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Neuromodulation of the right temporoparietal junction alters amygdala functional connectivity to authority pressure

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Abstract

Past historical events and experimental research have shown that complying with orders from an authority has a strong impact on harming/destructive behavior, but no one has ever looked into the potential intervention and its neural underpinning to reveal the toll of coercion. We used a paradigm of virtual obedience to authority, in which an experimenter ordered a volunteer to press a handheld button to initiate actions that carried different consequences, including harming or helping others. In this study, we scanned the brain with functional neuroimaging and applied transcranial direct current stimulation (tDCS) to modulate the activation of the right temporoparietal junction (rTPJ) in healthy volunteers in a single-blinded, sham-controlled, crossover trial with anodal, cathodal, and sham stimulation. We observed that cathodal stimulation, compared to anodal and sham stimulation, significantly reduced reaction times (RTs) to initiating harming actions. The effect of tDCS on the rTPJ, orbitofrontal cortex, and anterior cingulate cortex had opposite directions depending on coercive harming or helping actions. Cathodal tDCS-induced changes in the strength of the functional connectivity between the rTPJ and amygdala predicted the effect of cathodal tDCS on harming RTs. The findings provide evidence supporting the rTPJ having a role in coercion-induced changes in the sense of agency. Neuromodulation with tDCS might help in unveiling the power of authority and assisting in the emergence of prosocial behavior, thus shedding light on coping strategies against coercion beyond merely examining its effects.

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KEYWORDS

coercion, intervention, right temporoparietal junction (rTPJ), sense of agency, tDCS

1 | INTRODUCTION

There are many examples in the history of humankind that when people obeyed orders from an authority, they were able to perform highly immoral acts toward others (e.g., Arendt, 1951; Arendt, 1963; Herman & Chomsky, 1988). Even past experimental research, mainly the work of Stanley Milgram (1963, 1974), showed that many people complied with coerced orders to inflict an unbearable electric shock on a person for the sake of the experiment in which they were involved. However, very few studies have looked into the potential intervention approach to examine the toll of coercion, and none of them disentangled its neural underpinning.

The phenomenon of a reduction in agency and outcome processing under command is called the coercion effect (Caspar et al., 2016; Caspar et al., 2018; Caspar, Loumpa, et al., 2020; Caspar, Lo Bue, et al., 2020), as indicated by the intentional binding and auditory N1 amplitude. Receiving coercive orders reduces the sense of agency over potentially harmful actions. Note that a strict definition of “coercion” refers to the use of force or threat of force to persuade someone to do something that they would normally be unwilling to do—but this cannot and should not be studied experimentally, since it clearly violates ethical codes. Herein, we use the conventional term “coercion” to refer to an experimental situation in which people obey orders to inflict harm to another individual.

The “sense of agency” is the experience of being in control of one's actions and the outcomes of those actions. A sense of agency can explicitly be measured, by asking people to report their experiences, or implicitly by recording the perceived time interval between actions and outcomes (intentional binding). A complex brain network subserves the sense of agency, and the temporoparietal junction (TPJ) is one of its main nodes (Zito, Anderegg, et al., 2020; Zito, Wiest, & Aybek, 2020). The TPJ is amenable to neuromodulation, including transcranial direct current stimulation (tDCS) (Hughes, 2018; Tang et al., 2017; Wang et al., 2019).

Via tDCS, a low and direct electrical current that differentiates anodal and cathodal stimulation by modulating the resting membrane potential of the neurons stimulated, can be applied to modulate cognitive and motor skills (Nitsche & Paulus, 2000). Anodal stimulation increases the probability of action potentials occurring by depolarizing the neurons, whereas cathodal stimulation hyperpolarizes neurons, thus decreasing the likelihood of action potentials occurring (Nitsche et al., 2008). Traditionally, a weak electrical current was emitted via the placement of two electrodes attached to the scalp of a participant. However, some montages that place the reference electrode extracranially, for example on the upper arm, have one important advantage of excluding the effect of the reference electrode on cortical modulation, thus greatly focalizing the current in the active electrode (Nitsche & Paulus, 2011). On the other hand, bihemispheric montages

(also known as “dual” stimulation) can be used if the positioning of both target electrodes is important and the hypothesis concerns both areas (Thair et al., 2017). In a recent tDCS study of moral judgments, Sellaro et al. (2015), respectively placed stimulant and return electrodes at the rTPJ and the left supraorbital area, where both regions were considered of great importance in mediating belief attribution for moral judgments. Thus, tDCS can mimic minor TPJ lesions and help delineate the TPJ's functions (Dalong et al., 2021; Stewart et al., 2001; Zito, Anderegg, et al., 2020).

In a recent study, we demonstrated that social coercion affects an individual's experience of agency and responsibility (Cheng et al., 2021). In a virtual obedience paradigm, participants watching the first image of a social interaction scenario mini-clip were forced (as ordered by textual instructions) to press a button in order to initiate successive actions that carried different consequences, including harming actions, along with visual feedback of such scenarios. Participants reported higher guilt ratings and exhibited longer reaction times (RTs) to initiate harming than neutral actions. Harming RTs under coercion were closely correlated with guilt ratings. RTs to initiate actions are therefore a valuable measure of implicit behaviors in response to coercive power.

Herein, using tDCS and functional magnetic resonance imaging (fMRI), we performed a single-blinded, sham-controlled study to explore how neuromodulation of the right TPJ (rTPJ) alters destructive/harming behaviors under authority pressure. While performing a virtual obedience paradigm, participants received 1.0-mA active anodal, cathodal, or sham tDCS, in a crossover within-subject design. When receiving the cathodal tDCS stimulation, activation of the rTPJ, considered a pivotal region in the function of a sense of agency (Zito, Wiest, & Aybek, 2020), is suppressed, and the participants' sense of agency is decreased (with the addition of a coercive effect exerted on the agents), which in turn would allow a participant to initiate harming actions more promptly. If so, we hypothesized that by increasing the sense of agency (as opposed to the coercive effect) via anodal tDCS administration to the rTPJ, we might have a chance to help subjects, who were negatively affected by a coercive power regain a sense of agency and hence alter their social behaviors, which underpin neural correlates and functional connectivity under coercion. To the best of our knowledge, this is one of the first studies to use tDCS to explore the function of the rTPJ in processing coercive behaviors.

2 | MATERIALS AND METHODS

2.1 | Participants

Forty-one healthy volunteers (20 males and 21 females) with no history of psychiatric or neurological disorders (e.g., dementia or

seizures), a head injury, or alcohol or substance abuse, and who were all ethnic Chinese, right-handed, and aged 20–30 (mean = 23.46, standard deviation [SD] = 2.17) years were enrolled in the study. Participants were recruited from local community colleges through an online survey. All participants had normal or corrected-to-normal vision. This study was prospectively approved by the Ethics Committee of National Yang Ming Chiao Tung University Hospital (Yilan, Taiwan; Institutional Review Board no.: 2016B008), conducted in accordance with the *Declaration of Helsinki*, and retrospectively registered in a publicly accessible database of [ClinicalTrials.gov](https://www.clinicaltrials.gov) (tDCS, Moral Decision-Making, fMRI; NCT04681391).

2.2 | Procedures

A virtual obedience paradigm inspired by prior studies on obedience to authority (Caspar et al., 2016; Caspar et al., 2018; Caspar, Loumpa, et al., 2020; Caspar, Lo Bue, et al., 2020; Cheng et al., 2021), in which an experimenter ordered a subject to inflict harm to a third party, was designed to measure participants' behavior under authority power (Figure 1). During fMRI scanning, participants watching the first image of a mini-clip of a social interaction were forced (ordered via textual instructions) to press a button in order to initiate successive actions that carried different consequences, including harming, neutral, and helping actions, along with visual feedback of each scenario. This task was based on stimuli used in previous research (Akitsuki & Decety, 2009; Decety et al., 2008). Each action was animated by three still images shown consecutively with no duration limit set for the first image, but a 200 ms duration set for the second image, and a 1000 ms duration set for the third image. Each animation portrayed the following scenarios: (1) a person who is alleviating the physical pain of a suffering person (helping), (2) a person who is taking an action to physically harm another person (harming), and (3) a baseline stimulus depicting a person carrying out an action that is irrelevant to

another person (neutral). The faces of the protagonists were not visible to ensure that no emotional reactions could be seen by participants. The participant observed the first image of the animation (with no duration limit set) so as to gauge their reaction time, then were forced (coercively ordered via textual instructions) to press the button to cause the remaining two images to play. In the beginning part of the action of the first image, there was no harm cue in any of the harming, neutral, or helping conditions. The outcome was shown in the third image. After MRI scanning, participants were ordered to undergo the same procedures that they did within the scanner. The visual stimuli were presented (five trials each for the harming, neutral, and helping scenarios), and participants were asked to indicate how much the order to commit the action (coercion) violated their own will. The ratings were on a 1–7 Likert scale, from (1) “my will was not violated at all” to (7) “my will was strongly violated.”

2.3 | Transcranial direct current stimulation stimulation

Transcranial direct current stimulation, a noninvasive neuromodulatory technique, delivers a weak current to the scalp to respectively enhance or reduce cortical excitability via anodal or cathodal tDCS. In the present study, we used a DC Brain Stimulator Plus (NeuroConn, Ilmenau, Germany) to stimulate the rTPJ. The target electrode was placed over CP6, the location of the rTPJ (Santesteban et al., 2012), according to the international 10–20 system for electroencephalographic electrode placement; in contrast, the return electrode was placed over the left supraorbital area. That is, during anodal tDCS, the anode was placed over CP6, and the cathode was placed over the left supraorbital area; conversely, during cathodal tDCS, the cathode was placed over CP6, and the anode was placed over left supraorbital area (Figure 2). For active stimulation, utilizing both anodal and cathodal tDCS, a constant current of 1 mA was delivered through a 35-cm²

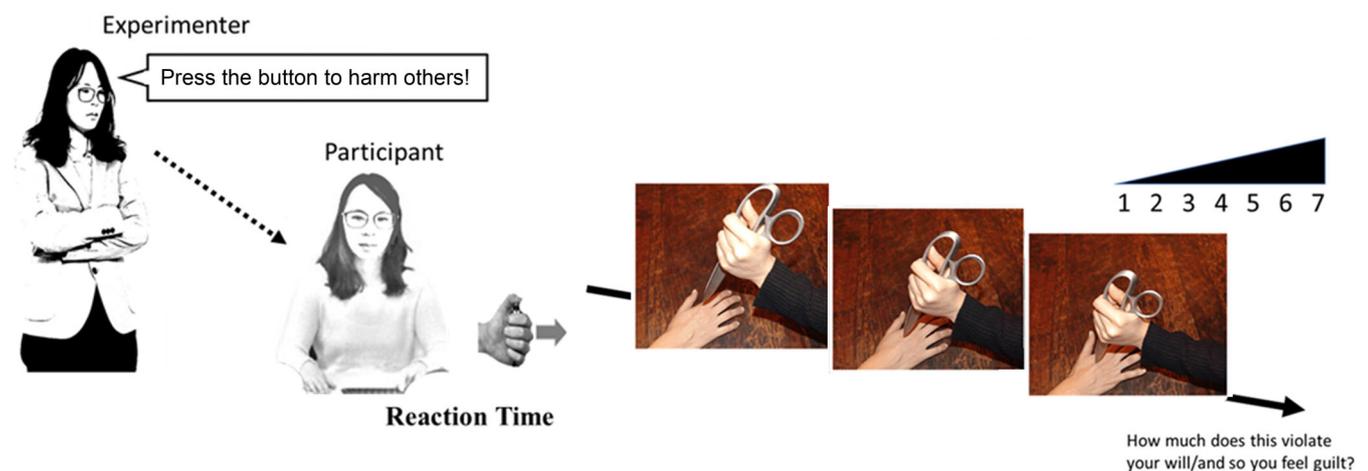


FIGURE 1 Schematic representation of the paradigm for coercive commands. Through textual instructions, the experimenter ordered a participant to initiate socially interactive behaviors by pressing a trigger button in a virtual computerized program along with visual feedback of the scenarios.

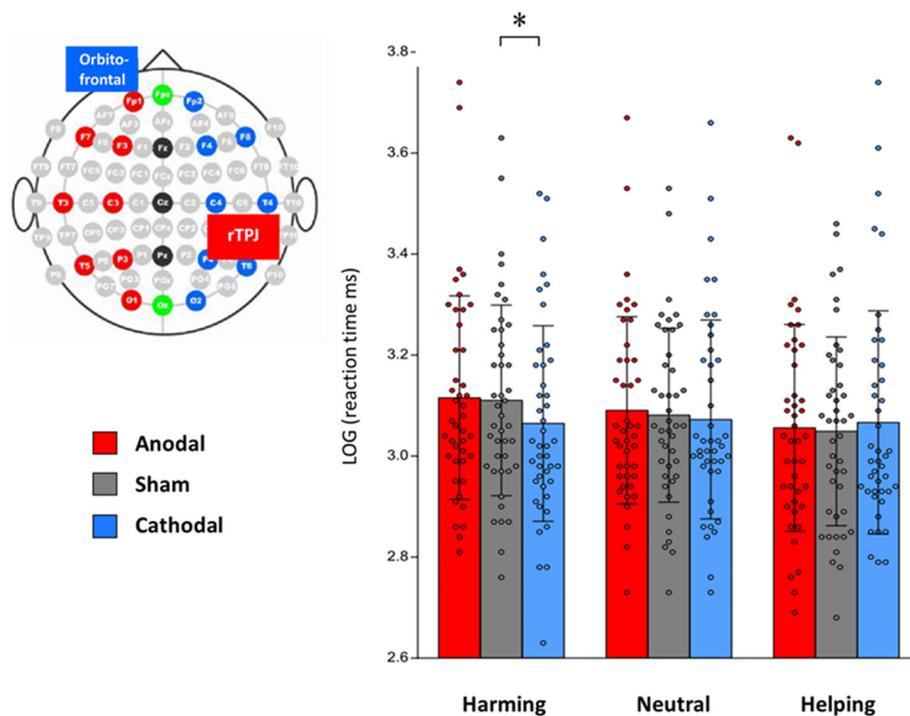


FIGURE 2 Effects of transcranial direct current stimulation (tDCS) on reaction times (RTs) under pressure of coercion. While the RTs for initiating helping behaviors under authority pressure were shorter (3.057 ± 0.028 s, mean \pm SE), compared to neutral (3.082 ± 0.026 s, $p = .003$) and harming actions (3.097 ± 0.026 s, $p = .005$), the tDCS effect had opposite directions depending on the scenario factor. Cathodal tDCS accelerated harming RTs (cathodal vs. sham: 3.066 ± 0.03 vs. 3.11 ± 0.029 s, $p = .019$), whereas anodal tDCS did not affect harming RTs (anodal vs. sham: 3.12 ± 0.031 vs. 3.11 ± 0.029 s, $p = .843$).

electrode for 20 min with fade-in and fade-out of 10 s each, producing a current density of 0.029 mA/cm². On the other hand, the same fade-in, fade-out, and current density were applied for sham stimulation, but the duration of current delivery only lasted 35 s. Therefore, participants could feel the skin sensation but did not experience tDCS after-effects (Nitsche & Paulus, 2000). In order to ensure that participants did not feel discomfort during or after the stimulation, we had them fill out a tDCS adverse effects questionnaire. The questionnaire asked them to rate if they felt (1) a headache, (2) neck pain, (3) nausea, (4) muscle contractions in the face and/or neck, (5) a stinging sensation under the electrodes, (6) a burning sensation under the electrodes, (7) uncomfortable (generic) feelings, and (8) other sensations and/or adverse effects rated on a scale of 1 (“no sensation”) to 5 points (“very uncomfortable”).

Each participant received three sessions of tDCS—*anodal*, *cathodal*, and *sham* (as a control condition) tDCS—with an interval of at least 1 month (average time pause: 64 ± 34 days, mean \pm SD) to prevent a learning effect in any test. The order of the tDCS stimulation was counterbalanced across participants in a single-blind manner. Regarding the sham tDCS condition, the electrical current was ramped up for 35 s at the beginning of stimulation and decreased in the same manner at the end of the 20-min session. This pattern was shown to be a validated and reliable sham-procedure to simulate the sensations observed at the beginning of active stimulation without modifying cortical excitability (Cosmo et al., 2015; Gandiga et al., 2006; Nitsche et al., 2008). In each experimental session, tDCS was first applied over the rTPJ for 20 min (Figure S1). The 20 min application of tDCS could induce an after-effect of more than 1 h throughout the entire experiment (Nitsche & Paulus, 2000). After that, the virtual obedience paradigm was carried out during fMRI scanning, followed by a sense-of-

agency evaluation to rate how much the order to commit the action (coercion) violated their own will.

2.4 | Functional magnetic resonance imaging acquisition and analysis

Participants underwent three sessions of fMRI scanning (*anodal*, *cathodal*, and *sham* tDCS) on different days. Stimuli were presented with E-prime software (Psychology Software Tools, Pittsburgh, PA, USA) and MRI-compatible goggles (VisualStimDigital, Resonance Technology, Northridge, CA, USA) in a three-level within-subject design of social-interaction scenarios (*harming* vs. *neutral* vs. *helping*). Scanning followed a block design (25.4 ± 0.1 s “on”/ 13.2 ± 4.4 s “off”) in two runs. Each run consisted of six “on” blocks (two *harming*, two *helping*, and two *neutral* scenarios) intermixed with six “off” blocks. Each “on” block consisted of five trials, and five inter-stimulus intervals (ITIs, of a 2200-ms duration each) with a fixation cross presented against a gray background. While the ITI was set to 2200 ms, the duration of each fMRI regressor was modeled on each participant’s actual RTs. Because the RT varied across trials and participants, the modeled duration self-served as jittering in nature, leaving the average length of each “on” block as 2541 ± 100 ms (mean \pm SE, *helping*: 2492 ± 107 ms; *harming*: 2599 ± 103 ms; *neutral*: 2532 ± 96 ms). The sequence of the scenarios (*harming*, *helping*, and *neutral*) was pseudorandomized within each run. The order of runs was counterbalanced across participants. Scanning was performed on a 3T Siemens Magnetom Trio-Tim magnet. For functional changes, changes in blood oxygenation level-dependent (BOLD) T2*-weighted MR signals were collected along the AC-PC plane using a gradient echo-planar imaging (EPI) sequence

($t_{...}$ (TR) = 2200 ms, $t_{...}$ (TE) = 30 ms, field of view (FOV) = 220 mm, flip angle = 90°, matrix = 64 × 64, 36 transversal slices, voxel size = 3.4 × 3.4 × 3.0 mm, and no gap). High-resolution structural T1-weighted images were acquired with a 3D magnetization-prepared rapid gradient echo sequence (TR = 2530 ms, TE = 3.5 ms, FOV = 256 mm, flip angle = 7°, slice thickness = 1 mm, matrix = 256 × 256, and no gap). Functional images were processed with SPM12 (Wellcome Department of Imaging Neuroscience, London, UK) in MATLAB 9.0 (MathWorks, Sherborn, MA, USA). Structural T1 images were coregistered to mean functional images, and a skull-stripped image was created from the segmented gray matter, white matter, and cerebrospinal fluid images. These segmented images were combined to create a subject-specific brain template. EPI-created images were realigned and filtered (with a 128-s cutoff), then coregistered to these brain templates, normalized to the Montreal Neurologic Institute (MNI) space, and smoothed (8 mm full width at half maximum). The hemodynamic response function was time-locked to the stimulus onset. Data were input into a general linear model, with movement parameters as nuisance regressors. A two-stage general linear model was used to examine the effect size of each condition. At the first level of analysis, three conditions (harming, helping, and neutral) were separately modeled with a duration of a participant's RT beginning at the onset of each "on" block. The null event (fixation) was modeled with a duration of 13.2 ± 4.4 s. Linear contrasts were applied to obtain parameter estimates. At the second level of analysis, images of parameter estimates from the first-level analysis (helping > neutral; harming > neutral) were collapsed into a repeated-measure factorial design with scenario (helping vs. harming) and tDCS administration (anodal, cathodal, and sham) as within-subject variables.

Group-wise effects for subsequent whole-brain activation contrasts were corrected for a multiple-comparisons family-wise error rate at $p < .05$. Monte Carlo simulation was implemented using 3dClustSim: https://afni.nimh.nih.gov/pub/dist/doc/program_help/3dClustSim.html with a 10-voxel extent at an uncorrected height threshold of $p < .001$ (cutoff, $t = 3.178$) which yielded a FEW-corrected threshold of $p < .05$ that accounted for spatial correlations in neighboring voxels (significance level: voxel $p = .001$, $\alpha = .05$ with 5000 Monte Carlo simulations after gray matter masking). An anatomically defined gray matter mask was created based on the MNI avg152T1 template and explicitly specified and applied to the whole-brain analysis.

Finally, to elucidate the tDCS effect on brain function modulated by coercion, a region-of-interest (ROI) analysis was conducted for the right and left TPJs, and left orbitofrontal cortex (OFC), based on tDCS placement, and the anterior cingulate cortex (ACC), anterior insula cortex (AIC), and amygdala. ROIs were determined by recent publications on coercion (Caspar, Ioumpa, et al., 2020; Cheng et al., 2021). Beyond the existing literature on the effect of authority power during coercive harming, there may be additional cortical regions which are pivotal to the sense of agency. Therefore, the coordinates for the posterior cingulate cortex and precuneus were determined on the basis of neuroanatomical atlases and meta-analyses of the sense of agency

(Kühn et al., 2013; Zito, Wiest, & Aybek, 2020). ROI data are reported for significant contrast image peaks within 10 mm of these a priori coordinates. Data extraction for the ROI analyses was performed using the MarsBaR toolbox (<http://marsbar.sourceforge.net/>) implemented in SPM12.

2.5 | Functional connectivity analysis

Based on the tDCS placement and the behavioral and fMRI contrast results that showed a significant cathodal tDCS effect (vs. sham) on RTs of coercive harming, the psychophysiological interaction (PPI) analysis was seeded in the rTPJ (56, -50, 18) and OFC (-46, 50, -8) to estimate how cathodal tDCS administration (vs. sham) altered the functional connectivity of the rTPJ and OFC during coercive harming (harming vs. neutral). The time series of the first eigenvariables of the BOLD signal were temporally filtered, mean-corrected, and deconvolved to generate a time series of the neuronal signal for the source region, i.e., the rTPJ and OFC, as the physiological variable in the PPI. The PPI analysis assessed the hypothesis that the activity in one brain region can be explained by an interaction between cognitive processes and hemodynamic activity in another brain region. As the rTPJ and OFC were selected as the PPI source region, the physiological regressor was denoted by activities in the rTPJ and OFC. Coercive harming (harming vs. neutral) was the psychological regressor. The interaction between the first and second regressors represented the third regressor. The psychological variable was used as vector coding for the specific task (1 for harming, -1 for neutral) convolved with the hemodynamic response function. Individual time series of rTPJ and OFC were obtained by extracting the first principle component from all raw voxel time series in a sphere (of 4 mm in radius) centered on activation of the coordinates of the subject-specific rTPJ and OFC. These time series were mean-corrected and high-pass-filtered to remove low-frequency signal drifts. PPI analyses were then carried out for each subject by creating a design matrix with the interaction term, psychological factor, and physiological factor as regressors. PPI analyses were separately performed for the cathodal tDCS and sham to identify brain regions showing significant changes in functional coupling with rTPJ and OFC activation during coercive harming in relation to cathodal tDCS administration. Subject-specific contrast images were then entered into the random-effects analyses.

3 | RESULTS

3.1 | Reaction times and subjective ratings

Given that the data on RTs were not normally distributed, RT data were log-transformed and subject to a 3 (administration: anodal vs. sham vs. cathodal) × 3 (scenario: coercive harming vs. helping vs. neutral) repeated-measures analysis of variance (ANOVA). There was a main effect of scenario ($F_{2,84} = 7.11$, $p = .011$, $\eta^2 = 0.15$) and an interaction between administration and scenario ($F_{4,168} = 3.08$,

$p = .029$, $\eta^2 = 0.07$). Follow-up analyses replicated previous findings and indicated that the RTs in helping (3.057 ± 0.028 s, mean \pm SE) were shorter than those of neutral (3.082 ± 0.026 s, $p = .003$) and harming (3.097 ± 0.026 s, $p = .005$). The tDCS effect had opposite directions depending on the scenario factor. Cathodal tDCS accelerated harming RTs (cathodal vs. sham: 3.066 ± 0.03 vs. 3.11 ± 0.029 s, $p = .019$), whereas anodal tDCS did not affect harming RTs (anodal vs. sham: 3.12 ± 0.031 vs. 3.11 ± 0.029 s, $p = .843$) (Figure 2). Subjective ratings were also subject to a 3 (administration: anodal vs. sham vs. cathodal) \times 3 (scenario: coercive harming vs. helping vs. neutral) repeated-measures ANOVA. There was a main effect of scenario ($F_{2,84} = 838.76$, $p < .001$, $\eta^2 = 0.95$), indicating that under coercion, participants were less willing (i.e., more self-reported violation to their own will) to do harming (5.15 ± 0.16) than to help (4.46 ± 0.18). Neither the main effect of tDCS ($F_{2,84} = 0.4$, $p = .67$, $\eta^2 = 0.009$) nor its interaction with scenario ($F_{4,168} = 0.67$, $p = .61$, $\eta^2 = 0.016$) reached significance on subjective ratings.

3.2 | Functional magnetic resonance imaging results

Table 1 lists the brain regions showing significant hemodynamic activation to coercive harming and helping after anodal, cathodal, and sham tDCS administration. In response to coercive harming (vs. neutral), both anodal and cathodal administration showed activation of the supramarginal gyrus, caudate, thalamus, supplementary motor area (SMA), dorsomedial prefrontal cortex (dmPFC), AIC, precentral gyrus, inferior frontal gyrus, dorsolateral prefrontal cortex (dlPFC), postcentral gyrus, midcingulate cortex, hippocampus, and OFC. In contrast, anodal tDCS administration (vs. sham) significantly decreased activities in the dlPFC, dmPFC, inferior frontal gyrus, supramarginal gyrus, angular gyrus, ITPJ, ACC, rTPJ, and OFC, while cathodal tDCS significantly increased activity in the dmPFC and decreased activities in the superior frontal gyrus, inferior frontal gyrus/AIC, OFC, SMA, rTPJ, ACC, and AIC during coercive harming.

Regarding the ROI results (Figure 3), significant interactions of tDCS administration (anodal vs. cathodal vs. sham) with scenario (coercive harming vs. helping) were observed in the rTPJ ($F_{1,76} = 5.15$, $p = .026$, $\eta^2 = 0.06$), ITPJ ($F_{1,76} = 4.89$, $p = .03$, $\eta^2 = 0.06$), left OFC ($F_{1,76} = 4.89$, $p = .03$, $\eta^2 = 0.06$), and ACC ($F_{1,76} = 5.87$, $p = .018$, $\eta^2 = 0.07$). The follow-up analyses indicated that the tDCS administration effect in the rTPJ, ITPJ, left OFC, and ACC had opposite directions depending on the scenario factor (coercive harming vs. helping). Cathodal tDCS administration decreased activity in the ACC during harming (cathodal vs. anodal: -0.2 ± 0.12 vs. 0.07 ± 0.12), whereas it increased activity during helping (0.32 ± 0.15 vs. -0.07 ± 0.12). For the rTPJ, ITPJ, and left OFC, cathodal relative to anodal tDCS administration increased their activities during harming (rTPJ: 0.09 ± 0.13 vs. -0.31 ± 0.22 ; ITPJ: 0.02 ± 0.03 vs. -0.11 ± 0.06 ; left OFC: 0.12 ± 0.09 vs. -0.12 ± 0.13), whereas it decreased their activities during helping (rTPJ: -0.1 ± 0.11 vs. 0.27 ± 0.2 ; ITPJ: -0.01 ± 0.04 vs. 0.13 ± 0.09 ; left OFC: -0.33 ± 0.14 vs. 0.04 ± 0.16).

3.3 | Functional connectivity

While behavioral results showed a significant effect of the acute cathodal tDCS intervention (vs. sham) on changes in RTs during coercive harming, a PPI functional connectivity analysis was further conducted to estimate how cathodal tDCS administration altered the functional connectivity of the rTPJ and OFC (according to tDCS placement) during coercive harming (harming vs. neutral) (Table 2, Figure 4). Cathodal tDCS (vs. sham) triggered significant patterns in functional coupling (Figure 4). When seeded in the rTPJ, cathodal tDCS administration significantly increased functional coupling with the right amygdala (20, 22, 42), left amygdala (20, 36, -18), and ACC (4, 22, -6). When seeded in the OFC, cathodal tDCS administration significantly increased functional coupling with the posterior cingulate cortex (0, -50, 22) and precuneus (16, -52, 36) (Table 2, Figure S2). Notably, cathodal tDCS-induced effects found in changes of harming RTs could be predicted by the tDCS-induced effects on functional connectivity (rTPJ-left amygdala connectivity: $r = 0.348$, $p = .026$; rTPJ-right amygdala: $r = 0.355$, $p = .023$; OFC-precuneus: $r = 0.372$, $p = .017$; OFC-PCC: $r = 0.358$, $p = .021$).

4 | DISCUSSION

Combining the use of tDCS and fMRI in a paradigm of virtual obedience to authority, we aimed to look for a potential intervention approach to determine the toll of coercion. Unfortunately, contrary to our hypothesis, we failed to determine a way for anodal tDCS administration on the rTPJ to regain a sense of agency under authority pressure.

At the behavioral level, the tDCS effect existed in RTs but not in subjective ratings. RTs did exhibit an interaction between administration and scenario, as indicated by opposite directions of the tDCS effect depending on the scenario factor. Cathodal tDCS accelerated harming RTs, whereas anodal tDCS did not exert such an effect. The present findings replicated a previous study (Cheng et al., 2021), regarding longer RTs and more self-reported violation of subjects' own will for harming than helping. However, as opposed to our hypothesis, enhancing a sense of agency by applying anodal tDCS to the rTPJ did not change behaviors under authority pressure. This null result of anodal tDCS might be ascribed to the electrode layout in which the positioning of both stimulant electrode (rTPJ) and return electrode (IOFC) are important for simultaneously upregulating (anodal current) one area and downregulating (cathodal current) the other area. While both the rTPJ and OFC are involved in theory of mind and sense of agency (Piras et al., 2020; Sabbagh, 2004), inhibition of the IOFC might counteract the exhilarating effect of the rTPJ on RTs. However, inhibiting the rTPJ by cathodal tDCS resulted in shortened RTs to follow harming orders. It is reasonable to suppose that cathodal tDCS over the rTPJ might enhance the coercive effect exerted on a reduced sense of agency, which in turn caused shortened RTs. Although Sellaro et al. (2015) once provided indirect evidence showing that stimulation of the rTPJ was at the origin of the observed

TABLE 1 Brain regions showing significant blood oxygenation level-dependent (BOLD) activities to coercive harming and helping as well as transcranial direct current stimulation (tDCS) administration

Brain regions	Side	MNI coordinates			t
		x	y	z	
Coercive harming versus neutral					
AIC	R	36	14	-16	4.72
AIC	L	-36	4	-14	5.45
OFC	L	-46	50	-8	2.14*
Hippocampus	L	-16	-32	-4	4.06
dIPFC	L	-56	14	8	3.94
dIPFC	L	58	14	34	3.62
Occipital cortex	R	24	-88	10	5.82
Thalamus	R	8	-16	18	5.66
Inferior frontal gyrus	L	-50	8	18	4.13
Caudate	R	16	-18	22	6.23
dmPFC	-	0	56	28	5.57
Supramarginal gyrus	L	-58	-24	30	7.17
Supramarginal gyrus	R	66	-22	36	5.67
Midcingulate cortex	R	2	-2	40	4.32
Precentral gyrus	L	-48	2	52	4.74
Postcentral gyrus	R	28	-44	56	4.48
SMA	R	-8	12	68	5.32
SMA	L	-8	16	70	6.14
Coercive helping versus neutral					
OFC	L	-46	50	-8	-2.65*
Occipital cortex	R	28	-84	8	4.38
Supramarginal gyrus	R	54	-22	24	3.49
Midcingulate cortex	R	10	12	42	3.35
Anodal tDCS versus sham coercive harming					
Inferior frontal gyrus	R	50	34	2	-3.45
OFC	L	-44	48	4	-2.4*
Inferior frontal gyrus	R	48	20	10	3.55
Inferior frontal gyrus	L	-42	16	16	-3.64
rTPJ	R	60	-52	22	-2.9*
ITPJ	L	-48	-48	28	-3.31
Supramarginal gyrus	L	-60	-36	24	-3.52
Anterior cingulate cortex	L	-8	38	26	-3.2
dIPFC	R	30	52	36	-4.48
dmPFC	R	10	60	38	-3.9
Angular gyrus	L	-40	-64	46	-3.47
Cathodal tDCS versus sham coercive harming					
OFC	L	-46	24	-12	-3.56
AIC	R	38	20	-10	-2.34*
AIC	L	-38	18	-4	-2.4*
Inferior frontal gyrus/AIC	L	-50	20	0	-3.71
rTPJ	R	62	-48	28	-1.98*
Anterior cingulate cortex	R	6	24	32	-2.18*
Superior frontal gyrus	L	-38	16	54	-3.73
dmPFC	L	-6	36	56	3.42
SMA	L	-6	24	66	-3.44

(Continues)

TABLE 1 (Continued)

Brain regions	Side	MNI coordinates			t
		x	y	z	
Anodal tDCS versus sham coercive helping					
rTPJ	R	56	-46	18	2.91*
Cathodal tDCS versus sham coercive helping					
dIPFC	R	32	46	40	2.38*
(Anodal helping-cathodal helping) > (anodal harming-cathodal harming)					
OFC	L	-32	44	-2	1.87*
rTPJ	R	58	-50	20	2.61*
ITPJ	L	-38	-46	28	3.22
(Anodal helping-cathodal helping) < (anodal harming-cathodal harming)					
Anterior cingulate cortex	-	0	32	-4	2.98*

Note: Pooled group results for all participants ($N = 41$). All clusters were significant at a voxel-wise family-wise error (FWE)-corrected $p < .05$, except those marked with an asterisk, which were taken from a priori predefined regions of interest (ROIs) and were significant at an uncorrected $p < .05$.

Abbreviations: AIC, anterior insula cortex; dIPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; ITPJ, left temporoparietal junction; L, left; OFC, orbitofrontal cortex; R, right; rTPJ, right temporoparietal junction; SMA, supplementary motor area.

* $p < .05$.

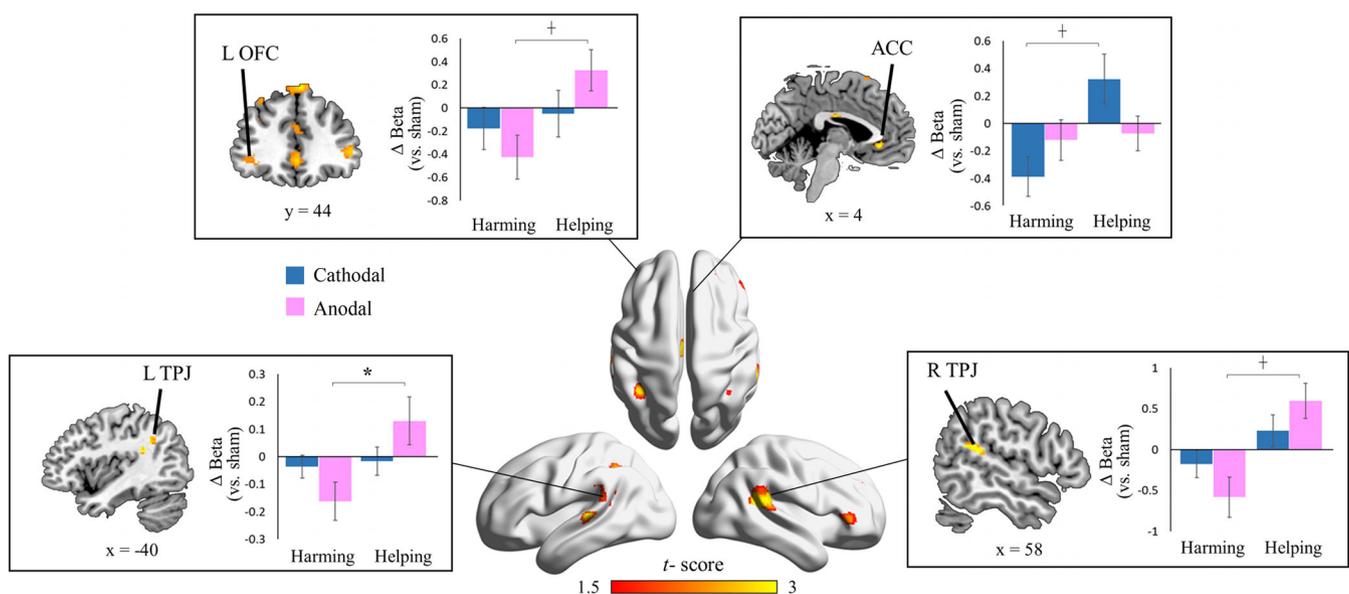


FIGURE 3 Brain regions that showed an interaction between transcranial direct current stimulation (tDCS) effects and the scenario of coercive behaviors. Effects of tDCS administration in the right temporoparietal junction (rTPJ), left TPJ (ITPJ), left orbitofrontal cortex (IOFC), and anterior cingulate cortex (ACC) had opposite directions depending on the scenario factor (coercive harming vs. helping). Acute cathodal tDCS administration (vs. anodal tDCS) decreased brain activity during coercive harming in the ACC, whereas cathodal tDCS increased ACC activity during coercive helping. For the rTPJ, ITPJ, and IOFC regions of interest (ROIs), acute anodal tDCS administration (vs. cathodal tDCS) decreased brain activity during coercive harming, whereas anodal tDCS increased brain activity during a helping condition. $^{\dagger}p < .1$, $*p < .05$.

effect when both the rTPJ and IOFC were simultaneously stimulated, future studies using specific montages of electrodes (e.g., using an extracephalic reference electrode setup) to directly test relative contributions of the rTPJ and OFC to the effect of coercion are warranted (Sellaro et al., 2015).

At the neural level, irrespective of anodal or cathodal tDCS, coercive harming and helping scenarios showed distinct brain

activations. For ROIs, the tDCS effect exhibited opposite directions depending on the scenario factor. Given that we have consciousness at all relates to how evolution has shaped our neurobiology for social living (Churchland, 2019), and helping might not be as harming in reducing the sense of agency under authority pressure. That is why we observed distinct tDCS effects between harming and helping others.

TABLE 2 fMRI results of the functional connectivity showing significant main effects of cathodal transcranial direct current stimulation (tDCS) (vs. sham) during coercive harming

Brain region	Side	MNI coordinates			t	Cluster size
		x	y	z		
Seeded in the rTPJ						
Amygdala	R	22	-4	-12	2.22 ^a	27
Amygdala	L	-30	-4	-14	1.88 ^b	69
Anterior cingulate cortex	L	-2	46	-4	2.07 ^c	44
Seeded in the OFC						
Posterior cingulate cortex	-	0	-50	22	3.6 ^d	505
Precuneus	L	16	-52	36	3.81 ^d	505

Abbreviations: MNI, Montreal Neurologic Institute; OFC, orbitofrontal cortex; rTPJ, right temporoparietal junction.

^a $p = .014$.

^b $p = .031$.

^c $p = .02$.

^d $p < .001$.

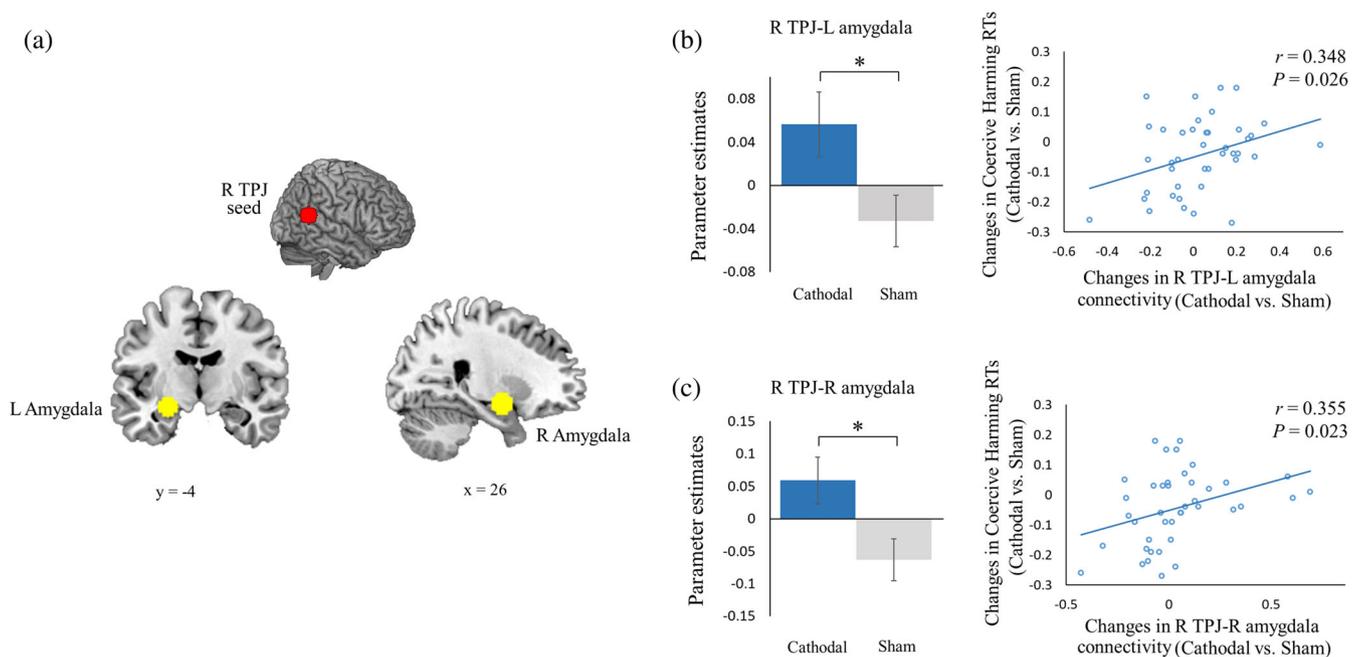


FIGURE 4 Effects of cathodal transcranial direct current stimulation (tDCS) on functional coupling between the right temporoparietal junction (rTPJ) and amygdala. (a) Illustration of the rTPJ showing significant changes in functional coupling with the bilateral amygdala as revealed by the contrast between cathodal tDCS and sham stimulation. (b) Parameter estimates of rTPJ-left amygdala connectivity as a function of the acute cathodal tDCS intervention. Error bars indicate standard errors. Cathodal tDCS-induced changes in the strength of rTPJ-left amygdala connectivity predicted cathodal tDCS effects on harming reaction times (RTs). (c) Parameter estimates of rTPJ-right amygdala connectivity as a function of an acute cathodal tDCS intervention. Error bars indicate standard errors. Cathodal tDCS-induced changes in the strength of rTPJ-right amygdala connectivity predicted the cathodal tDCS effects on harming RTs.

Irrespective of harming or helping, ACC activation responded more strongly to cathodal tDCS, whereas the others did so to anodal tDCS (as shown in Figure 3). Anodal tDCS modulated the neural level instead of behavioral performance (i.e., RTs). Cathodal tDCS also significantly reduced RTs for coercive harming. Neuroimaging studies have consistently found that the ACC is involved in interpersonal guilt (Basile et al., 2011; Bastin et al., 2016; Cheng et al., 2021; Wagner et al., 2011). Cathodal tDCS administration can cause ACC activation to decrease during harming, whereas it may increase during helping. It

is reasonable to suppose that the effect of tDCS administration was in opposite directions depending on the scenario factor (coercive harming vs. helping), which might be associated with the experience of guilt. Cathodal tDCS inhibited the rTPJ for processing a sense of agency, which in turn decreased guilt-related processing in the ACC and prompted RTs to harming others.

Cathodal tDCS induced decreased TPJ and OFC activation along with heightened functional connectivity among the rTPJ-amygdala, OFC-precuneus, and OFC-posterior cingulate cortex in response to

coercive harming. We suppose that there should be a compensatory mechanism that operates to offset inhibition via cathodal tDCS. Such heightened functional connectivity in brain regions might lead to altered functions of the sense of agency during coercive harming. Notably, tDCS modulated the functional connectivity between the stimulated area and the sense-of-agency brain network (posterior cingulate cortex and precuneus). tDCS enables induction of modulation of resting-state functional connectivity in older adults (Antonenko et al., 2017). Despite compensation with heightened neural connectivity in response to the cathodal rTPJ by tDCS, behavioral results still followed the ameliorating effect on the sense of agency. This might be indicative of individual differences under coercion, i.e., some participants might fight harder not to obey an inappropriate coercive command or hence undergo a higher level of anxiety (Cheng et al., 2021). It was not surprising to see that cathodal tDCS-induced changes in harming RTs could predict corresponding changes in the functional connectivity between the rTPJ and amygdala. Specifically, cathodal tDCS (vs. shame) induced more-positive connectivity between the rTPJ and amygdala which was associated with a stronger sense of agency, as indicated by greater changes in harming RTs.

A few limitations of the current work should be clarified for future research. First of all, despite the simple anodal-increase and cathodal-decrease rules of thumb, many studies observed that beyond tDCS polarity, inter- and intra-individual differences, including genetics, age, gender, physiological differences, and baseline task performance, might determine the modulating effect through their interactions with tDCS (Cheeran et al., 2008; Hsu et al., 2016; Krause & Cohen Kadosh, 2014; Mattay et al., 2003; Veniero et al., 2019). Herein, this tDCS study used a within-subject crossover design to control for inter-individual differences to a certain degree. Second, while the rTPJ is also a significant neural marker for theory of mind (Krall et al., 2015), cognitive empathy (Decety & Jackson, 2004; Decety & Sommerville, 2003), and self-referential processing (Qin et al., 2020), future studies incorporating relevant dispositional assessments (Chen et al., 2020) with a larger sample size are encouraged to corroborate the present findings.

Taken together, using a paradigm of virtual obedience to authority, this fMRI study showed that tDCS could alter the sense of agency at the neural connectivity level and a behavioral index. To the best of our knowledge, this should be the first step in finding an approach to determine the toll of coercion. Although anodal tDCS failed to regain a sense of agency, we learned that cathodal tDCS induced a greater reduction in the sense of agency, prompted coercive harming behavior, and strengthened the neural underpinning and connectivity between the rTPJ and amygdala. Overall, being on the right tract, we should take individual differences into account when investigating how to overcome coercive control.

AUTHOR CONTRIBUTIONS

Yawei Cheng and Chenyi Chen conceived and conceptualized the study. Chenyi Chen, Yang-Teng Fan, and Yu-Chun Chen collected and analyzed the data. Yawei Cheng and Chenyi Chen conducted the necessary literature reviews and drafted the first manuscript. All authors contributed toward the writing and revision of the final draft.

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CONFLICT OF INTEREST

None of the authors has any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study and the code used for data analysis are available upon reasonable request to the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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