

Where is my Mind? Separating the Self from the Body through Perspective Taking

D.M.L. de Boer^{1,3*}, P.J. Johnston^{1,3}, G. Kerr^{2,3}, M. Meinzer^{4,5}, A. Cleeremans⁶.

Affiliations

¹ School of Psychology and Counseling, Faculty of Health, Queensland University of Technology, Kelvin Grove, Queensland 4059, Australia.

² School of Exercise and Nutrition Science, Faculty of Health, Queensland University of Technology, Kelvin Grove, Queensland 4059, Australia.

³ Institute of Health and Biomedical Innovation, Queensland University of Technology, Brisbane, Australia.

⁴ Centre for Clinical Research, The University of Queensland, Brisbane, Australia.

⁵ Department of Neurology, University Medicine Greifswald, Greifswald, Germany.

⁶ Consciousness, Cognition, and Computation Group (CO3), Centre for Research in Cognition and Neurosciences (CRCN), ULB Neuroscience Institute (UNI), Université libre de Bruxelles (ULB), Avenue F.D. Roosevelt 50, CP191, 1050 Brussels, Belgium.

*Correspondence to: debbie.boer@hdr.qut.edu.au

One Sentence Summary: The right Angular Gyrus is causally involved in spatiotemporal self-location (perspective-taking) that can be decoupled from the bodily self, explaining phenomena associated with disembodiment.

Abstract

Recent theories suggest that self-consciousness, in its most elementary form, is separate from the own body. Patients with psychosis frequently misattribute their thoughts and actions to external sources; and in certain out-of-body experiences, lucid states, and dreams body-ownership is absent but self-identification is preserved. We hypothesized that self-identification depends on inferring self-location at the right Angular Gyrus (perspective-taking). This process relates to the discrimination of self-produced signals (endogenous attention) from environmental stimulation (exogenous attention). We combined a Full-body Illusion paradigm with brain stimulation (HD-

tDCS) and found a clear causal association between right Angular Gyrus activation and alterations in self-location (perspective-taking). Anodal versus sham HD-tDCS resulted in: a more profound out-of-body shift (with reduced sense-of-agency); and a weakened ability to discriminate self from other perspectives. We conclude that self-identification is mediated in the brain by inferring self-location (perspective-taking). Self-identification can be decoupled from the bodily self, explaining phenomena associated with disembodiment.

Introduction

Recent theories suggest that self-consciousness, in its most elementary form, is separate from the own body (see discussion on *Minimal Phenomenal Selfhood* 1, 2). In out-of-body experiences the brain perceives the locus of the Self as being outside of the body (3); and in hallucinations and delusions thoughts and actions are frequently misattributed to external sources (see *psychosis* 4). Here, it is proposed that these forms of *disembodiment* arise by unusual right Angular Gyrus activation and failure of the brain to identify self-produced signals (resp. *exogenous vs. endogenous attention* 5, **Fig. 1**). To examine this hypothesis, we combined a full-body illusion paradigm with brain stimulation using high-definition tDCS. These paradigms manipulate body-ownership and offer a way to examine how (bodily) self-consciousness is constructed (1; for a critical review 6). In a typical full-body illusion people observe a virtual body a few feet in front of them through a Head-mounted Display. For a few minutes they see in front of them what they feel happening to them (e.g., back stroking). This leads people to identify with the virtual body and judge their spatial location to be closer to the external body than their actual location (7, 8). However, because of technical restrictions and safety issues, paradigms involving Head-mounted Displays are difficult to combine with existing neuroscience techniques. Due to this, the neural

mechanisms underlying such illusions remain understudied (for one study [9](#)). To address this problem, we developed a stereoscopic 3D-projection of a Full-body Illusion: video-captured images were LIVE-streamed to a computer and in real-time merged and projected onto a large screen. Unlike previous paradigms, this allowed us to simultaneously modify the brain function of healthy volunteers undergoing a full-body illusion and characterize the role of self-location, i.e., where someone experiences themselves to be. Previous studies have shown that electrical stimulation of the right Angular Gyrus induces out-of-body experiences ([10](#), [11](#) & Penfield in [3](#)); and hinders the recognition of self-produced signals and self-identification ([12-14](#); also see [15](#)). What connects these findings and the precise role of the right Angular Gyrus remains unclear.

The brain's ability to recognize and discriminate self-produced signals from external stimulation is tied to the process of sensory gating. Sensory information is transformed in the brain through a complex system of gating steps that filter out irrelevant noise and excessive sensory information ([16](#)). When you lift your arm, for instance, efference copies are generated. Efference copies are neural representations or 'copies' of motor commands that travel to the sensory cortex and attenuate feedback stemming from our own sensory systems (see also *comparator models* [17](#)). Sensory attenuation ([18](#)) thus informs the brain whenever it is stimulating itself, and accounts for why we cannot tickle ourselves ([17](#), [19](#)) and why we are unaware of our eye-saccades ([20](#), [21](#)). In psychosis these systems appear to be compromised ([16](#)). Recent studies ([22-25](#)) show that people who experience hallucinations and delusions are unable to monitor self-produced signals (prospective agency), but are able to compensate for this by relying on external cues to attribute actions to oneself (retrospective agency). A defect in predicting one's own body signals thus causes the brain to no longer recognize being in control of them (sense-of-agency [26](#), [27](#)),

resulting in altered sensations and perceptions. Interestingly, recent studies in psychosis (25, 28) and Movement Disorders (29) report decreased and altered connectivity between the frontoparietal control network and the right Angular Gyrus. Furthermore, a recent meta-analysis of tDCS studies found a causal link between sense-of-agency and action selection in the dorsolateral prefrontal cortex (dlPFC) (30). It appears that exactly the inverse coupling between the dlPFC (endogenous attention) and the right Angular Gyrus (exogenous attention) is impaired in psychosis: when the brain selects a voluntary movement, the inhibitory control of the frontal cortex to the right Angular Gyrus is lost (25). These recently overlooked findings shed light on the origin of disembodied phenomena and neural basis of self-identification, see **Fig. 1**.

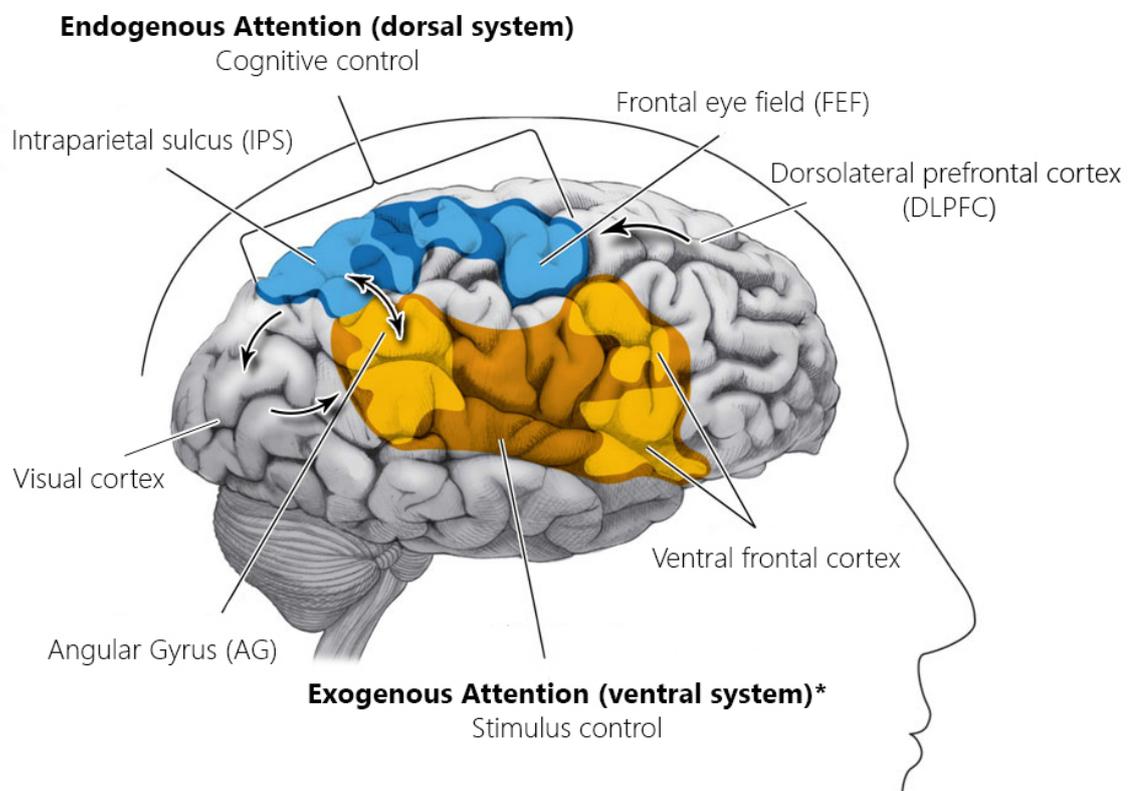


Fig. 1. Endogenous (dorsal) versus Exogenous (ventral) Attention Systems.

Dorsal (blue) and ventral (yellow) frontoparietal attention systems (as outlined by Corbetta & Schulman, 2002).

Humans can perceive the world from different perspectives: from an endogenous (Self) versus exogenous (Other) focus of attention. Self-produced signals are predicted in the brain (e.g., by efference copies), whereas external signals are not. These predictions allow the brain to early discriminate self-produced signals from external stimulation and keep track of its own spatiotemporal location (perspective).

Endogenous attention: the dorsal system is goal-directed and processes self-produced signals. ‘Cognitive control’ enables the top-down voluntary selection of stimuli and responses, resp.: dorsolateral prefrontal cortex (dlPFC), frontal eye field (FEF), intraparietal sulcus (IPS) & visual cortex. **Exogenous attention** * lateralized to the right hemisphere: the ventral system is stimulus-driven and processes external signals. ‘Stimulus control’ enables the automatic orientation and bottom-up detection of behaviorally relevant stimuli, resp.: visual cortex, angular gyrus (AG; as part of the larger temporoparietal junction) & the ventral frontal cortex. These attention systems keep external and self-produced signal processing separated and interconnect at the right AG (**double arrow**). At any given time, the right AG may orient attention outwards to salient or unexpected external events, acting as a ‘circuit breaker’ for the dorsal system; in return, when the dlPFC detects self-produced signals AG’s function is inhibited, silencing the ventral system. When this decoupling fails, self-produced signals are processed as if uncontrolled by oneself (e.g., delusion of control [4](#)); and (over)stimulation of the right AG (e.g., electrical stimulation, epileptic seizures) results in signals being processed as if they are localized outside the own body (i.e., out-of-body experience). Endogenous = ‘of internal origin;’ exogenous = ‘of external origin.’ Figure adapted from [\(5\)](#).

In the present study we sought to obtain direct evidence for a causal link between abnormal right Angular Gyrus activation and altered spatiotemporal self-location (perspective-taking). To achieve this, right Angular Gyrus function was systematically manipulated with high-definition transcranial direct current stimulation (HD-tDCS) while healthy volunteers (i) underwent a full-body illusion, and (ii) carried out a perspective-taking task. It was hypothesized that anodal (vs. sham) right Angular Gyrus stimulation would: (i) make individuals feel more localized towards the virtual body; while (ii) reducing their ability to discriminate between perspectives. This set-

up allowed us to look at self-identification separately from body-ownership. Our results suggest that self-location (perspective-taking) is the key mechanism of self-identification.

Results

The experiment had two sessions that each included a (i) Full-body Illusion (FBI) paradigm; and a (ii) Self-Other perspective-taking (PT) task (i.e., Own-body Transformation (OBT) vs. control Lateralization (LAT) task [31](#)). The two tasks were randomized and counterbalanced over HD-tDCS conditions. This resulted in four experimental conditions: FBI-PT with active stimulation on Session 1 (FBI-PT 1) or Session 2 (FBI-PT 2); and PT-FBI with active stimulation on Session 1 (PT-FBI 1) or Session 2 (PT-FBI 2). Sham stimulation was presented on all other occasions. Thirty-six prescreened participants (see **Materials and Methods**) were randomly assigned to one of the four conditions, resulting in nine participants in each group. One participant was excluded from the FBI-analysis due to unforeseen technical problems (group PT-FBI 1; female; FBI $N = 35$). Two other participants were excluded from the PT-analysis because of chance-level performance (group PT-FBI 1 & FBI-PT 2; females; OBT & LAT $N = 34$). Occasional outliers in reaction times ($< 1\%$ data points LAT: RT < 160 ms / > 1000 ms; OBT: RT < 200 ms / > 2000 ms) and missing values ($< 3\%$ data points PT-task) were replaced by mean values. Statistical analyses were performed in SPSS v25.0 and are reported using a 0.05 significance level.

Full-body Illusion (FBI)

Statistics pooled over the sessions revealed that the average reported displacement towards the projected image was 69.1 cm in Session 1 and 72.4 cm in Session 2. Participants reported that the displacement occurred “*After a while*” ($N = 22$ Session 1; $N = 19$ Session 2) or after 3

minutes ($M = 3.6$, $SD = 1.8$). This was experienced “*Many short times*” ($N = 15$ Session 1; $N = 17$ Session 2) followed by “*Continuously*” ($N = 5$ Session 1; $N = 8$ Session 2) and “*Once shortly*” ($N = 7$ Session 1; $N = 2$ Session 2). Maximal displacement was reported on nine occasions (180-200 cm); while 1/6 of participants reported no displacement (17.1%). The exit-interview consisted of 15 items (incl. 3 control items), answered on 5-point Likert scales ranging from ‘1 = *Strongly Disagree*’ to ‘5 = *Strongly Agree*.’ The items measured: ‘*Displacement*,’ ‘*Self-Identification*,’ and ‘*Sense-of-Agency*’ (see **Supplementary Materials**). Most prominently, participants perceived the displacement as: (i) a “*loss of control*” (Item 8, Agency low; $N = 24$ Session 1, $N = 25$ Session 2); followed by (ii) a sense of dissociation from the bodily self “*I felt a shift out of my body towards the virtual body*” (Item 2, Main Displacement; $N = 19$ Session 1, $N = 23$ Session 2); and (iii) subsequent identification with the virtual self (Items 5, 6, 10, & 15; Self-Identification; $M_{tot} = 15$ Session 1, $M_{tot} = 15.6$ Session 2). A large subset also reported (iv) a regain in control “*I felt as if I could stand up and walk away with the virtual body,*” i.e., adopting a first-person perspective in the illusion (Item 11, Agency high; $N = 14$ Session 1, $N = 15$ Session 2). “*Total Exit Interview Scores*” were calculated excluding the control items.

As expected, a first mixed ANOVA found a significant main effect for displacement in pre- and posttest scores over sessions, $F(1,31) = 62.8$, $p < 0.001$, $\eta p^2 = 0.67$ (behavioral measure). A second mixed ANOVA performed over “*Total Exit Interview Score*” also indicated a significant main displacement effect over sessions, $F(1,31) = 5.2$, $p = 0.03$, $\eta p^2 = 0.14$ (psychometric measure). These results confirmed that the new 3D FBI-paradigm had been successful. Furthermore, a significant effect of HD-tDCS to the right Angular Gyrus was found. The previous mixed ANOVA measured a significant interaction in displacement scores between

experimental groups, $F(3,31) = 4.4, p = 0.01, \eta^2 = 0.30$. There was no specific hypothesis based on task order (FBI-PT vs. PT-FBI), nor did Levene’s test for homogeneity indicate unequal group variances, $F < 1$. Therefore, in subsequent analyses the results were taken together comparing two groups differing in stimulation order. These analyses revealed a significant interaction between displacement scores and stimulation, $F(1,33) = 10.5, p = 0.003, \eta^2 = 0.24$ (**Fig. 2**); as also between “*Total Exit Interview Scores*” and stimulation, $F(1,33) = 4.8, p = 0.035, \eta^2 = 0.13$ (**Fig. 3**). Group 1: HD-tDCS S1 ‘Yes’ $M = 42.8(6.4)$ vs. S2 ‘No’ $M = 42.9(7.1)$; Group 2: HD-tDCS S1 ‘No’ $M = 37.3(8.3)$ vs. S2 ‘Yes’ $M = 42.7(8.4)$, Bonferroni corrected. Note: to provide more details Fig. 3 includes the original four groups. In short, both the behavioral and psychometric measure confirmed that more displacement was reported when the right Angular Gyrus received active versus sham stimulation. Moreover, a strong correlation between the amount of displacement and interview scores was found, $r(33) = 0.57, p < 0.01$ (Session 1) and $r(33) = 0.51, p < 0.01$ (Session 2), one-tailed Bonferroni corrected.

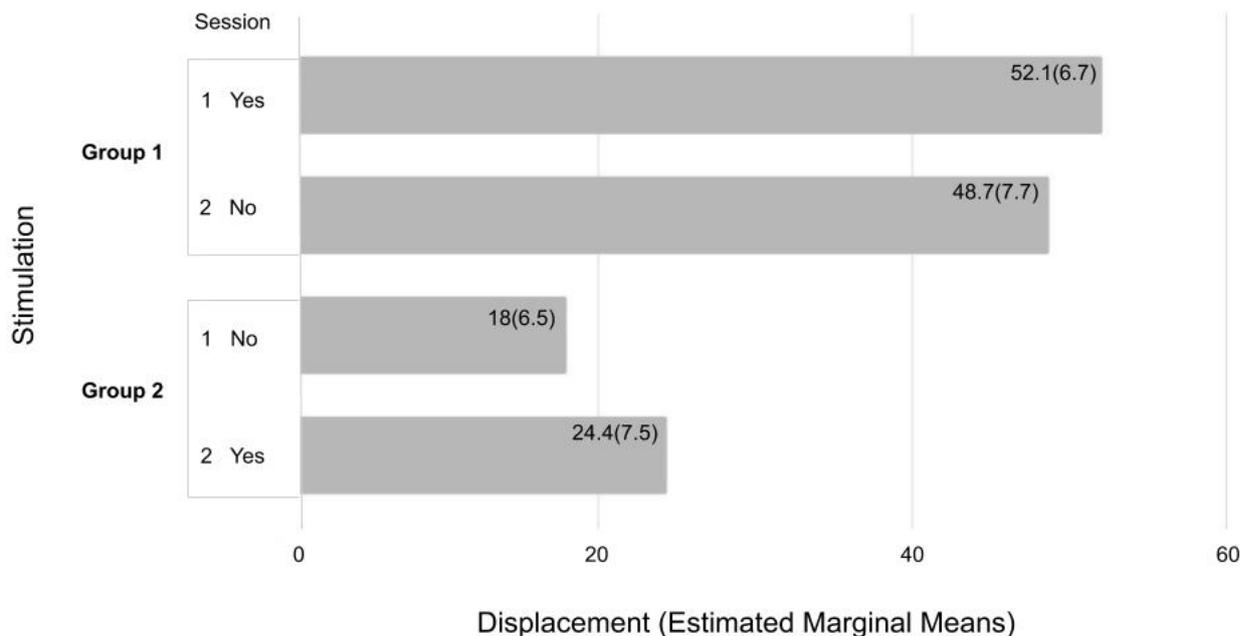


Fig. 2. Behavioral measure: Full-body Illusion Displacement * Stimulation.

Reported 'Displacement' by 'Group 1' active stimulation on Session 1 'Yes' vs. Session 2 'No' & 'Group 2' active stimulation on Session 1 'No' vs. Session 2 'Yes.' Estimated Marginal Mean (Standard Error) Bonferroni corrected; Group 1: FBI-PT 1 & PT-FBI 1 ($N = 17$); Group 2: FBI-PT 2 & PT-FBI 2 ($N = 18$).

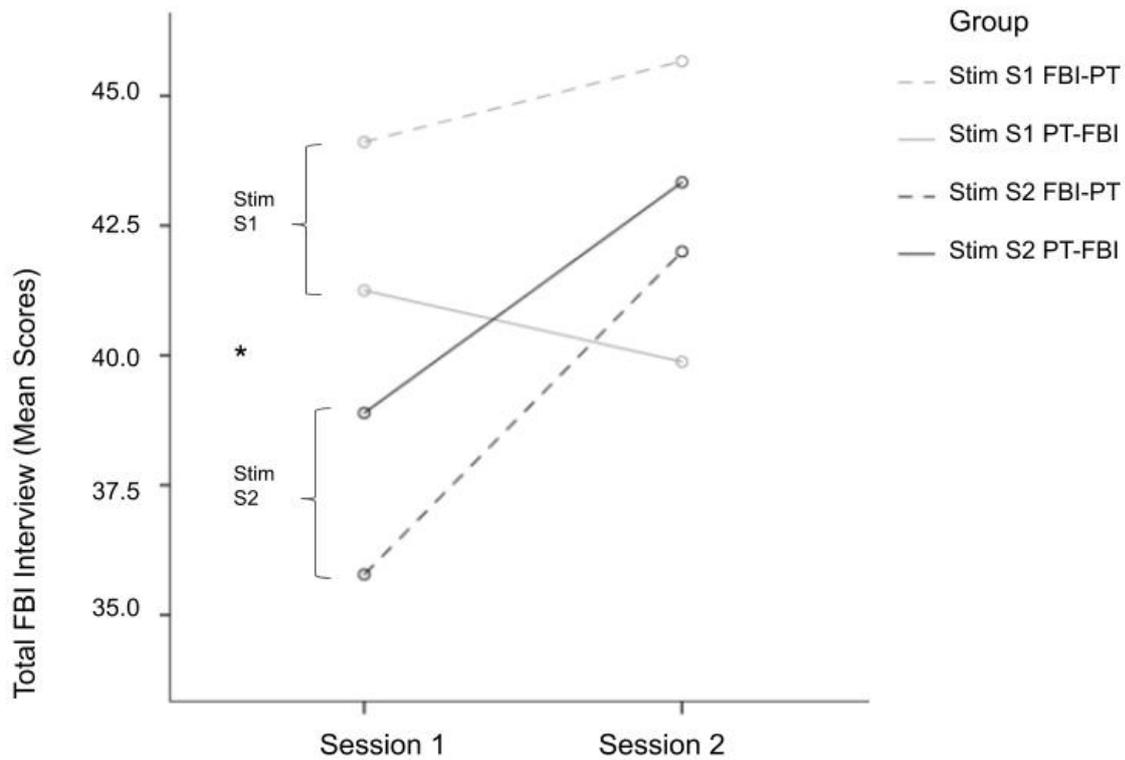


Fig. 3. Psychometric measure: Full-Body Illusion Exit Interview * Stimulation.

Mean Total Exit Interview scores per Session plotted by Group: solid & dashed grey lines received active stimulation on Session 1 (FBI-PT 1 $N = 9$ & PT-FBI 1 $N = 9$); solid & dashed black lines received active stimulation on Session 2 (FBI-PT 2 $N = 8$ & PT-FBI 2 $N = 9$). Stim = Stimulation; S1 = Session 1; S2 = Session 2; FBI = Full-body Illusion; PT = Perspective Taking; p -value $< 0.05 = *$ (Groups: Stim S1 $N = 18$ vs. Stim S2 $N = 17$).

Perspective Taking (OBT & LAT tasks)

First, we confirmed that participants responded faster on the control Lateralization task ($M = 348$ ms $SD = 50$ LAT) than on the more cognitively demanding Own-body Transformation task ($M =$

699 ms $SD = 124$ OBT). A strong learning effect on the OBT-task was found over consecutive blocks; this was not found on the control task, where participants had to make simple left-right judgments, $ps < 1$. A repeated MANOVA performed over the Own-body transformations demonstrated a significant improvement in response times over blocks, $F(2,29) = 12.6, p < 0.001, \eta p^2 = 0.46$, and between sessions, $F(1,30) = 77.6, p < 0.001, \eta p^2 = 0.72$, see **Fig. 4**. Furthermore, stimulation had a significant effect on OBT-task performance. As expected, this effect was in the opposite direction to that of the full-body illusion, making it harder to perform the Self-Other transformations. The first mixed ANOVA demonstrated a significant interaction between OBT response times and stimulation over blocks, Pillai's Trace = 0.86, $F(15,84) = 2.2, p = 0.011, \eta p^2 = 0.29$. This interaction was also significant in the univariate within-subjects results, $F(15,30) = 1.8, p = 0.047, \eta p^2 = 0.15$. Overall response times had been longer when the right Angular Gyrus received active versus sham stimulation (**Table 1**). No significant group differences were found, $ps < 1$.

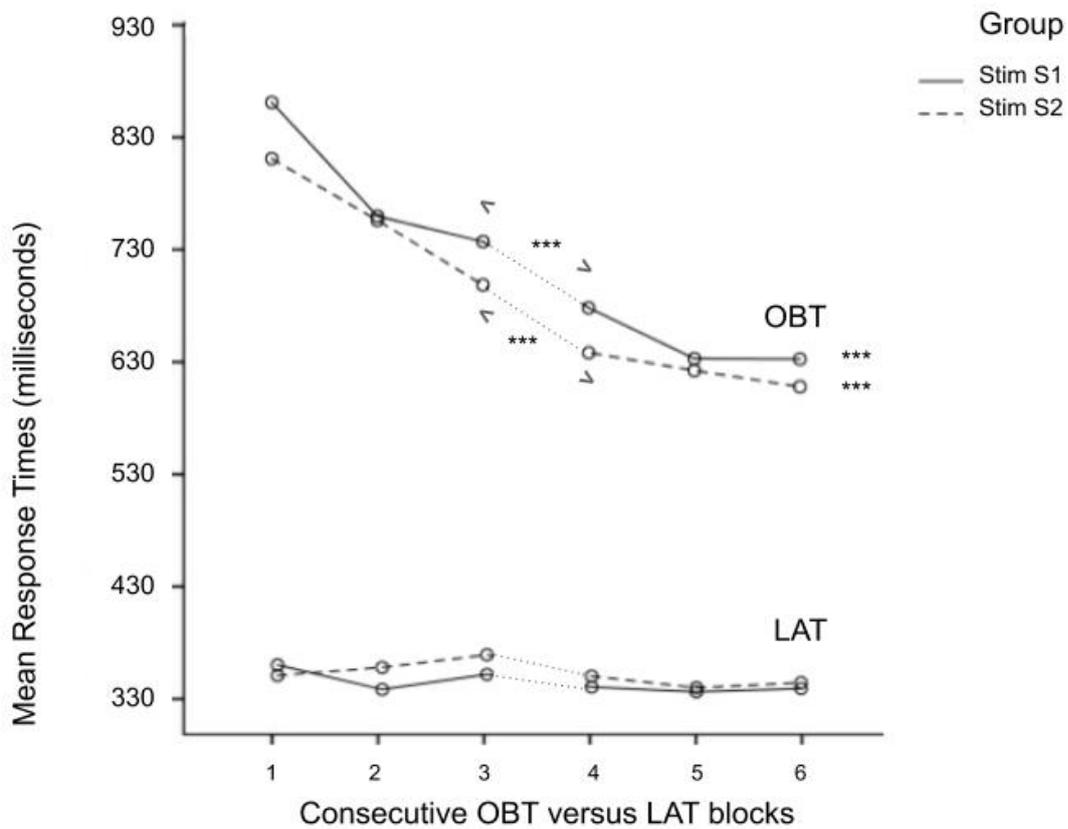


Fig. 4. Improvement in Mean Response Times (milliseconds) OB versus LAT blocks.

Mean Response Times of OB versus LAT blocks plotted by Group: solid lines received active stimulation on Session 1 ($N = 17$; FBI-PT 1 & PT-FBI 1); dashed lines received active stimulation on Session 2 ($N = 17$; FBI-PT 2 & PT-FBI 2). Stim = Stimulation; S1 = Session 1 (blocks 1-3); S2 = Session 2 (blocks 4-6); OB = Own-body Transformations; LAT = left-right decision-making; p -value $< 0.001 = ***$ over blocks ($< *** >$ between sessions).

OBT-task	Condition	M	SD	N	LAT-task	Condition	M	SD	N
Session 1					Session 1				
Block 1	1 FBI-PT Stimulation	789	181	9	Block 1	1 FBI-PT Stimulation	367	102	9
	2 FBI-PT Sham	779	127	8		2 FBI-PT Sham	319	21	8
	3 PT-FBI Stimulation	928	273	8		3 PT-FBI Stimulation	352	58	8
	4 PT-FBI Sham	829	155	9		4 PT-FBI Sham	379	63	9
Block 2	1 FBI-PT Stimulation	736	149	9	Block 2	1 FBI-PT Stimulation	346	42	9
	2 FBI-PT Sham	747	131	8		2 FBI-PT Sham	338	35	8
	3 PT-FBI Stimulation	777	175	8		3 PT-FBI Stimulation	329	37	8
	4 PT-FBI Sham	755	129	9		4 PT-FBI Sham	375	63	9
Block 3	1 FBI-PT Stimulation	706	142	9	Block 3	1 FBI-PT Stimulation	355	47	9
	2 FBI-PT Sham	677	126	8		2 FBI-PT Sham	341	65	8
	3 PT-FBI Stimulation	763	166	8		3 PT-FBI Stimulation	347	56	8
	4 PT-FBI Sham	711	106	9		4 PT-FBI Sham	393	74	9
Session 2					Session 2				
Block 1	1 FBI-PT Sham	696	96	9	Block 1	1 FBI-PT Sham	344	55	9
	2 FBI-PT Stimulation	621	55	8		2 FBI-PT Stimulation	319	21	8
	3 PT-FBI Sham	652	197	8		3 PT-FBI Sham	335	33	8
	4 PT-FBI Stimulation	649	113	9		4 PT-FBI Stimulation	377	68	9
Block 2	1 FBI-PT Sham	646	75	9	Block 2	1 FBI-PT Sham	339	46	9
	2 FBI-PT Stimulation	626	96	8		2 FBI-PT Stimulation	330	24	8
	3 PT-FBI Sham	613	93	8		3 PT-FBI Sham	333	30	8
	4 PT-FBI Stimulation	616	83	9		4 PT-FBI Stimulation	348	35	9
Block 3	1 FBI-PT Sham	648	82	9	Block 3	1 FBI-PT Sham	339	44	9
	2 FBI-PT Stimulation	567	48	8		2 FBI-PT Stimulation	327	21	8
	3 PT-FBI Sham	610	74	8		3 PT-FBI Sham	338	36	8
	4 PT-FBI Stimulation	641	99	9		4 PT-FBI Stimulation	359	36	9

Table 1. Mean Response Times (milliseconds) OBT and LAT blocks.

Mean response time (M), standard deviation (SD), and population size (N) reported per experimental condition (1 FBI-PT; 2 FBI-PT; 3 PT-FBI; 4 PT-FBI) for OBT and control LAT blocks. FBI = Full-body Illusion; PT = Perspective Taking task; OBT = Own-body Transformations; LAT = left-right decision-making.

Largely similar results were obtained when examining the accuracy of the Own-body Transformations (i.e., number of correct responses). A repeated MANOVA demonstrated a significant improvement in accuracy over sessions, $F(1,30) = 7.8, p = 0.009, \eta^2 = 0.21$; while no improvement was found on the control task, $ps < 1$. Importantly, a mixed ANOVA performed over blocks found a significant interaction between the accuracy in Own-body Transformations and stimulation, $F(15,74) = 2.2, p = 0.015, \eta^2 = 0.31$. This interaction was marginally

significant in the univariate within-subjects results, $F(6,60) = 2.0$, $p = 0.079$, $\eta^2 = 0.17$. No interactions were found between the accuracy on the control task and stimulation, $ps < 1$.

Discussion

Self-consciousness, in its most elementary form, may be disconnected from the own body (1, 2). Patients with psychosis frequently misattribute their thoughts and actions to external sources; and in certain out-of-body experiences, lucid states, and dreams body-ownership is absent but self-identification is preserved. A common factor between these experiences appears to be abnormal activation of the right Angular Gyrus, but its role in self-identification remained unclear. We hypothesized that self-identification depends on inferring self-location at the right Angular Gyrus (perspective-taking). This process relates to the discrimination of self-produced signals (endogenous attention) from environmental stimulation (exogenous attention; Fig. 1). In a fully randomized, double-blind and sham-controlled HD-tDCS experiment we found a clear causal relation between right Angular Gyrus activation and alterations in self-location. Confirming our hypothesis, anodal versus sham HD-tDCS (i.e., stimulating the ‘other’ perspective) resulted in: (i) a more profound out-of-body shift in a full-body illusion; and (ii) a reduction in people’s ability to discriminate self from other perspectives. Disembodiment appeared to be specifically characterized by an initial loss in sense-of-agency (i.e., decoupling of endogenous attention), but not in self-identification. Healthy volunteers controlled for susceptibility factors consistently reported: (i) more displacement towards the virtual body in centimeters; and (ii) stronger out-of-body experiences when receiving active versus sham HD-tDCS. Furthermore, the stronger the self-identification with the virtual ‘other,’ the more displacement in centimeters was reported (i.e., alteration in self-location). Correspondingly, anodal versus sham HD-tDCS led to longer

response times and less accuracy in judging self from other perspectives. In short, our results confirm a causal role of the right Angular Gyrus in spatiotemporal self-location (perspective-taking). Self-identification can be decoupled from the bodily self, explaining phenomena associated with disembodiment.

Recent evidence suggests that the brains' ability to accurately infer its own location is closely tied to the discrimination of self and other signals. Distinct attention networks appear responsible for the processing of endogenous (self) versus exogenous (other) signals (5), and this allows the brain to keep track of different perspectives (see Fig. 1). As was addressed in the **Introduction**, in order to adequately process self-produced signals (i.e., endogenous attention) the brain needs to actively inhibit external stimulation (i.e., exogenous attention). This mechanism is inextricably tied to the predictability of self-produced signals (i.e., sense-of-agency). Previous studies have shown that when self-produced signals are recognized as one's own, the right Angular Gyrus is inhibited by the frontal control network (22-25). However, when this decoupling fails, voluntary movements are experienced as not controlled by oneself (cf. *movement disorders*, 29) and sometimes even misattributed as being caused by external sources (e.g., *delusion of control*, 4). How the brain directs its attention appears to be critical. Out-of-body experiences and full-body illusions are unusual instances where self-produced signals are temporarily interrupted, while the right Angular Gyrus is (over)stimulated (3, 10-11 & this study). These findings indicate that disembodied reference frames result from an initial failure of the brain to recognize one's own body's signals, an *agency dysfunction*, while the Self as the center of awareness is preserved. Altered perceptions like these reveal that there are different ways to identify with the Self: one directly related to the bodily self and the predictability of self-produced signals; and another,

more reflective way of relating to the world and someone else's perspective (i.e., the right Angular Gyrus). The respective roles of the dorsal and ventral attention systems in these processes need further examination (Fig. 1). The present study focused on explaining the unusual phenomena associated with disembodiment by elucidating the role of the right Angular Gyrus in self-identification (perspective-taking). More studies, however, confirm a critical role of the right Angular Gyrus when attention for self-produced signals is lacking. Together, these findings demonstrate why its' functional disruption seems to be particularly detrimental for (bodily) self-consciousness, then: we can no longer recognize ourselves in the mirror (13); we feel ourselves disconnected from our own bodies and body parts (e.g., 6); and the sharp distinction between our bodily selves and others is lost from us (e.g., 4). The most fundamental aspect of ourselves appears to stay with us: the sense of being a discrete entity localized in the here (space) and now (time), perceiving the world from an immersive, first-person perspective (2).

Conclusion: The present study reports a clear causal relation between right Angular Gyrus activation and alterations in spatiotemporal self-location (perspective-taking). Self-identification can be decoupled from the bodily self, explaining phenomena associated with disembodiment.

Materials and Methods

Experimental Design

This study comprised a fully randomized, double-blind and sham-controlled HD-tDCS experiment. The experiment had a crossover, mixed factorial design with two repeated measures (i.e., sessions) on the dependent variables and one independent grouping factor with four levels (the four experimental

conditions, see **Results**). In each session, healthy volunteers controlled for susceptibility factors (see **Participants**) completed a (i) Full-body Illusion paradigm and (ii) a (control) Perspective Taking task. Half of the participants received active stimulation on Session 1 versus sham stimulation on Session 2 (see **HD-tDCS** section & double-blinding procedure). The Full-body Illusion paradigm had two dependent variables: (i) the pre- and posttest displacement scores (*behavioral measure* with two levels) and (ii) the total exit-interview scores (*psychometric measure*). The Perspective Taking task (composed of an OBT-task & control LAT-task) had four dependent variables with three levels: (i) mean response times and (ii) accuracy scores were calculated for each of three blocks per task (see **Procedure and Tasks**).

Participants

Thirty-six naive right-handed adults with normal vision, hearing and vestibular function volunteered for the experiment (24 females, 12 males; mean age = 24.7; SD = 6.1). All received reimbursement in the form of course credit or gift cards. Sample size reflected the need to counterbalance four experimental groups and was based on *N* sizes reported in similar tDCS studies (see [12](#)). Participants were recruited through an online research participant pool of the Queensland University of Technology (QUT) and study advertisements sent to staff email addresses (Brisbane, Australia). Potential participants were prescreened online for (i) age, (ii) handedness ([32](#)), (iii) tDCS safety ([33-34](#)), (iv) pre-existing susceptibility to body illusions ([35](#)), (v) (history of) psychological or neurological disorders, and (vi) visual or vestibular problems viewing 3D content. Two participants reported prior Out-of-Body Experience during childhood (unrelated to a medical injury or near death experience). Susceptibility was assessed with the 20-item *time Perceptual Aberration Scale* (tPAS) and identified no individuals scoring within the top 10% of the scale. Past research found a strong correlation between the tPAS and the Perceptual Aberration Scale (i.e., measuring vulnerability to schizophrenia spectrum disorders), and between high tPAS scores and right Angular Gyrus (AG) dysfunction ([35](#)). See **Table S1** for a full list of exclusion criteria. Participants gave written informed consent and performed the experiment twice in two sessions scheduled one week apart.

Informed consent to publish identifying images was obtained. This study was approved by the University Human Research Ethics Committee (QUT-UHREC) and conducted according to the Declaration of Helsinki (WMA, version October 2013).

HD-tDCS

Stimulation was administered to the right Angular Gyrus (rAG) using a one-channel direct current stimulator (DC Stimulator Plus, NeuroConn) and a concentric centre-ring montage with two rubber electrodes (36-37). A small circular electrode (diameter: 3 cm) served as the anode and was placed over the target region (rAG); while a concentric ring return electrode (inner/outer diameter: 7.5/10cm) was placed evenly spaced around the anode. Electrodes were held into position with electroconductive paste (Ten20, Weaver) and an EEG-cap to ensure consistent adhesion to the scalp. The position of the centre electrode was determined using the 10-10 International EEG system (right AG, P4-P6; Brodmann Area 39), **Fig. S1**. Unlike conventional tDCS, where the current is projected between two large and distant electrodes, the concentric centre-ring montage constrains current flow safely to the target regions as demonstrated in previous modeling studies (36-37, 15). Recent studies have reliably measured regional (36, 15) and task-specific (15) behavioral modulation with this set-up. In two counterbalanced sessions participants received either 25 minutes (1500 sec) of anodal stimulation or “sham” stimulation to the rAG. In both sessions the current was gradually ramped up and down to 1 mA (50 sec). This elicited a physical sensation on the scalp to ensure blinding of the participants, but did not modulate neural function in the sham stimulation condition. Blinding of the researchers was achieved by using the ‘study mode’ of the DC-Stimulator (a preassigned code triggered one of two stimulation conditions). To assure safe administration and blinding, participants rated the intensity of 11 potential adverse effects in each session (e.g., ‘Headache’ ranging from ‘1 = Absent,’ ‘2 = Mild,’ ‘3 = Moderate,’ to ‘4 = Severe’), for details see **Table S2 (38)**. Participants and the researcher were unable to guess stimulation order, respectively: (i)

when the manipulation was revealed at study completion; and (ii) based on differences, e.g., in skin redness (which were absent). Sessions were held a week apart to avoid carryover effects.

3D live-streaming Full-body Illusion paradigm

A new 3D Full-body Illusion (FBI) was developed that included a montage of two action cameras to capture and live-stream 3D-images that were in real-time projected onto a large screen. The video cameras live-captured participants from behind, while they looked at themselves being stroked on the back projected live-size in 3D in front of them. Therefore, participants could ‘observe’ in front of them what they ‘felt’ happening to themselves. This created the illusion of an Out-of-Body Experience; see **Fig. S2** for the experimental setup. Furthermore, with the use of plastic 3D-goggles, for the first time participants were able to observe the illusion while simultaneous stimulation could be administered safely. (Note: it was not possible to recreate an FBI using a VR-paradigm and Head-mounted Display. The electrical stimulation of the brain would interfere with the electronic equipment and this could potentially be unsafe.) The equipment used for the live stereoscopic 3D-streaming consisted of a set of two 3D-mounted action cameras (brand: Xiaomi Yi; 2K resolution) that were connected to an ASUS ROG Strix gaming laptop by two AGPtek USB 3.0 capture cards. In return, the gaming laptop was connected via a high-speed HDMI cable to an Optoma HD 3D-projector. At 60 frames per second it projected full HD stereoscopic 3D images onto a white screen positioned four meters away and two meters in front of the observer. To ensure the best quality projection, the room was kept dark except for two spotlights that illuminated participants’ backs from opposite directions (surroundings were blacked out). Real-time merging of the two separate video streams, and any necessary adjustments (e.g., image-size corrections; left camera horizontal flip; zooming of streams), were done in Bino 3D player-software 1.6.7 ([39](#)) using a Linux operating system (Ubuntu 18.04 LTS software with kernel 4.19.5).

Procedure and Tasks

At the start of the experiment participants either sat comfortably behind a desk at arm's length distance from a 17.3 inch 1920x1080 resolution laptop screen (PT); or two meters from a large projection screen (FBI; the laptop was removed during this task). They were instructed to sit motionless for the duration of the tasks. Short breaks were inserted between the tasks and blocks to take time to rest.

For (A) *the Self-Other Perspective Taking task* the classical Own-body Transformation (OBT) versus control Lateralization (LAT) task was chosen (31). In the OBT-task participants saw sequences of either front-faced or back-faced human figures and were required to judge whether one of the marked hands (i.e., appearing to wear a grey glove) was the right or left hand of the figure, see **Fig. S3** for task stimuli A-D. To ensure that the participants did not adopt a strategy, they were instructed to perform the mental transformations on each trial by imagining themselves in the position of the figure and only then to make a response. Participants completed a short 60 second trial session before commencing the actual task (8 trials). The OBT task consisted of three blocks of 80 items each. In each block, one of the four stimuli (A-D) appeared 20 times in a randomized order. Stimuli were shown in the center of the screen (5.0 X 6.1° visual angle) for a duration of 200 ms. In between a centered fixation cross could be observed (1000 ms ISI). Participants were instructed to keep focusing on the fixation cross and upon seeing the figure to make a response as quickly and accurately as possible. Responses were made with the right hand using the index ('<' left arrow key) and middle fingers ('>' right arrow key). In a control condition, i.e., *the lateralization task*, the same visual stimuli were presented in three blocks. However, this time participants only had to indicate on which side of the screen the marked hand was shown (without performing mental transformations). The OBT and LAT tasks are known to only differ from each other in the 'own-body

transformations,' i.e., in mental rotation and Self-Other perspective (40). Therefore, tasks were identical except for the degree of transformations required. The perspective switching task lasted 10-15 minutes and ran on PsychoPy v1.90.3 (41).

To standardize (B) *the Full-body Illusion* between experimental sessions participants wore a white T-shirt with no prints on the back. Upon arrival, they were invited to comfortably sit down on a stool behind a large table located in the middle of the room. The table was positioned about 200 cm from a large white projection screen. In the middle of the table, directly in front of the stool, a measuring tape was visible that stretched out over the total width of the table. Hence, the tape started counting 0 cm from the participants' body out towards the screen. First, participants were asked to indicate their perceived location on the measuring tape (i.e., pretest score). Subsequently, they were asked to wear 3D goggles and place their hands loosely on top of the table. Their hands were covered by a black sheet that matched a black table cloth that covered the table. Before beginning, participants were instructed to keep completely still during the illusion and to focus on what was happening in front of them. In the following eight minutes participants were stroked on the back (with a brush fastened on top of a stick) while this was live-captured from behind and the images in real-time projected in front of them. The stroking centered on the upper part of the middle back over a length of 20 cm and was carefully executed at a pace of 50 strokes per minute (i.e., the researcher had received previous training with a metronome). In short, during a continuous period of eight minutes participants could 'observe' in front of them what they 'felt' happening to them.

The effectiveness of the FBI was measured in two-fold: (i) '*Displacement scores*' were taken before (pretest score) and after the illusion (posttest score) using the measuring tape fixed onto the desk in front of the participants. In case participants indicated to have felt a displacement towards the virtual body, they were asked to point out in centimeters to what extent they had felt the displacement. Pointing '0 cm' on

the tape localized participants to their body (i.e., no displacement); while pointing '200 cm' on the tape localized participants to the virtual body (range 0-200 cm). Directly after the illusion (ii) *an exit-interview* was completed that explicitly asked participants about their experience (5 min duration). Participants indicated their agreement to 15 statements intended to measure displacement, e.g., '*I felt I was in front of my body,*' scored on 5-point Likert scales ranging from '*1 = strongly disagree*' to '*5 = strongly agree,*' see **Table S3** for a full list of statements. In addition, they were asked to estimate (a) the onset time of the displacement from '*0 = never,*' '*1 = after a while*' to '*2 = fairly quickly,*' (b) the onset time in minutes, and (c) the frequency of the displacement from '*0 = never,*' '*1 = once shortly,*' '*2 = many short times*' to '*3 = continuously.*' In completion, participants provided a written description of their experience. The next week participants returned and completed the same routine. Each session lasted ~90 minutes and was scheduled approximately at the same time of day.

Statistical Analysis

The experiment had six dependent variables spread over two tasks (Full-body Illusion FBI; Perspective Taking PT) with two repeated measures (Session 1 & 2) and one grouping variable (the four experimental conditions, see **Results**). Each of the dependent variables (e.g., "*Total Exit Interview Score*") was analyzed separately in a mixed ANOVA with one between-subjects factor (e.g., "*Experimental Condition*" with four levels) and one within-subjects factor (e.g., "*Session*" with two levels). Where appropriate, the four experimental groups were taken together creating an independent variable "*Stimulation Order*" with two levels: stimulation Session 1 (FBI-PT 1 & PT-FBI 1) versus stimulation Session 2 (FBI-PT 2 & PT-FBI 2). In addition, the dependent variables of the PT-task were analyzed in a one-way repeated measures MANOVA including an additional dependent variable for "*Time*" to check for task-learning effects over consecutive blocks and sessions irrespective of stimulation order.

H2: Supplementary Materials

Table S1 – S3

Fig. S1 – S3

External Databases S1

Data S2

References (32 – 41)

References and Notes

1. T. Metzinger, Why are dreams interesting for philosophers? The example of minimal phenomenal selfhood, plus an agenda for future research. *Front. Psychol.* **4**, 746 (2013).
2. J.M. Windt, The Immersive Spatiotemporal Hallucination Model of Dreaming. *Phenom. Cogn. Sci.* **9**, 295-316 (2010).
3. F. Tong, Out-of-body experiences: from Penfield to present. *Trends Cogn. Sci.* **7**, 104-106 (2003).
4. C. Frith, The self in action: Lessons from delusions of control. *Conscious. Cog.* **14**, 752–770 (2005).
5. S.M. Breedlove, & N.V. Watson, “Chapter 18: Attention and Higher Cognition” in *Biological Psychology. An Introduction to Behavioral, Cognitive, and Clinical Neuroscience* (Sinauer Associates, Sunderland, MA, ed. 7, 2013), pp. 561-596.
6. J.E. Aspell, B. Lenggenhager, & O. Blanke, “Chapter 24: Multisensory Perception and Bodily Self-Consciousness. From Out-of-Body to Inside-Body Experience” in Murray, M.M. & Wallace, M.T. (Eds.). *The Neural Bases of Multisensory Processes*. (CRC Press/Taylor & Francis, Boca Raton, FL, 2012).
7. H.H. Ehrsson, The experimental induction of out-of-body experiences. *Science* **317**, 1048 (2007).

8. B. Lenggenhager, T. Tadi, T. Metzinger, & O. Blanke, Video ergo sum: manipulating bodily self-consciousness. *Science* **317**, 1096–1099 (2007).
9. A. Guterstam, M. Björnsdotter, G. Gentile, & H.H. Ehrsson, Posterior Cingulate Cortex Integrates the Senses of Self-Location and Body Ownership. *Curr. Biol.* **25(11)**, 1416–1425 (2015).
10. O. Blanke, S. Ortigue, T. Landis, & M. Seeck, Stimulating illusory own-body perceptions. *Nature* **419(6904)**, 269–270 (2002).
11. D. De Ridder, K. Van Laere, P. Dupont, T. Menovsky, & P. Van de Heyning, Visualizing Out-of-Body Experience in the Brain. *New Engl. J. Med.* **357(18)**, 1829–1833 (2007).
12. L.Q. Uddin, I. Molnar-Szakacs, E. Zaidel, M. Iacoboni, rTMS to the right inferior parietal lobule disrupts self-other discrimination. *Soc. Cogn. Affect. Neur.* **1**, 65–71 (2006).
13. S. Payne, & M. Tsakiris, Anodal transcranial direct current stimulation of right temporoparietal area inhibits self-recognition. *Cogn. Affect. Beh. Ne.* **17**, 1–8 (2017).
14. H. Fukushima, Y. Goto, T. Maeda, M. Kato, & S. Umeda, Neural Substrates for Judgment of Self-Agency in Ambiguous Situations. *PLoS One* **8(8)**, e72267 (2013).
15. A.K. Martin, J. Huang, A. Hunold, & M. Meinzer, (2018). Dissociable Roles Within the Social Brain for Self–Other Processing: A HD-tDCS Study. *Cereb. Cortex* **29(8)**, 3642–3654 (2018).
16. L.K. Pynn, & J.F.X. DeSouza, The function of efference copy signals: implications for symptoms of schizophrenia. *Vision Res.* **76**, 124–133 (2013).
17. S.J. Blakemore, D. Wolpert, & C.D. Frith, Why can't you tickle yourself? *Neuroreport* **11**, R11–R16 (2000).

18. K.E. Cullen, Sensory signals during active versus passive movements. *Curr. Opin. Neurobiol.* **14**, 698-706 (2004).
19. A.L. Lemaitre, M. Luyat, & G. Lafargue, Individuals with pronounced schizotypal traits are particularly successful in tickling themselves. *Conscious. Cog.* **41**, 64-71 (2016).
20. M. Spering, E.C. Dias, J.L. Sanchez, A.C. Schütz, & D.C. Javitt, Efference Copy Failure during Smooth Pursuit Eye Movements in Schizophrenia. *J. Neurosci.* **33(29)**, 11779-11787 (2013).
21. K.N. Thakkar, J.D. Schall, S. Heckers, & H. Park, Disrupted Saccadic Corollary Discharge in Schizophrenia. *J. Neurosci.* **35(27)**, 9935–9945 (2015).
22. M. Synofzik, P. Thier, D.T. Leube, P. Schlotterbeck, & A. Lindner, Misattributions of agency in schizophrenia are based on imprecise predictions about the sensory consequences of one’s actions. *Brain* **133**, 262–271 (2010).
23. M. Voss, J. Moore, M. Hauser, J. Gallinat, A. Heinz, & P. Haggard, Altered awareness of action in schizophrenia: a specific deficit in predicting action consequences. *Brain* **133**, 3104–3112 (2010).
24. F. Garbarini, A. Mastropasqua, M. Sigaud, M., Rabuffetti, A. Piedimonte, L. Pia, & P. Rocca, Abnormal Sense of Agency in Patients with Schizophrenia: Evidence from Bimanual Coupling paradigm. *Front. Behav. Neurosci.* **10**, 43 (2016).
25. M. Voss, V. Chambon, D. Wenke, S. Khün, & P. Haggard, In and out of control: brain mechanisms linking fluency of action selection to self-agency in patients with schizophrenia. *Brain* **140**, 2226–2239 (2017).
26. S. Gallagher, Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn. Sci.* **4(1)**, 14-21 (2000).

27. P. Haggard, & V. Chambon, Sense of agency. *Curr. Biol.* **22**, R390–R392 (2012).
28. T.J. Whitford, D.H. Mathalon, M.E. Shenton, B.J. Roach, R. Bammer, R.A. Adcock, S. Bouix, M. Kubicki, J. De Siebenthal, A.C. Rausch, J.S. Schneiderman, & J.M. Ford, Electrophysiological and diffusion tensor imaging evidence of delayed corollary discharges in patients with schizophrenia. *Psychol. Med.* **41**, 959–969 (2011).
29. C.W. Maurer, K. LaFaver, R. Ameli, S.A. Epstein., M. Hallett, & S.G. Horowitz, Impaired self-agency in functional movement disorders: A resting-state fMRI study. *Neurology* **87**, 564-570 (2016).
30. N. Khalighinejad, S. Di Costa, & P. Haggard, Endogenous action selection processes in dorsolateral prefrontal cortex contribute to sense of agency: a meta-analysis of tDCS studies of ‘intentional binding.’ *Brain Stimul.* **9**, 372–379 (2016).
31. O. Blanke, C. Mohr, C.M. Michel, A. Pascual-Leone, P. Brugger, M. Seeck, T. Landis, & G. Thut, Linking Out-of-Body Experience and Self Processing to Mental Own-Body Imagery at the Temporoparietal Junction. *J. Neurosci.* **25(3)**, 550–557 (2005).
32. R.C. Oldfield, The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* **9(1)**, 97–113 (1971).
33. S. Rossi, M. Hallett, P.M. Rossini, A. Pascual-Leone, The Safety of TMS Consensus Group. Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clin. Neurophysiol.* **120**, 2008–2039 (2009).
34. S. Rossi, M. Hallett, P.M. Rossini, A. Pascual-Leone, Screening questionnaire before TMS: An update. *Clin. Neurophysiol.* **122**, 1686 (2011).

35. S. Arzy, C. Mohr, I. Molnar-Szakacs, & O. Blanke, Schizotypal Perceptual Aberrations of Time: Correlation between Score, Behavior and Brain Activity. *PLoS ONE* **6(1)**, e16154 (2011).
36. O. Gbadeyan, M. Steinhauser, K. McMahon, & M. Meinzer, Safety, Tolerability, Blinding Efficacy and Behavioural Effects of a Novel MRI-Compatible, High-Definition tDCS Set-Up. *Brain Stimul.* **9(4)**, 545–552 (2016).
37. M. Bortoletto, C. Rodella, R. Salvador, P.C. Miranda, & C. Miniussi, Reduced Current Spread by Concentric Electrodes in Transcranial Electrical Stimulation (tES). *Brain Stimul.* **9(4)**, 525–528 (2016).
38. A.R. Brunoni, J. Amadera, B. Berbel, M.S. Volz, B.G. Rizzerio, & F. Fregni, A systematic review on reporting and assessment of adverse effects associated with transcranial direct current stimulation. *Int. J. Neuropsychoph.* **14(8)**, 1133-1145 (2011).
39. M. Lambers, Bino: free 3d video player. Retrieved from <http://bino3d.org> (2012, June 24).
40. L. Schwabe, B. Lenggenhager, O. Blanke, The timing of temporo-parietal and frontal activations during mental own body transformations from different visuo-spatial perspectives. *Hum. Brain Mapp.* **30(6)**, 1801-1812 (2009).
41. J.W. Peirce, PsychoPy--Psychophysics software in Python. *J. Neurosci. Meth.* **162 (1-2)**, 8-13 (2007).

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