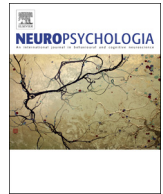




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The role of the temporoparietal junction in implicit and explicit sense of agency

Gethin Hughes

Department of Psychology, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, UK



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ABSTRACT

The experience of being in control of one's actions and their 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 temporoparietal 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, 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.

1. 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 temporoparietal junction (TPJ) in detecting the mismatch between actions and visual outcomes (Farrer et al., 2003; Farrer and 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 and 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 and 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 et al., 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 and 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 and 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 that TMS to left inferior parietal lobe disrupts prospective agency judgments, but no previous research has used brain stimulation to influence comparator-based agency judgments.

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 et al., 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

E-mail address: ghughes@essex.ac.uk.

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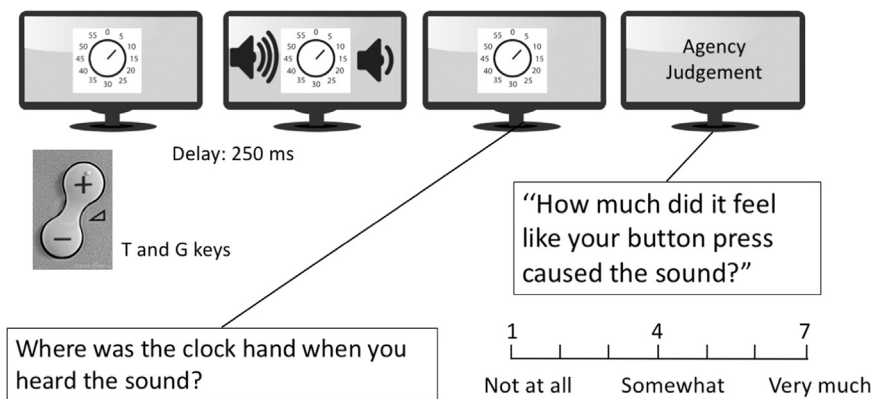


Fig. 1. A schematic overview of the experimental design in the current studies. Participants pressed one of two keys on the keyboard to either increase or decrease the volume of the computer. A loud or quiet tone was presented 250 ms after their button press. Participants were asked to report the time 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.

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., 2012). 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., 2012) 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 and 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 likert scale (Ebert and 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 ITPJ; Khalighinejad and 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.

2. Methods

2.1. 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 Smirnov-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.

2.2. Experimental design and procedure

Participants completed the same agency task in both experiments (Fig. 1). The behavioural task was presented using the psychophysics toolbox (Brainard, 1997) in Matlab (MathWorks). 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 100 ms duration were presented via the speaker of an apple iMac computer, with an approximate volume of 80 dB and 70 dB for the loud and quiet 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 (250 ms after the participant's action), the clock continued to rotate for a random period between 1 and 3 s. Then, after a blank screen of 300 ms 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 1–7 on the keyboard, and pressed the spacebar to confirm their response.

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