Behavioural Brain Research 303 (2016) 71–75

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Research report

Modulating activity in the orbitofrontal cortex changes trustees' cooperation: A transcranial direct current stimulation study

Guangrong Wang[a,b,c,*], Jianbiao Li[b,c], Xile Yin[b,c], Shuaiqi Li[b,c], Mengxing Wei[d]

[a] *Neural Decision Science Laboratory, Weifang University, PR China*
[b] *Selten Laboratory, Nankai University, PR China*
[c] *China Academy of Corporate Governance, Nankai University, PR China*
[d] *The University of Leicester, UK*

HIGHLIGHTS

- The right OFC is the guilt-specific brain region.
- Anodal tDCS over the right OFC increased the degree of cooperation.
- The right OFC is involved in pure cooperative motives.

ARTICLE INFO

Article history:
Received 10 November 2015
Received in revised form 15 January 2016
Accepted 20 January 2016
Available online 22 January 2016

Keywords:
OFC
tDCS
Reciprocity
Cooperation
Trust game

ABSTRACT

Trust is one of the most important factors in human society, as it pervades almost all domains of the society. The trusting behavior of trustors is dependent on the belief about the cooperative (reciprocal) level of trustees. Thence what are the motives underlying the cooperative behavior? An important explanation is that guilt aversion can motivate cooperative behavior. The right orbitofrontal cortex (OFC) is the guilt-specific region, while there is little understanding on the causal effect of this network. We explored the causal effect of the OFC on cooperative behavior using transcranial direct current stimulation (tDCS). Sixty participants played the trust game as trustees, and they received either anodal tDCS over the right OFC and simultaneously cathodal electrode over the right dorsolateral prefrontal cortex (DLPFC), or sham stimulation. Experimental results showed that participants as trustees transferred back more money in the tDCS treatment than sham stimulation. This suggests that the activity of the right OFC has causal effects on cooperative behavior.

1. Introduction

Social interactions are governed by social norms and expectations that enable us to learn the reputation of others in order to establish social relationships [1–3]. Trust is predicated on a notion of reciprocity, which means people are frequently nice and cooperative in response to generous or kind behavior; conversely, they are frequently nasty in response to hostile behavior [4–6]. Therefore, the nature of trust is belief, i.e., the expectation of trustworthiness of trustees [7,8].

What are the motives underlying trust and cooperation? Behavioral economists developed a number of models that emphasized other-regarding preferences to answer this question [9–13]. On the other hand, enormous neuroscience studies investigated the neural basis of the trust behavior [14–17]. However, few studies focused on the neural system underlying the cooperative behavior of the trustee [17,18]. In fact, these studies explored neural basis of external factors such as reputation, risk and benefit when the trustee reciprocating. Nevertheless, neural correlates of the trustee's pure cooperative motives still need to be investigated.

Some recent studies focused on the effects of guilt aversion on cooperative behavior [19,20]. In the context of psychological game theory, people might feel guilty in proportion to the degree to which they do not live up to others' expectations [21,22]. Chang et al. [19] suggested that the cooperation level might be enhanced on avoidance of the guilt feeling. Additionally, they utilized functional magnetic resonance imaging (fMRI) to identify brain regions that mediate cooperative behavior while participants decided whether or not to honor the partner's trust. Nihonsugi et al. [20] suggested

* Corresponding author at: Neural Decision Science Laboratory, Weifang University, 5147# Dongfeng Street, Weifang 261061, PR China. Fax: +86 536 8785821.
E-mail address: grongw@126.com (G. Wang).

http://dx.doi.org/10.1016/j.bbr.2016.01.047

both guilt and inequity aversion affected cooperative behavior, and guilt had much more significant effect.

Wagner et al. [23] identified specific brain regions associated with guilt by comparison with the two most closely related emotions-shame and sadness- using fMRI in healthy volunteers. Their experimental results demonstrated that the right orbitofrontal cortex (OFC) was specifically recruited by guilt.

Previous studies mainly utilized fMRI to explore activation of brain regions related to guilt. When the trustee chose whether or not to honor the trust, many factors including guilt, reward and inequality affected the neural activity. The observed neural activation could spuriously correlate with task performance but need not necessarily play a causal role in task execution [24,25]. Consequently, previous fMRI studies could not make causal inferences about the effect of brain processes on cooperative behavior. In contrast, brain stimulation techniques such as tDCS interfere non-invasively with the activity of defined areas in the human cortex, thus it enables researchers to observe the behavioral impact of an increase or decrease in the cortical excitability of the stimulated brain regions. Therefore, we aimed to use tDCS to explore the causal effect of guilt related brain regions on the cooperative behavior.

Because the right OFC is the specific brain region involved in guilt aversion [23]. if modulating the activity in the right OFC affects cooperative behavior of the trustee, it means that guilt aversion indeed plays a crucial role on cooperation. Hence, we enhanced the activity in the right OFC using tDCS while participants playing the trust game as trustees. The right DLPFC is the crucial brain region involved in the conflict processes and cognitive control [26,27]. Previous studies have demonstrated that enhancing the activity of the right DLPFC would increase the cooperation of trustees [19,20]. Hence, to test the role of the right OFC, we depressed the activity of the right DLPFC when enhancing the activity of the right OFC. We predicted that increases in the cortical excitability of the right OFC by means of tDCS would evoke more cooperative behavior of trustees if the right OFC is indeed involved in processes of guilt aversion.

2. Method

2.1. Subjects

60 healthy college students (25 men and 35 women; mean age: 22.37; ranging from 20 to 25 years old) were recruited to participate in our experiment. All subjects were right-handed without ex ante knowledge of tDCS or trust game tasks. All of them had no history of psychiatric illness or neurological disorders. All subjects were randomly assigned to receive anodal tDCS over the right OFC and simultaneously cathodal tDCS over the right DLPFC ($n = 30$, 12 men; mean age: 22.73, SD = 2.44851) or sham stimulation ($n = 30$, 13 men; mean age: 22, SD = 3.09616). Informed consent was obtained from each participant prior to the study. The experiment was performed in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of Business School of Nankai University. Each participant was paid according to their own offers and decisions of their partners. On average, each participant received 62.60 Chinese yuan (about 10 US$). No participants reported any adverse side effects concerning pain on the scalp or headaches after the experiment.

2.2. Transcranial direct current stimulation (tDCS)

Transcranial direct current stimulation (tDCS) involves the application of a weak direct current to the scalp via two, saline-soaked surface sponge electrodes (9 cm^2). The current is constant and delivered by a battery-driven stimulator (Neuro Conn,

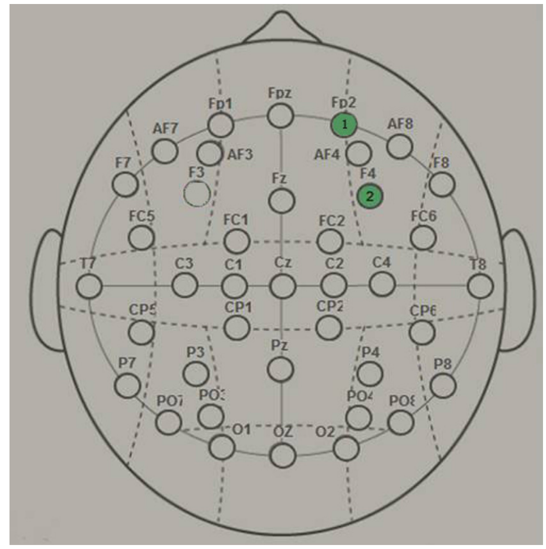

Fig. 1. Schematic drawing of electrode positions.
The anodal electrode was placed over the right Fp2 and the cathodal electrode was placed over the right F4 according to the 10–20 system.

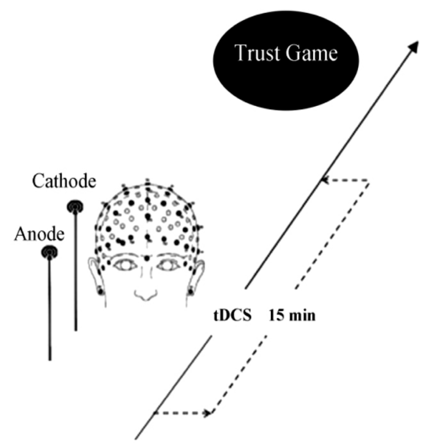

Fig. 2. Schematic representation of the experimental design.
After 15 min of stimulation, each participant completed Trust Game for 10 periods with 10 different anonymous trustors.

Germany). tDCS induces changes in cortical excitability by means of a weak electrical field applied transcranially, which de- or hyperpolarizes neuronal membranes on a subthreshold level. Anodal tDCS increases, whereas cathodal tDCS decreases, excitability [28]. For the subjects receiving the tDCS, the anodal electrode was placed over the right Fp2 according to the international EEG 10–20 system, while the cathodal electrode was placed over the right F4 (see Fig. 1). For sham stimulation, the procedures were the same but the current lasted only for the first 30 s. The participants may have felt the initial itching, but there was actually no current for the rest of the stimulation. The current was constant and of 2 mA intensity with 15 s of ramp up and down. After 15 min of stimulation, participants were then asked to complete the trust game task (see Fig. 2).

2.3. Task and procedure

The Trust Game (TG) is the classical paradigm to study trust and cooperation (reciprocity) [4]. In the standard trust game, there are two players: a trustor and a trustee. The trustor firstly decides how much of an endowment to transfer to the trustee. Once transferred,