Neural correlates of an illusive sense of agency caused by virtual reality

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Abstract

As a part of self-consciousness, sense of agency (SoA) refers to our sensation that we initiate actions that lead to ensuing perceptual consequences. Previous neuroimaging studies manipulated voluntary actions to create differential levels of SoA, and found that the SoA network largely overlaps with the sensorimotor network. It is thus unclear whether effects observed in these regions are attributable to SoA or some specific aspects of action processes (e.g., intentionality of action) related to voluntary action control, or both. To disentangle the effect of action processes, here we utilized virtual reality (VR) technology to induce an illusive SoA in the absence of voluntary action, and examined it by functional magnetic resonance imaging (fMRI). Participants' experience of controlling an avatar hand elicited a persistent increase in temporal binding, a behavioral marker of SoA, when they merely observed the avatar hand's movement in the scanner. fMRI results showed that the SoA with the non-action was associated with a cluster centered in right angular gyrus, extending to right inferior parietal lobule and the right precuneus. These high-level associative areas have been implicated in SoA with voluntary actions for their role in perceptual-motor mismatch detection and action awareness. Other traditional SoA areas, especially those governing action intentionality and motor planning, were not implicated. Hence, controlling a virtual body can generate a salient SoA whose neural correlates are distinct from those supporting action control but partially overlapping with those governing post voluntary-action SoA processes. These findings also highlight the role of angular gyrus in giving rise to the self-consciousness changes associated with virtual body embodiment in VR and metaverse.

Introduction

Sense of agency (SoA) is the sensation that self-initiated actions influence the external environment. As an integral part of self-consciousness, SoA enables one to feel fluent control over one's surroundings (Haggard, 2017), distinct from others (Kahl & Kopp, 2018), and responsible for one's own actions (Haggard & Tsakiris, 2009).

Previous neuroimaging studies on SoA have tested the brain activities by contrasting conditions where SoA is accompanied by voluntary actions that are perceptually perturbed. Researchers either manipulated the authorship of the action, e.g., externally moving people's effector to generate passive "actions" (e.g., Balslev et al., 2006; Kuhn et al., 2013; Straube et al., 2017; Tsakiris et al., 2010; Uhlmann et al., 2020; van Kemenade et al., 2017, 2019; Zapparoli et al., 2020), or perturbed the sensory feedback of the movement or its outcome with temporal and spatial discrepancies (e.g., Balslev et al., 2006; Chambon et al., 2013; David et al., 2007; de Bezenac et al., 2016; Di Plinio et al., 2020; Farrer et al., 2003, 2008; Farrer & Frith, 2002; Kikuchi et al., 2019; Kuhn et al., 2013; Leube, Knoblich, Erb, Grodd, et al., 2003; Leube, Knoblich, Erb, & Kircher, 2003; Matsuzawa et al., 2005; Nahab et al., 2011; Ohata et al., 2020; Sasaki et al., 2018; Schnell et al., 2007; Spengler et al., 2009; Uhlmann et al., 2020; van Kemenade et al., 2019; Yomogida et al., 2010; Zapparoli et al., 2020). Such contrast between voluntary action and perturbed action yielded extensive cortical areas distributed over frontal, parietal, temporal, and insula cortices and subcortical regions such as the cerebellum and striatum (Charalampaki et al., 2022; Haggard, 2017; Seghezzi et al., 2019). In particular, a wide network of sensorimotor areas is implicated, including pre-supplementary motor area (pre-SMA), putamen, SMA proper, postcentral gyrus, cerebellum, insula, temporoparietal junction (TPJ), and angular gyrus (AG). These areas govern various aspects of actions, including action selection, movement planning and initiation, motor execution,

sensory predictions of action consequences, somatosensory feedback, action awareness, and comparison or integration of the predictions and actual sensory feedback. The large overlap between the SoA network and the sensorimotor network is in line with the comparator model of action awareness (Frith et al., 2000; Wolpert et al., 1995), which posits that SoA arises as a subjective experience of action processing (Frith, 2005). However, it is unclear whether effects observed in these regions are attributable to SoA or some specific aspects of action processes related to voluntary action control, or both.

SoA can indeed be elicited without voluntary action (Buehner, 2012; Kong et al., 2017; Suzuki et al., 2019). As a sign of implicit SoA, people's timing judgment of an action (e.g., a key press) and its consequence (e.g., a resulting beep sound) are biased towards each other whenever the action is voluntary as compared to unintentionally made (e.g., the finger pushed by others or triggered by transcranial magnetic stimulation). This temporal binding phenomenon has thus been coined intentional binding (Haggard et al., 2002). Interestingly, temporal binding can occur without self-action but based on the mere presence of causality between a movement and its outcome (Buehner, 2012; Kong et al., 2017; Suzuki et al., 2019). Buehner showed that the perceptual experience of seeing a human's or even a machine's causal action (i.e., a key press) could subsequently lead to temporal binding while seeing a non-causal event (i.e., an LED flash) could not (Buehner, 2012). Our recent behavioral study showed that the avatar movement, not intentionally controlled by the virtual reality (VR) user, could lead to enhanced temporal binding after a brief VR exposure (Kong et al., 2017). The type of observation-elicited binding effect is in line with the so-called apparent mental causation account of SoA (Wegner & Wheatley, 1999), which conceptualizes the SoA as a consequence of a post hoc inference after movements (Buehner & Humphreys, 2009; Desantis et al., 2011; Tramacere, 2021; Wegner, 2003; Wegner & Wheatley, 1999). Such settings allow us

to disentangle potential effects of SoA without voluntary action (and motor planning), but so far their underlying neural correlates have not been examined.

Here we combine VR and brain imaging to elucidate the neural basis underpinning the SoA in the absence of action. Based on the temporal binding elicited by observing the avatar's "action" (Kong et al., 2017), the present study examined the SoA arising in the absence of voluntary action with fMRI scans before and after the VR exposure. Two questions can be addressed with this novel paradigm: first, if the binding effect is driven by action processes only, we should find neural correlates in sensorimotor regions, especially those prefrontal and frontal areas (e.g., pre-SMA and SMA proper) implicated in motor intention and planning (Seghezzi et al., 2019; Sperduti et al., 2011). Relatedly, since action observation itself could also trigger action processes, especially those related to motor simulations (Binkofski & Buccino, 2006; Hari et al., 1998; Molnar-Szakacs et al., 2006; Rizzolatti et al., 1996), we further examined whether the SoA arising from non-actions but with action observation (Buehner, 2012; Kong et al., 2017; Suzuki et al., 2019) is associated with changes in the action observation network (Caspers et al., 2010). Second, VR experience can change people's self-consciousness (Banakou & Slater, 2014; Slater et al., 2009), but previous neuroimaging studies have only focused on the sense of bodily ownership (Bach et al., 2012; Bekrater-Bodmann et al., 2014; Pamplona et al., 2022) and self-localization (Ionta et al., 2011; Lenggenhager et al., 2011), leaving the neural basis of SoA over a virtual body unchecked. Our second goal is thus to shed important light on the neural basis of self-consciousness changes yielded by VR experience in general.

Methods

Participants

Our study recruited 48 college students as paid volunteers. Half of the participants were randomly assigned to the experimental group and half to the control group. Both groups were exposed to a VR environment, but only the experimental group viewed an avatar hand. Four participants, inattentive in a task during fMRI scanning (rate of successful judgment < 80%, details in Procedures), were excluded from data analyses, leaving twenty-three participants in the experimental group (mean age = 23.69 ± 2.37 years, 12 females) and twenty-one participants in the control group (mean age = 21.99 ± 2.75 years, 13 females). Power analysis with a previously reported effect size of 0.5 (Kong et al., 2017) indicated that a sample size of n = 14 would lead to a power of 0.9 with an α level of 0.05 (G*Power; Faul et al., 2007). The two groups were matched in age (t_{42} = .639, p = .526) and gender (χ^2 = .424, p = .515). All participants were right-handed, had normal or corrected-to-normal vision, and reported no neurological diagnoses. The experiment was conducted according to the principles of the Declaration of Helsinki and was approved by the Ethical Committee of the School of Psychological and Cognitive Sciences at Peking University.

Procedures

Experimental procedure overview

Each participant went through three consecutive phases of the experiment, i.e., a pre-test, VR exposure, and a post-test. In the pre-test and post-test, participants performed the classical temporal binding task and a hand laterality judgment task (hand laterality task, Ferri et al., 2012) in a sequel in the MRI scanner (T1 functional scan was acquired before pre-test); each test lasted about 35 minutes. The laterality task was designed for studying questions unrelated to the purpose of the

current investigation. Due to a lack of measurement evaluating participants' attention in the temporal binding task, four participants showing inattentive performance in the laterality task (rate of successful judgment < 80%) were excluded from the current data analyses out of prudence. After the pre-test, the participants walked into the waiting room next to the scanning room to receive VR exposure for about 30 minutes. During VR exposure, participants wore a head-mounted display (HMD, HTC Vive Pro) and performed four gamified motor tasks by controlling an avatar hand with their right hand (see below). The VR exposure aimed to enable participants to embody the avatar hand by controlling it for goal-directed movements. The experimental group could view the avatar hand, whose motion spatially and temporally matched with that of their actual right hand. The control group, never given a chance to see the avatar hand, performed the same motor tasks. After finishing the VR exposure, the participants removed the HMD and walked with their eyes closed to the scanning room under the guidance of the experimenter. They were instructed not to open their eyes until they were properly positioned in the scanner to get ready for the post-test. This procedure was employed to minimize the visual experience of the real settings and to preserve the effect of VR exposure. After the post-test, participants re-entered the waiting room and were asked to evaluate their subjective sense of embodiment (SoO and SoA) during the post-test by means of questionnaires.

Temporal binding task

The temporal binding task performed was a replicate of the same task in our previous study, though it was performed with the HMD previously (Kong et al., 2017). In brief, participants judged the timing of an auditory stimulus with the aid of a Libet clock projected in the MRI scanner in keeping to the temporal binding task outside of the VR (Haggard et al., 2002).

The task involved temporal judgments of tones in a series of trials. Two types of trials, baseline, and operant trials, were presented in blocks. For each operant trial (top panel in Figure 1a), the Libet clock started to rotate clockwise from a random location. After a random interval of 2560 - 5120 ms, the right avatar hand pressed the white button. A tone would be presented 250 ms later (100 ms in duration). Note that the participant was required to refrain from any movement during the stimulus presentation. The clock hand kept rotating after the tone for a random duration of 1280 - 2560 ms, then reset its position to 12 o'clock. Participants were required to report the location of the clock hand when the tone was perceived. They reported by pressing the left and right keys using the left middle and index finger to move the clock hand clockwise and counterclockwise, respectively. They then confirmed their estimated position by pressing the button with the right index finger when the clock hand arrived at the desired location. The report was self-paced. The baseline trial (bottom panel in Figure 1a) was identical to the operant trial, except that the tone would be presented without the button press, i.e., the avatar's hand remained static all the time. The timing of the tone followed the same random uniform distribution as for the operant trial.

Participants familiarized themselves with the temporal binding task before the formal experiment by conducting four operant trials and four baseline trials outside the scanner. Both pre-test and post-test comprised of two operant runs and two baseline runs whose orders were random and counterbalanced between participants. Each run contained 20 trials.

All the visual stimuli, including the Libet clock, a pair of avatar hands, and a white button under the index finger of the right avatar hand, were back-projected onto a translucent screen located inside the scanner (resolution: 1024×768; refresh rate: 60Hz; Figure 1a). The avatar hand

resembled the one that the participants visually controlled during the VR exposure outside the scanner. The clock had a 10-pixel-long hand, which rotated with a period of 2560 ms per circle. The clock face (radius = 110 pixels) was marked with conventional “1 min” intervals. The participants wore a pair of headphones to receive the auditory stimuli and to reduce noise. Before the formal data collection, participants familiarized themselves in the scanner with the temporal binding task. We adjusted the volume of the auditory stimulus on the individual basis to ensure that they could hear the stimuli clearly and comfortably in the scanner. The viewing distance was about 90 cm. The rendering was controlled by a customized program coded using Psychtoolbox 3.0.16 in MATLAB (R2019a, MathWorks).

VR exposure

During VR exposure that was sandwiched between the pre-test and the post-test, participants wore the HMD with a dual-display giving a 110° field of view and a resolution of 1080 × 1200 per eye. In the VR scene, they could see a virtual desk located at approximately the same location as the physical desk at which they sat. Participants wore a motion tracking glove (Noitom Hi5 VR Glove; sampling rate 100 Hz) on their right hand to control a right avatar hand in the VR environment. The motion of the avatar hand was always temporally and spatially congruent with the real right hand. For participants from the experimental group, the avatar hand resembled their own right hand in size and skin tone, which were adjusted before the experiment. For control participants, no avatar hand was shown, and all the VR tasks were performed with the “invisible” hand. The games were designed to provide a sensorimotor experience of controlling avatar's hand to interact with the virtual environment (Figure 1b), including the gesture-imitation task, the bubble-poking task, the cube-picking task, and the pad-tapping task (customized by using the Unity3D game engine).

In the gesture-imitation task, a left-hand avatar was displayed in front of the participants at their eye height. This avatar hand would present a hand gesture randomly selected from 20 possible gestures, e.g., a closed fist, a thumb-up, and a V-sign. The participant was required to replicate the same gesture with their right avatar hand. Once the gesture was reproduced, the next target gesture would appear until all 40 trials (two repetitions for each different gesture) were successfully finished. In the bubble-poking task, a transparent bubble would appear at a random location on the desk, moving at a random speed and direction. Participants were asked to poke the bubble with the index finger of the avatar before it fell off the desk. After a bubble was poked or dropped off the desk, the next bubble would appear. This task lasted until 60 target bubbles were shown and poked. In the cube-picking task, forty cubes with different sizes, colors (red or blue), and labeled numbers (1 or 2) were placed randomly on the virtual desk. Participants were required to control the avatar hand to grab specific cubes and drop them on the floor. Participants performed this task three times with different verbal instructions each time, including “pick all the red cubes and drop them on the floor," “pick all the cubes labeled as number 1 and drop them on the floor”, and “pick all the red cubes labeled as number 1 and drop them on the floor”. In the pad-tapping task, a multi-digit number would appear before disappearing after 2~4 s. Participants were required to memorize the number and then replicate the number by tapping on a virtual number pad. Forty numbers, ranging from 3-digit to 10-digit, were presented in random order for each participant. Each of the four VR tasks lasted for about 6-7 minutes, resulting in a total VR exposure time of about half an hour.

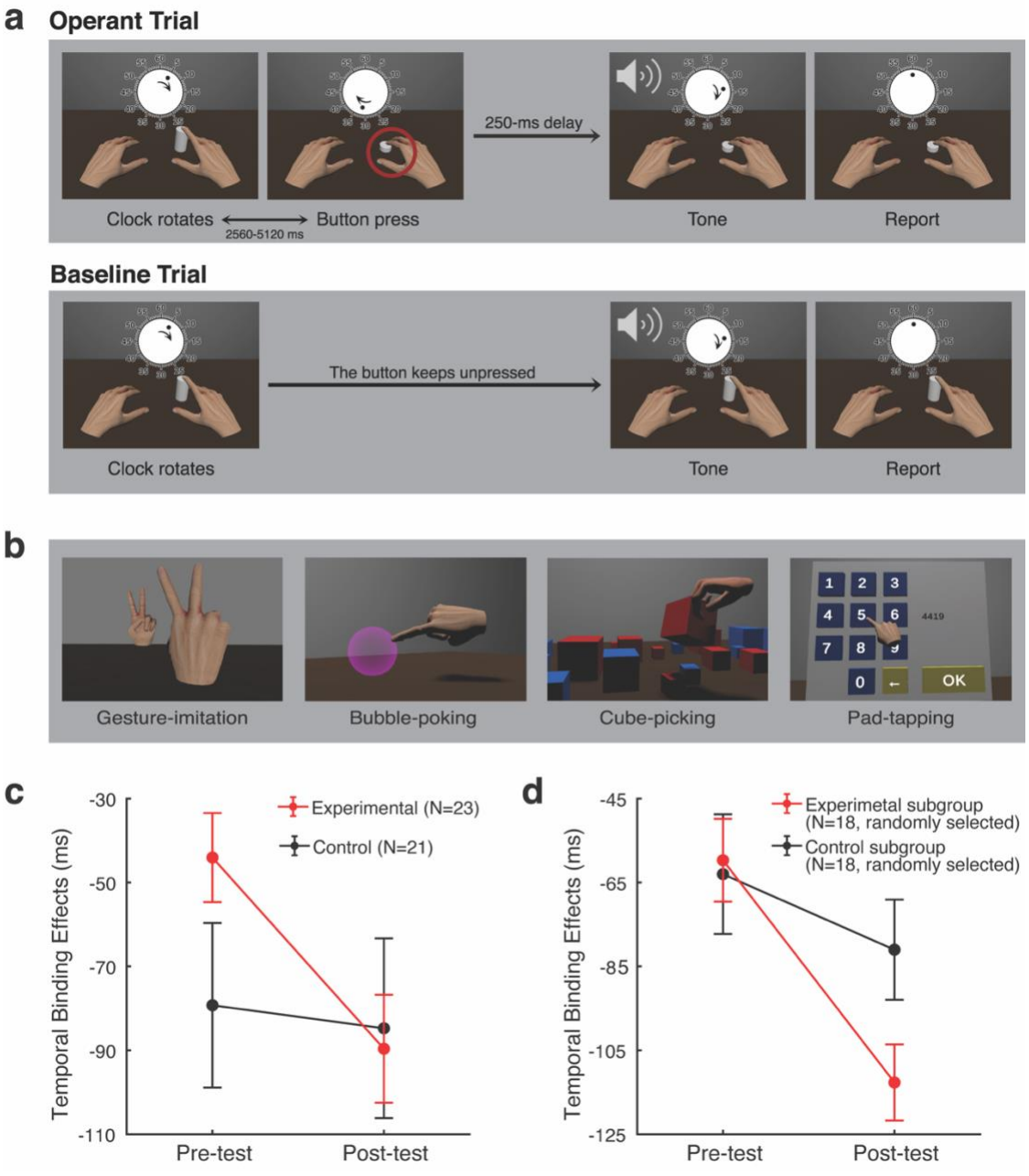


Figure 1. (a) Graphical illustration of an operant trial (top panel) and a baseline trial (bottom panel) in the temporal binding task. (b) Scenes of motor tasks in virtual reality. Participants performed four VR motor tasks: the gesture-imitation task: bending right-hand fingers to match a target gesture, shown by the distant avatar hand; the bubble-poking task: poking the bubble with the right index finger; the cube-picking task: picking target cubes that are specified by color or shape in instructions; the pad-tapping task: memorizing a multi-digit number before it

disappears, and then recalling it by tapping on a keypad. The experimental group viewed the avatar hand (shown here), but the control group did not. (c) Temporal binding effects from all the participants. The temporal binding effect is quantified by perceptual shifts evoked by the avatar's movement. The average binding effects in pre-test and post-test are shown for two groups separately. (d) Temporal binding effects from two randomly selected subgroups of participants matched based on pre-test performance.

Questionnaire

We assessed the subjective feeling of embodiment by means of questionnaires in the post-test (Table 1). The questions were identical to the ones used in our previous study on VR embodiment (Kong et al., 2017). The items were designed to assess SoA and SoO or to control for possible response bias by using the reversed items (control items, SoA-control).

Table 1. Questionnaire on embodiment evaluation. All questions were rated on a Likert scale from 1 (strongly disagree) to 7 (strongly agree).

Category	Questions: During the current experiment condition in Virtual Reality,	Order of questions
Sense of ownership	I felt like I was looking at my own hand.	1
	I felt like the avatar was part of my body.	6
	It seemed as if my hand was pressing when I saw the avatar's movement.	5
Sense of agency	It seemed as if the avatar moved, obeying my will.	4
	It seemed as if the avatar pressed the button instead of me.	3
	If I moved my finger, I felt that the virtual finger would move in the same way.	7
Sense of agency-control	I felt as if the movement of the avatar had no relationship with me.	8
	It seemed as if the avatar had a will on its own.	2

Data analysis

Behavioral data analysis

To examine whether VR exposure could enhance participant's implicit SoA associated with an avatar hand, we compared the temporal binding effect by using a two-way mixed-design ANOVA with Phase as the within-group factor (pre versus post) and Group as the between-group factor (experimental versus control group). Each trial yielded a perceptual error of temporal judgment, quantified as the difference between the reported and the actual onset of the tone. The temporal binding effect is operationally defined as the difference in perceptual error, i.e., a perceptual shift, between the operant condition and the baseline condition. A negative perceptual shift indicates the temporal binding effect.

For the subjective measures of embodiment from questionnaires, we calculated the median scores for SoA, SoO, and SoA-control separately. Between-group comparisons were performed by the Wilcoxon Signed Ranks test. Spearman correlation was used to test the association between the binding effects and the subjective feelings of embodiment.

Since the two groups happened to differ in the binding effect during the pre-test, we randomly selected 18 participants from each group for a subgroup analysis to match their initial performance and performed all the analyses based on these baseline-matched samples (n = 18 each). Major fMRI results of this subset remained the same as those of the whole set of participants (see the Supplementary Material).

fMRI data analysis

All functional and structural MRI data were acquired on a Siemens 3T Prisma scanner with a 64-channel head-neck coil at the Center for MRI Research, Peking University. High-resolution functional images were acquired using a multi-band echo-planar sequence (62 axial slices, repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle (FA) = 90°, field of view (FOV) = 224 × 224 mm^2, matrix size = 112 × 112, slice thickness = 2.0 mm, voxel size = 2 × 2 × 2 mm^3, multi-band factor = 2). High-resolution 3D T1-weighted anatomical images were acquired using the magnetization-prepared rapid-acquisition gradient-echo sequence (192 sagittal slices, TR = 2530 ms, TE = 2.98 ms, inversion time = 1100 ms, FA = 7°, FOV = 224 × 256 mm^2, matrix size = 224 × 256, interpolated to 448 × 512, slice thickness = 1.0 mm, voxel size = 0.5 × 0.5 × 1 mm^3). Functional images were preprocessed using Statistical Parametric Mapping (SPM) software (Version 12; Wellcome Trust Center for Neuroimaging, London, UK, http://www.fil.ion.ucl.ac.uk/spm12/). For each individual participant, the first five volumes of each functional run were discarded. The remaining images were corrected for slice timing and head motion and spatially normalized to Montreal Neurological Institute (MNI) space via unified segmentation (resampling into 2 × 2 × 2 mm^3 voxel size). No participant had head motion larger than 3 mm/3°. These images were spatially smoothed using a 6-mm full-width half-maximum (FWHM) Gaussian kernel for univariate contrast analyses.

We carried out a whole-brain univariate analysis to test whether exposure with/without an avatar hand in VR would lead to differential brain activity for the temporal binding task. At the first level, preprocessed functional images were modeled in a general linear model (GLM) corresponding to the onset of the beep time in each trial, with four regressors for the condition (operant or baseline) and the phase (pre-test or post-test) of different runs (the condition was consistent in a single run),

convolved with the canonical hemodynamic response function (HRF). The GLM also included six additional predictors of no interest representing head motion parameters in each run. The high-pass filter was set at 128 s. After model estimation, we first obtained whole-brain contrast images of operant condition versus baseline condition in the pre-test and post-test, respectively, for each participant. One-sample *t*-tests of these contrast images represented the general neural responses of the temporal binding effects (operant error – baseline error). The between-phase (post-test versus pre-test and pre-test versus post-test) effects of such neural responses were analyzed by paired-sample *t*-tests. Besides, the VR exposure-related neural activities were quantified by subtracting the whole-brain contrast images of the pre-test (operant versus baseline) from the post-test (operant versus baseline) for each participant. VR exposure-related neural signals were entered into the second-level analyses, testing the between-group effect by a two-sample *t*-test. All the results reported survived at a voxel-wise uncorrected threshold at $p < .005$ and a cluster-level FWE correction at $p < .05$.

To investigate whether the classical agency-related regions (based on studies with voluntary actions) would be activated in our novel paradigm, we chose seven regions of interest (ROI) reported associated with agency in a recent meta-analysis (Seghezzi et al., 2019), used the reported peaks to form 8-mm-radium spherical ROIs (top panel in Figure 3a, peak coordinates in Table 2) on the VR exposure-related contrast images, extracted the averaged beta values, and conducted two-sample *t*-tests to compare between the two groups. For completeness, these seven ROIs cover clusters associated with both self-agency (agency attributed to self; their Table 1) and external-agency (agency attributed to others; their Table 3). For regions showing nonsignificant between-group differences, Bayesian factors were conducted with the default prior scale = 0.707.

To verify that the SoA-related neural activities were not simply caused by action observation, we examined possible group differences in action observation-related ROIs. We chose fourteen ROIs reported in association with observation of general hand actions from a meta-analysis (Caspers et al., 2010), used the reported peaks to form 8-mm-radium spherical ROIs (top panel in Figure 3b, peak coordinates in Table 3) on the VR exposure-related contrast images and conducted two-sample *t*-tests to compare the two groups. Notably, action observation in our present temporal binding task was elicited by the key press in the operant trials. Thus, action observation-related ROIs particularly associated with the avatar hand were defined as regions showing significantly stronger activation in the operant condition relative to the baseline in the pre-test for all participants (voxel-wise uncorrected $p < .005$ and cluster size > 10). Bilateral lateral occipitotemporal cortex (LOTC) was selected (top panel in Figure 3c and peak coordinates in Table 3; L LOTC: 144 voxels, R LOTC: 211 voxels), and two-sample *t*-tests were conducted.

To probe the link between brain activity and behavior, we intended to select the regions showing significant neural effects to calculate the participants' neural signals. We used Spearman correlation to test whether the neural signals were correlated with changes in temporal binding or subjective embodiment ratings after VR exposure. To examine whether the correlation can be explained away by group difference, we also regressed neural signals on behavioral changes with group label as a covariate.

All of the surface brain maps were visualized with the BrainNet Viewer (Version 1.7; Xia et al., 2013; http:// www.nitrc.org/projects/bnv/). All statistical tests were conducted by R (version 4.1.1).

Results

Behavioral results: The temporal binding effects

Before the VR exposure (pre-test phase), both groups of participants showed a moderate level of temporal binding effect (Figure 1c). In the baseline condition, when the avatar hand remained stationary, the temporal judgment error amounted to an average of -26.45 ms (SE = 14.58 ms, same below) and -38.05 (16.25) ms for the experimental and control groups, respectively. In the operant condition with the avatar hand suddenly pressing the button before the tone, the judgment error was -70.49 (17.06) ms and -117.30 (27.44) ms for the experimental and control groups, respectively. Thus, in the pre-test, both groups showed a negative perceptual shift in timing judgment of the tone, an indicator of temporal binding.

Crucially, after the VR exposure in the post-test, the experimental group increased their binding effects by 45.59 ms (10.57) with the baseline and operant error of -7.81 (15.09) ms and -97.45 (19.66) ms, respectively. The control group's binding effects remained largely unchanged (differed from the pre-test by -5.49 ± 13.32 ms). This group difference was confirmed by a mixed ANOVA (within-group factor: Phase; between-group factor: Group): both the interaction ($F_{1, 42}$ = 5.706, p = .021) and the main effect of Phase ($F_{1, 42}$ = 9.255, p = .004) reached significance, while the main effect of Group was not significant ($F_{1, 42}$ = .493, p = .487). Post-hoc comparisons indicated that the experimental group showed enhanced binding effects in the post-test (-89.64 ± 16.92 ms) than in the pre-test (-44.04 ± 15.05 ms; t_{42}= 3.931, Bonferroni-corrected p <.001, Cohen's d = 0.829), while the same effect was absent in the control group (t_{42}= .452, Bonferroni-corrected p =.654, Cohen's d = .100). These behavioral results and their effect size were similar to those in our

previous study (Kong et al., 2017), indicating that seeing and controlling an avatar hand increases the temporal binding effect.

We noticed that the two groups tended to differ in the binding effect at the pre-test, though statistically insignificant (t_{42}= 1.616, p = .113). To test group differences in the neuroimaging data robustly, we randomly selected 18 participants from each group to match their pre-test performance and subsequently contrasted these two subgroups' fMRI data. A pair of exemplary subgroups were shown (Figure 1d), with a matched pre-test performance ($F_{1, 34}$ = .037, p = .849) and a significant Group by Phase interaction ($F_{1, 34}$ = 5.914, p = .020). The imaging analysis was conducted for all participants and for the pre-test matched random subsets. The fMRI results shown below were based on all participants; see supplemental material for results on the subset shown in Figure 1d.

Behavioral results: The subjective feeling of SoA and SoO

Besides using temporal binding as the implicit measure of SoA, we also used a questionnaire to explicitly measure their sense of embodiment for the avatar hand in the post-test. We did not find significant group difference in SoA and SoO ratings (z = -.131, p = .896 for SoA; z = -.095, p = .925 for SoO). Across the two groups, the average scores of the SoA-control questions were significantly higher than those of the SoA questions (z = -3.428, p = .001), indicating that the participants correctly followed the instructions to fill in the questionnaire.

As expected, the subjective SoA and SoO were positively correlated (ρ = .597, p < .001). However, neither of them was correlated with the temporal binding effects in the post-test or the binding changes between the pre- and post-test (binding effects: ρ = -.187, p = .225 and ρ = -.065, p = .676

for SoA and SoO in the post-test, respectively; changes in binding effects: ρ = -.017, p = .878 and ρ = .043, p = .783 for SoA and SoO, respectively).

Imaging results: The basic operant binding effects

To investigate the neural responses of the binding effects (operant error - baseline error) in the temporal binding task, we first generated whole-brain contrast images of the operant condition versus baseline, separately for different phases (pre-test and post-test) and groups (experimental group and control group). Note the difference captured by these contrast images is that the avatar hand made a quick keypress movement in the operant condition while it remained static in the baseline condition. All the contrasts except the experimental group in the pre-test showed significant activation in bilateral occipito-temporal cortex (LOTC; Figure 2a) with a voxel-wise uncorrected threshold at $p < .005$ and a cluster-level FWE correction at $p < .05$. The experimental group in the pre-test showed a trend in this region but failed to reach the significant level.

Imaging results: The VR binding effects (Pre- vs. Post-test) in Experimental vs. Control group

For the experimental group who behaviorally showed enhanced binding effects in the post-test, we observed increased activation in the post-test (versus pre-test) in three clusters (Figure 2b, voxel-wise uncorrected threshold at $p < .005$ and cluster-level FWE correction at $p < .05$), located in left precentral gyrus (MNI peak coordinates: -7, -4, 69; cluster size = 255, t_{22} = 4.33), right precentral gyrus (MNI peak coordinates: 26, -12, 56; cluster size = 237, t_{22} = 4.97), and right postcentral gyrus (MNI peak coordinates: 20, -40, 68; cluster size = 627, t_{22} = 5.08). No significant activation in the pre-test (versus post-test) was found in the experimental group. For the control group, however, no region displayed a significant effect between two phases (post-test versus pre-test and pre-test versus post-test) under the same threshold (voxel-wise uncorrected threshold at $p < .005$

and cluster-level FWE correction at $p < .05$), which echoed their stable binding effects throughout the experiment.

Behaviorally, the VR exposure-induced binding changes were quantified by subtracting the binding effects (operant error - baseline error) of the pre-test from that of the post-test. Similarly, the VR exposure-related neural activities were analyzed by obtaining whole-brain contrast images between the pre-test (operant versus baseline) and the post-test (operant versus baseline). We then contrasted these contrast images between the experimental and control groups who performed the same temporal binding task during imaging and differed only in whether they had visually controlled the avatar hand during the VR exposure outside of the scanner.

Critically, compared to the control group, the experimental group showed increased activation in a single cluster centered around right angular gyrus (MNI coordinate of peak: 40, -50, 36; cluster size = 290 voxels), extending into right inferior parietal lobule and the right precuneus (Figure 2c). While the reported cluster contained a few voxels (13.1%) in precuneus, none of the reporter subpeaks landed there and thus we focused the discussion on angular gyrus and inferior parietal lobule. Specifically, for the experimental group, the activation related to the operant versus baseline effects within this cluster increased from -2.583 (.982) in the pre-test to 1.444 (1.058) in the post-test, while for the control group, such activation decreased from 2.020 (1.028) in the pre-test to -1.124 (1.107) in the post-test (Figure 2c). Notably, a recent meta-analysis (Seghezzi et al., 2019) reported that agency was associated with the right angular gyrus. The reported peak coordinates were 13.2 mm from the peak of our cluster. No significantly greater activation was detected in the control group when compared with the experimental group at the same threshold.

Imaging results: Associations between neural activities and temporal binding effects

Although three clusters showed greater activation in the post-test (relative to the pre-test) for the experimental group, the averaged neural signals from these clusters did not significantly correlate with the temporal binding effects (left precentral gyrus: ρ = -.126, p = .403; right precentral gyrus: ρ = -.095, p = .531; right postcentral gyrus: ρ = -.185, p = .217). However, the activation changes in the cluster centered on the right angular gyrus, which showed a significant between-group effect, were significantly correlated with the temporal binding changes (ρ = -.342, p = .023; Figure 2d). Thus, the larger the binding effect, the smaller the activation changes in right angular gyrus. The multiple regression analysis, using the group label as an additional predictor, revealed that group was significant (β = .505, p = .001) but the binding change was no longer significant (β = -.109, p = .437). This result thus suggested that the correlation between the VR exposure-related neural activities and the binding changes was largely driven by group differences. Lastly, we did not find any significant correlation between VR exposure-related activation changes and subjectively-reported SoA (ρ = .157, p = .308) or SoO (ρ = .116, p = .452).

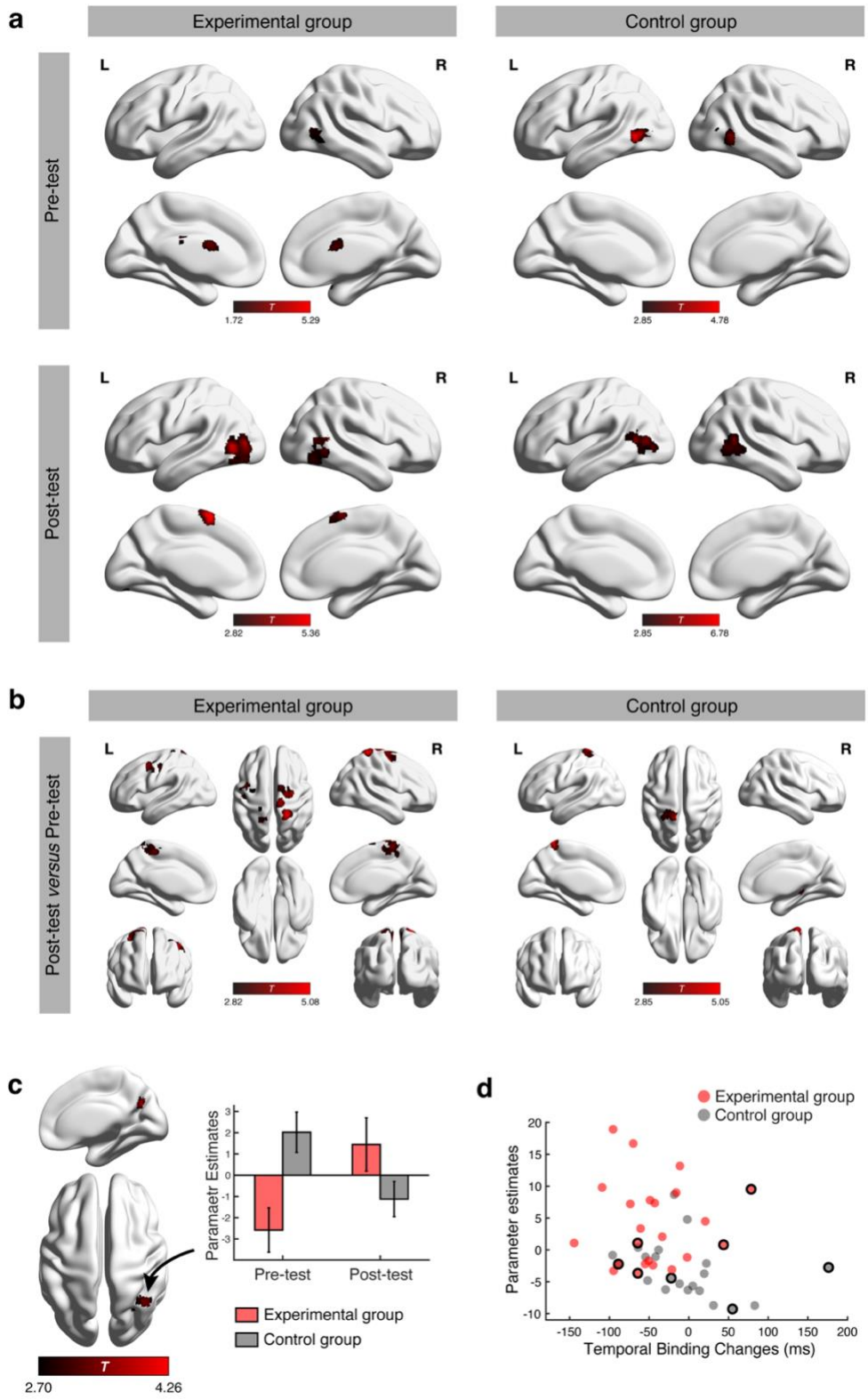


Figure 2. (a) Whole-brain contrast images of operant versus baseline plotted separately for different phases (pre-test and post-test) and different groups (experimental group and control

group). A lenient threshold was applied at voxel-wise uncorrected $p < .05$ and cluster size > 10 for the experimental group in the pre-test, while the threshold of the other three conditions was applied at voxel-wise uncorrected $p < .005$ and cluster-level FWE correction at $p < .05$; (b) Whole-brain comparison for the neural response of the binding effect (operant - baseline) before and after VR exposure (post-test versus pre-test), plotted separately for the experimental group and control group. The experimental group revealed three clusters with greater activation in the post-test relative to the pre-test (voxel-wise uncorrected threshold at $p < .005$, cluster-level FWE correction at $p < .05$. The control group displayed no significant activation at the same threshold, and its activation map was shown with a more lenient threshold at voxel-wise uncorrected $p < .005$ and cluster size > 30; (c) The whole-brain between-group comparison of the VR exposure effect that is depicted in (b). Greater activation with the experimental group relative to the control group (voxel-wise uncorrected threshold at $p < .005$, cluster-level FWE correction at $p < .05$) was observed at 40, -50, 36 (MNI coordinate) with a cluster size of 290 voxels. The right bar graph depicts the magnitude of neural activation of the whole cluster, as represented by the average parameter estimates across participants (operant versus baseline); (d) Association between the VR exposure-related neural signals and the temporal binding changes. The enclosed dots are from the participants excluded from the supplementary subgroup analysis that equates the pre-test performance between the two groups (see Supplemental Material).

ROI analysis 1: VR binding effects in the previously reported SoA ROIs

Unlike previous imaging studies using voluntary actions to study SoA, our paradigm modulated implicit SoA (temporal binding effect) without voluntary actions. We specifically examined whether the previously reported SoA-related brain regions showed the VR-elicited SoA effects, when voluntary action is not involved. We obtained seven ROIs associated with agency in a recent

meta-analysis (Seghezzi et al., 2019). Using the reported peaks to form 8-mm-radium spherical ROIs (top panel in Figure 3a and Table 2) on the VR exposure-related contrast images (used in the between-group comparison above), we compared the ROI signals between two groups. No significant group difference was detected among these ROIs, and Bayes factors (BF) indicated that for 3 out of 7 ROIs, the null hypothesis of no difference between groups was more than 3 times more likely than the alternative hypothesis (bottom panel in Figure 3a and Table 2). The ROI at right angular gyrus (AG) was marginally significant (p = 0.051, BF = 1.46), but it distanced from our cluster center by 13.2mm. The ROI at right STG was not significant with a distance of 19.8mm. Thus, these results showed that the voluntary action-based SoA regions were not reliably implicated in our data where the observation-elicited SoA was observed.

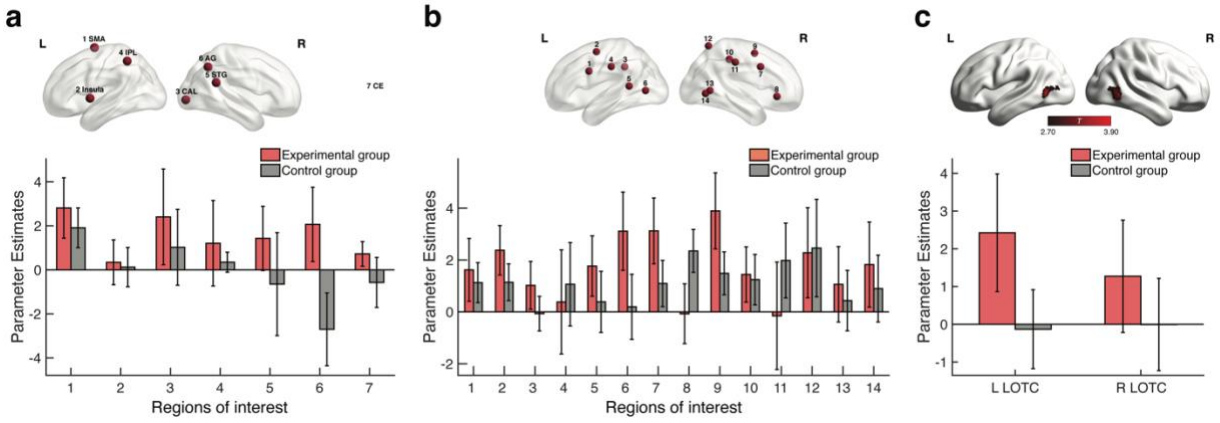


Figure 3. Group-based ROI results. (a) SoA-related ROI results. Top panel: SoA ROIs defined by a recent meta-analysis (Seghezzi et al., 2019). Bottom panel: The experimental (red) and control (gray) information in each ROI. SMA = Supplementary motor area, Insula = Posterior insula, CAL = Calcarine scissure, IPL = Inferior parietal lobule, AG = Angular gyrus, STG = Superior temporal gyrus, CE = Cerebellum; (b) ROIs results from observation of general hand actions. Top panel: ROIs associated with the observation of hand actions. They were defined by a recent meta-analysis

(Caspers et al., 2010). Bottom panel: The experimental (red) and control (gray) information in each ROI. 1 = L IFG / PrG, 2 = L lat dPMC, 3 = L SI / IPS, 4 = L IPL, 5 = L STS / pMTG, 6 = L lat occipital, 7 = R IFG / PrG, 8 = R IFG, 9 = R lat dPMC / MFG, 10 = R SI, 11 = R IPL, 12 = R SPL, 13 = R STS / pMTG, 14 = R lat occipital; (c) ROIs results from particular observation of the avatar hand actions (operant condition) in the pre-test. Top panel: ROIs defined by the contrast of operant vs. baseline in the pre-test at the group level. Bottom panel: The experimental (red) and control (gray) information in each ROI.

Table 2. Between-group comparison for ROI signals in SoA-related regions.

Brain regions	**MNI coordinates**			***t***	***p***	**Cohen's *d***	**BF**
	x	***y***	***z***				
Supplementary motor area	-7	-4	69	–.55	.585	-.16	.335
Posterior insula	-41	2	1	–.16	.872	–.05	.301
Calcarine scissure	18	-90	-1	–.49	.625	–.15	.328
Inferior parietal lobule	-46	-48	51	–.61	.543	–.19	.347
Superior temporal gyrus	54	-49	22	–1.07	.292	–.32	.470
Angular gyrus	45	-60	43	–2.01	.051	–.61	1.46
Cerebellum	24	-53	-27	–.52	.607	–.16	.332

ROI analysis 2: VR binding effects in the hand-action observation network

Apart from voluntary action, observing others' actions could also elicit extensive activations in motor-related regions. As the temporal binding effect here was elicited by observing the "action" of the avatar hand, it might be supported by action observation-related regions. ROIs associated with the observation of hand actions were first defined by a recent meta-analysis (Caspers et al.,

2010). We used the reported peaks to form 8-mm-radium spherical ROIs (top panel in Figure 3b and Table 3) on the VR exposure-related contrast images (used in the between-group comparison above) and compared the ROI signals between the two groups. We did not obtain significant group differences in these ROIs (All *p*s >.05). Bayes factors were between 0.298 and 0.912, indicating anecdotal evidence for null hypothesis of no difference between groups (bottom panel in Figure 3b and Table 3). For 6 out of the 14 ROIs, the null hypothesis was more than 3 times more likely than the alternative hypothesis.

Furthermore, for the present temporal binding task, action observation was specifically elicited by the key press of the avatar hand in the operant trials. Thus, the particular ROIs associated with action observation of the avatar hand were defined as regions showing significantly stronger activation in the operant condition relative to the baseline in the pre-test for all participants (voxel-wise uncorrected $p < .005$ and cluster size > 10), and bilateral LOTC were selected (top panel in Figure 3c and Table 3; L LOTC: 144 voxels, R LOTC: 211 voxels). We did not obtain significant group differences in these two ROIs (*p*s >.05 with BF = 0.607 and 0.354, respectively; bottom panel in Figure 3c and Table 3). In sum, ROI analyses failed to support that the temporal binding is associated with neural response changes in observation-related regions.

Table 3. Between-group comparison for ROI signals in regions associated with the observation of general hand actions (Caspers et al., 2010) and the avatar hand actions (operant condition) in the pre-test.

	Brain regions	**MNI coordinates**			***t***	***p***	**Cohen's *d***	**BF**
		x	***y***	***z***				
General hand actions	Left IFG / PrG	-50	6	30	–.34	.733	–.10	.312
	Left lat dPMC	-26	-4	56	–1.02	.312	–.31	.454
	Left SI / IPS	-36	-42	36	–.94	.352	–.28	.425
	Left IPL	-58	-24	36	.26	.795	.08	.306
	Left STS / pMTG	-56	-48	10	–.83	.411	–.25	.393
	Left lat occipital	-46	-70	4	–1.47	.149	–.44	.705
	Right IFG / PrG	52	8	36	–1.29	.205	–.39	.577
	Right IFG	56	30	-4	1.68	.101	.51	.912
	Right lat dPMC / MFG	36	0	54	–1.43	.162	–.43	.647
	Right SI	42	-34	46	–.14	.892	–.04	.300
	Right IPL	60	-26	42	.83	.411	.25	.393
	Right SPL	22	-62	64	.07	.944	.02	.298
	Right STS / pMTG	52	-60	4	–.33	.741	–.10	.311
	Right lat occipital	50	-66	0	–0.44	.664	–.13	.322
Avatar hand actions	Left LOTC	-52	-66	2	–1.36	.181	–.41	.607
	Right LOTC	50	-66	-4	–.66	.515	–.20	.354

IFG: inferior frontal gyrus, PrG: precentral gyrus, dPMC: dorsal premotor cortex, SI: primary somatosensory cortex, IPS: intraparietal sulcus, IPL: inferior parietal lobule, STS: superior temporal sulcus, pMTG: posterior middle temporal gyrus, MFG: middle frontal gyrus, SPL: superior parietal lobule, LOTC: lateral occipitotemporal cortex, lat: lateral.

Discussion

We examined the brain activation pattern supporting SoA elicited by “embodied” observation as opposed to voluntary action, using the classical temporal binding paradigm before and after VR exposure. Behaviorally, we replicated our previous findings that controlling an avatar for a short period of time gives people an illusive SoA over the avatar hand: when the actual hand stays immobile, the avatar's hand movement leads to an increased temporal binding that has been traditionally associated with the intentionality of voluntary actions (Kong et al., 2017). Extending the previous finding, here we show that this VR embodiment effect persists after exiting the VR setting and remains robust when the same avatar hand is then depicted in a two-dimensional display in the fMRI scanner. Our neuroimaging results indicate that the binding effect observed in the experimental group is associated with increased activation in a cluster centered at the right angular gyrus, extending to the inferior parietal lobule and precuneus. Furthermore, typical areas related to voluntary action-elicited SoA, especially those frontal or prefrontal areas involved in motor planning or intentionality, are not implicated. The action observation network is also not implicated. As expected, the revealed neural correlates for VR-induced SoA are distinct from neural correlates for other VR-induced self-consciousness changes such as bodily ownership and self-localization. Our findings suggest that the temporal binding elicited by experience of controlling a virtual body is unlikely subserved by sensorimotor processes associated with voluntary actions or action observation, and SoA by non-action has its distinct neural representations.

The enhanced temporal binding is unlikely to be explained away by mere use of VR or repeated testing of the temporal binding task. The control group, who had similar VR experience but had no controlling experience of the avatar hand, did not show enhanced SoA. The other trivial

explanation for the enhanced SoA is so-called ideomotor learning, which refers to the learning of the association between action and its effect (Elsner & Hommel, 2001). After ideomotor learning, if presented with the action effect without actual action, the learner would show increased activation in various motor areas, including premotor and somatosensory cortices, SMA, and cerebellum (Kuhn et al., 2011; Melcher et al., 2008). However, we did not observe the same motor activation when our participants passively heard the tone, the action effect of the avatar. Thus, the enhanced temporal binding after controlling the avatar hand was unlikely explained by ideomotor learning either. The increase in temporal binding, induced without a voluntary action after "embodying" the avatar hand, is in line with the causal account of SoA that the acquired association and/or causality between action and its sensory event is sufficient to generate SoA (Buehner & Humphreys, 2009; Desantis et al., 2011).

Importantly, the SoA from VR exposure enabled us to reveal distinct neural underpinning of SoA from non-actions. Previous investigations have extensively examined the activation foci for SoA by contrasting condition pairs with presumably different levels of SoA, i.e., voluntary action versus rest, voluntary action versus stimulus-driven action, actions with higher visuomotor congruency versus those with lower congruency (see a recent review, Seghezzi et al., 2019). Of note, all these contrasting analyses involve voluntary actions. Thus the identified extensive brain network for SoA includes sensorimotor areas, especially those related to action intentionality and motor planning (Seghezzi et al., 2019). For example, dorsolateral prefrontal cortex is associated with action selection (Khalighinejad et al., 2016), pre-SMA with the intentionality (Yomogida et al., 2010; Zapparoli et al., 2018) and the temporal binding in particular (Kuhn et al., 2013), and SMA proper with motor planning and initiation (Passingham & Lau, 2019). All these prefrontal and frontal areas, dealing with generating action before action feedback, returned null effect in our

analyses, supporting that the observed SoA from non-actions does not involves action selection and planning.

Instead, our experiment showed that the SoA in the absence of voluntary action can be attributed to right AG (extended to IPL and precuneus), a cluster not directly tied to intentionality, motor planning and initiation, or action observation. Right AG and IPL have been previously associated with prospective SoA, i.e., the feeling or judgement of agency *after* action. This is consistent with SoA in the absence of action in our experiment: the temporal binding effect is elicited by observing the avatar's movement, which invokes post-hoc processing of "actions". Indeed, right AG has been associated with awareness of the mismatch between intended and actual action consequences and with explicit judgement of agency, both occurring after action (Chambon et al., 2013; Farrer et al., 2003, 2008; Farrer & Frith, 2002). For right IPL, it not only involved in explicit judgement of agency but also in various types of causal processing. Explicit judgment of both physical and social causality involves neural activations in right IPL, along with other areas (Renes et al., 2015; Wende et al., 2013). Even seeing a causal event, such as object collision, elicits more activations in right IPL than seeing a non-causal event such as object launching (Fugelsang et al., 2005). Relatedly, anosognosia patients who have illusive agency over non-actions and often assert that they performed an action with their paralyzed, immobile limb (Fotopoulou et al., 2008) typically have lesions in the right parietal lobule. These previous findings thus imply that both right AG and right IPL are involved in post-hoc attribution of causality for perceptual events and agency. Thus, the fact that they are involved in the SoA arising in the absence of voluntary action lends indirect support for the causal account of action awareness, which emphasizes the involvement of retrospective processing of causality in generating SoA (Buehner & Humphreys, 2009; Desantis et al., 2011; Tramacere, 2021; Wegner, 2003; Wegner & Wheatley, 1999).

Right AG has been implicated in SoA studies based on voluntary actions for long. A recent meta-analysis described it as a common region for processing motor intention and SoA (Seghezzi et al., 2019). Other meta-analyses of neuroimaging studies emphasize that the role of TPJ, with right AG included, in attributing agency to others (external agency, Sperduti et al., 2011) or the reduction of SoA (negative agency, Zito et al., 2020). While our ROI analysis found that the right AG estimated by these studies was marginally significant, it is noteworthy that the peak of the right AG we estimated in the context of an absence of voluntary action was 13.2mm away from the peak estimated from the meta-analysis based on voluntary action-related SoA (Seghezzi et al., 2019). Thus, the SoA driven by retrospective processing of action feedback, shown by the current VR setting, and the SoA driven by both prospective processes (e.g., action intentionality and planning) and retrospective processing, shown by the meta-analysis, converge on the right AG. Whether the retrospective processing of action feedback from both voluntary actions and observation are computed by the same mechanisms here in the AG region desires further investigations.

The enhanced SoA arguably reflects a change of self-consciousness after controlling an avatar body in VR. Indeed, VR affects users' self-consciousness (Banakou & Slater, 2014; Slater et al., 2009). With a brief exposure to VR, people erroneously feel that they own a virtual body part or even a full virtual body (Blanke et al., 2015; Petkova et al., 2011), mislocate themselves (Ehrsson, 2007), or change the perception of one's identity (Banakou et al., 2013; Petkova et al., 2011). Neuroimaging studies have shown that premotor cortex and TPJ are key areas for bodily ownership (Bekrater-Bodmann et al., 2014; Pamplona et al., 2022) and self-location (Ionta et al., 2011; Lenggenhager et al., 2011). However, the neural substrate of agency changes in VR has not been explored before. Our findings provide compelling evidence that sensorimotor control experience

with an avatar can lead to agency changes whose neural correlates center at the right AG, a key area that is also associated with SoA arising from actions in real settings. Given this cluster covers high-order associative regions, we postulate that the VR embodiment effect is potentially generalizable to other tasks beyond the temporal binding. For instance, SoA arising from voluntary actions contributes to perceptual attenuation of action-induced sensory stimuli (Blakemore et al., 1998; Shergill et al., 2005) or self-other distinction (Kahl & Kopp, 2018). Whether these perceptual tasks are affected by similar avatar-control experience in VR warrants further investigations.

Our findings raised possible problems for the era of VR or metaverse. First, despite that our participants did not change their self-reported explicit SoA with the brief VR experience, it is still possible that people's explicit judgment of agency can be modulated by long-term VR use. Second, individuals with neurological and psychiatric disorders experience disrupted SoA and illusions in their daily life (Edwards & Bhatia, 2012; Frith et al., 2000), and even neurotypical individuals can occasionally experience faulty SoA, say, with sensory priming (Aarts et al., 2005; Wegner & Wheatley, 1999). Whether certain population's self-consciousness is negatively affected by the experience of controlling an avatar is an important open question from the perspective of psychopathology. Third, given the observed immediate behavioral and neural effect of an embodied avatar on SoA, we expect that unintended "actions" of the avatar, accidentally caused by technical glitches in the virtual worlds, might affect the avatar owner's SoA and even lead to psychological harm (Cheong, 2022). These novel scenarios might lead to potential legal issues about how to account for the responsibility of compromising someone's sense of agency in the metaverse.

In conclusion, SoA arising in the absence of voluntary action is subserved not by traditional sensorimotor areas (e.g., pre-SMA) implicated by studies on SoA arising from voluntary actions. The two types of SoA, though, share the right AG as their common node, consistent with its role in action awareness. Given that people's sense of agency over an avatar can be built up, both behaviorally and neurologically, by a brief period of avatar control in immersive VR, how the embodiment of virtual body affects our self-consciousness and other psychological constructs would pose as a novel problem when our populace spends increasing time in virtual or digital worlds.

Reference

Aarts, H., Custers, R., & Wegner, D. M. (2005). On the inference of personal authorship: Enhancing experienced agency by priming effect information. *Consciousness and Cognition*, *14*(3), 439–458. https://doi.org/10.1016/j.concog.2004.11.001

Bach, F., Cakmak, H., Maass, H., Bekrater-Bodmann, R., Foell, J., Diers, M., Trojan, J., Fuchs, X., & Flor, H. (2012). Illusory Hand Ownership Induced by an MRI Compatible Immersive Virtual Reality Device. *Biomedical Engineering-Biomedizinische Technik*, *57*, 718–720. https://doi.org/10.1515/bmt-2012-4084

Balslev, D., Nielsen, F. A., Lund, T. E., Law, I., & Paulson, O. B. (2006). Similar brain networks for detecting visuo-motor and visuo-proprioceptive synchrony. *Neuroimage*, *31*(1), 308–312. https://doi.org/10.1016/j.neuroimage.2005.11.037

Banakou, D., Groten, R., & Slater, M. (2013). Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. *Proceedings of the National Academy of Sciences*, *110*(31), 12846–12851. https://doi.org/10.1073/pnas.1306779110

Banakou, D., & Slater, M. (2014). Body ownership causes illusory self-attribution of speaking and influences subsequent real speaking. *Proceedings of the National Academy of Sciences*, *111*(49), 17678–17683. https://doi.org/10.1073/pnas.1414936111

Bekrater-Bodmann, R., Foell, J., Diers, M., Kamping, S., Rance, M., Kirsch, P., Trojan, J., Fuchs, X., Bach, F., Çakmak, H. K., Maaß, H., & Flor, H. (2014). The Importance of Synchrony and Temporal Order of Visual and Tactile Input for Illusory Limb Ownership Experiences – An fMRI Study Applying Virtual Reality. *PLoS ONE*, *9*(1), e87013. https://doi.org/10.1371/journal.pone.0087013

Binkofski, F., & Buccino, G. (2006). The role of ventral premotor cortex in action execution and action understanding. *Journal of Physiology-Paris*, *99*(4–6), 396–405. https://doi.org/10.1016/j.jphysparis.2006.03.005

Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, *1*(7), 635–640. https://doi.org/10.1038/2870

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, *88*(1), 145–166. https://doi.org/10.1016/j.neuron.2015.09.029

Buehner, M. J. (2012). Understanding the Past, Predicting the Future: Causation, Not Intentional Action, Is the Root of Temporal Binding. *Psychological Science*, *23*(12), 1490–1497. https://doi.org/10.1177/0956797612444612

Buehner, M. J., & Humphreys, G. R. (2009). Causal Binding of Actions to Their Effects. *Psychological Science*, *20*(10), 1221–1228. https://doi.org/10.1111/j.1467-9280.2009.02435.x

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, *50*(3), 1148–1167. https://doi.org/10.1016/j.neuroimage.2009.12.112

Chambon, V., Wenke, D., Fleming, S. M., Prinz, W., & Haggard, P. (2013). An Online Neural Substrate for Sense of Agency. *Cerebral Cortex*, *23*(5), 1031–1037. https://doi.org/10.1093/cercor/bhs059

Charalampaki, A., Karabanov, A. N., Ritterband-Rosenbaum, A., Nielsen, J. B., Siebner, H. R., & Christensen, M. S. (2022). Sense of agency as synecdoche: Multiple neurobiological mechanisms may underlie the phenomenon summarized as sense of agency.

Consciousness and Cognition, *101*, 103307. https://doi.org/10.1016/j.concog.2022.103307

Cheong, B. C. (2022). Avatars in the metaverse: Potential legal issues and remedies. *International Cybersecurity Law Review*, *Journal Article*. https://doi.org/10.1365/s43439-022-00056-9

David, N., Cohen, M. X., Newen, A., Bewernick, B. H., Shah, N. J., Fink, G. R., & Vogeley, K. (2007). The extrastriate cortex distinguishes between the consequences of one's own and others' behavior. *Neuroimage*, *36*(3), 1004–1014. https://doi.org/10.1016/j.neuroimage.2007.03.030

de Bezenac, C. E., Sluming, V., Gouws, A., & Corcoran, R. (2016). Neural response to modulating the probability that actions of self or other result in auditory tones: A parametric fMRI study into causal ambiguity. *Biological Psychology*, *119*, 64–78. https://doi.org/10.1016/j.biopsycho.2016.07.003

Desantis, A., Roussel, C., & Waszak, F. (2011). On the influence of causal beliefs on the feeling of agency. *Consciousness and Cognition*, *20*(4), 1211–1220. https://doi.org/10.1016/j.concog.2011.02.012

Di Plinio, S., Perrucci, M. G., Aleman, A., & Ebisch, S. J. H. (2020). I am Me: Brain systems integrate and segregate to establish a multidimensional sense of self. *Neuroimage*, *205*, 116284. https://doi.org/10.1016/j.neuroimage.2019.116284

Edwards, M. J., & Bhatia, K. P. (2012). Functional (psychogenic) movement disorders: Merging mind and brain. *Lancet Neurology*, *11*(3), 250–260. https://doi.org/10.1016/S1474-4422(11)70310-6

Ehrsson, H. H. (2007). The Experimental Induction of Out-of-Body Experiences. *Science*, *317*(5841), 1048–1048. https://doi.org/10.1126/science.1142175

Elsner, B., & Hommel, B. (2001). Effect anticipation and action control. *Journal of Experimental Psychology-Human Perception and Performance*, *27*(1), 229–240. https://doi.org/10.1037/0096-1523.27.1.229

Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J., & Jeannerod, A. (2003). Modulating the experience of agency: A positron emission tomography study. *Neuroimage*, *18*(2), 324–333. https://doi.org/10.1016/S1053-8119(02)00041-1

Farrer, C., Frey, S. H., Van Horn, J. D., Tunik, E., Turk, D., Inati, S., & Grafton, S. T. (2008). The Angular Gyrus Computes Action Awareness Representations. *Cerebral Cortex*, *18*(2), 254–261. https://doi.org/10.1093/cercor/bhm050

Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs another person as being the cause of an action: The neural correlates of the experience of agency. *Neuroimage*, *15*(3), 596–603. https://doi.org/10.1006/nimg.2001.1009

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/bf03193146

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012). A Sensorimotor Network for the Bodily Self. *Journal of Cognitive Neuroscience*, *24*(7), 1584–1595. https://doi.org/10.1162/jocn_a_00230

Fotopoulou, A., Tsakiris, M., Haggard, P., Vagopoulou, A., Rudd, A., & Kopelman, M. (2008). The role of motor intention in motor awareness: An experimental study on anosognosia for hemiplegia. *Brain*, *131*, 3432–3442. https://doi.org/10.1093/brain/awn225

Frith, C. D. (2005). The self in action: Lessons from delusions of control. *Consciousness and Cognition*, *14*(4), 752–770. https://doi.org/10.1016/j.concog.2005.04.002

Frith, C. D., Blakemore, S. J., & Wolpert, D. M. (2000). Explaining the symptoms of schizophrenia: Abnormalities in the awareness of action. *Brain Research Reviews*, *31*(2–3), 357–363. https://doi.org/10.1016/S0165-0173(99)00052-1

Fugelsang, J. A., Roser, M. E., Corballis, P. M., Gazzaniga, M. S., & Dunbar, K. N. (2005). Brain mechanisms underlying perceptual causality. *Cognitive Brain Research*, *24*(1), 41–47. https://doi.org/10.1016/j.cogbrainres.2004.12.001

Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, *18*(4), 196–207. https://doi.org/10.1038/nrn.2017.14

Haggard, P., Clark, S., & Kalogeras, J. (2002). Voluntary action and conscious awareness. *Nature Neuroscience*, *5*(4), 382–385. https://doi.org/10.1038/nn827

Haggard, P., & Tsakiris, M. (2009). The Experience of Agency: Feelings, Judgments, and Responsibility. *Current Directions in Psychological Science*, *18*(4), 242–246. https://doi.org/10.1111/j.1467-8721.2009.01644.x

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(25), 15061–15065. https://doi.org/10.1073/pnas.95.25.15061

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R., & Blanke, O. (2011). Multisensory Mechanisms in Temporo-Parietal Cortex Support Self-Location and First-Person Perspective. *Neuron*, *70*(2), 363–374. https://doi.org/10.1016/j.neuron.2011.03.009

Kahl, S., & Kopp, S. (2018). A Predictive Processing Model of Perception and Action for Self-Other Distinction. *Frontiers in Psychology*, *9*, 2421. https://doi.org/10.3389/fpsyg.2018.02421

Khalighinejad, N., Di Costa, S., & Haggard, P. (2016). Endogenous Action Selection Processes in Dorsolateral Prefrontal Cortex Contribute to Sense of Agency: A Meta-Analysis of tDCS Studies of 'Intentional Binding.' *Brain Stimulation*, *9*(3), 372–379. https://doi.org/10.1016/j.brs.2016.01.005

Kikuchi, T., Sugiura, M., Yamamoto, Y., Sasaki, Y., Hanawa, S., Sakuma, A., Matsumoto, K., Matsuoka, H., & Kawashima, R. (2019). Neural responses to action contingency error in different cortical areas are attributable to forward prediction or sensory processing. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-46350-1

Kong, G., He, K., & Wei, K. (2017). Sensorimotor experience in virtual reality enhances sense of agency associated with an avatar. *Consciousness and Cognition*, *52*, 115–124. https://doi.org/10.1016/j.concog.2017.04.018

Kuhn, S., Brass, M., & Haggard, P. (2013). Feeling in control: Neural correlates of experience of agency. *Cortex*, *49*(7), 1935–1942. https://doi.org/10.1016/j.cortex.2012.09.002

Kuhn, S., Keizer, A. W., Colzato, L. S., Rombouts, S. A. R. B., & Hommel, B. (2011). The Neural Underpinnings of Event-file Management: Evidence for Stimulus-induced Activation of and Competition among Stimulus-Response Bindings. *Journal of Cognitive Neuroscience*, *23*(4), 896–904. https://doi.org/10.1162/jocn.2010.21485

Lenggenhager, B., Halje, P., & Blanke, O. (2011). Alpha band oscillations correlate with illusory self-location induced by virtual reality. *European Journal of Neuroscience*, *33*(10), 1935–1943. https://doi.org/10.1111/j.1460-9568.2011.07647.x

Leube, D. T., Knoblich, G., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. J. (2003). The neural correlates of perceiving one's own movements. *Neuroimage*, *20*(4), 2084–2090. https://doi.org/10.1016/j.neuroimage.2003.07.033

Leube, D. T., Knoblich, G., Erb, M., & Kircher, T. T. J. (2003). Observing one's hand become anarchic: An fMRI study of action identification. *Consciousness and Cognition*, *12*(4), 597–608. https://doi.org/10.1016/S1053-8100(03)00079-5

Matsuzawa, M., Matsuo, K., Sugio, T., Kato, C., & Nakai, T. (2005). Temporal Relationship between Action and Visual Outcome Modulates Brain Activation: An fMRI Study. *Magnetic Resonance in Medical Sciences*, *4*(3), 115–121. https://doi.org/10.2463/mrms.4.115

Melcher, T., Weidema, M., Eenshuistra, R. M., Hommel, B., & Gruber, O. (2008). The neural substrate of the ideomotor principle: An event-related fMRI analysis. *Neuroimage*, *39*(3), 1274–1288. https://doi.org/10.1016/j.neuroimage.2007.09.049

Molnar-Szakacs, I., Kaplan, J., Greenfield, P. M., & Iacoboni, M. (2006). Observing complex action sequences: The role of the fronto-parietal mirror neuron system. *Neuroimage*, *33*(3), 923–935. https://doi.org/10.1016/j.neuroimage.2006.07.035

Nahab, F. B., Kundu, P., Gallea, C., Kakareka, J., Pursley, R., Pohida, T., Miletta, N., Friedman, J., & Hallett, M. (2011). The Neural Processes Underlying Self-Agency. *Cerebral Cortex*, *21*(1), 48–55. https://doi.org/10.1093/cercor/bhq059

Ohata, R., Asai, T., Kadota, H., Shigemasu, H., Ogawa, K., & Imamizu, H. (2020). Sense of Agency Beyond Sensorimotor Process: Decoding Self-Other Action Attribution in the Human Brain. *Cerebral Cortex*, *30*(7), 4076–4091. https://doi.org/10.1093/cercor/bhaa028

Pamplona, G. S. P., Salgado, J. A. D., Staempfli, P., Seifritz, E., Gassert, R., & Ionta, S. (2022). Illusory Body Ownership Affects the Cortical Response to Vicarious Somatosensation. *Cerebral Cortex*, *32*(2), 312–328. https://doi.org/10.1093/cercor/bhab210

Passingham, R. E., & Lau, H. C. (2019). Acting, seeing, and conscious awareness. *Neuropsychologia*, *128*, 241–248. https://doi.org/10.1016/j.neuropsychologia.2017.06.012

Petkova, V. I., Bjornsdotter, M., Gentile, G., Jonsson, T., Li, T.-Q., & Ehrsson, H. H. (2011). From Part- to Whole-Body Ownership in the Multisensory Brain. *Current Biology*, *21*(13), 1118–1122. https://doi.org/10.1016/j.cub.2011.05.022

Renes, R. A., Van Haren, N. E. M., Aarts, H., & Vink, M. (2015). An exploratory fMRI study into inferences of self-agency. *Social Cognitive and Affective Neuroscience*, *10*(5), 708–712. https://doi.org/10.1093/scan/nsu106

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*(2), 131–141. https://doi.org/10.1016/0926-6410(95)00038-0

Sasaki, A. T., Okamoto, Y., Kochiyama, T., Kitada, R., & Sadato, N. (2018). Distinct sensitivities of the lateral prefrontal cortex and extrastriate body area to contingency between executed and observed actions. *Cortex*, *108*, 234–251. https://doi.org/10.1016/j.cortex.2018.08.003

Schnell, K., Heekeren, K., Schnitker, R., Daumann, J., Weber, J., Hesselmann, V., Moeller-Hartmann, W., Thron, A., & Gouzoulis-Mayfrank, E. (2007). An fMRI approach to particularize the frontoparietal network for visuomotor action monitoring: Detection of incongruence between test subjects' actions and resulting perceptions. *Neuroimage*, *34*(1), 332–341. https://doi.org/10.1016/j.neuroimage.2006.08.027

Seghezzi, S., Zirone, E., Paulesu, E., & Zapparoli, L. (2019). The Brain in (Willed) Action: A Meta-Analytical Comparison of Imaging Studies on Motor Intentionality and Sense of Agency. *Frontiers in Psychology*, *10*, 804. https://doi.org/10.3389/fpsyg.2019.00804

Shergill, S. S., Samson, G., Bays, P. M., Frith, C. D., & Wolpert, D. M. (2005). Evidence for sensory prediction deficits in schizophrenia. *American Journal of Psychiatry*, *162*(12), 2384–2386. https://doi.org/10.1176/appi.ajp.162.12.2384

Slater, M., Perez-Marcos, D., Ehrsson, H. H., & Sanchez-Vives, M. V. (2009). Inducing illusory ownership of a virtual body. *Frontiers in Neuroscience*, *3*(2), 214–220. https://doi.org/10.3389/neuro.01.029.2009

Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Was it me or was it you? How the sense of agency originates from ideomotor learning revealed by fMRI. *Neuroimage*, *46*(1), 290–298. https://doi.org/10.1016/j.neuroimage.2009.01.047

Sperduti, M., Delaveau, P., Fossati, P., & Nadel, J. (2011). Different brain structures related to self- and external-agency attribution: A brief review and meta-analysis. *Brain Structure & Function*, *216*(2), 151–157. https://doi.org/10.1007/s00429-010-0298-1

Straube, B., Van Kemenade, B. M., Arikan, B. E., Fiehler, K., Leube, D. T., Harris, L. R., & Kircher, T. (2017). Predicting the Multisensory Consequences of One's Own Action: BOLD Suppression in Auditory and Visual Cortices. *PLoS ONE*, *12*(1), e0169131. https://doi.org/10.1371/journal.pone.0169131

Suzuki, K., Lush, P., Seth, A. K., & Roseboom, W. (2019). Intentional Binding Without Intentional Action. *Psychological Science*, *30*(6), 842–853. https://doi.org/10.1177/0956797619842191

Tramacere, A. (2021). A causal view of the sense of agency. *Philosophical Psychology*, 1–24. https://doi.org/10.1080/09515089.2021.1985102

Tsakiris, M., Longo, M. R., & Haggard, P. (2010). Having a body versus moving your body: Neural signatures of agency and body-ownership. *Neuropsychologia*, *48*(9), 2740–2749. https://doi.org/10.1016/j.neuropsychologia.2010.05.021

Uhlmann, L., Pazen, M., Kemenade, B. M., Steinsträter, O., Harris, L. R., Kircher, T., & Straube, B. (2020). Seeing your own or someone else's hand moving in accordance with your action: The neural interaction of agency and hand identity. *Human Brain Mapping*, *41*(9), 2474–2489. https://doi.org/10.1002/hbm.24958

van Kemenade, B. M., Arikan, B. E., Kircher, T., & Straube, B. (2017). The angular gyrus is a supramodal comparator area in action-outcome monitoring. *Brain Structure & Function*, *222*(8), 3691–3703. https://doi.org/10.1007/s00429-017-1428-9

van Kemenade, B. M., Arikan, B. E., Podranski, K., Steinstraeter, O., Kircher, T., & Straube, B. (2019). Distinct Roles for the Cerebellum, Angular Gyrus, and Middle Temporal Gyrus in Action-Feedback Monitoring. *Cerebral Cortex*, *29*(4), 1520–1531. https://doi.org/10.1093/cercor/bhy048

Wegner, D. M. (2003). The mind's best trick: How we experience conscious will. *Trends in Cognitive Sciences*, *7*(2), 65–69. https://doi.org/10.1016/S1364-6613(03)00002-0

Wegner, D. M., & Wheatley, T. (1999). Apparent mental causation—Sources of the experience of will. *American Psychologist*, *54*(7), 480–492. https://doi.org/10.1037/0003-066X.54.7.480

Wende, K. C., Nagels, A., Blos, J., Stratmann, M., Chatterjee, A., Kircher, T., & Straube, B. (2013). Differences and commonalities in the judgment of causality in physical and social contexts: An fMRI study. *Neuropsychologia*, *51*(13), 2572–2580. https://doi.org/10.1016/j.neuropsychologia.2013.07.027

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An Internal Model for Sensorimotor Integration. *Science*, *269*(5232), 1880–1882. https://doi.org/10.1126/science.7569931

Xia, M., Wang, J., & He, Y. (2013). BrainNet Viewer: A Network Visualization Tool for Human Brain Connectomics. *PLoS ONE*, *8*(7), e68910. https://doi.org/10.1371/journal.pone.0068910

Yomogida, Y., Sugiura, M., Sassa, Y., Wakusawa, K., Sekiguchi, A., Fukushima, A., Takeuchi, H., Horie, K., Sato, S., & Kawashima, R. (2010). The neural basis of agency: An fMRI study. *Neuroimage*, *50*(1), 198–207. https://doi.org/10.1016/j.neuroimage.2009.12.054

Zapparoli, L., Seghezzi, S., Scifo, P., Zerbi, A., Banfi, G., Tettamanti, M., & Paulesu, E. (2018). Dissecting the neurofunctional bases of intentional action. *Proceedings of the National Academy of Sciences*, *115*(28), 7440–7445. https://doi.org/10.1073/pnas.1718891115

Zapparoli, L., Seghezzi, S., Zirone, E., Guidali, G., Tettamanti, M., Banfi, G., Bolognini, N., & Paulesu, E. (2020). How the effects of actions become our own. *Science Advances*, *6*(27), eaay8301. https://doi.org/10.1126/sciadv.aay8301

Zito, G. A., Wiest, R., & Aybek, S. (2020). Neural correlates of sense of agency in motor control: A neuroimaging meta-analysis. *PLoS ONE*, *15*(6), e0234321. https://doi.org/10.1371/journal.pone.0234321

Supplemental Material

Selection of subgroup participants

We noticed that the two groups tended to differ in the binding effect at pre-test, though statistically insignificant (t_{42}= 1.616, p = .113; see Figure 2c). To test group differences in the neuroimaging data robustly, we randomly selected 18 participants from each group to match their pre-test performance. A pair of exemplary subgroups (see Figure 2d), were selected to validate the results of whole-group participants.

Behavioral results of subgroup participants

The temporal binding effects

The mixed ANOVA of the temporal binding effects revealed a significant Group*Phase interaction ($F_{1, 34}$ = 5.913, p = .020) and a significant main effect of Phase ($F_{1, 34}$ = 24.363, p < .001), while the main effect of Group was not significant ($F_{1, 34}$ = .950, p = .337). The Group*Phase interaction was further examined by post hoc comparisons, with participants from experimental group showing larger temporal binding effects in the post-test (M = -113.67, $S.E.$ = 10.61) than in the pre-test (M = -59.69, $S.E.$ = 12.26): t_{34}= 5.210, Bonferroni-corrected p <.001, Cohen's d = 1.246. The temporal binding effects of control group showed no significant difference between the post-test (M = -81.02, $S.E.$ =10.61) and the pre-test (M = -63.01, $S.E.$ = 12.26): t_{34}= 1.771, Bonferroni-corrected p =.086, Cohen's d = .423.

The subjective feeling of SoA and SoO

For all the subgroup participants, the average scores of SoA-control were significantly higher than those of SoA (z = -2.759, p = .006), indicating that they correctly understood the instructions in

the questionnaire. The perceived SoA and SoO did not differ between two groups (z = -.448, p = .654 for SoA z = -.111, p = .911 for SoO).

As expected, the subjective SoA and SoO were positively correlated (ρ = .683, p < .001). However, neither of them was correlated the TB effect in the post-test and the TB changes between the pre- and post-test (ρ = -.224, p = .189 for SoA and TB effect in post-test; ρ = -.223, p = .191 for SoO and TB effect in post-test; ρ = -.082, p = .635 for SoA and TB changes; ρ = -.044, p = .800 for SoO and TB changes).

fMRI results of subgroup participants

Operant binding effects (operant versus baseline) in different conditions

For the subgroup participants, we generated whole-brain contrast images of the operant condition versus baseline, and contrasted these images within different phases (pre-test and post-test) and groups (experimental subgroup and control subgroup). Similar with the whole group analysis, only experimental subgroup showed no significant activation in the pre-test at a voxel-wise uncorrected threshold at p < .005 and a cluster-level FWE correction at p < .05 (Figure S1). Other three conditions still displayed similar activation in bilateral Occipito-temporal cortex (LOTC; Figure S1), replicating the general activation of operant condition relative to baseline from the whole group.

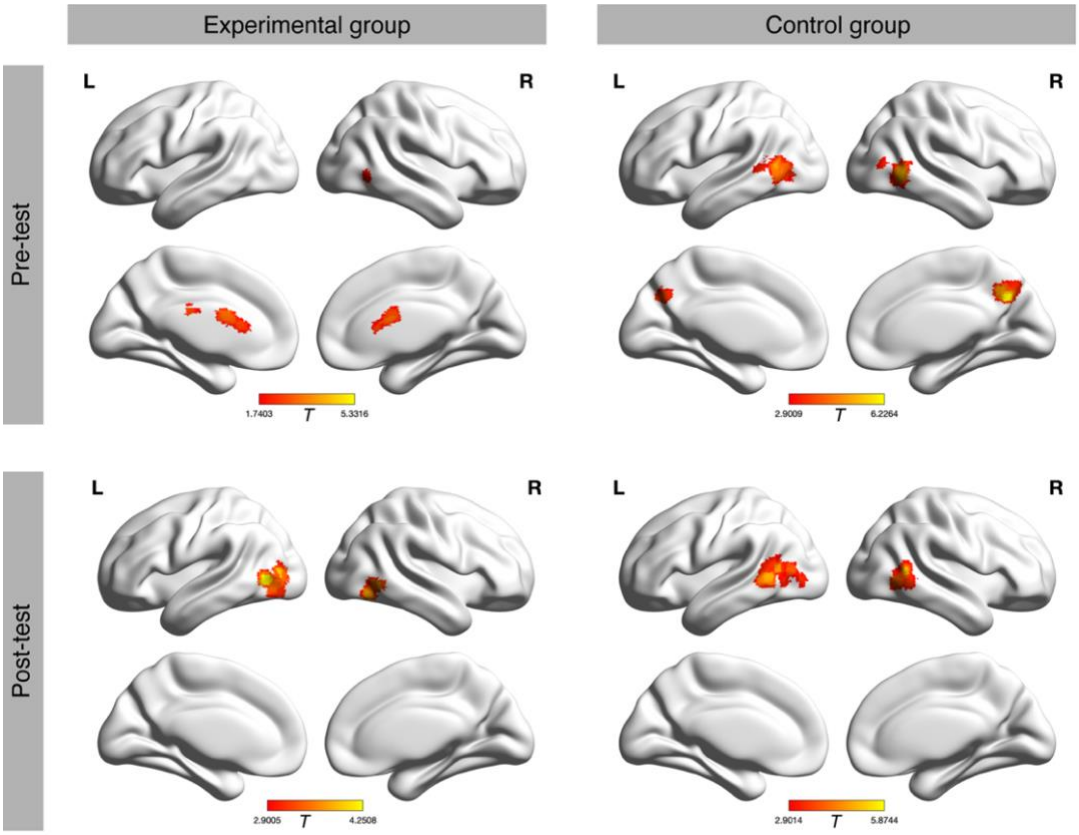


Figure S1. Whole-brain contrast images (visualized using BrainNet Viewer; Xia et al., 2013) of operant versus baseline under different phases (pre-test and post-test) in different subgroups (experimental subgroup and control subgroup). A lenient threshold was applied at voxel-wise uncorrected $p < .05$ and cluster size > 10 for the experimental subgroup in the pre-test, while threshold of other three conditions were applied at voxel-wise uncorrected $p < .005$ and cluster-level FWE correction at $p < .05$.

VR exposure-related neural (post-test versus pre-test) in different groups

For either the experimental subgroup or the control subgroup, no region displayed a significant effect between two phases (post-test versus pre-test and pre-test versus post-test; voxel-wise uncorrected threshold at $p < .005$ and cluster-level FWE correction at $p < .05$).

Between-subgroup comparison for VR exposure-related neural changes

The whole-group analysis revealed a significant VR exposure-related neural effect centered in the angular gyrus (Figure 2c). To verify this effect in the subgroup, we calculated the neural changes of this cluster and conducted a Group*Phase mixed ANOVA, showing a significant Group*Phase interaction ($F_{1, 34}$ = 15.355, p < .001), while the main effect of Group ($F_{1, 34}$ = .931, p = .174) and Phase ($F_{1, 34}$ = 1.158 p = .289) were not significant. Specifically, for the experimental subgroup, activation related to the operant versus baseline effects within this cluster increased from -3.359 (1.102) in the pre-test to 1.480 (1.220) in the post-test, while for the control subgroup, such activation decreased from 2.283 (1.102) in the pre-test to -.471 (1.220) in the post-test.

Correlation and regression analyses for neural changes and behavioral performance

Association between neural changes and temporal binding changes. The cluster at the right precuneus were selected to calculate the VR exposure-related neural changes for each participant. We then found a significant correlation between VR exposure-related neural changes and temporal binding changes (ρ = -.427, p = .009). In the regression, beta coefficients for group were statistically significant and positive (β = .477, p = .004), indicating a general group difference of neural changes. However, temporal binding changes showed insignificant predictability (β = -.211, p = .175). This suggested that the correlation between VR exposure-related neural changes and temporal changes was largely caused by group differences.

Association between neural changes and subjective feelings. VR exposure-related neural changes had no significant correlation with subjective feelings of SoA (ρ = .244, p = .152) or SoO (ρ = .138, p = .421).

Between-subgroup comparison for agency-related ROI signals

We did not obtain significant group difference in the all the agency-related ROIs (*All p*s >.05), but all the Bayes factors were above 1/3 but below 3, indicating that the data were insensitive whether the identified SoA-related regions could underlie the neural basis of observation-elicited SoA. See Table S1.

Table S1. Between-subgroup comparison for ROI signals in agency-related regions (Seghezzi et al., 2019).

Brain regions	**MNI coordinates**			***t***	***p***	**Cohen's *d***	**BF**
	x	***y***	***z***				
Supplementary motor area	-7	-4	69	–.85	.400	–.28	.427
Posterior insula	-41	2	1	–.37	.710	–.12	.340
Calcarine scissure	18	-90	-1	–.66	.516	–.22	.381
Inferior parietal lobule	-46	-48	51	–.56	.579	–.19	.364
Superior temporal gyrus	54	-49	22	–1.28	.210	–.43	.606
Angular gyrus	45	-60	43	–1.63	.112	–.54	.895
Cerebellum	24	-53	-27	–.75	.456	–.25	.402

Between-subgroup comparison for action observation-related ROI signals

We did not obtain significant group differences in the ROIs associated with the observation of general hand actions and bilateral LOTC (All *p*s >.05 and all BF < 1). Thus, there is no conclusive evidence for significant group difference.

Table S2. Between-group comparison for ROI signals in regions associated with the observation of general hand actions (Caspers et al., 2010) and the avatar hand actions (operant condition) in the pre-test.

	Brain regions	**MNI coordinates**			***t***	***p***	**Cohen's**	**BF**
		x	***y***	***z***			***d***	
General hand actions	Left IFG / PrG	-50	6	30	–.72	.481	–.24	.393
	Left lat dPMC	-26	-4	56	–.99	.332	–.33	.470
	Left SI / IPS	-36	-42	36	–1.04	.306	–.35	.489
	Left IPL	-58	-24	36	.25	.806	.08	.329
	Left STS / pMTG	-56	-48	10	–.88	.383	–.29	.436
	Left lat occipital	-46	-70	4	–1.64	.110	–.55	.906
	Right IFG / PrG	52	8	36	–1.66	.109	–.55	.922
	Right IFG	56	30	-4	1.63	.116	.54	.888
	Right lat dPMC / MFG	36	0	54	–1.26	.218	–.42	.597
	Right SI	42	-34	46	–.01	.990	–.00	.322
	Right IPL	60	-26	42	1.07	.292	.36	.504
	Right SPL	22	-62	64	.57	.576	.19	.364
	Right STS / pMTG	52	-60	4	–.78	.443	–.26	.407
	Right lat occipital	50	-66	0	–.83	.414	–.28	.420
Avatar hand actions	Left LOTC	-52	-66	2	–1.42	.166	–.47	.703
	Right LOTC	50	-66	-4	–.96	.345	–.32	.460

Reference

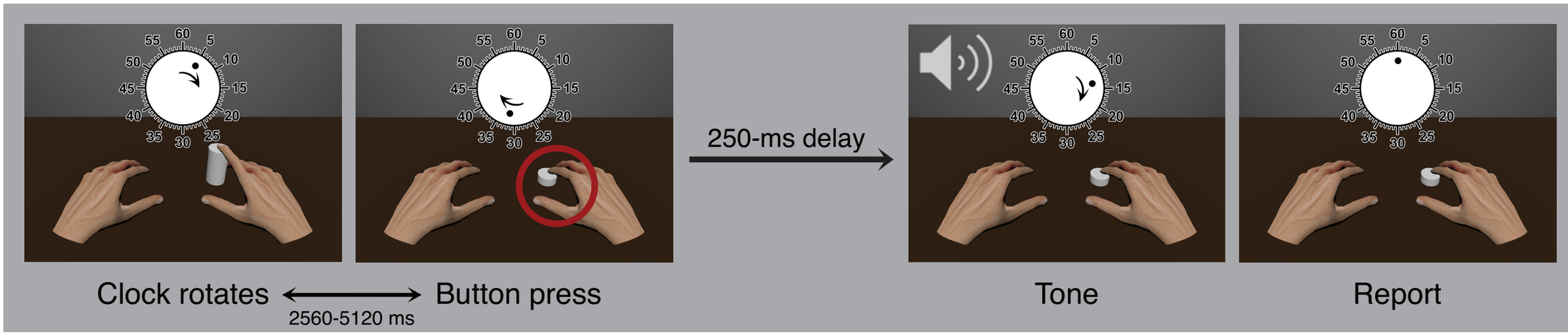
Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, *50*(3), 1148–1167. https://doi.org/10.1016/j.neuroimage.2009.12.112

Seghezzi, S., Zirone, E., Paulesu, E., & Zapparoli, L. (2019). The Brain in (Willed) Action: A Meta-Analytical Comparison of Imaging Studies on Motor Intentionality and Sense of Agency. *Frontiers in Psychology*, *10*, 804. https://doi.org/10.3389/fpsyg.2019.00804

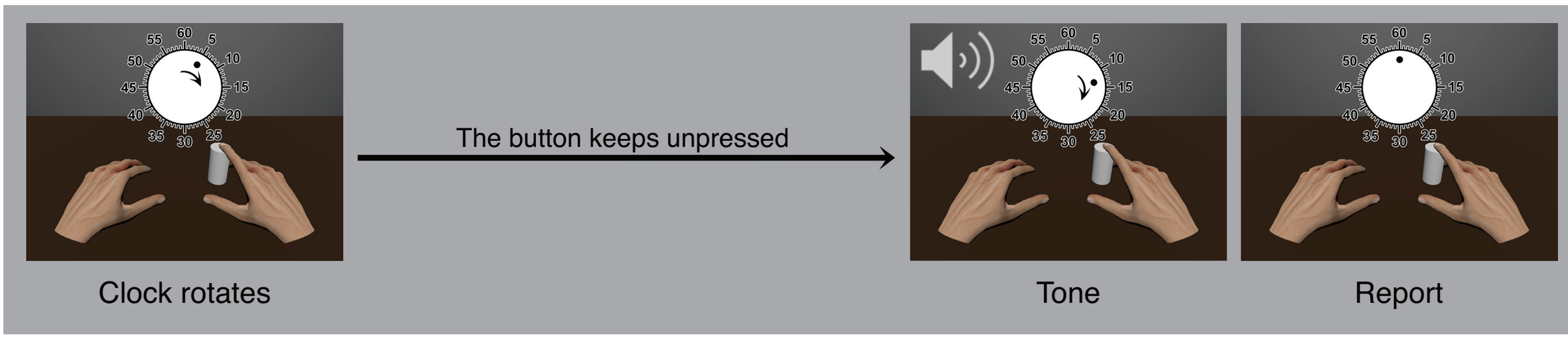
Xia, M., Wang, J., & He, Y. (2013). BrainNet Viewer: A Network Visualization Tool for Human Brain Connectomics. *PLoS ONE*, *8*(7), e68910. https://doi.org/10.1371/journal.pone.0068910

a

Operant Trial



Baseline Trial



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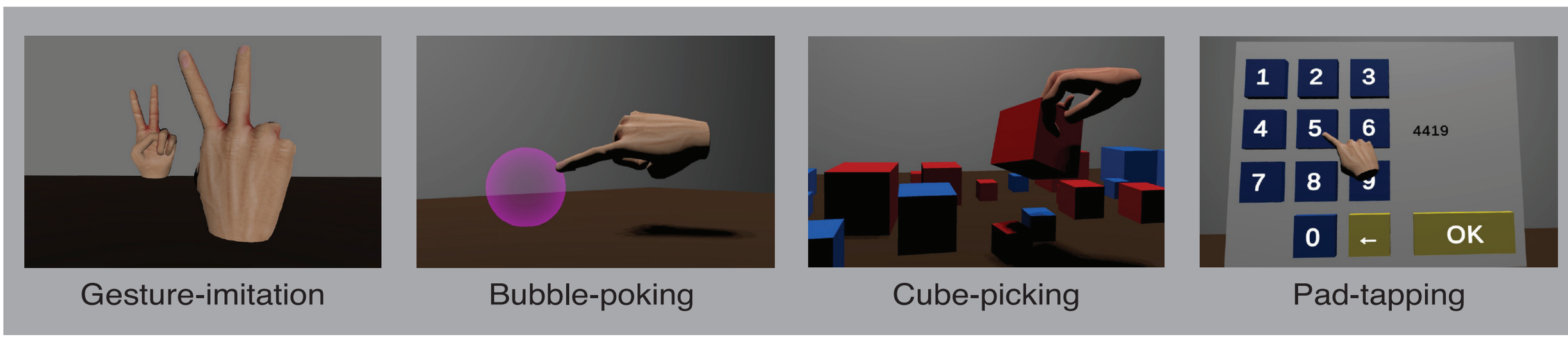

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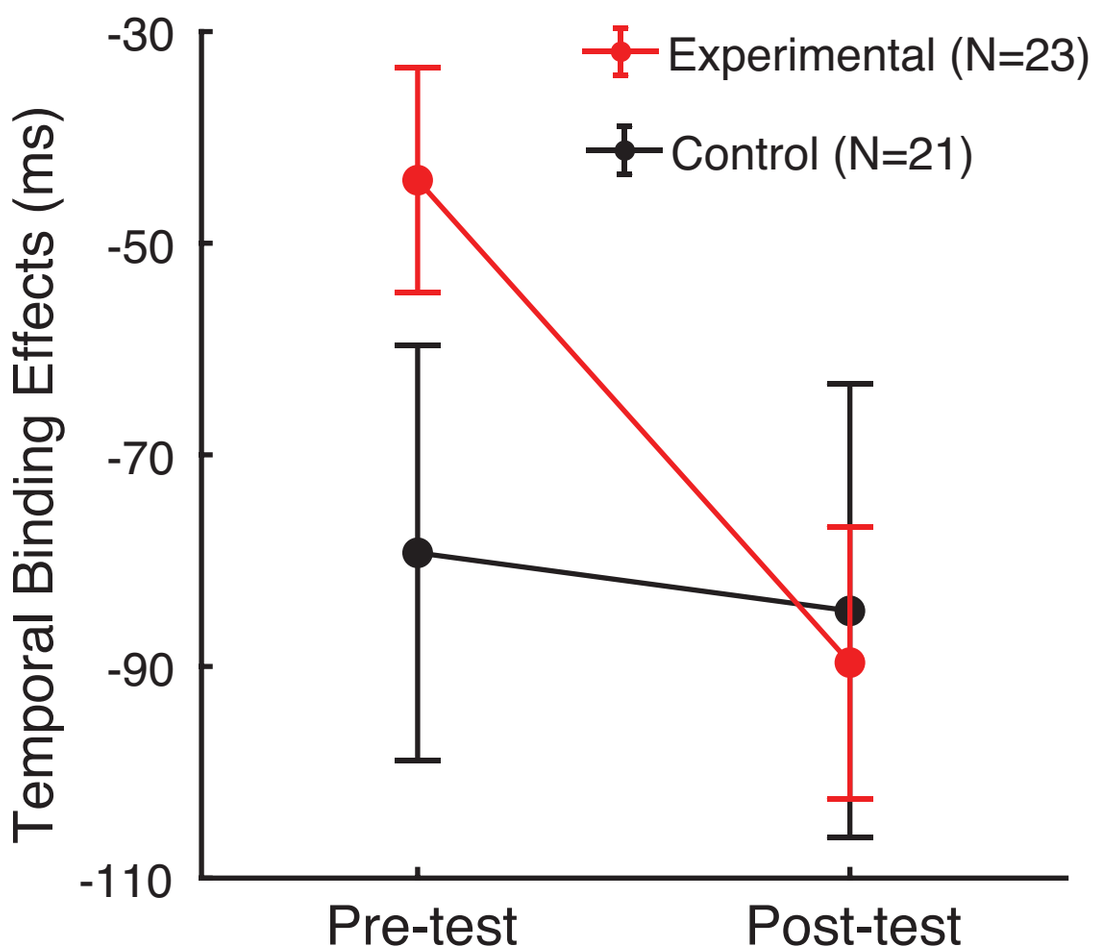

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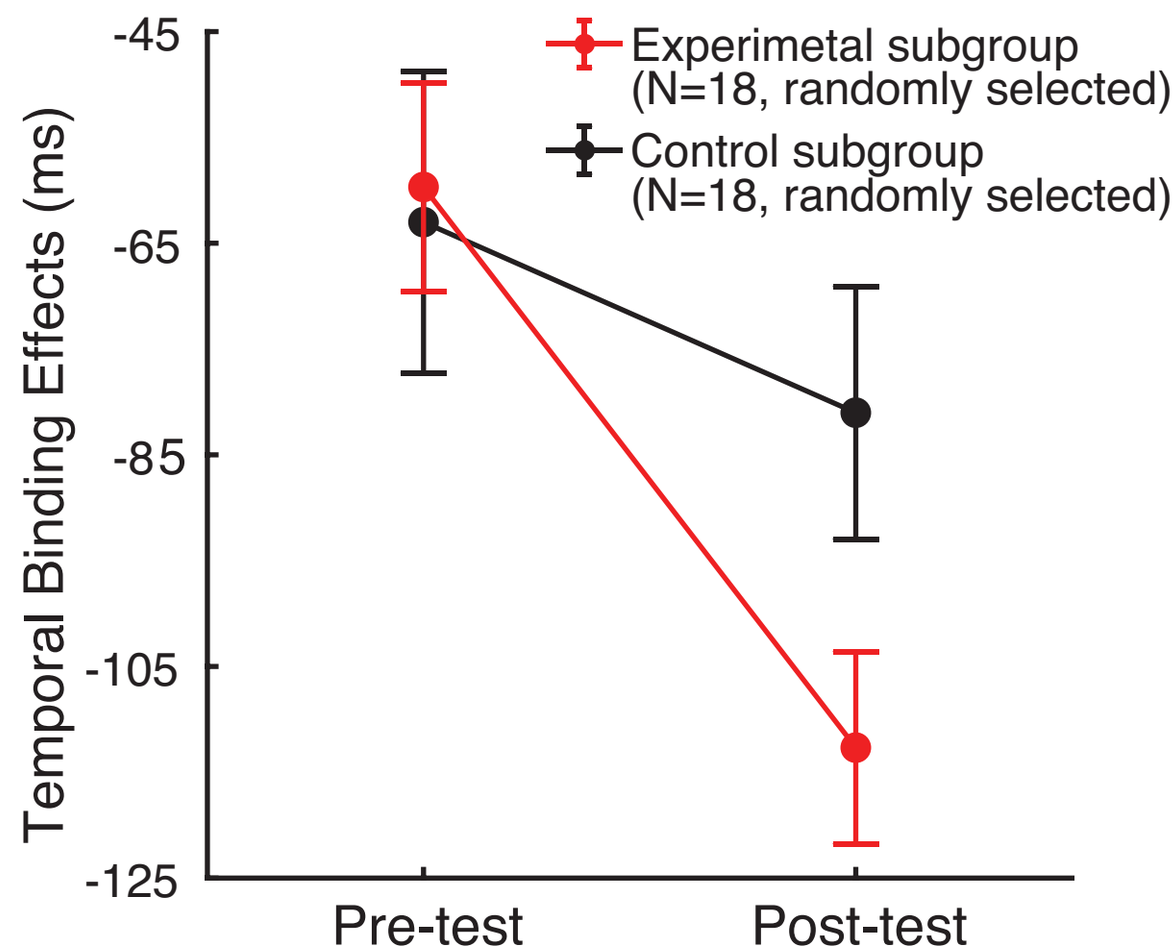
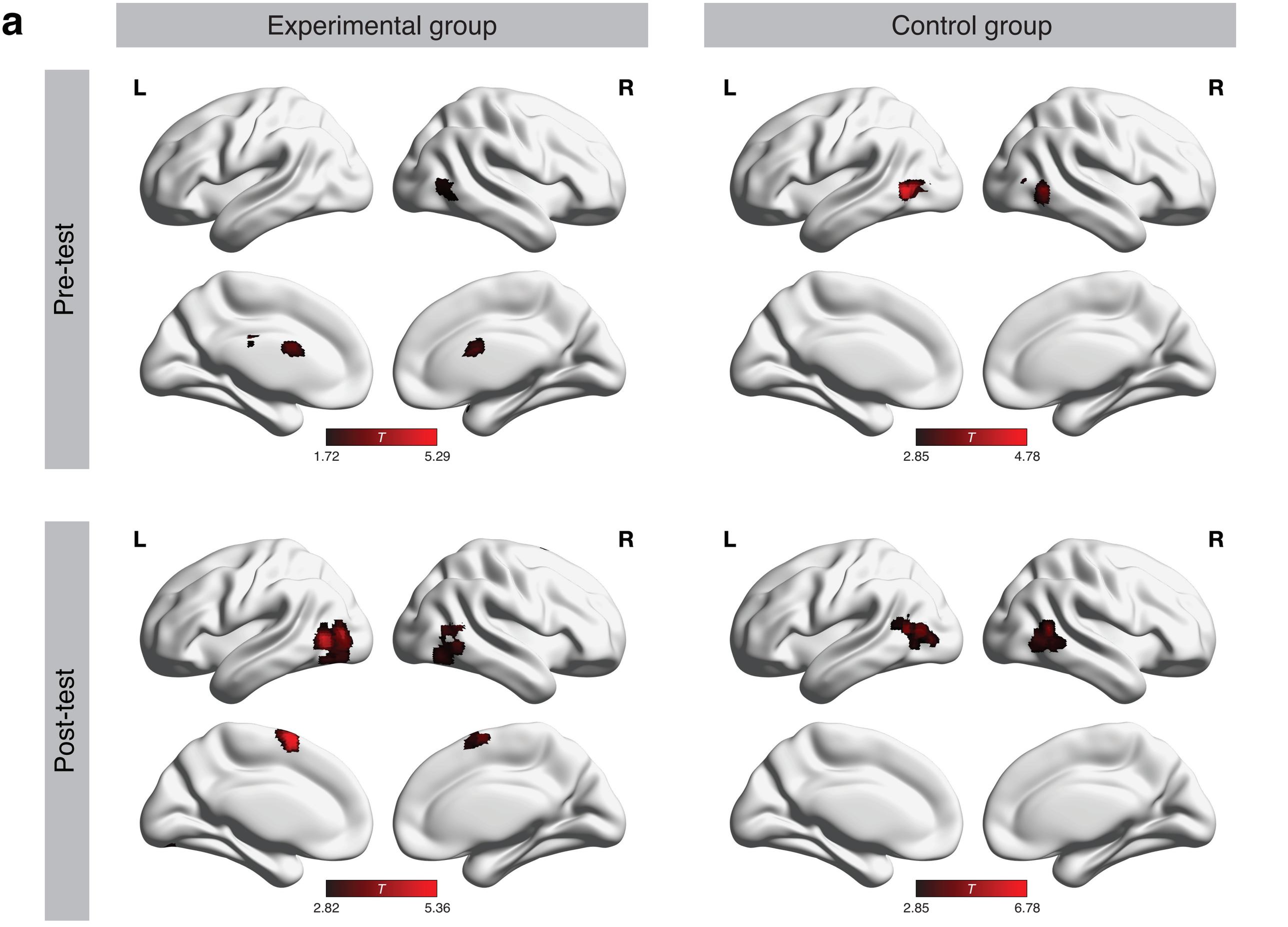
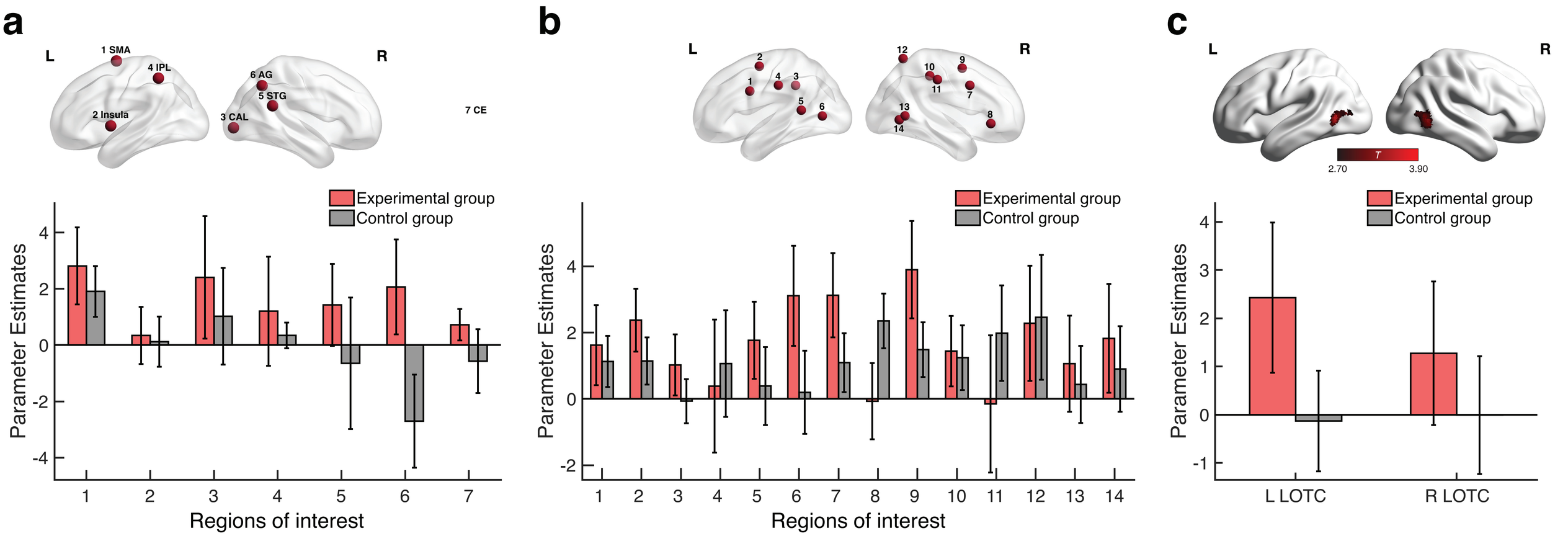
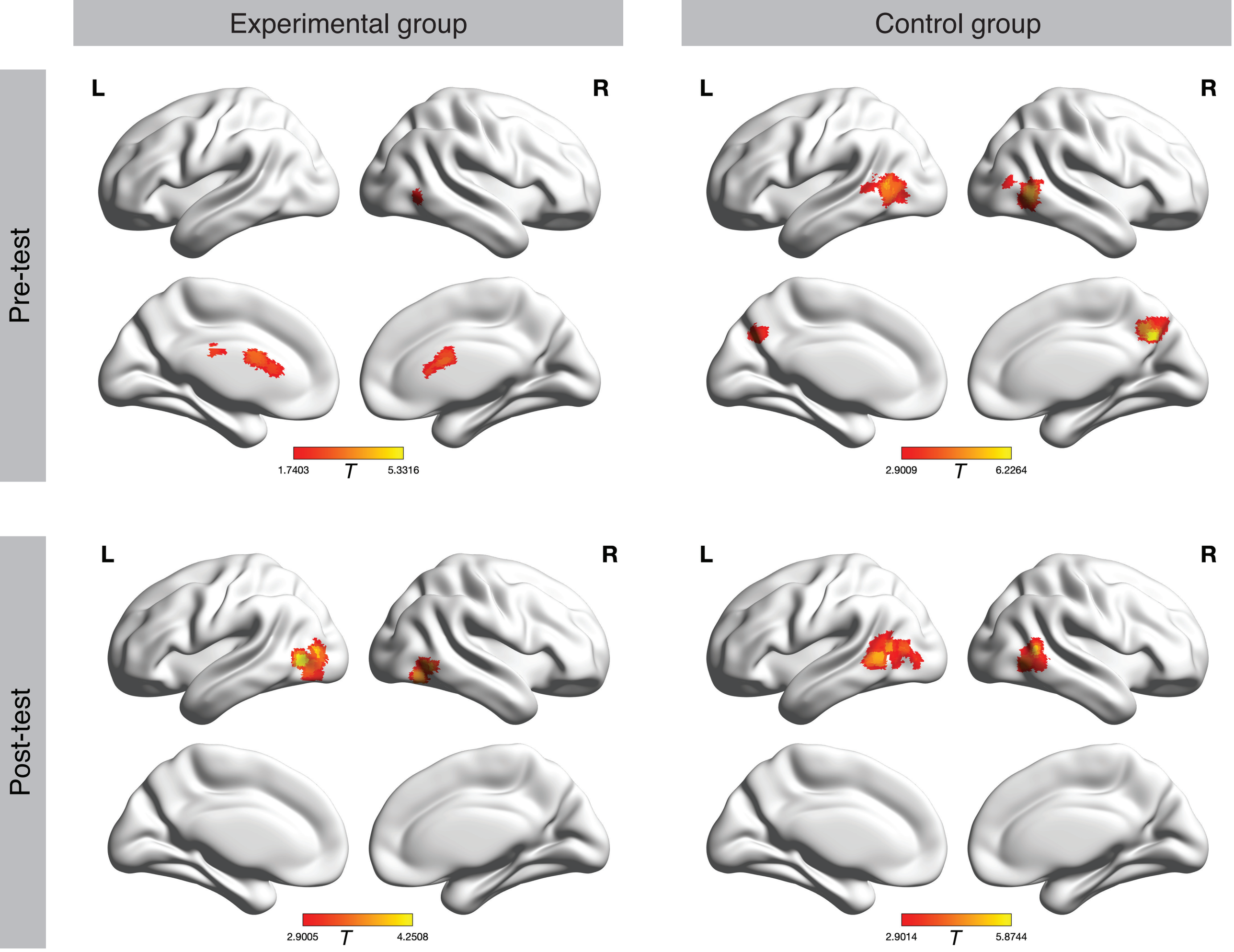



a
Experimental group
Control group
Pre-test
Post-test
L
R
T
1.72
5.29
2.85
4.78
2.82
5.36
2.85
6.78
b
Post-test versus Pre-test
2.82
5.08
2.85
5.05
c
2.70
4.26
Paramaetr Estimates
Pre-test
Post-test
Experimental group
Control group
d
Parameter estimates
Temporal Binding Changes (ms)


a
L
R
1 SMA
4 IPL
2 Insula
6 AG
5 STG
3 CAL
7 CE
Experimental group
Control group
Parameter Estimates
Regions of interest
b
L
R
Experimental group
Control group
Parameter Estimates
Regions of interest
c
L
R
T
2.70
3.90
Experimental group
Control group
Parameter Estimates
L LOTC
R LOTC


Experimental group
Control group
Pre-test
Post-test
L
R
1.7403
T
5.3316
2.9009
T
6.2264
2.9005
T
4.2508
2.9014
T
5.8744