



Transcranial direct current stimulation of superior medial frontal cortex disrupts response selection during proactive response inhibition



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ABSTRACT

Cognitive control is a vital executive process that is involved in selecting, generating, and maintaining appropriate, goal-directed behaviour. One operation that draws heavily on this resource is the mapping of sensory information to appropriate motor responses (i.e., response selection). Recently, a transcranial direct current stimulation (tDCS) study demonstrated that the left posterior lateral prefrontal cortex (pLPFC) is causally involved in response selection and response selection training. Correlational brain imaging evidence has also implicated the superior medial frontal cortex (SMFC) in response selection, and there is causal evidence that this brain region is involved in the proactive modulation of response tendencies when occasional stopping is required (response inhibition). However, to date there is only limited causal evidence that implicates the SMFC in response selection. Here, we investigated the role of SMFC in response selection, response selection training (Experiment 1) and response selection when occasional response inhibition is anticipated (Experiments 2 and 3) by employing anodal, cathodal, and sham tDCS. Cathodal stimulation of the SMFC modulated response selection by increasing reaction times in the context of proactive response inhibition. Our results suggest a context dependent role of the SMFC in response selection and hint that task set can influence the interaction between the brain and behaviour.

1. Introduction

Cognitive control enables individuals to flexibly select task-relevant responses (i.e., response selection) and to suppress inappropriate and automatic responses (i.e., response inhibition) according to their goals (Luria, 1970). Extensive research using functional magnetic resonance imaging (fMRI) has shown that a wide range of tasks that engage cognitive control, tap a distributed network of brain regions, including the dorsolateral prefrontal cortex, superior medial frontal cortex (SMFC), anterior cingulate cortex, motor cortex, parietal regions, and the basal ganglia (Duncan, 2010; Miller and Cohen, 2001). However, it is currently unknown whether response selection and response inhibition reflect the same or distinct cognitive operations, and the extent to which they draw on overlapping neural substrates (Mostofsky and Simmonds, 2008; van Gaal et al., 2008).

Response selection – the mapping of sensory information onto motor responses – is an amodal information processing operation that is thought to underlie our inability to multitask efficiently (Pashler, 1984). In the lab, increased reaction time (RT) latency is commonly observed when choosing the correct response from a large subset of response alternatives (single response selection task) relative to a low response

selection load, or when individuals attempt to respond to two stimuli in close succession (dual-task). Such multitasking deficits are thought to reflect capacity limitations at the central response selection stage (Dux et al., 2006; Pashler, 1984). Neuroimaging studies suggest that the left hemisphere posterior lateral prefrontal cortex (pLPFC) plays an important role in this bottleneck (Dux et al., 2006, 2009; Jiang and Kanwisher, 2003; Miller and Cohen, 2001). For example, fMRI studies have shown that dual tasks activate this area to a greater extent than single tasks, and that this difference is attenuated as training reduces dual task costs (Dux et al., 2009).

More recently, causal evidence from transcranial direct current stimulation (tDCS) studies implicates the left pLPFC in single- and dual-task response selection, and response selection training effects (Filmer et al., 2013a; Filmer et al., 2013b). tDCS is a non-invasive brain stimulation method that can be employed to modulate cortical activity and establish a causal role of specific regions or functionally/anatomically connected networks in behaviour (Liang et al., 2014; Yu et al., 2015). In addition, it can shed light on the systems-level neural mechanisms of specific cognitive operations by influencing performance in a polarity-specific manner (Filmer et al., 2014). Filmer et al. (2013b) used a combined behavioural and tDCS paradigm to investigate whether the pLPFC

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directly contributes to response selection and response selection training gains. Participants learned the stimulus response mappings for six and two alternative force choice (AFC; high- and low-response selection load respectively) discrimination tasks. Anodal (excitatory), cathodal (inhibitory), or sham stimulation were applied in different sessions with one group receiving stimulation to the left pLPFC and another the right pLPFC. Results demonstrated that under high-load conditions, anodal and cathodal tDCS over the left pLPFC disrupted response selection training benefits relative to sham but this was not observed for the right pLPFC group. These results were also obtained using an alternate reference electrode location and replicated by [Filmer et al. \(2013a\)](#).

Another brain region that has been implicated in response selection operations is the pre-supplementary motor area (pre-SMA; [Dux et al., 2006](#); [Isoda and Hikosaka, 2007](#); [Tombu et al., 2011](#)), a region within the SMFC with extensive pre-frontal connections ([Nachev et al., 2008](#)). Recent tDCS and transcranial magnetic stimulation (TMS) studies provide causal evidence that this area is involved in response selection processes that occur in contexts with increased task conflict, such as selecting responses when automatic and impulsive response tendencies need to be overridden with an incongruent response ([Duque et al., 2013](#); [Herz et al., 2014](#); [Soutschek et al., 2013](#); [Spieser et al., 2015](#)), or when switching between tasks ([Rushworth et al., 2002](#)). To date, however, the causal role of this area in single-task response selection and training has not been established.

While there is limited causal evidence that the SMFC is a key neural substrate of single-task response selection and training, there is extensive research demonstrating that this area is part of a fronto-subcortical network critical for response inhibition (for a review see [Aron, 2011](#)). Indeed, greater pre-SMA Blood-Oxygen-Level-Dependent (BOLD) activity is observed for successful compared to failed stopping ([Aron et al., 2007](#); [Boehler et al., 2010](#)) and TMS and tDCS over the SMFC has been found to disrupt inhibitory control processes ([Cai et al., 2012](#); [Chen et al., 2009](#); [Hsu et al., 2011](#); [Obeso et al., 2013](#); [Watanabe et al., 2015](#)). In addition, fMRI ([Chikazoe et al., 2009](#); [Jahfari et al., 2010](#)), EEG ([Boulinguez et al., 2009](#)), TMS ([Jahfari et al., 2010](#); [Obeso et al., 2013](#)) and tDCS ([Reinhart and Woodman, 2014](#)) studies have further implicated the SMFC in the modulation of response tendencies when participants anticipate that they might have to stop. Such proactive control processes prepare the brain for implementing executive operations. While we refer to this as ‘proactive inhibitory response selection control’, we note that it could also be described as proactive inhibitory control, favoring accuracy over speed, increased response caution, or preparation for a cognitively demanding event. In contrast to reactive control mechanisms, which are triggered by external events, proactive control is guided by endogenous signals. Consequently, RTs are prolonged when participants anticipate the occurrence of a stop-signal (e.g., maybe stop condition) during a stop-signal task (SST) compared to experimental blocks in which no stop-signals are presented (e.g., never stop; [Jahfari et al., 2010](#)).

Given that the SMFC has been implicated separately in both response selection and response inhibition processes, in tasks using distinct stimuli and methodologies, we examined whether this brain area is causally involved in both operations. Specifically, we ran three tDCS experiments that carefully differed in response selection and response inhibitory requirements while controlling stimulus-processing demands. In Experiment 1, we employed the same paradigm as [Filmer et al. \(2013b\)](#) to investigate the role of SMFC in single-task response selection and training processes. In order to test the role of SMFC in response selection and response inhibition, in Experiment 2 we modified the response selection paradigm to incorporate a stop-signal component. This allowed us to investigate whether the SMFC plays a causal role in modulating inhibitory behaviour. Finally, in Experiment 3 we divided the paradigm into response selection only blocks (i.e., Never Stop condition, no inhibitory context) and blocks where outright stopping was occasionally required (i.e., Maybe Stop condition, inhibitory context present). We did this to examine whether SMFC recruitment in response selection is influenced by the context in which it is performed.

2. Experiment 1

2.1. Method

2.1.1. Participants

Eighteen participants (12 females, mean age=24, range 21–33 years) from The University of Queensland participated in the experiment and were paid \$60 for taking part. All participants were right-handed, reported normal or corrected-to-normal visual acuity, passed a tDCS safety screening questionnaire, and had no history of psychiatric or neurological impairment. Written informed consent was obtained and The University of Queensland Human Research Ethics Committee approved the study protocol. The sample size and subject exclusion criteria were determined before data collection and based on the same number of participants recruited in the study by [Filmer et al. \(2013b\)](#), which found a significant stimulation-induced effect on response selection processes.

2.1.2. Stimulation protocol

Each participant underwent three tDCS sessions (anodal, cathodal or sham), which were administered a minimum of 48 h apart. For each session, two 5×5 cm saline-soaked surface sponge electrodes were placed on the scalp. The cortical region of interest (MNI: x=2, y=12, z=56), targeting the SMFC (and specifically pre-SMA; see [Fig. 1A](#)), was based on a recently published meta-analysis into the differential activation effects of two primary response inhibition tasks ([Swick et al., 2011](#)). The reference electrode was placed over the right mastoid (A2), a region commonly used as a reference electrode site when targeting cognitive control operations with tDCS ([Utz et al., 2010](#)). Given the resolution of tDCS, despite targeting pre-SMA, neighbouring regions (e.g., SMA) may well have been stimulated (all be it to a lesser degree). Thus, as is

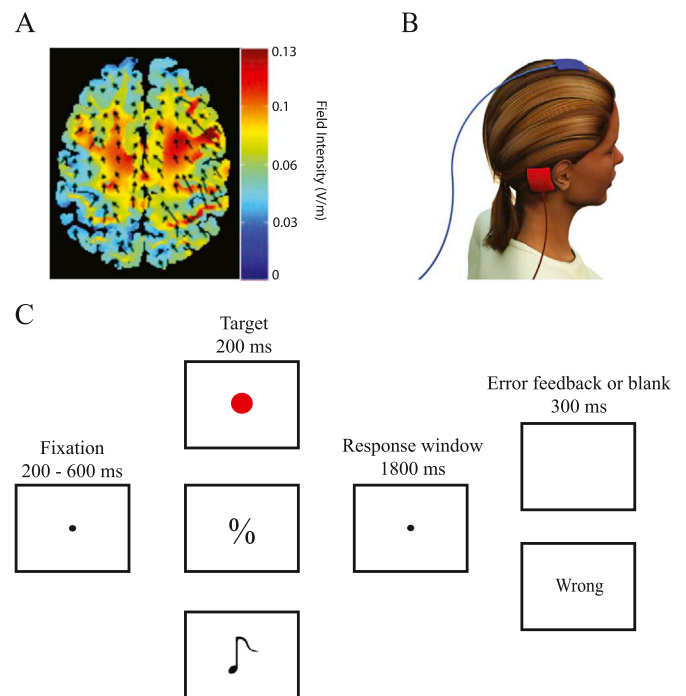


Fig. 1. tDCS model and experiment design. (A) A modeled distribution of electric field during active tDCS on an axial view shown projected through a 3D reconstruction of the cortical surface. The forward model is based on pre-SMA cathode and right mastoid anode electrode locations. (B) tDCS electrode montage. The target electrode was placed 1 cm posterior to Fz, located with reference to the 10–20 EEG system ([Jasper, 1958](#)). The reference electrode was placed over the right mastoid (A2). (C) Schematic representation of trials for the response selection paradigm (see also [Filmer et al. \(2013b\)](#)). All participants completed the response selection paradigm with a different variant of the task (coloured circles, symbols and sounds) used in each session (to control for across session training effects). Participants completed low-load (2 alternative forced choice) and high-load (6 alternative forced choice) blocks.

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