The role of the temporoparietal junction in implicit and explicit sense of agency.

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Abstract

The experience of being in control of one's actions and outcomes is called the sense of agency. This is a fundamental feature of our human experience, and may underpin important social functions such as morality and responsibility. Sense of agency can be measured explicitly, by asking people to report their experience, or implicitly by recording the perceived time interval between actions and outcomes (intentional binding). The current studies used transcranial direct current stimulation to assess the role of left and right temporal-parietal junction in both implicit and explicit sense of agency. Participants were informed that they could control the volume output of the computer with one of two buttons. Participants experienced reduced sense of agency when the outcome was inconsistent with their action. However, temporal binding did not differ between congruent and incongruent action-outcomes. The modulation of explicit agency ratings by action-outcome congruency was significantly reduced by right TPJ stimulation (experiment 1) but not left TPJ stimulation (experiment 2). Implicit agency was not affected in either stimulation condition. These findings are discussed in terms of the possible neural mechanisms of implicit and explicit sense of agency.

Keywords: Agency; intentional binding; forward model; comparator; tDCS.

Introduction

Sense of Agency refers to the feeling of being in control of your actions, and through them, events in the world (Haggard, 2017). Previous research robustly shows that when outcomes are inconsistent with our expectations, we experience a reduced sense of agency. Numerous neuroimaging studies have implicated the temporal parietal junction (TPJ) in detecting the mismatch between actions and visual outcomes (Farrer et al., 2003; Farrer & Frith, 2002; Nahab et al., 2011; Schnell et al., 2007; Yomogida et al., 2010). Similarly, this region has been implicated in implicit measures of agency, such as intentional binding (Khalighinejad & Haggard, 2015). The current studies aimed to provide new evidence for the role of parietal comparator processes in implicit and explicit sense of agency.

One key marker for the sense of agency is the consistency between the intended and observed outcome of an action (Wegner 2002; Sato & Yasuda, 2005; Sato 2009). One influential theory suggests that this discrepancy is determined by comparing predictions generated by a forward model (Wolpert 1997), with the observed consequences of an action. Although originally envisaged as a model of motor control, this comparator model has also been used to explain agency processing (Blakemore, Wolpert & Frith, 2002).

Investigating the neural underpinnings of this comparator process has consistently shown greater activation of the temporoparietal junction (see Sperduti et al., 2011), when there is a mismatch between predicted and observed action outcomes. Greater brain activation has been reported for both temporal (Balslev et al., 2006; Farrer et al., 2008; Leube, et al., 2003; Matsuzawa et al., 2005; Nahab et al., 2011; Tsakiris et al., 2010; Yomogida et al., 2010) and spatial discrepancy (Farrer et al., 2003; Farrer & Frith, 2002; Nahab et al., 2011; Schnell et al., 2007; Yomogida et al., 2010). However, the precise nature of this activation remains unclear. For instance since these regions are a core part of the exogenous attention network (Corbetta & Shulman, 2002), this activation during agency processing may reflect reallocation of attention driven by this conflict, rather than sensorimotor conflict per se. The current study aims to provide causal evidence for the role of TPJ in agency processing, by using brain stimulation. One previous study (Chambon et al., 2014) has shown the TMS to left inferior parietal lobe disrupts prospective agency judgments, but no previous research has used brain stimulation to influence comparator based agency judgements.

While research on explicit sense of agency finds consistent evidence of TPJ based comparator processes, research on implicit agency is less clear. Implicit agency is typically assessed using the intentional binding paradigm (Haggard, Clark, & Kalogeras, 2002), whereby people are asked to estimate the time of actions and action outcomes using a rotating Libet clock (Libet et al., 1983). When comparing these time judgements to baseline conditions including only actions or sensory events, actions and outcomes appear to be bound together. More specifically, actions that produce sensory outcomes are experienced later, while the outcomes themselves are experienced earlier. Although these implicit agency measures are typically explained in terms of comparator processes, this interpretation has recently been challenged (Hughes et al., 2013). Indeed, one previous study failed to show any modulation of intentional binding dependent on action outcome predictability or action outcome congruency (Desantis et al., 2013). However, outcomes in this study were high or low pitch tones, which had no meaningful association with the actions that produced them.

In contrast, Ebert and Wegner (2010) showed that both explicit judgements of agency and intentional binding were greater for congruent action outcomes. They asked participants to move a joystick either towards themselves or away from themselves. These movements triggered the objects presented on screen to become either larger or smaller. As such, the outcomes in this study were more intuitively linked to the actions –

participants either pulled objects towards themselves or pushed them away. This is in contrast to most other binding studies (including Desantis et al., 2013) that use simple tones as action outcomes. In such studies, participants are normally trained to arbitrarily associate one action, with a particular outcome. As such, one possibility is that comparator processes might only influence binding in tasks where the action outcome is more intuitively linked to the action.

Neuroscientific evidence for comparator based processes influencing intentional binding is also mixed. One previous neuroimaging study showed that activity in supplementary motor area and not angular gyrus correlated with the magnitude of intentional binding (Kuhn et al., 2013). However, one recent tDCS study found that stimulation of left TPJ but not right TPJ reduced the magnitude of intentional binding, possibly because tDCS boosted mismatch detection in TPJ (Khalighinejad & Haggard, 2015). Nonetheless, in that particular task (as is the case in most studies on intentional binding) no mismatch ever occurs, as only one action and one outcome was used on every trial. The current study will assess whether tDCS stimulation of TPJ influences the degree to which binding might be modulated by the match or mismatch between the predicted and observed consequences of an action.

We report data from two experiments investigating the role of right (experiment 1) and left (experiment 2) TPJ on both explicit and implicit (intentional binding) measures of agency. Participants pressed one of two buttons (up or down) to trigger loud or quiet tones. Implicit agency was assessed on each trial by asking participants to report the time of the outcome using the position of the clock hand on a Libet clock. Explicit agency was also assessed on each trial using a 7 point lickert scale (Ebert & Wegner, 2010). If intentional binding is driven by comparator processes, we would expect greater binding for congruent action-outcomes. We would also predict TPJ stimulation (particularly lTPJ; Khalighenejad & Haggard, 2015) to modulate the degree to which this congruency influences binding. In line with previous neuroimaging studies, we expect TPJ (particularly rTPJ) stimulation to influence the degree to which action-outcome congruency influences explicit agency ratings.

Methods

Participants

In total, 65 participants were recruited from the University of Essex. Participants confirmed before the experiment that they did not have a history of seizure, fainting, epilepsy or any neurological or psychiatric disorder or any metallic object in their head that may be affected by stimulation. Experiment 1 included 40 participants (16 males mean age = 25.4; SD = 7.4), and experiment 2 included 25 participants. Three participants were excluded from experiment 2 by the Smirnoff-Grubbs test for outliers (Grubbs, 1950), leaving 22 participants (10 male, mean age = 24.3 ; SD = 4.05). Ethical approval was provided by the Department of Psychology Neuromodulation Committee.

Experimental Design and Procedure

Participants completed the same agency task in both experiments. The behavioural task was presented using the Psychtoobox (Brainard, 1997). Sense of Agency was measured using both a temporal measure of the outcome (intentional binding) and an explicit judgement of agency. Temporal judgements were provided using a Libet Clock, rotating at one revolution every 2800 ms. In the operant block, participants were asked to press either one of two buttons (T or G on a UK QWERTY keyboard). They were informed that the buttons would trigger a tone to be presented, and that the up key (T) would serve to increase the volume of the computer and the (G) would decrease the volume. As such, participants were guided to expect a loud tone following an up button press and a quiet tone following a down button press. 500 Hz tones of 100ms duration were presented via the speaker of an apple iMac computer, with an approximate volume of 80dB and 70dB for the loud and quite tones respectively. Half the trials were congruent with the instructed stimulus response mapping (e.g. a loud tone following an up press) and half were incongruent (e.g. a quiet tone following an up press). Following the presentation of the tone (250ms after the participant's action), the clock continued to rotate for a random period between 1 and 3 seconds. Then, after a blank screen of 300ms the clock reappeared without the clock hand, and participants were asked to report the time at which the tone was presented using any whole number between 0 and 59. Their response appeared under the clock as they typed, and they could delete any errors, before confirming their answer by pressing the spacebar. Next, participants were asked to provide an explicit judgement of the whether they felt like the tone was caused by them pressing the button on the keyboard. They were presented with a 7-point scale on the screen with the anchors "not at all" "somewhat" and "very much" over points 1, 4, and 7 respectively. They responded with the letters 1 to 7 on the keyboard, and pressed the spacebar to confirm their response. Following an inter-trial interval of 0.7 to 1.1 seconds, then next trial began with a rotating Libet clock starting in a random position.

In the baseline blocks, tones were triggered by the computer between 3 and 7 seconds after trial onset (following a normal distribution). Half of the sounds were quiet and half were loud. As in the operant blocks, participants were asked to judge the timing of the sound using the Libet clock. Participants completed six practice trials of the baseline condition, followed by a single block of 40 trials (20 loud and 20 quiet tones). Next, they completed six practice trials of the operant condition followed by 2 blocks of 40 trials (20 congruent and 20 incongruent). Intentional binding was calculated as the difference in the perception of the time of the tone in the operant condition compared to the baseline condition (relative to the actual time of the sound).

Positive values reflect an earlier experience of the tone in operant blocks. Binding was calculated separately for congruent trials and incongruent trials.

TDCS Protocol

Both experiments used offline tDCS stimulation. Experiment 1 used the same protocol previously used to modulate self-other distinction (Santiesteban *et al*., 2012). The anodal electrode was placed over the right TPJ, centered on electrode CP6 in the electroencephalography 10/20 system, with the reference mastoid placed over the vertex (Cz). Electrodes were placed into saline soaked sponges 35cm2 in size and delivered by a battery powered HDCstim stimulator. In the stimulation condition, a weak electrical current (1 MA) was delivered to the participant through these electrodes for 20 minutes, prior to completing the agency task. In the sham condition, participants experienced 30 seconds of stimulation, to induce the sensation of stimulation, but this was ramped down to zero for the rest of the 20-minute period. Evidence has shown that stimulation of 13 minutes sustains cortical excitability for up to 90 minutes after stimulation (Nitsche & Paulus, 2001) and the behavioural task lasted around 25-40 minutes depending on the participant. Thus, the protocol of the stimulation in this experiment should have been sufficient to maintain the effects of stimulation during the course of the behavioural task. Experiment 1 used the same stimulation protocol except that the anodal electrode was placed over the left TPJ (electrode position CP5). Experiment 1 used a between-subjects design, with 20 participants in each stimulation condition. Experiment 2 used a repeated measures design in which all participants completed one stimulation session and one sham session (order counterbalanced, separated by 24 hours).

Data Analysis

Each experiment had two dependent variables, the intentional binding score, and the mean agency rating. Each experiment also included two factors: stimulation condition (stimulation and sham), and congruency of the action-outcome (congruent versus incongruent. Experiment 1 was analysed using a mixed ANOVA (where stimulation condition was a between-subjects factor), while experiment 2 was analysed using a repeated measures ANOVA. Significant effects on the omnibus tests were followed up by *t*-tests.

Results

Experiment 1

ANOVA on agency ratings revealed a significant main effect of congruency (F (1,38) = 32.5; p < .001; η_p^2 = .46), with participants experiencing a greater sense of agency for congruent outcomes (M = 5.3; SEM = .18), compared to incongruent outcomes (M = 3.8; SEM = .26). There was no significant main effect of stimulation group (F (1,38) < 1; η_p^2 = .02). However, there was a significant interaction between congruency and stimulation group (F (1,38) = 7.2; p = .011; η_p^2 = .16). Figure 2 shows that effect of congruency on agency ratings is smaller in the anodal stimulation condition. Follow-up tests confirmed a significant congruency effect in the sham condition (t (19) = 5.23; p < .001; Cohen's d = 1.207), and a significant, but reduced effect in the anodal condition (t (19) = 2.53; p = .021; Cohen's d = .574). Independent samples t-tests showed no significant difference between groups on congruent trials (t (38) = 1.1; p = .27; Cohen's d = .354), and a near significant difference on incongruent trials (t (38) = 1.99; p = .054; Cohen's d = .630). Overall these findings show that tDCS stimulation of rTPJ significantly reduced the degree to which participants' agency ratings were modulated by whether the action outcome was consistent with their expectation.

Since we did not record individual differences in the use of the agency rating scale prior to our tDCS manipulation (i.e. a baseline measure of agency), the effects we observed could stem from an allocation bias, whereby random group allocation was ineffective in adequately controlling for any such individual difference. To assess this possibility, we randomly reallocated each participants' agency ratings for the two conditions (congruent and incongruent) to two different groups, and conducted a mixed ANOVA (congruency by group) to look for the significant congruency by group interaction observed in our data. We ran 10,000 permutations, re-randomising the group allocations on each permutation, conducting the ANOVA, and recording the *F* value and *p* value for the interaction. A significant (p <. 05) interaction was revealed in 471 (< 5%) of these tests. Furthermore, on only 92 tests (< 1%) was the *F* value at or above the observed value for this interaction in our data (7.1598). This strongly suggests that the effect we observed was a genuine effect of our tDCS manipulation, rather than group allocation not adequately controlling individual differences in the use of the agency rating scale.

Binding was observed on both congruent and incongruent trials, in both stimulation conditions, such that timing estimates were significantly earlier in the operant condition compared to the baseline condition (all at $p < .001$). ANOVA on binding scores revealed no significant effect of congruency (F (1,38) = 1.2; $p = .28$; η_p^2 = .03), no effect of stimulation group ($F < 1$; $\eta_p^2 < .01$), and no stimulation group by congruency interaction ($F < 1$; $\eta_p^2 < .01$). These findings confirm that stimulation of rTPJ did not influence intentional binding.

Discussion

In line with our predictions, experiment 1 showed that stimulation of right TPJ influences explicit agency ratings, but not intentional binding. Given recent evidence that left TPJ stimulation influences the amount of binding (Khalighinejad & Haggard, 2015), experiment 2 stimulated lTPJ while measuring both implicit and explicit sense of agency.

Experiment 2

ANOVA on agency ratings revealed a significant main effect of congruency (F (1,21) = 25.1; $p < .001$; $\eta_p^2 = .55$), with participants experiencing a greater sense of agency for congruent outcomes (M = 5.76; SEM = .23), compared to incongruent outcomes (M = 3.8; SEM = .42). There was no significant main effect of stimulation group (F (1,21) < 1; $\eta_p^2 < .01$), and no significant congruency by stimulation group interaction (F (1,21) < 1; $\eta_p^2 < .01$). These findings suggest that stimulation of lTPJ has no effect on explicit agency ratings.

Binding was observed on both congruent and incongruent trials, in both stimulation conditions, such that timing estimates were significantly earlier in the operant condition compared to the baseline condition (all at $p < .001$). ANOVA on binding scores revealed no significant effect of congruency ($F < 1$; $\eta_p^2 = .04$), no effect of stimulation group ($F < 1$; $\eta_p^2 < .01$), and no stimulation group by congruency interaction (F (1,21) = 3.2; $p = .087$; $\eta_p^2 = .13$).

General Discussion

In line with previous neuroimaging studies (Farrer et al., 2003; Farrer & Frith, 2002; Nahab et al., 2011; Schnell et al., 2007; Yomogida et al., 2010) we found that stimulation of right TPJ influenced comparator-based judgements of agency. We found no effect of left TPJ stimulation on explicit agency ratings, confirming previous reports of a right lateralisation in comparator processes in inferior parietal regions (Balslev et al., 2005; Balslev et al., 2006; Farrer et al., 2008). Across two studies we found no effect of action outcome congruency on intentional binding, nor did we find any effect of tDCS stimulation of parietal regions in intentional binding. These findings support previous suggestions that intentional binding is not based on the comparison between predicted and observed action outcomes (Desantis et al., 2013; Hughes et al., 2013).

Although previous neuroimaging studies have reliably found rTPJ to be involved in comparator based agency judgements (Balslev et al., 2005; Balslev et al., 2006; Farrer et al., 2003; Farrer & Frith, 2002; Nahab et al., 2011; Schnell et al., 2007; Yomogida et al., 2010), the activation of these regions could be related to shifts of exogenous attention triggered by the unexpected action outcome (Corbetta & Shulman, 2002). By showing that electrical stimulation of right TPJ influenced the degree to which action-outcome mismatch feeds into agency, we provide novel evidence for the role of this region in comparator based agency judgements. The significant interaction between stimulation group and congruency in experiment 1 was driven by a reduced congruency effect in the anodal stimulation group compared to the sham stimulation condition. Since anodal stimulation is thought to increase the excitability of underlying brain tissue (Nitsche & Paulus, 2001), one might expect increased mismatch detection in this condition. One possible explanation for our findings is that in addition to increasing correct detection of incongruent outcomes, increase excitability of rTPJ could also increase the number of false alarms, resulting in an overall reduction in the sensitivity of mismatch processing. Alternatively, the effect in the current study could constitute a negative effect of tDCS. Indeed, previous evidence suggests that while tDCS stimulation of 13 minutes leads to increased cortical excitability, longer stimulation (26 minutes) can lead to decreases in cortical excitability (Monte-Silva at al., 2013). As the stimulation period (20 minutes) in the current study lies between these two values, it is possible that this could result in decreased cortical excitability.

Previous studies have shown inconsistent findings with regard to whether intentional binding is modulated by action outcome congruency. Desantis et al. (2013) found no modulation of binding dependent on action-effect predictability or action-effect tones. In contrast, Ebert and Wegner (2010) showed that intentional binding did vary dependent on whether the change in size of an object presented on the screen corresponded with the direction of their joystick movement. Despite using similarly intuitive action outcomes in the current studies, we observed no modulation of binding by congruency. The consistent modulation of explicit agency ratings confirms that participants did experience reduced agency for incongruent sounds. One possible explanation for this difference is that while the current study used the Libet clock to measure participants experience of the timing of the action outcome, Ebert and Wegner (2010) measured binding by asking participants to explicitly report the interval between action and outcome. Previous research shows that while transcranial magnetic stimulation to pre-supplementary motor area (pre-SMA) disrupts outcome binding, it does not influence action binding (Moore et al., 2010). Since pre-SMA seems to be involved in making predictions that feed into comparator systems (Waszak et al., 2012), this suggests that while outcome binding may be linked to forward model based comparator mechanisms, action binding is likely partially driven by postdictive processes. Crucially, the time estimation measure used by Ebert and Wegner (2010) cannot distinguish action and outcome binding, and therefore the congruency effects may be partially driven by postdictive processes (Hughes et al., 2013). In other words, in Ebert and Wegner's (2010) study participants explicit belief that they caused the outcome, might retrospectively influence them to give a shorter time estimate. The findings from the current study are consistent with the suggestion that outcome binding, measured by the Libet clock method is not generated by prediction based comparator mechanisms (Desantis et al., 2013; Hughes et al., 2013).

This conclusion is further supported by the observation that although TPJ stimulation influenced explicit sense of agency, it did not influence intentional binding. Given the wealth of research supporting the role of this region in comparator based agency processing (Farrer et al., 2003; Farrer & Frith, 2002; Nahab et al., 2011; Schnell et al., 2007; Yomogida et al., 2010), if intentional binding indeed recruits the same mechanisms, then tDCS stimulation to this region should have influenced intentional binding. Although the absence of an effect must be treated with some caution, the overall findings of the two studies do further question whether intentional binding is driven by comparator processes in parietal lobe. It is also worth noting that one previous study did observe significant modulation of binding following left but not right TPJ modulation (Khalighinejad & Haggard, 2015). Given the different paradigms and different stimulation protocols used in these studies it is difficult to speculate what the reason might be for these divergent results. Nonetheless, it is worth noting that in that study, as in almost all studies on binding (see Hughes et al., 2013) comparator mechanisms need not be invoked, since action outcomes were always the same (a 1000 Hz tone of fixed volume). As such, tDCS stimulation in those experiments might influence binding through some other mechanisms than comparator processes.

According to the preactivation account of intentional binding (Waszak et al., 2012), intentional binding comes about through preactivation of sensory brain regions coding for the predicted response. Under such an account this implicit measure of intentional binding need not invoke comparator processes in TPJ, as it is caused by the fact that stimuli that are predicted reach the threshold for conscious awareness earlier due to preactivation. As discussed above, most binding studies do not in fact require a comparison of predicted and observed action outcomes, since there is normally only one outcome. The current studies provide further evidence that in a situation where the task does invoke the comparator, intentional binding is not modulated by action-outcome congruency and is not influenced by brain stimulation. This is despite the fact that explicit ratings of agency varied dependent on action outcome congruency, and were modulated by stimulation of right TPJ. As such, the current findings fit with the idea that intentional binding is driven by preactivation of sensory brain regions rather than by an explicit comparison between predicted and observed action-outcomes.

The current studies provide novel evidence for the role of rTPJ in comparator-based agency judgements. These findings build on previous neuroimaging results by showing that electrical stimulation of rTPJ (but not lTPJ) modulates the degree to which action outcome mismatches inform the sense of agency. The absence of similar effects on intentional binding, suggests that this implicit measure of agency might be less dependent on these parietal-based comparator processes.

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Figure Legends

Figure 1: A schematic overview of the experimental design in the current studies. Participants pressed one of two keys on the keyboard to either increase or decrease the volume of the computer. A loud or quiet tone was presented 250ms after their button press. Participants were asked to report the time of the sound using a rotating clock. Next, they were asked to rate their sense of agency on the current trial. For full details and timings refer to text.

Figure 2: Agency and binding scores for experiment 1 (RTPJ) and experiment 2 (LTPJ) separately for congruent (dark grey) and incongruent (light grey) trials. * = $p < .05$ ** = $p < .001$. Error bars reflect standard error.