

1 **Modulating human sense of agency with non-invasive brain stimulation**

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21 **Abstract**

22 Human voluntary actions are accompanied by a distinctive subjective experience termed “sense of
23 agency”. We performed three experiments using transcranial direct current stimulation (tDCS) to
24 modulate brain circuits involved in control of action, while measuring stimulation-induced changes in
25 one implicit measure of sense of agency, namely the perceived temporal relationship between a
26 voluntary action and tone triggered by the action. Participants perceived such tones as shifted towards
27 the action that caused them, relative to baseline conditions with tones but no actions. Actions that
28 caused tones were perceived as shifted towards the tone, relative to baseline actions without tones.
29 This ‘intentional binding’ was diminished by anodal stimulation of the left parietal cortex (targeting
30 the angular gyrus (AG)), and, to a lesser extent, by stimulation targeting the left dorsolateral
31 prefrontal cortex (DLPFC), (Experiment 1). Cathodal AG stimulation had no effect (Experiment 2).
32 Experiment 3 replicated the effect of left anodal AG stimulation for actions made with either the left
33 or the right hand, and showed no effect of right anodal AG stimulation. The angular gyrus has been
34 identified as a key area for explicit agency judgements in previous neuroimaging and lesion studies.
35 Our study provides new causal evidence that the left angular gyrus plays a key role in the perceptual
36 experience of agency.

37 **Keywords:** sense of agency; angular gyrus; dorsolateral prefrontal cortex; intentional binding; tDCS

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1. Introduction

46 Healthy human adults have the feeling that they are able to control their own actions, and, through
47 them, external events. This is referred to as the sense of agency. Sense of agency is central to
48 individual goal-directed action, and also to social responsibility and punishment (Frith, 2014; Moretto,
49 Walsh, & Haggard, 2011). Moreover, many neurological and psychiatric disorders involve
50 abnormalities of agency (de Jong, 2011; Fletcher & Frith, 2009; Kranick & Hallett, 2013).

51 Despite extensive theoretical work on agency, its neural correlates are not fully understood.
52 Neuroimaging studies found activation of AG (Farrer et al., 2003; Farrer & Frith, 2002; Farrer et al.,
53 2008) and DLPFC (Fink et al., 1999) associated with agency tasks, but the activation of these areas
54 was always greater in the conflicting, non-agency condition than in the agency condition. In a recent
55 meta-analysis of sense of agency, the single most consistent result was activation of a broadly-defined
56 temporoparietal junction area conditions associated with reduced or absent sense of agency (Sperduti,
57 Delaveau, Fossati, & Nadel, 2011). This broad ‘non-agency’ area includes AG. Computational
58 models of predictive motor control offer an important theoretical framework for understanding
59 agency. An internal forward model uses efference copies of the motor command to predict outcomes
60 (Wolpert & Ghahramani, 2000). According to these models, sense of agency arises when there is a
61 match between the predicted and actual sensory outcome of the generated action. Conversely, if
62 current sensory information does not match the model’s prediction, then the corresponding sensory
63 event cannot be self-generated, and no sense of agency is experienced (Frith, Blakemore, & Wolpert,
64 2000).

65 Farrer et al., (2008) used this framework to interpret fMRI activations of AG in particular, suggesting
66 that AG processes discrepancies between intended action and its actual consequences. Her data
67 showed increased activations of AG when a detectable temporal discrepancy was inserted between an
68 action and visual feedback of the outcome, and also when participants explicitly rejected agency over
69 the viewed outcome.

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70 Most of these studies used explicit agency attribution tasks, in which participants *judge* whether they
71 did or did not cause a specific sensory event. Synofzik, Vosgerau, & Newen, (2008) noted that one
72 *feels* a sense of agency when acting, even without making any explicit judgements. One suitable
73 measure of this pre-reflective, sensorimotor feeling of agency is the perceived temporal relationship
74 between a voluntary action and its sensory outcome (Moore & Obhi, 2012). The perceived time of
75 voluntary actions and their sensory consequences are attracted towards each other. This ‘intentional
76 binding’ is absent, or less prominent, for involuntary movements, and for associations between
77 external events not involving voluntary actions (Cravo, Claessens, & Baldo, 2009).

78 The neural bases of such *feelings* of agency are poorly understood. One neuroimaging study found a
79 neural correlate of intentional binding in the medial frontal cortex (Kühn, Brass, & Haggard, 2013). A
80 ‘virtual lesion’ study showed that theta-burst stimulation over a slightly more anterior medial frontal
81 location reduced the intentional binding effect (Moore, Ruge, Wenke, Rothwell, & Haggard, 2010).
82 On the other hand, other lesion (Sirigu et al., 2004) and stimulation (Desmurget et al., 2009) studies
83 suggested an important role of parietal cortex in intentional action and agency, though these studies
84 did not use binding. To our knowledge, no previous causal study has investigated the influence of
85 both frontal and parietal areas on sense of agency using implicit measures. We therefore performed
86 three transcranial direct current stimulation (tDCS) experiments, to modulate excitability of key brain
87 circuits underlying the control of action, while measuring the effects on sense of agency, using
88 intentional binding. Our experiments investigated the respective contributions of parietal and frontal
89 areas to intentional binding as a proxy measure of agency (Experiment 1), their susceptibility to both
90 up- and down-regulation (Experiment 2), and their hemispheric specialisation (Experiment 3).

91 Based on the existing neuroimaging data investigating explicit agency judgement (Farrer et al., 2003;
92 Farrer & Frith, 2002; Farrer et al., 2008), we predicted that anodal stimulation of putative AG should
93 also influence the sense of agency, as measured by intentional binding. Importantly, such a result
94 would identify a causal role for AG in sense of agency, but would not conclusively identify *how* AG
95 computes agency. We also investigated the role of prefrontal areas in sense of agency. Studies of
96 frontal contributions to sense of agency are more equivocal. Neurostimulation (Moore et al., 2010)

1 97 and neuroimaging (Kühn et al., 2013) studies of intentional binding found evidence for medial
2 98 prefrontal involvement, but studies of explicit agency judgements in tasks requiring a choice between
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4 99 alternative actions (Chambon, Wenke, Fleming, Prinz, & Haggard, 2013) identified a more lateral
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6 100 prefrontal focus. DLPFC has also been identified as a key area for initiation (Jahanshahi et al., 1995)
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8 101 and monitoring of voluntary action (Rowe, Hughes, & Nimmo-Smith, 2010). Given the relative
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10 102 inaccessibility of medial prefrontal cortex to neurostimulation, we focussed here on the lateral
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12 103 prefrontal cortex. The stimulations targeted primarily the left hemisphere, and participants made
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14 104 actions with their right hand (experiments 1,2), or with either hand (experiment 3).
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18 105 **2. Materials and Methods**

19 106 2.1. Participants

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22 107 In total 55 healthy volunteers, 18-35 years of age (25 females) were recruited from the Institute of
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24 108 Cognitive Neuroscience subject data pool for three separate experiments. All participants were right
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26 109 handed, had normal or corrected to normal vision, had no history or family history of seizure, epilepsy
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28 110 or any neurologic or psychiatric disorder and did not have any metallic or electronic object in the
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30 111 head. Participants affirmed that they had not participated in any other brain stimulation experiment in
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32 112 the last 48 hours, nor had consumed alcohol in the last 24 hours. The sample for Experiment 1
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34 113 consisted of 18 participants (8 females), Experiment 2 consisted of 19 participants (10 females) and
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36 114 Experiment 3 consisted of 18 participants (7 females). One participant failed to finish Experiment 2
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38 115 due to lack of concentration, and was therefore excluded. Experimental design and procedure were
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40 116 approved by the UCL research ethics committee, and followed the principles of the Declaration of
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42 117 Helsinki. Transcranial stimulation followed established safety procedures (Nitsche et al., 2003;
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44 118 Poreisz, Boros, Antal, & Paulus, 2007). Participants were paid a minimum amount for participating in
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46 119 each session of the experiment. Participants were paid a small additional bonus at the end of the last
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55 121 2.2. Behavioural task

122 We used intentional binding paradigm as an implicit measure of agency (Fig. 1). The task was based
123 on previous studies (Haggard, Clark, & Kalogeras, 2002), and was programmed in LabVIEW 2012
124 (Austin, Texas). Participants viewed a clock hand rotating on a computer screen which was located
125 60cm in front of the participants in a quiet room. The initial clock position was random. Clock
126 rotation was initiated by participants pressing the return key on a keyboard. Each full rotation lasted
127 2560ms. Participants were instructed to look at the centre of the clock. They made voluntary actions,
128 when instructed, by pressing the return key with their right index finger (Experiments 1, 2), or by
129 pressing F9 or F4 with their right or left index finger, respectively (Experiment 3). Participants chose
130 for themselves when to make these voluntary actions. After each key press, the clock hand stopped at
131 a random location, participants made a time judgement according to condition (see later). Each
132 experimental session consisted of four types of trials, presented in separate blocked and randomised
133 conditions. At the beginning of each block, brief instructions for the relevant condition were displayed
134 on the screen. In the *baseline action* condition, participants had to press the key at a time of their own
135 free choice. The clock hand stopped after 1500-2500ms (at random), and participants then judged the
136 clock hand position at the time of their key press, entering their response on the keyboard. In this
137 condition, the participant's actions produced no sensory outcome. In the *baseline tone* condition,
138 participants were instructed to look at the clock but not to press any key. While the clock was rotating,
139 a pure tone (1000Hz, 100ms duration) was played over a loudspeaker, 1750-4000ms (at random) after
140 the onset of the trial. Participants were then asked to judge the clock hand position at the time of the
141 tone. In the *operant action* condition, participants pressed a key at a time of their own choosing, and
142 each keypress produced a tone after 250ms. Participants judged the clock hand position at the moment
143 of pressing the key. Finally, the *operant tone* condition was similar to the operant action condition,
144 with the difference that participants had to judge the clock hand position at the time of the tone. Each
145 condition was tested in a separate block of 30 trials. The order of the blocks was randomised and there
146 was a 1 minute break between each block.

147 This common basic design was slightly changed according to the demands of each specific
148 experiment. In Experiment 3, text below and above the clock instructed participants to reply with

149 either their left or right index fingers. The order of hands was randomised in each block. The block
150 length was increased by 40 trials to allow sufficient trials for analysis of each hand's data.

151 Before each experiment, participants were trained and familiarised with the task. They were reminded
152 to look at the centre of the clock, to avoid following the clock hand with their eyes, to be spontaneous
153 in their key presses and to be as precise as possible in their judgements, in particular not confining
154 themselves to those numbers 5,10,15... marked on the clock face. Each experimental session
155 consisted of four blocks and took approximately 20 minutes. The short duration of each individual
156 session was planned to coincide with the known effective period of tDCS.

157 2.3. tDCS

158 Direct current stimulation was delivered by StarStim noninvasive wireless neurostimulator
159 (Neuroelectronics, Barcelona, Spain). Circular rubber electrodes (25cm²) were covered in saline-soaked
160 sponges, installed in a 27 channel neoprene cap, and connected to a wireless current generator. tDCS
161 was then controlled by Neuroelectronics Instrument Controller (NIC v1.2) through a separate computer.
162 Current strength was set at 1mA in all experiments, generating a current density of 0.04mA/cm² at the
163 scalp surface. For each experiment, all participants underwent three separate sessions of tDCS, two
164 effective stimulations and one sham session. The order of the sessions was randomised and
165 counterbalanced across participants. There was a minimum of 48 hours (and a maximum of 1 week)
166 between each stimulation session to minimise any potential carry over effects of tDCS (Nitsche et al.,
167 2008). The duration of stimulation in each session was set at 25 minutes, including 30s to ramp-up
168 and down the stimulating current. For the sham condition, electrical current was only applied during
169 the first and last 30 seconds of the stimulation, so as to induce the same cutaneous sensation as real
170 stimulation, and thus blind the participants as to stimulation condition. During the first 5min of each
171 stimulation, participants were asked to relax on their seats and close their eyes. This delay was
172 designed to allow potential neuro-modulatory effects to build up (Zwissler et al., 2014). Next,
173 participants began the behavioural task while stimulation continued (Fig. 2). All participants finished
174 the behavioural task approximately after 20min, the same time as the end of stimulation. In case
175 participants finished the task prior to the end of stimulation they were asked to remain seated until the

176 end of the stimulation. In case the task outlasted the stimulation, they continued to perform the task
177 without further stimulation. The task period never exceeded the stimulation period by more than 2
178 minutes.

179 Fig. 2 shows tDCS montages of the three experiments. In Experiment 1, the anodal electrode was
180 placed on the left DLPFC (F3 according to the 10/20 international EEG electrode placement) or
181 putative left AG (position P3) (Okamoto et al., 2004; Spitoni et al., 2013) in separate sessions. During
182 the sham session, the position of the stimulating electrode was counterbalanced between F3 and P3. In
183 all three sessions, the return electrode (cathodal) was placed on the right supraorbital area. For
184 Experiment 2, anode and cathode were placed on the putative left AG in separate sessions while the
185 return electrode was placed on the right supraorbital area. This arrangement was retained during the
186 sham session. Experiment 3 used a biparietal montage (Cohen Kadosh, Soskic, Iuculano, Kanai, &
187 Walsh, 2010; Hecht, Walsh, & Lavidor, 2010). For anodal stimulation of the putative left AG, the
188 anode was placed over P3 and cathode was placed over P4. This arrangement was reversed for anodal
189 stimulation of the putative right AG. For sham stimulation, the anode was pseudorandomly placed
190 either at P3 or P4. After each session participants were asked as part of debriefing if they had
191 experienced any notable effects of stimulation. No effects were reported other than mild tingling
192 sensations localised to the electrodes.

193 2.4. Data analysis

194 The difference between the judged clock hand position and the actual onset of the corresponding
195 event was calculated, giving a judgement error for each trial. A perceptual delay was represented by a
196 positive judgement error, and an anticipation by a negative judgement error. The mean and standard
197 deviation of the judgement errors across trials were then measured for each condition. Action binding
198 was defined as the shift of action toward its outcome, and was calculated by subtracting each
199 participant's mean judgement error in the *baseline action* from that in the *operant action* condition.
200 Likewise, tone binding was defined as a shift in the perceived time of a tone towards the action that
201 caused it. Tone binding was calculated by subtracting each participant's mean judgement error in

202 *baseline tone* condition from that in the *operant tone* condition. Thus, perceptual association of an
203 action with a subsequent tone produced a positive value for action binding, and a negative value for
204 tone binding. We analysed action and tone binding separately, since there is evidence from both
205 cognitive studies (Wolpe, Haggard, Siebner, & Rowe, 2013), and previous neurostimulation studies
206 (Moore et al., 2010), that they are driven by distinct mechanisms.

207 Some participants were excluded because of highly variable time judgement. A standard deviation of
208 judgement error across trials of over 250ms in any condition was used as a marker of poor time
209 perception. As in previous intentional binding experiments (Haggard, Aschersleben, Gehrke, & Prinz,
210 2002), these participants were excluded. On this basis, two participants were excluded from
211 Experiment 1, two from Experiment 2, and four from Experiment 3. Importantly, these exclusion
212 criteria are orthogonal to the *mean* judgement errors used for statistical inference.

213 In Experiments 1 and 2, inferential statistics were based on one-way repeated measures ANOVA,
214 with paired-sample t-tests for follow-up testing. Because our ANOVA had only 3 levels, Bonferroni
215 correction was not required for follow-up testing after a significant result (Cardinal & Aitken, 2013;
216 Meier, 2006). Additionally, in Experiment 1, we used linear discriminant analysis to determine which
217 percepts were most strongly affected by stimulation condition. Experiment 3 used repeated measures
218 ANOVA, with the additional factor of acting hand (right hand responses vs. left hand responses). A
219 final pooled analysis was performed to compare effects of stimulation common to all conditions.

220 **3. Results**

221 3.1. Experiment 1: frontal vs parietal anodal stimulation

222 This experiment compared the effects of frontal (targeting left DLPFC) and parietal (targeting left
223 AG) cortex stimulation on intentional binding for actions and tones. One-way repeated measures-
224 ANOVA with the factor of stimulation type (anodal frontal vs. anodal parietal vs. sham) showed that
225 action binding was not significantly affected by the type of stimulation ($F(2, 30)=1.90, p=0.17,$
226 $\eta^2=0.11$). However, an identical ANOVA on tone binding showed significant differences ($F(2,$
227 $30)=4.30, p=0.02, \eta^2=0.22$). Follow-up testing showed that tone binding was significantly reduced by

228 anodal stimulation of the putative left AG compared to sham ($t(15)=2.67$, $p=0.02$, $d=0.43$). Anodal
229 stimulation of the left DLPFC showed a clear trend to reduce tone binding, which approached the
230 border of conventional significance ($t(15)=2.07$, $p=0.06$, $d=0.42$). There was no significant difference
231 between the frontal and parietal stimulation ($t(15)=-0.10$, $p=0.92$, $d=0.02$) (Fig. 3; see also
232 supplementary table A.1-6).

233 We additionally performed the same analysis using median rather than mean judgement error in each
234 condition (see supplementary table B.1-3), since median measures are more robust than means to the
235 influence of outliers. The patterns of statistical significance were unchanged.

236 Finally, to confirm that anodal stimulation of putative AG affected primarily the operant tone
237 condition and not the baseline tone, the effect of stimulation type on participants' judgement error in
238 *baseline* tone conditions was assessed using repeated-measure one-way ANOVA. There was no
239 significant main effect of stimulation type on baseline tone condition ($F(2, 30)=0.58$, $p=0.56$,
240 $\eta^2=0.04$). This suggests that stimulation influenced a neurocognitive process that is present primarily
241 in the operant condition.

242 We additionally applied multivariate linear discriminant analysis (Krzanowski, 2000) to identify the
243 linear combination of action binding and tone binding variables that optimally discriminates the
244 different stimulation conditions. Linear discriminant analysis significantly differentiated the three
245 stimulation conditions (Wilks' Lambda=0.59, approx. $F(4,58)=4.36$, $p<0.01$). Inspection of canonical
246 coefficients showed that this difference was primarily due to tone binding (standardized canonical
247 coefficient 1.86) rather than action binding (-0.93) (The scores of the individual participants on the
248 first discriminant variate are shown in supplementary Fig. A.1). Post-hoc comparisons between
249 conditions showed a highly significant difference between parietal and sham stimulation ($p<0.01$;
250 standardised coefficients -1.03 for action binding, 2.19 for tone binding), and also a significant
251 difference between frontal and sham stimulation ($p=0.04$; standardised coefficients -0.82 for action
252 binding, 1.55 for tone binding). Interestingly, the frontal effect thus involved a slightly larger action
253 binding coefficient, considered relative to the tone binding coefficient, than did the parietal effect,

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254 though no inferential statistics can be applied to this ratio. Frontal and parietal stimulation did not
255 differ significantly ($p=0.74$).

256 3.2. Experiment 2: anodal vs cathodal parietal stimulation

257 If anodal stimulation boosts activity in the left AG then cathodal stimulation of the same area should
258 lead to its suppression. Thus, if anodal stimulation decreases intentional binding, cathodal stimulation
259 should increase it. To test this hypothesis, putative left AG was exposed to anodal, cathodal or sham
260 stimulation in different sessions, and effects on intentional binding were evaluated.

261 One-way repeated measures-ANOVA with the factor of stimulation type (anodal parietal vs. cathodal
262 parietal vs. sham) was used for analysis. Action binding was not significantly affected by the type of
263 stimulation ($F(2, 30)=0.50$, $p=0.61$, $\eta^2=0.03$). Tone binding was also unaffected by type of stimulation
264 ($F(2, 30)=0.45$, $p=0.64$, $\eta^2=0.03$), contrary to our predictions from Experiment 1. Nevertheless, the
265 numerical effect of anodal stimulation of the putative left AG was in the same direction as Experiment
266 1, namely a decreased tone binding compared to sham and cathodal stimulation (Fig. 4; see also
267 supplementary table A.7-12).

268 We additionally performed the same analysis using median rather than mean judgement error in each
269 condition (see supplementary table B.4-6). The patterns of statistical significance were unchanged.

270 3.3. Experiment 3: left vs right parietal stimulation

271 Experiment 3 aimed to replicate the effects of Experiment 1, and additionally investigated the
272 lateralisation of intentional binding using a biparietal montage. The biparietal montage may provide a
273 higher local current density, because of the relatively short path between anode and cathode. In
274 addition, this montage controls for any possible effect of cathodal stimulation of prefrontal areas that
275 may occur with the conventional supraorbital placement of the cathode. Therefore, putative left and
276 right AG were exposed to anodal stimulation in separate sessions, and a third session involved sham
277 stimulation. We also investigated whether the putative AG involvement in intentional binding is hand-
278 specific or hemisphere-specific, by asking participants to make actions with either the left or right

279 hand, choosing randomly on each trial. Analysis of action binding showed no significant main effect
280 of stimulation type ($F(2, 26)=0.06, p=0.94, \eta^2=0.01$) or acting hand $F(1, 13)=0.10, p=0.76, \eta^2=0.01$
281 and no significant interaction ($F(2, 26)=0.89, p=0.42, \eta^2=0.06$). Analysis of tone binding showed a
282 highly significant main effect of stimulation ($F(2, 26)=5.93, p<0.01, \eta^2=0.31$). Follow-up testing
283 showed that anodal stimulation of the putative left AG significantly decreased tone binding relative to
284 both sham stimulation ($t(13)=2.55, p=0.02, d=0.40$), and relative to anodal stimulation of the putative
285 right AG ($t(13)=2.90, p=0.01, d=0.56$). No significant difference was observed between anodal
286 stimulation of the putative right AG and sham ($t(13)=-0.75, p=0.47, d=0.10$) (Fig. 5; see also
287 supplementary table A.13-18). Acting hand had no significant main effect on tone binding ($F(1,$
288 $13)=0.01, p=0.94, \eta^2<0.01$) and no interaction was observed between the stimulation and acting hand
289 ($F(2, 26)=0.15, p=0.86, \eta^2=0.01$).

290 We additionally performed the same analysis using median rather than mean judgement error in each
291 condition (see supplementary table B.7-9). The patterns of statistical significance were unchanged.

292 To check whether the decrease in tone binding was primarily due to shifts in the operant tone, or in
293 the baseline tone condition, participants' judgement errors in the baseline tone condition were
294 compared across the stimulation groups. Analysis showed no significant main effect of stimulation
295 type on baseline tone condition ($F(2, 26)=0.50, p=0.60, \eta^2=0.04$).

296 3.4. Pooled data: anodal parietal vs sham stimulation

297 Anodal stimulation of the putative left AG was common to all three experiments reported here, as was
298 a sham stimulation condition, although the experiments differed in other respects. Therefore, we
299 pooled the data in these specific conditions across the 46 participants (21 female) from the three
300 experiments, in a single analysis. We found that anodal stimulation of putative left AG significantly
301 reduced the perceptual shift of tone toward action compared to sham ($t(45)= 3.28, p<0.01, d=0.35$),
302 but had no effect on action binding ($t(45)=-1.37, p=0.18, d=0.22$).

303 The anodal montage in the third session used a different return (cathode) location compared to the
304 first and second experiments. Our decision to pool data of the three studies was based on the common

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305 placement of the anode across these three experiments, and the general observation that cathodal
306 effects on cognitive function are rare (Jacobson, Koslowsky, & Lavidor, 2012). In that case,
307 differences in cathode location may be relatively unimportant, and need not prevent pooling across
308 studies. However, because we cannot entirely exclude some contribution of cathodal location to our
309 main results, we ran a further pooled analysis using the left anodal stimulation conditions of
310 experiments 1 and 2 only, which share a supraorbital cathode location, but excluding experiment 3.
311 This analysis again found that anodal stimulation of putative left AG significantly reduced the
312 perceptual shift of tone toward action compared to sham ($t(31)=2.45$, $p=0.02$, $d=0.35$), but had no
313 effect on action binding ($t(31)=-1.48$, $p=0.15$, $d=0.32$).

314 To investigate the generality of the anodal AG effect across experiments, we performed a mixed
315 ANOVA with a between-subject factor of experiments (1, 2 or 3), and a repeated-measures factor of
316 stimulation type (anodal left AG vs. sham). The main effect of stimulation type ($F(1, 43)=10.7$,
317 $p<0.01$, $\eta^2=0.20$) recapitulating the pooled t-test reported above. There was no significant main effect
318 of experiment ($F(2, 43)=0.80$, $p=0.45$, $\eta^2=0.04$). Importantly, there was no hint of interaction between
319 experiment and stimulation ($F(2,43)=0.96$, $p=0.39$, $\eta^2=0.04$).

320 Our main inferences above are based on comparing experimental stimulation with sham. We therefore
321 additionally investigated whether sham stimulation had different effects in the three experiments. We
322 found no significant difference among the sham conditions for the 3 experiments for action binding
323 ($F(2,43)=2.20$, $p=0.12$), or tone binding ($F(2,43)=1.10$, $p=0.33$).

324 **4. Discussion**

325 4.1. Stimulation-induced modulation of the left parietal cortex

326 We performed a series of three tDCS experiments to investigate the neural circuits responsible for the
327 sense of agency, as measured by the perceptual association between the time of a voluntary action and
328 the time of a resulting auditory tone. We found a significant decrease in the binding of outcomes
329 towards actions after anodal stimulation of the putative left AG (Experiment 1). Anodal stimulation of
330 the left DLPFC also decreased action and tone binding compared to sham. DLPFC affected tone

331 binding as much as AG stimulation, but its effects were less consistent across participants.

332 Nevertheless, our discriminant analysis showed a significant effect of DLPFC stimulation compared
333 to sham, when action and tone binding were considered together.

334 Our tDCS stimulation of putative AG could have widespread effects across the inferior parietal cortex
335 (IPC), since tDCS has quite low spatial specificity. For example, anterior parts of the IPC may also be
336 affected. IPC is routinely activated in neuroimaging studies when participants judge whether their
337 own action, or some other cause, is responsible for a specific sensory event. In a study by Farrer and
338 Frith (2002), the IPC area was more active when participants attributed a visual event to another
339 person, rather than to themselves. Similarly, a PET study (Farrer et al., 2003) observed that neural
340 activity in IPC increased with the level of discrepancy between the executed and the observed action
341 on the screen. In an fMRI study (Farrer et al., 2008), the subjective feeling of loss of control
342 correlated with BOLD response in the AG, as did the awareness of temporal discrepancy between
343 action and feedback. The authors of those studies suggested that AG houses the comparison between
344 the efference copy of the intended action and the actual sensory outcome. Any mismatch between
345 these signals will then give rise to the explicit awareness of non-agency, or an external source of
346 action.

347 Our overall results are consistent with this view. We found that anodal stimulation of the putative AG
348 *decreases* intentional binding, our proxy measure for agency. Anodal stimulation is generally thought
349 to *increase* the activity of the cortical region immediately under the electrode. However, AG
350 activation is routinely associated with *lack of agency*, rather than with experience of positive agency
351 (Farrer & Frith, 2002; Farrer et al., 2008; Sperduti et al., 2011). Therefore, excitation of a neural
352 substrate of non-agency might be expected to *decrease* intentional binding. The conventional polarity-
353 specific (anode-boosting, cathode-suppressing) framework of tDCS was developed on the basis of
354 effects in primary motor cortex stimulation (Nitsche & Paulus, 2000). Its applicability to non-primary
355 areas and cognitive processing has recently been questioned (Horvath, Forte, & Carter, 2014).
356 Nevertheless, our findings are broadly compatible with the conventional polarity-specific view.

357 4.2. Stimulation-induced modulation of the left frontal cortex

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3 358 Since DLPFC is normally thought to *facilitate* intentional action, one may question why prefrontal
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5 359 anodal tDCS did not *increase* intentional binding. Rowe et al., (2010) questioned whether DLPFC
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7 360 played any important role in initiation of simple voluntary actions, such as those tested here, and
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9 361 suggested a role in monitoring sequential action patterns instead. Fink et al., (1999) observed
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11 362 activation of DLPFC using PET when an intentional action and its sensory outcome were
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13 363 incompatible. Anodal tDCS over DLPFC might correspond to an increased coding for action-outcome
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15 364 conflict, even though our task did not explicitly manipulate action-outcome compatibility. Our
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17 365 discriminant analysis found some evidence consistent with this interpretation. However, this effect
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19 366 was investigated in only one experiment, and achieved statistical significance in multivariate analysis,
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21 367 but not in univariate analyses of action binding and tone binding separately. Therefore, further
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23 368 research is required before a strong statement about frontal tDCS effects on sense of agency can be
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25 369 made.

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31 370 4.3. Polarity-specific effects of tDCS

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34 371 Experiment 2 aimed to investigate whether parietal stimulation effects were polarity-specific. On one
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36 372 model, tDCS would simply add neural noise, irrespective of polarity. On another model, anodal
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38 373 stimulation would upregulate putative non-agency coding in AG, while cathodal stimulation should
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40 374 down-regulate it. The result of anodal left AG stimulation in experiment 2 followed the expected
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42 375 trend for tone binding, but did not reach statistical significance. Replication of statistically significant
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44 376 results is an important and controversial issue in modern neuroscience (Cumming, 2005). All effects
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46 377 measured in experiments represent a combination of the underlying ‘true’ effect, and noise.
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48 378 Importantly, when a nonzero true effect indeed exists, but is modest in size, it is quite likely for the
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50 379 effect to reach statistically significant levels in one study, but not in another. Thus, absence of a
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52 380 significant anodal tDCS effect in experiment 2 does not prove that no true effect exists: we return to
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54 381 this point later.

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382 Experiment 2 found no significant difference between cathodal and sham stimulation, although we
383 had predicted that cathodal stimulation might enhance intentional binding. Although inhibitory
384 cathodal effects on motor function are well established, a recent review of 34 studies found that
385 cathodal inhibitory effects on cognitive function are rare (Jacobson, Koslowsky, et al., 2012). Another
386 possible reason for the absence of any significant cathodal AG effect in Experiment 2 could be the
387 placement of the anode electrode on the supraorbital area. This location is standard for tDCS studies
388 of action (Nitsche et al., 2008). However, it causes a strong current density close to the frontopolar
389 and prefrontal areas, where the anode is located. These areas may also contribute to intentional action
390 (Brass & Haggard, 2007). Thus, our montage for cathodal stimulation of AG in experiment 2 involved
391 anodal stimulation at a frontopolar site, which may not be strictly neutral for sense of agency. Future
392 studies could address this issue by using extracephalic cathode placement.

25 393 4.4. Hemispheric specialisation of the sense of agency

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394 Experiment 3 avoided the potential confound of frontopolar stimulation using a biparietal montage.
395 This produces a higher current density in a small region surrounding the electrodes (Cohen Kadosh et
396 al., 2010; Nathan, Sinha, Gordon, Lesser, & Thakor, 1993), compared to the conventional supra-
397 orbital location. This might result in a more focal stimulation. More importantly, the biparietal
398 montage excludes the possibility that the significant effects of anodal AG stimulation in experiments
399 1 and 2 were in fact caused by cathodal frontopolar stimulation. Specifically, if the effects in
400 experiments 1 and 2 were merely due to cathodal frontopolar stimulation, then no effect of stimulation
401 should be found in experiment 3. The biparietal montage also allowed us to investigate lateralisation
402 of agency by varying both tDCS polarity and the hand used for action. Similar approaches have been
403 used previously in other studies (Bardi, Kanai, Mapelli, & Walsh, 2013; Jacobson, Goren, Lavidor, &
404 Levy, 2012).

405 The results of the third experiment replicated our previous findings. Anodal stimulation of putative
406 left AG significantly decreased tone binding compared to both sham and cathodal stimulation of the

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2 407 same area. The tDCS effect was statistically equivalent whether the action was made with the left or
3 408 the right hand. No effects were observed with anodal stimulation of the putative right AG.

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5 409 Experiment 3 does not support the alternative interpretation of experiments 1 and 2 based on a
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7 410 putative cathodal frontopolar stimulation. In contrast, experiment 3 supports the interpretation of an
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9 411 anodal left AG effect. We cannot conclusively rule out some contribution of frontopolar stimulation to
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11 412 our results, but we can rule in a specific contribution of the left AG.

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15 413 Experiment 3 adds several important elements to the previous studies. First, it demonstrates an
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17 414 involvement of AG in a task involving randomised, stimulus-driven selection between alternative
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19 415 actions, as opposed to mere repetition of a simple action. Second, it suggests that left, but not right
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21 416 AG is responsible for action-outcome binding for actions made by either hand. We found no
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23 417 interaction between stimulation and hand used for action. Previous neuroimaging studies have
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25 418 reported activation corresponding to non-agency judgements in both left and right AG. Interestingly,
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27 419 right AG activations appeared to dominate (Farrer et al., 2003; Farrer & Frith, 2002; Farrer et al.,
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29 420 2008), in contrast to our finding. However, in a more recent fMRI study, Lee & Reeve, (2013)
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31 421 reported higher activity in the left AG during non-self-determined behaviour, consistent with our
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33 422 hypothesis in Experiment 1 that anodal AG stimulation activates a neural code for ‘non-agency’.
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35 423 Finally, hemispheric specialisation of agency could plausibly depend on the task used, and the type of
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37 424 agency judgement. Previous neuroimaging studies generally used explicit judgements of agency, and
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39 425 often used complex manual actions with visual feedback (Farrer & Frith, 2002; Farrer et al., 2008;
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41 426 Sperduti et al., 2011). We are not aware of any neuroimaging study investigating the hemispheric
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43 427 lateralisation of low-level implicit measures of agency.

44 428 4.5. Limitations

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49 429 The results of experiment 3 by themselves could not distinguish between an effect of anodal
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51 430 stimulation of the putative left AG from an effect of cathodal stimulation of the putative right AG.
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53 431 However, this result does allow us to exclude a model in which tDCS simply acts to increase neural
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55 432 noise, irrespective of polarity. Moreover, our experiment 1 found some evidence of a left-hemisphere

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433 anodal tDCS effect, while our experiment 2 found no evidence of any cathodal effect (though in the
434 left hemisphere, rather than the right). Cathodal stimulation effects in cognitive tasks are reported to
435 be weak (Jacobson, Koslowsky, et al., 2012). Therefore, we provisionally favour an interpretation of
436 experiment 3 based on a left parietal anodal effect, rather than a right-hemisphere cathodal effect.
437 Further research would be required to draw a definitive conclusion.

438 Our study is further limited because we did not control for cases of crossmodal binding in the absence
439 of active movement. Therefore, we cannot exclude the possibility that AG stimulation influenced
440 some general feature of time perception, as opposed to temporal processing specific to agency.
441 However, several studies have shown stronger binding between voluntary actions and outcomes than
442 between other, similarly paired, events, including involuntary movements and outcomes (Engbert,
443 Wohlschläger, Thomas, & Haggard, 2007; Haggard et al., 2002) or pairs of sensory stimuli (Haggard,
444 Aschersleben, Gehrke, & Prinz, 2002; Haggard, Martin, Taylor-Clarke, Jeannerod, & Franck, 2003).
445 Moreover, other studies have investigated effects of parietal tDCS on time perception in general, in
446 the absence of action: and these studies found no effect (Woods et al., 2014). Thus, the weight of
447 other studies suggests that the intentional binding phenomenon reflects a distortion of perceptual
448 timing that is, at least partly, specific to voluntary action.

449 450 4.6. Dissociation between action binding and tone binding

451 Anodal stimulation over putative left AG was a common condition in all 3 experiments. Accordingly,
452 we could perform a pooled analysis of intentional binding results to compare this to the sham
453 stimulations that were also included in each experiment. This analysis showed a highly significant
454 reduction in tone binding with anodal stimulation of the putative left AG. We found no overall effect
455 on action binding. Dissociations between action binding and tone binding have been reported
456 previously (Wolpe et al., 2013), so it is possible that left parietal cortex is concerned primarily with
457 tone binding, rather than with action binding. This conclusion would be consistent with previous
458 studies suggesting that the AG processes mismatches in action outcomes (Farrer et al., 2008). On the
459 other hand, recent studies of explicit agency judgement suggest that AG also processes prospective,

1 460 premotor information arising during action selection (Chambon, Moore, & Haggard, 2014; Chambon
2 461 et al., 2013).

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5 462 Both online prospective and retrospective processes contribute to the intentional binding phenomenon
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7 463 (Moore and Haggard, 2008). The experimental design used here cannot identify the independent
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9 464 contribution of each process. However, binding of action towards outcome may rely more on
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11 465 prospective processes during action selection, while perceptual shift of outcome toward action may
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13 466 depend on retrospective, more inferential processes, triggered by reafferent signals about action
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15 467 outcome (Chambon, Moore, & Haggard, 2014). Future studies may address this issue by designing
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17 468 new paradigms which dissociate prospective and retrospective components of agency and examine the
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19 469 role of dLPFC and AG in each of these components.
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22 23 24 470 4.7. Conclusion and clinical implications

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27 471 Sense of agency is an important and distinctive feature of human voluntary action. We used a causal
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29 472 intervention (tDCS) and an implicit perceptual measure of sense of agency (intentional binding) to
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31 473 examine the role of different brain areas in sense of agency. Anodal stimulation of parietal cortex
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33 474 consistently reduced the binding of tones towards actions. We hypothesised that the angular gyrus
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35 475 might contribute to the sense of agency by monitoring the linkage of actions to outcomes, or,
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37 476 alternatively and equivalently, failures of such linkage. Anodal stimulation of this area may
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39 477 correspond to artificial boosting of a mismatch detection process.
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43 478 Sense of agency is altered following several classes of psychiatric and neurological disorders. In
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45 479 particular, patients with apraxia following lesions to the left parietal fail to recognise the source of a
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47 480 viewed manual gesture (Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999). This deficit is
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49 481 formally equivalent to an overestimation of agency in an explicit judgement task, consistent with
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51 482 damage to a neural centre detecting mismatches. The posterior form of ‘alien hand syndrome’ is also
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53 483 associated with contralateral parietal lesions (e.g., (Kloesel, Czarnecki, Muir, & Keller, 2010)).
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55 484 Interestingly, these patients show involuntary and spontaneous movements of the contralateral limb,
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57 485 but may correctly perceive that they are not agents over these actions. The capacity for voluntary
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2 486 movement is often preserved. Quantitative assessment of the implicit sense of agency in parietal
3 487 patients would be of considerable value in understanding the neural basis of sense of agency.

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8 489 **Competing interests**

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11 490 The authors declare no competing financial interests.

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13
14 491 **Acknowledgements**

15
16
17 492 This work was supported by the European Research Council Advanced Grant HUMVOL. PH was
18 493 additionally supported by a Professorial Research Fellowship from the ESRC. The funding sources
19
20 494 had no involvement, in study design; in the collection, analysis or interpretation of data; in the writing
21
22 495 of the report; or in the decision to submit the article for publication.

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24
25 496 We thank Andrea Desantis for helpful comments during the preparation of the manuscript.

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669 **Captions**

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3 670 Fig. 1. Schematic of intentional binding. Action and tone shifts are measured by subtracting each
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5 671 participant's mean judgement error in baseline conditions from judgement error in operant conditions.
6
7 672 These shifts serve as measures of intentional binding. Vertical bars and thin arrows represent mean
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9 673 judgement errors in each condition. Thick arrows represent binding effects. See text for full
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11 674 explanation.

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15 675 Fig. 2. A. tDCS montage and study design (anode +, cathode -). See text for explanation. In
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17 676 Experiment 1, to control for the cutaneous sensation of all three locations, all sponges were kept in
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19 677 place across the three sessions. However, only two of them were actually functioning in each session.
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21 678 B. Stimulation protocol. The order of conditions was randomised within each session.

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25 679 Fig. 3. Intentional binding in Experiment 1. A) The dashed line indicates the perceived time of either
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27 680 action or tone in the corresponding baseline condition. A separate baseline condition was used for
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29 681 each session, and differences in baseline values across sessions have been removed for display
30
31 682 purposes. Binding effects are drawn to scale, and values are in milliseconds. B) Mean binding effects
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33 683 in ms. The sign of tone binding effects has been inverted to allow for comparison with action binding.
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35 684 Error bars show standard error of the mean. * $p < 0.05$.

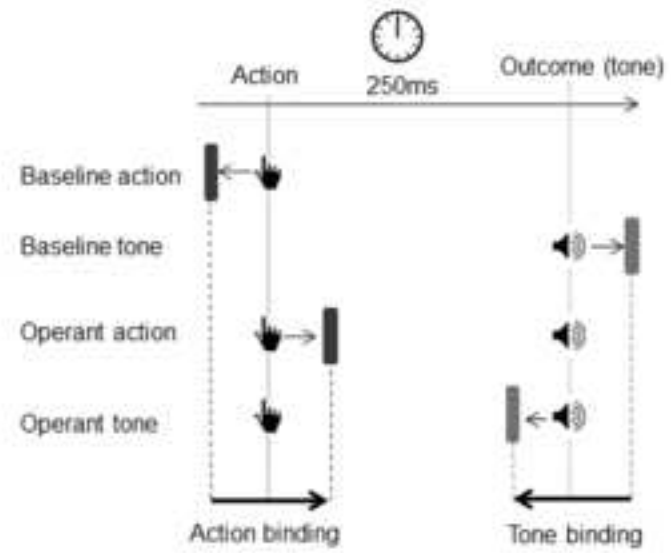
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39 685 Fig. 4. Intentional binding in Experiment 2. Format as in Fig. 3.

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42 686 Fig. 5. Intentional binding in Experiment 3. Format as in Fig. 3.

*Highlights

- Effects of tDCS on implicit measures of sense of agency were measured.
- Anodal stimulation of the left angular gyrus decreased 'intentional binding'.
- Cathodal stimulation had no effect.
- The left angular gyrus plays a key role in the experience of agency.

Figure1
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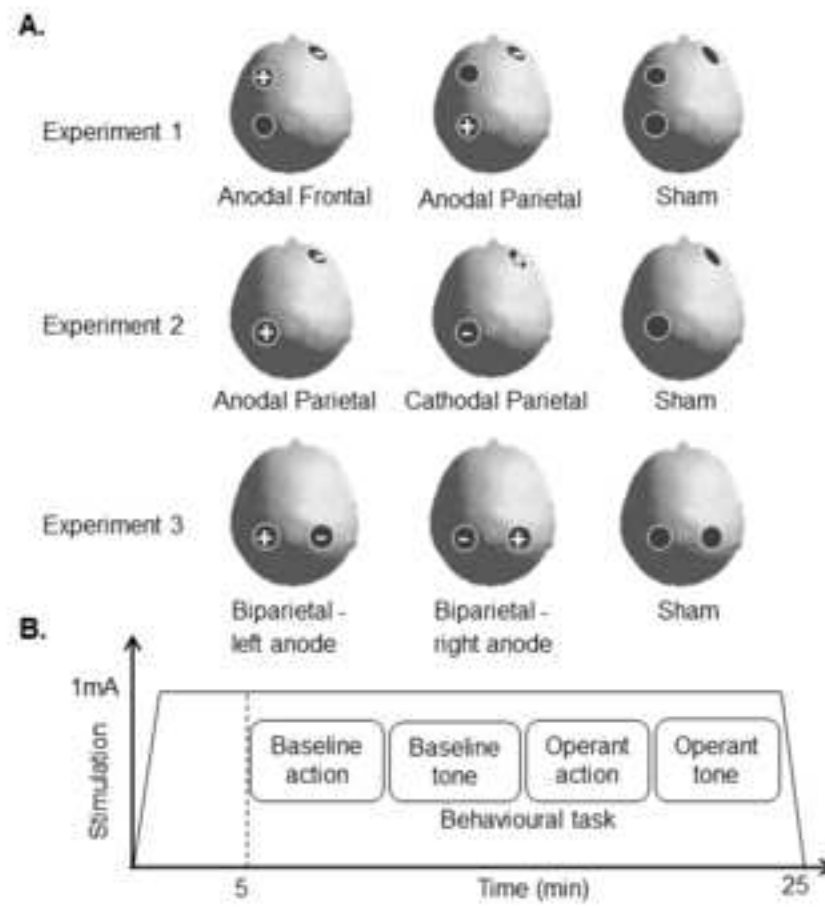


Figure3

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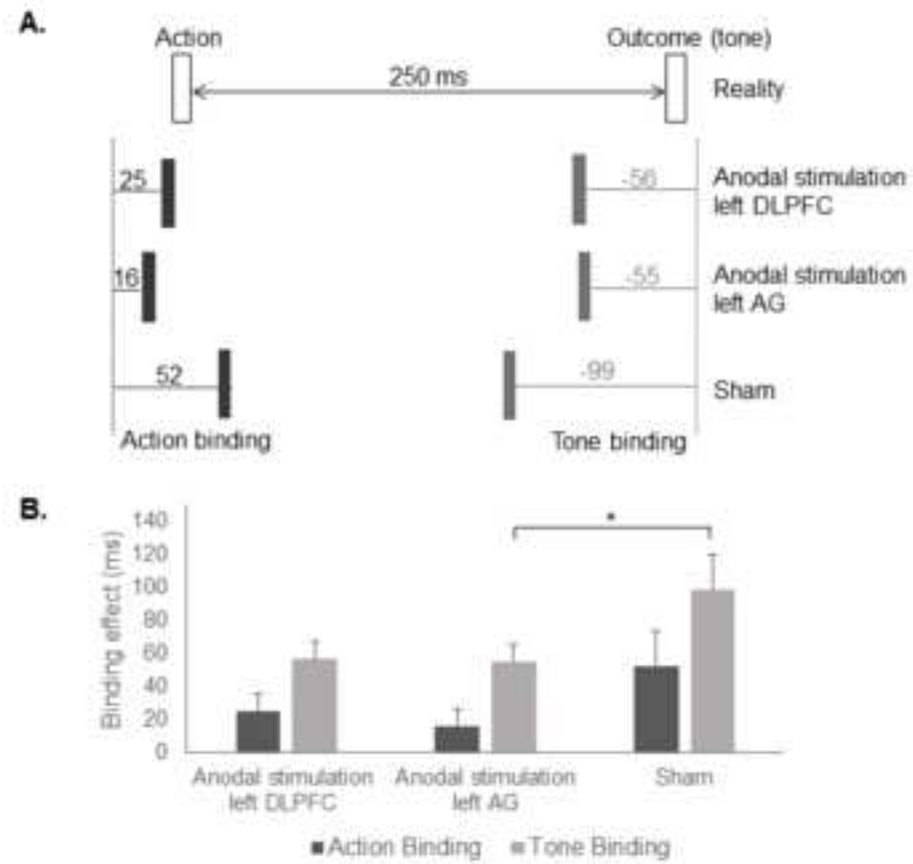


Figure4

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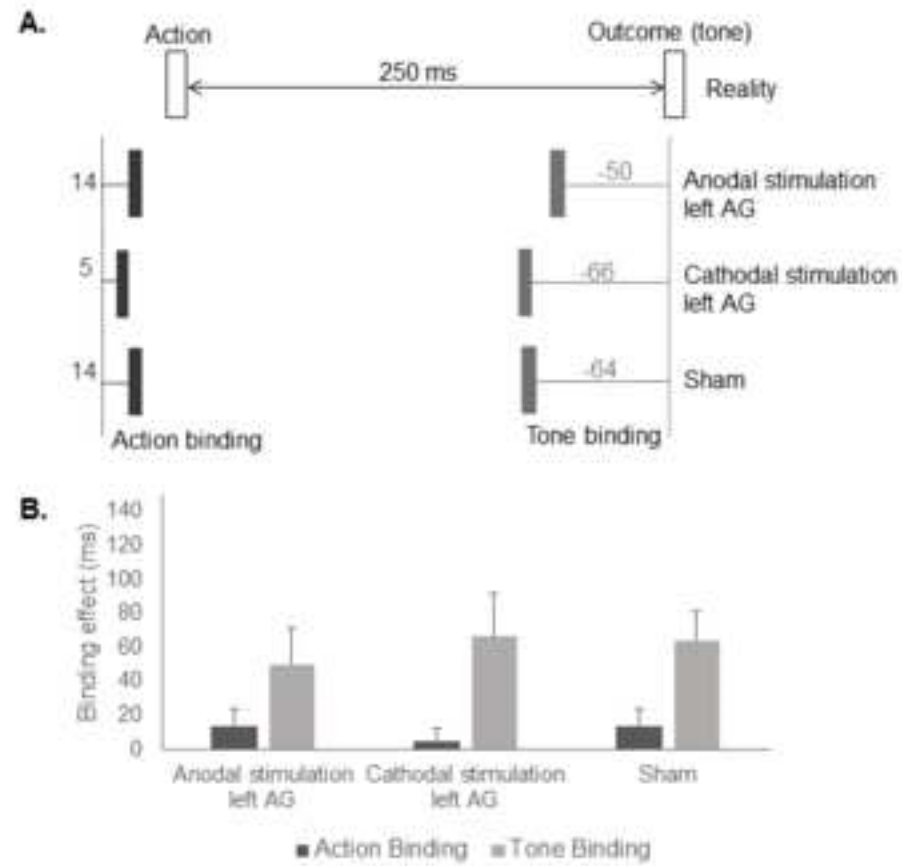
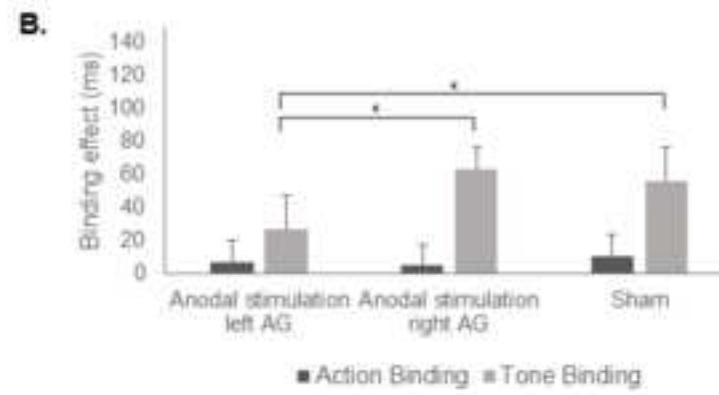
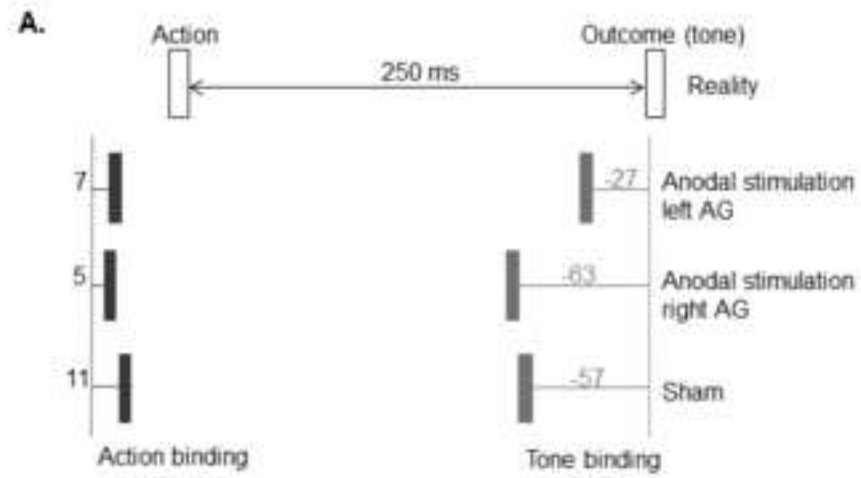


Figure 5

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