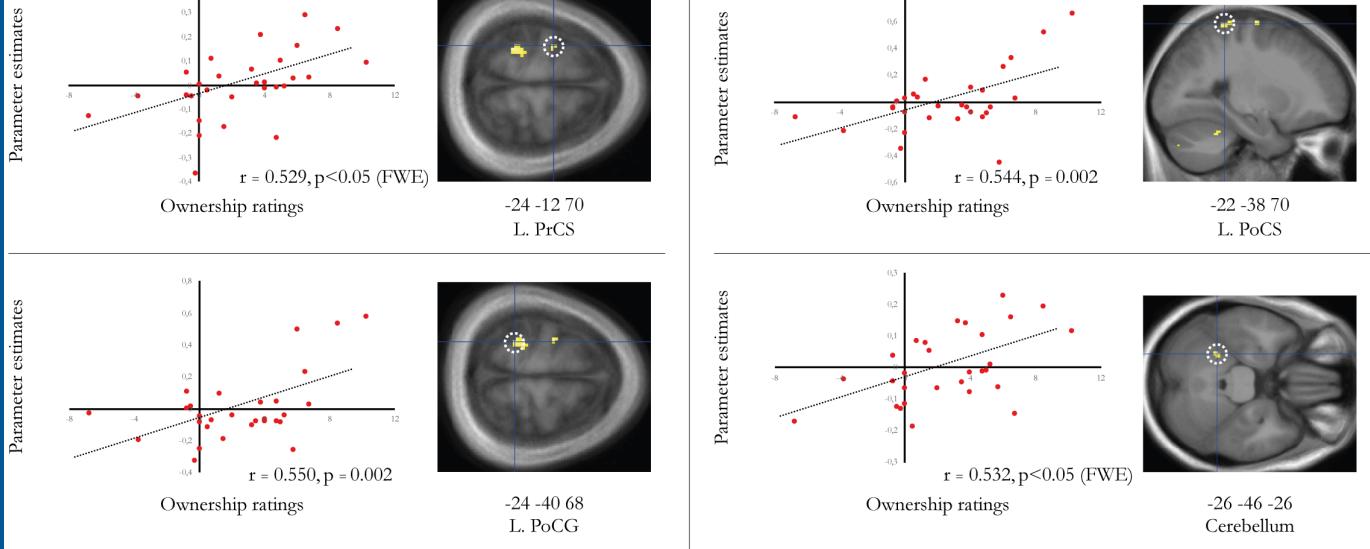
B

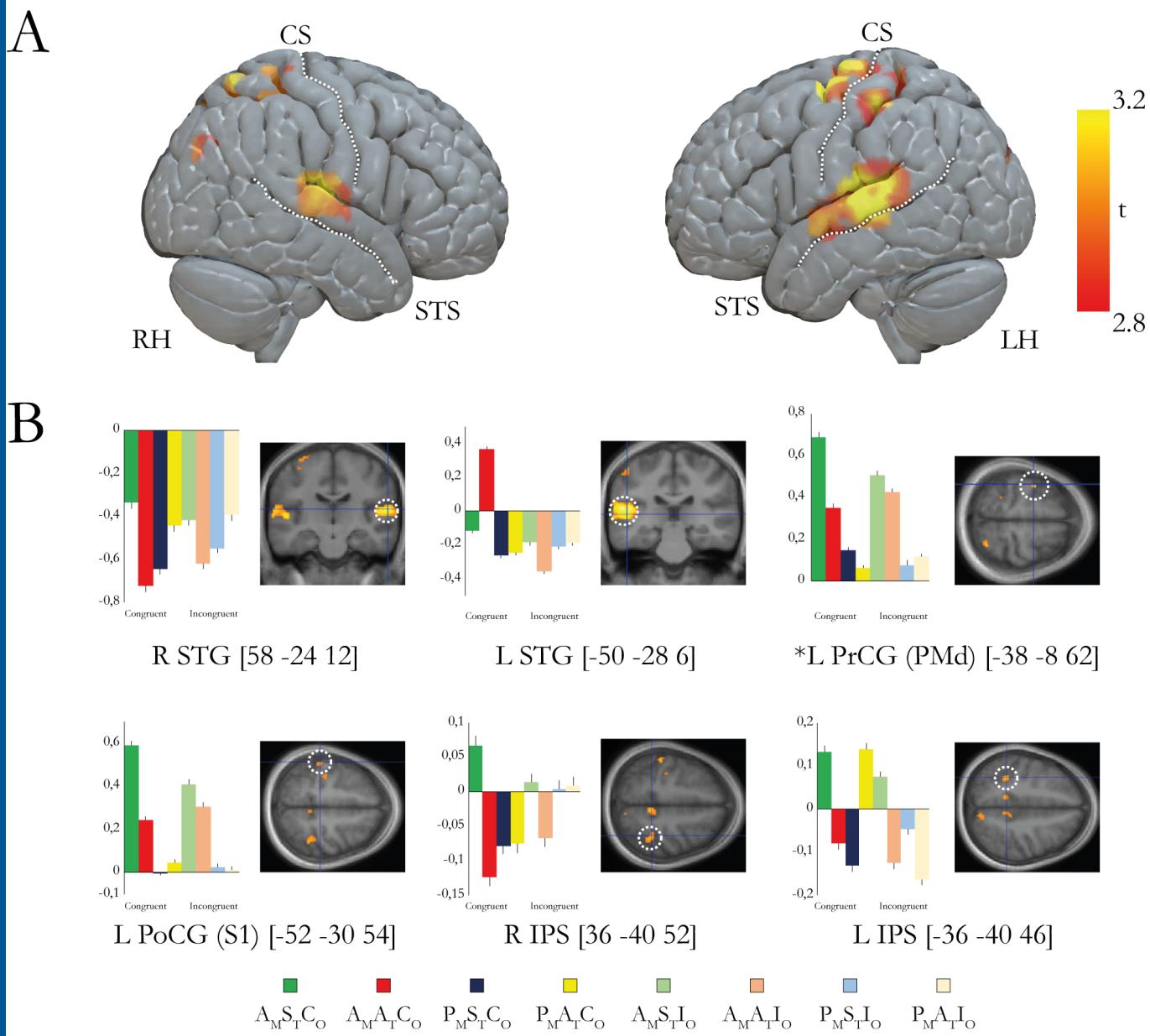
Condition	Acronym
Active/Synchronous/Congruent	$A_M S_T C_O$
Active/Aynchronous/Congruent	$A_M A_T C_O$
Passive/Synchronous/Congruent	$P_M S_T C_O$
Passive/Asynchronous/Congruent	$P_M A_T C_O$
Active/Synchronous/Incongruent	$A_M S_T I_O$
Active/Aynchronous/Incongruent	$A_M A_T I_O$
Passive/Synchronous/Incongruent	$P_M S_T I_O$
Passive/Asynchronous/Incongruent	$P_M A_T I_O$

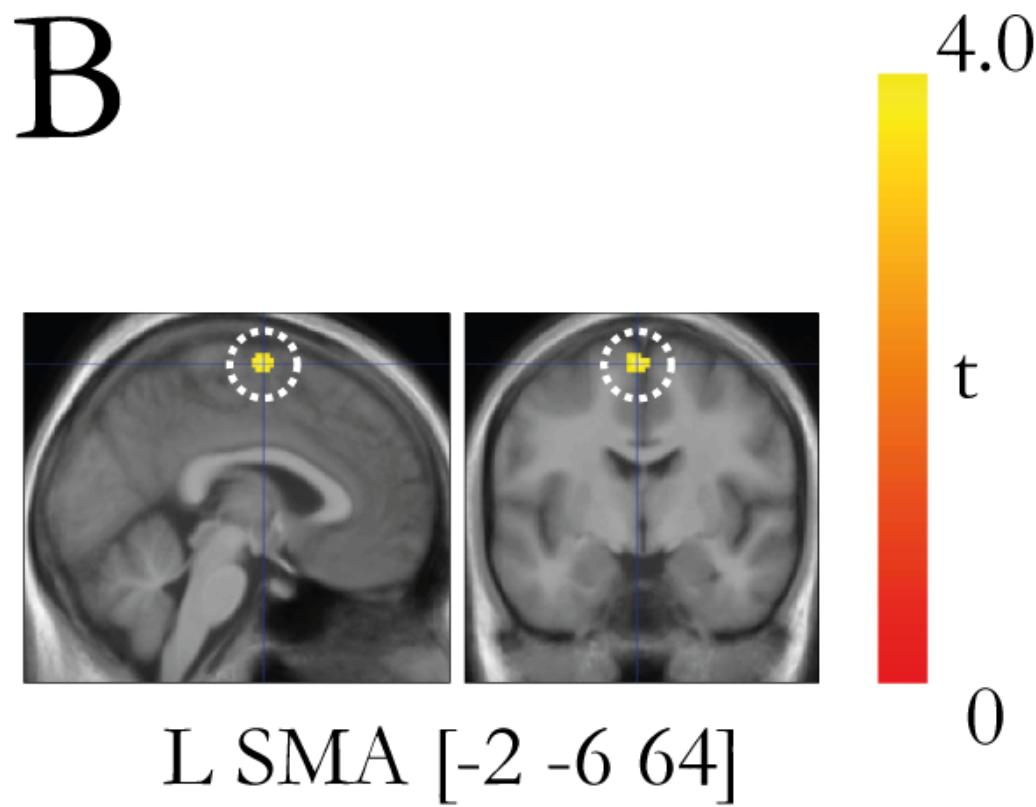
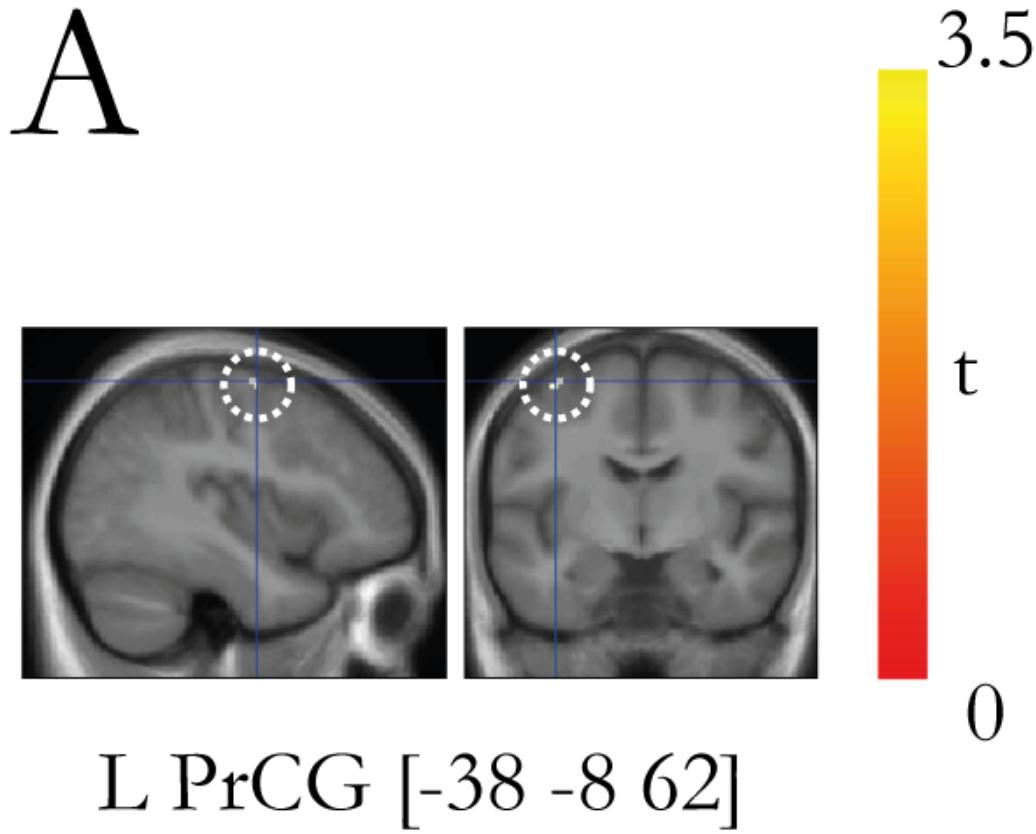


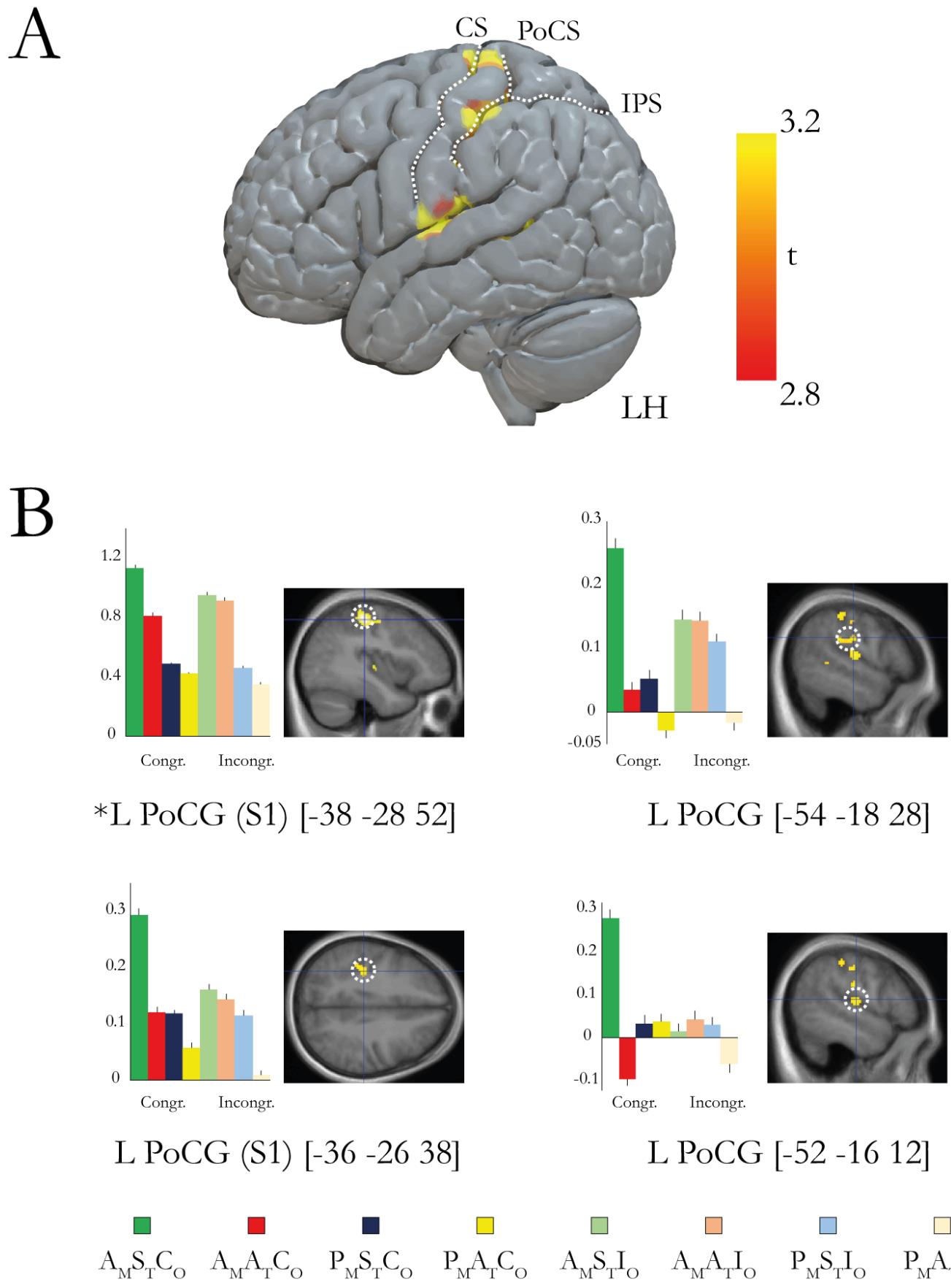


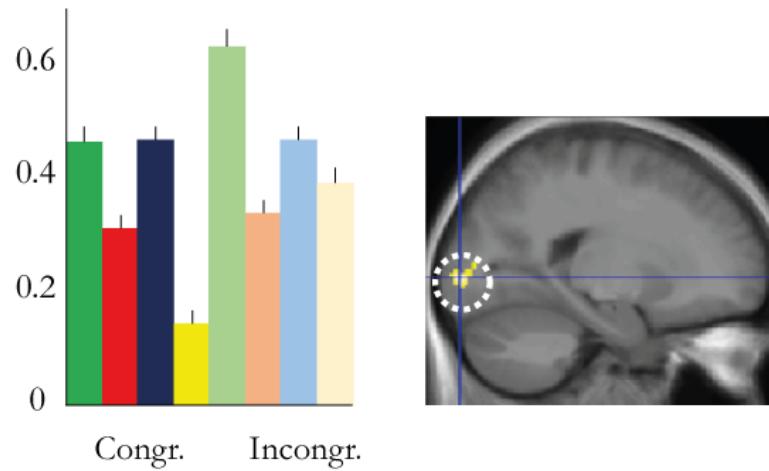
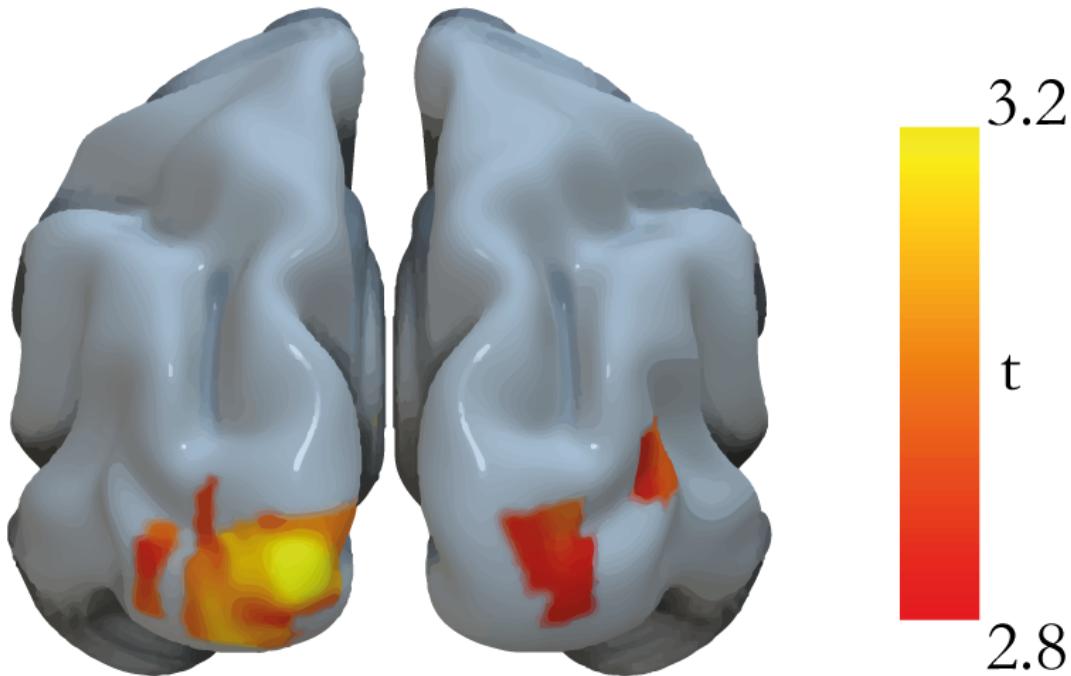




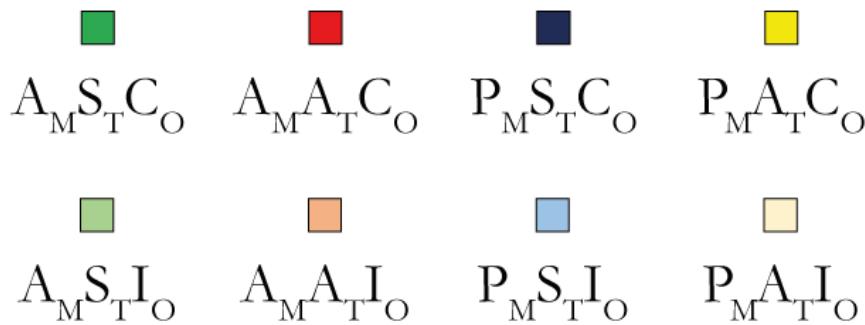


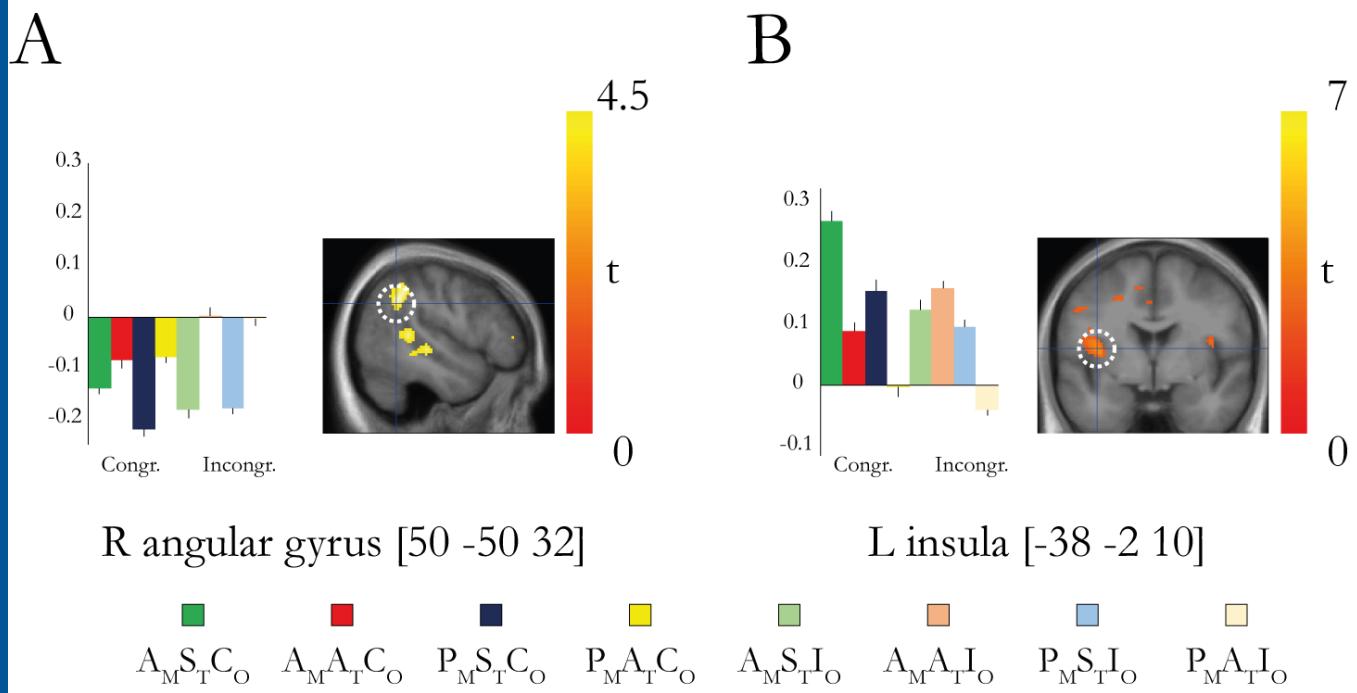


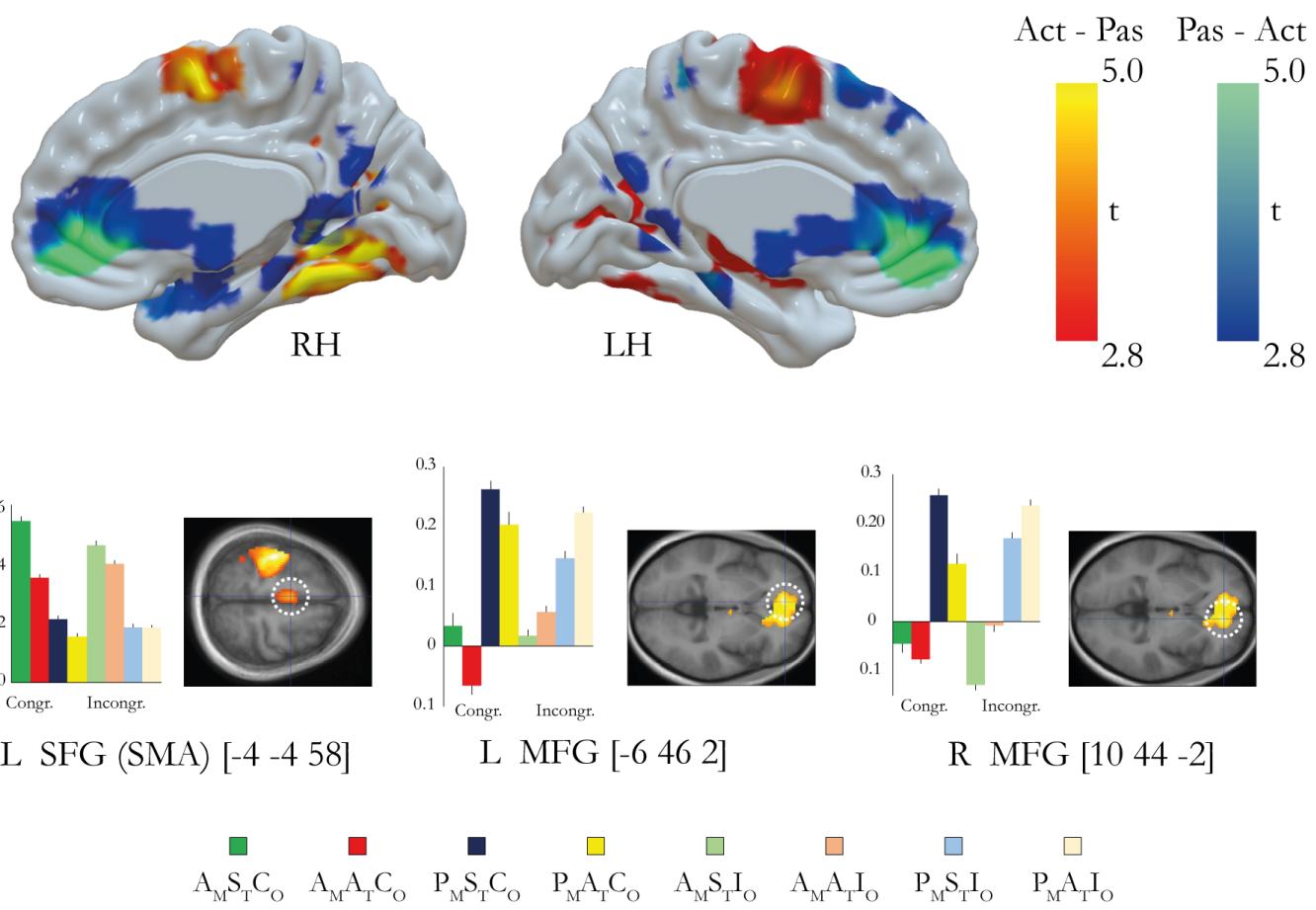


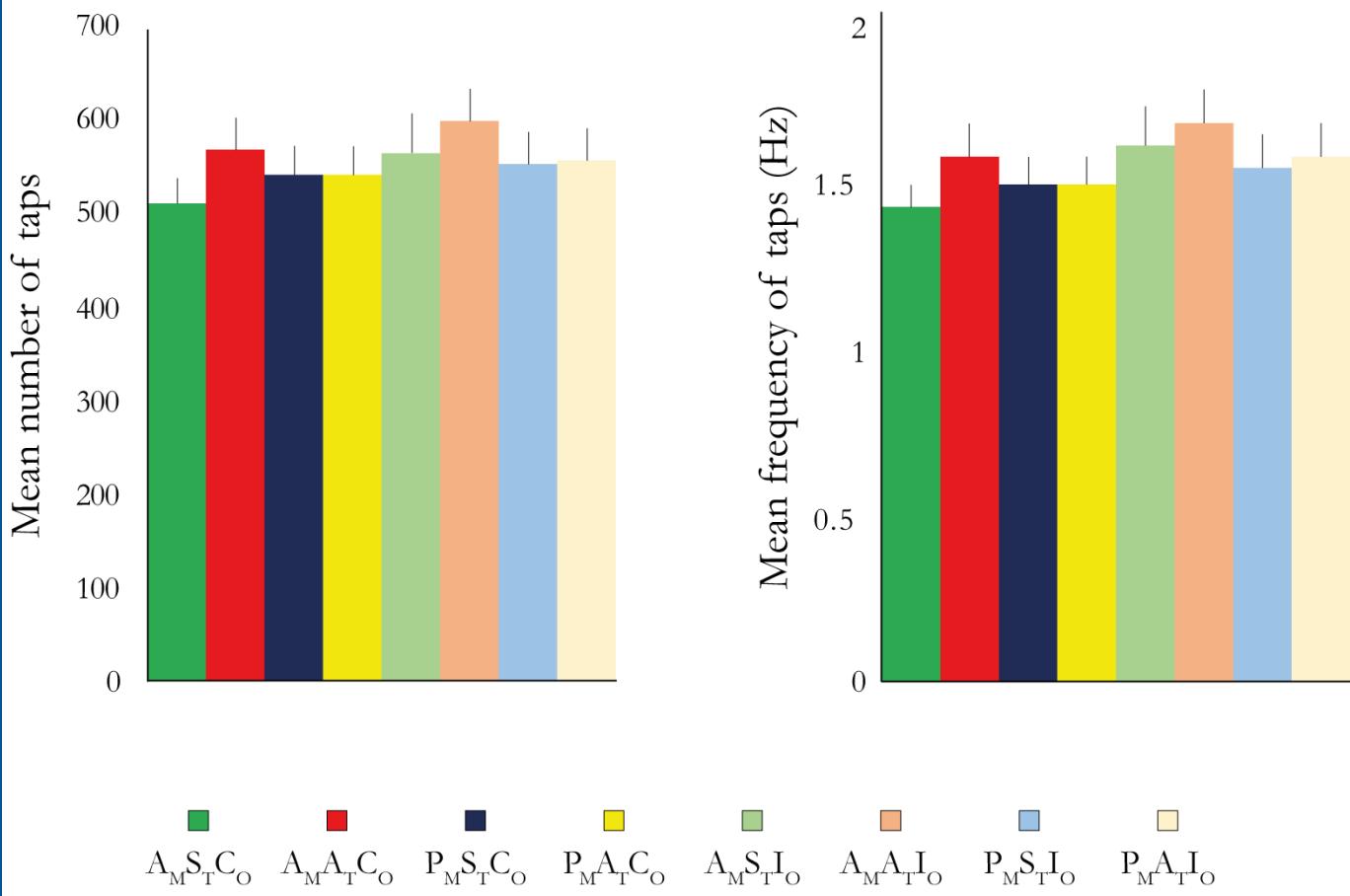


L MOG [-20 -94 0]









Assessment	Statement
Ownership	I felt as if I was looking at my own hand
	I felt as if the rubber hand was part of my body
	It seemed as if I were sensing the movement of my finger in the location where the rubber finger moved
	I felt as if the rubber hand was my hand
Agency	The rubber hand moved just like I wanted it to, as if it was obeying my will
	I felt as if I was controlling the movements of the rubber hand
	I felt as if I was causing the movement I saw
	Whenever I moved my finger I expected the rubber finger to move in the same way
Ownership control	I felt as if my real hand were turning rubbery
	It seems as if I had more than one right hand
	It appeared as if the rubber hand were drifting towards my real hand
	It felt as if I had no longer a right hand, as if my right hand had disappeared
Agency control	I felt as if the rubber hand was controlling my will
	I felt as if the rubber hand was controlling my movements
	I could sense the movement from somewhere between my real hand and the rubber hand
	It seemed as if the rubber hand had a will of its own

	Anatomical region	MNI x,y,z mm)	Peak t	p-value
A				
	L PrCG (PMd)	-42, -10, 58	4.66	0.009**
	L PrCG (PMd)	-34, -10, 64	4.30	0.019*
	L PrCG (PMd)	-42, -12, 56	4.13	0.010*
	L PrCG (PMd)	-36, -10, 62	3.99	0.014*
	L LSMG	-60, -48, 38	3.69	0.025*
	R Cerebellum (Vermis VIIa)	4, -68, -46	3.47	0.038*
	R Cerebellum (Crus I)	40, -74, -34	3.28	0.027*
	R Cerebellum (Crus I)	38, -72, -24	3.19	0.034*
	R ITG	42, -70, -8	3.38	0.046*
	L dlPFC	-24, 42, 38	4.42	0.001
	L mPFC	6, 50, 40	3.33	0.001
	L PrCG (M1)	-30, -22, 62	3.21	0.001
	L PoCG (S1)	-36, -22, 50	3.72	<0.001
	L PoCG	-46, -14, 52	3.51	<0.001
	L PoCG	-36, -32, 66	5.01	<0.001
	L PoCG	-56, -16, 40	3.05	0.003
	L IPS	-26, -76, 42	4.91	<0.001
	R IOG	44, -70, -12	2.97	0.003
B				
	R STG	58, -24, 12	4.03	0.051 [†]
	L PrCG (PMd)	-38, -8, 62	3.89	0.013*
	R STG	60, -20, 12	5.12	<0.001
	L STG	-50, -28, 6	4.88	<0.001
	L PoCG (S1)	-52, -30, 54	3.51	0.001
	R IPS	36, -40, 52	3.47	0.001
	L IPS	-36, -40, 46	3.69	<0.001
C				
	L PoCG (S1)	-38, -28, 52	4.21	0.007*
	L PoCG (S1)	-36, -26, 38	2.85	0.004
	L PoCG	-54, -18, 28	2.96	0.003
	L PoCG	-52, -16, 12	3.26	0.001
D				
	L MOG	-20, -94, 0	4.08	<0.001
	R MOG	26, -92, 4	3.08	0.002