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Transcranial electrical brain stimulation modulates neuronal tuning curves in perception of numerosity and duration

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ABSTRACT

Transcranial direct current stimulation (tDCS) is a non-invasive brain stimulation method with many putative applications and reported to effectively modulate behaviour. However, its effects have yet to be considered at a computational level. To address this we modelled the tuning curves underlying the behavioural effects of stimulation in a perceptual task. Participants judged which of the two serially presented images contained more items (*numerosity judgement task*) or was presented longer (*duration judgement task*). During presentation of the second image their posterior parietal cortices (PPCs) were stimulated bilaterally with opposite polarities for 1.6 s. We also examined the impact of three stimulation conditions on behaviour: anodal right-PPC and cathodal left-PPC (*rA-lC*), reverse order (*lA-rC*) and *no-stimulation condition*. Behavioural results showed that participants were more accurate in numerosity and duration judgement tasks when they were stimulated with lA-rC and rA-lC stimulation conditions respectively. Simultaneously, a decrease in performance on numerosity and duration judgement tasks was observed when the stimulation condition favoured the other task. Thus, our results revealed a double-dissociation of laterality and task. Importantly, we were able to model the effects of stimulation on behaviour. Our computational modelling showed that participants' superior performance was attributable to a narrower tuning curve — smaller standard deviation of detection noise. We believe that this approach may prove useful in understanding the impact of brain stimulation on other cognitive domains.

Introduction

Transcranial electrical brain stimulation has been claimed to be effective in the modulation of behaviour in many different applications; e.g. working memory (Fregni et al., 2005; Ohn et al., 2008), long-term memory (Javadi and Cheng, 2013; Javadi and Walsh, 2012; Javadi et al., 2012), motor tasks (Waters-Metenier et al., 2014; Zhou et al., 2014) as well as many clinical applications (da Silva et al., 2013; Fregni et al., 2005; Hummel et al., 2005), for review see (Madhavan and Shah, 2012; Nitsche and Paulus, 2011).

While such behavioural changes have been reported, the mechanisms underlying their responses are yet to be explored. To address this we created a computational model of the behavioural effects of tDCS stimulation of the left and right PPCs on neuronal tuning curves in numerosity processing and duration judgements. Although not conclusive, there is some evidence showing lateralisation of numerosity and duration judgement tasks (Cohen Kadosh et al., 2010; Dormal et al., 2008; Hauser et al., 2013; Vicario et al., 2013). Therefore we expected to see differential effects of stimulation based on laterality. This would have given us the chance to validate our model for different conditions.

Neurons tuned to numerosity were found in the macaque prefrontal and parietal cortices (Nieder and Miller, 2003, 2004). In line with these findings, Piazza et al. (2004) conducted an fMRI adaptation study which showed evidence for systematic modulation of magnitude processing in the parietal cortex of humans. Participants were required to judge the number of dots on a screen after being habituated to either 16 or 32 dots. Their responses followed a U-shaped tuning curve which indicated an internalised numerical scale centred on the habituation number. We hypothesised that the effects of brain stimulation found in past studies can therefore be explained using the concept of tuning curves: Higher accuracy and decreased variance in behaviour following brain stimulation (Hauser et al., 2013; Vicario et al., 2013) can be explained by narrower tuning curves.

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Methods

Participants

28 participants took part in this study. They were randomly assigned to one of the two tasks: the numerosity or the duration judgement task. Three participants were excluded from the analysis, either due to poor performance (n = 2), or due to displacement of electrodes (n = 1) leading to n = 12 for numerosity judgement task (7 females, age 22.80 ± 2.80) and n = 13 for duration judgement task (7 females, age 22.18 ± 2.18). All participants were healthy with no history of neurological or psychiatric disorders, had normal or corrected-to-normal vision and were naive to the purpose of the study. All were right-handed with a laterality quotient of at least 50 on the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave their written informed consent in accordance with the Declaration of Helsinki and the guidelines approved by the ethical committee of University College London (UCL).

Apparatus

Experiments were run on desktop computers with a 17-inch CRT monitor and 100 Hz refresh rate with the resolution 1024 × 768 pixels. The monitor was 53 cm from the participants' eyes. Stimuli presentation and response time recording were achieved using MATLAB (v7.5; MathWorks Company) and the Psychtoolbox v3 (Brainard, 1997; Pelli, 1997). Data analyses were performed using SPSS (v20.0; LEAD Technologies, Inc.). Responses were made on a conventional computer keyboard using the index and middle fingers of the right hand.

Procedure

The experiment adopted a mixed-design with stimulation condition (3 conditions, see below) as within-subjects factor and task (Numerosity/Duration) as between-subjects factor. Two sets of dots were presented in a virtual 800 × 600 rectangle (28.93° × 21.69° visual angle). Participants were asked to judge which of the two sets contained more dots (numerosity judgement task) or which of the two sets was presented longer (duration judgement task). The numerosity of dots and duration of presentation of dots varied between the trials depending on the task. In the numerosity judgement task, durations of presentation of the two sets were identical, while the number of dots changed. In the duration judgement task, the two sets contained equal numbers of dots but were presented with varying durations. The diameter of dots was adapted pseudo-randomly to achieve a similar overall covered area to avoid possible confounds such as luminance and space (minimum and maximum diameter of 39 and 61 pixels equivalent to 1.44° and 2.25° visual degrees, respectively) (Fig. 1).

The experiment was split over 6 blocks with 30 s rest after each block. Each block contained 50 trials plus 10 training trials at the beginning of the first block.

Transcranial direct current stimulation (tDCS)

Direct electrical current was administered using a neuroConn DC Brain Stimulator Plus unit (Rogue Resolutions, Wales, UK). It was delivered bilaterally via a pair of saline-soaked surface sponge electrodes (both 35 × 35 mm^2) onto the left and right PPCs (P3 and P4 based on 10–10 international system of electrode placement). In one condition, the anode electrode was placed over P3 and the cathode electrode was placed over P4 (*lA-rC* stimulation condition). In the second condition, the placement of the electrodes was reversed (*rA-lC* stimulation condition).

Stimulation was administered on a trial-by-trial basis. In each trial, there was either 1600 ms of stimulation (lA-rC and rA-lC stimulation conditions) or none (*no-stimulation* condition). The onset of the stimulation was 100 ms before the onset of the 2nd set of dots. A square wave form was used with 1.5 mA of amplitude (current density of 1.22 $\mu A/mm^2$). The stimulation was delivered during only the 2nd set of dots in each trial. This was followed by at least 3100 ms of no stimulation until presentation of the 1st set of dots of the next trial. Nitsche and Paulus (2001a) showed that the effect of stimulation of motor cortex on motor evoked potentials (MEP) does not last beyond the duration of stimulation for stimulations shorter than 5 min. Additionally Javadi et al. (2012) showed that the effects of 1600 ms of stimulation do not last beyond the duration of the stimulation Thus we did not expect any lasting effect beyond 1600 ms of stimulation. This method of stimulation has been shown to be effective in modulation of declarative memory (Javadi et al., 2012) and has been shown to be safe for humans (Iyer et al., 2005; Poreisz et al., 2007). The order of stimulation conditions was randomised throughout the session. Participants were informed that they would be stimulated briefly in each trial. They were acquainted with the sensation of the stimulation prior to the beginning of the experiment. All participants reported that they could feel the stimulation and none of them reported any discomfort.

The placement of the electrodes was switched between the blocks to achieve both lA-rC and rA-lC stimulation conditions. The placement of the initial polarity was counterbalanced between participants.

Modelling of tuning curves

Using computational modelling, we aimed to calculate the tuning curves for different stimulation conditions (No-Stimulation/lA-rC/rA-lC). Considering the short duration of brain stimulation used in this study, it is reasonable to assume that the effects of stimulation in the

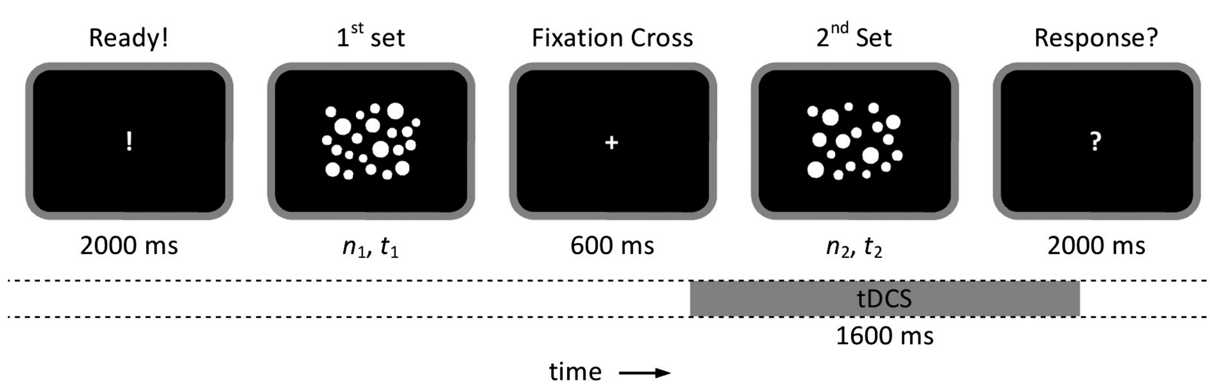

Fig. 1. Procedure of the experiment for both numerosity and duration judgement tasks. For the numerosity judgement task, the number of dots varied between the two sets ($n = \{30, 32, 34, 36, 38\}$) but they were presented for the same duration ($t = 1000$ ms). For the duration judgement task, the number of dots was kept constant ($n = 34$) but the duration of presentation of each set changed ($t = \{800$ ms, 900 ms, 1000 ms, 1100 ms, 1200 ms$\}$). The diameter of dots was controlled in such a way that the overall covered surface was constant between the two sets. Stimulation was initiated 100 ms before the onset of the second set.