Research report

Motor cortex guides selection of predictable movement targets

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HIGHLIGHTS

- We examine the role of the motor cortex in prediction-based target selection.
- tDCS was applied to motor cortex whilst participants reached and touched a target.
- tDCS modulated target selection when the target colour was predictable.
- Motor cortex involved in selecting predictable movement targets.

ARTICLE INFO

ABSTRACT

The present paper asks whether the motor cortex contributes to prediction-based guidance of target selection. This question was inspired by recent evidence that suggests (i) recurrent connections from the motor system into the attentional system may extract movement-relevant perceptual information and (ii) that the motor cortex cannot only generate predictions of the sensory consequences of movements but may also operate as predictor of perceptual events in general. To test this idea we employed a choice reaching task requiring participants to rapidly reach and touch a predictable or unpredictable colour target. Motor cortex activity was modulated via transcranial direct current stimulation (tDCS). In Experiment 1 target colour repetitions were predictable. Under such conditions anodal tDCS facilitated selection versus sham and cathodal tDCS. This improvement was apparent for trajectory curvature but not movement initiation. Conversely, where no predictability of colour was embedded reach performance was unaffected by tDCS. Finally, the results of a key-press experiment suggested that motor cortex involvement is restricted to tasks where the predictable target colour is movement-relevant. The outcomes are interpreted as evidence that the motor system contributes to the top-down guidance of selective attention to movement targets.

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1. Introduction

Selective attention is a crucial mechanism for dealing with the complexities of our visual world (see [1]; for a recent review). The deployment of selective attention is influenced by a range of bottom-up and top-down factors [2]. For instance, attentional deployment is more efficient when the colour of an odd-colour target is the same as on the previous trial [3]. This priming of pop-out (PoP) effect is often seen as the result of a bottom-up, short-term memory process [4]. Moreover, the PoP effect is further enhanced when the target colour is more likely to repeat than to switch over the course of a trial block [5,6]. In other words, attentional deployment is facilitated by predictability of the target colour (a top-down factor). The dorsal attentional network, including the posterior parietal cortex (PPC) and frontal eye fields (FEFs), has been shown to be crucially involved in the selection of a predictable target (see [7]; for a review). The present paper investigates whether the motor system is also involved in the selection of a predictable target.

Positing such a role for the motor system is at odds with traditional serial stage models of the brain. These models assume that the motor system 'simply' has to read out previous processing in order to execute a movement (e.g., [8,9]). Recently, however, converging evidence has revealed an interaction between motor and perceptual/attentional processes consistent with functional

connectivity between motor and posterior parietal regions (see [10]; for a review). For instance, the motor system has been implicated in cognitive operations traditionally thought to be completed 'upstream' [11,12]. It has been shown that the strength of beta oscillations in primary motor cortex varies with attention to task-relevant cues [13], and that the motor cortex accumulates perceptual evidence prior to executing a motor response [14,15]. Importantly, De Lange et al. [14] also demonstrated that the accumulation was biased by the choice of the participant on the previous trial. As well as perceptual information affecting activation in the motor cortex in a feedforward manner, the motor cortex has also been shown to bias perceptual judgments in a feedback fashion. For instance, learning processes in the motor system can change the psychophysical judgment of perceptual stimuli [16–18], and visual discrimination is better at locations that form movement targets than elsewhere [19,20].

Research has also demonstrated the involvement of the motor system in generating sensory predictions (see [21]; for a review). For example, Schubotz and von Cramon [22] asked participants to predict the size of a square based on a preceding size sequence. Analysis of fMRI activity showed that premotor cortex was activated by the attempt to predict the sequential perceptual pattern despite the lack of a movement component. Furthermore, the motor cortex has been shown to encode general uncertainty surrounding the presentation of a perceptual object based on the probability of a cue being a good predictor of a target over a trial block [23]. Bestmann et al. showed that when a high proportion of pre-cues validly predicted the target of a key-press decision pre-stimulus motor cortex activity was biased to a greater extent towards the cued effector than when pre-cues were less predictive.

1.1. The present studies

The studies outlined above suggest that the motor cortex encodes the predictability of perceptual stimuli. In Experiment 1 'streaks' of colour repetitions will be embedded within a trial block meaning that a target repeat is more likely than chance. We expect the motor system to be involved under such conditions. Conversely, we do not expect motor system involvement in Experiment 2 where target colour is unpredictable. Finally, we examine whether the predictable target needs to represent the end point of an overt movement in order to observe motor system involvement (Experiment 3).

To operationalise this movement aspect we combined an odd-colour search task with the choice reaching task (CRT) where participants are asked to reach and touch a target item (see [24]; for a review, and [25]; for a computational model of the CRT). Song and Nakayama [26] have previously demonstrated how the CRT is sensitive to predictable target repetitions. As the target colour predictably repeated there were reductions in both the time taken to initiate the reach (initiation latency; IL), and the maximum deviation of the reach trajectory (MD) from the ideal path (straight line; see Fig. 6). Thus, the ongoing competition between search items 'leaks' into the reach trajectory providing continuous insight into the target selection process (see [24]).

Evidence that the motor cortex can form representations of perceptual information if the information is strongly related to movements [27,28], gives additional credence to the hypothesised role of the motor system in our paradigm. For example, Zach et al. showed motor cortex neurons responded to the colour of a target when it was associated with the end point of a reaching movement. It is important to note that the present paper is not concerned with the roles of the cerebellum [29] or the superior colliculus [30] in movement control. Rather, it attempts to investigate the role of the motor system in prediction-based guidance of target selection.

In all studies transcranial direct current stimulation (tDCS) was applied to the motor cortex during task-completion. tDCS is known to increase (anodal tDCS) or decrease (cathodal tDCS) excitability of the underlying cortex [31]. In both cases, there are measurable behavioural consequences [32]. Although on the face of it, electrical stimulation over the motor cortex seems fairly non-specific, a recent study combining tDCS and electroencephalography demonstrated effects predominantly on the motor cortex and functionally-related areas [33].

2. Experiment 1: the effects of tDCS on reaching to a predictable target

In Experiment 1 target colour streaks introduced predictability into the experimental design. The proportion of target colour repeats to switches is 80%:20%, hence we expect the motor cortex to be recruited during task performance. Thus the repetition effect should be strengthened in the anodal stimulation group (AtDCS) but weakened in the cathodal stimulation group (CtDCS).

2.1. Method

2.1.1. Participants

27 University of Birmingham students were recruited in exchange for cash or course credit. Participants in all three experiments were right-handed and had normal or corrected-to-normal colour vision. Participants were randomly assigned to an AtDCS, CtDCS, or sham (StDCS) stimulation group. The participant information for each group was as follows: AtDCS: $n = 9$, 5 females, aged 18–29 (mean 22.1), StDCS: $n = 9$, 5 males, aged 20–35 (mean 25.9), CtDCS: $n = 9$, 7 females, aged 19–23 (mean 20.22). Procedures were approved by the local ethics committee at the University of Birmingham and informed consent was gathered from all participants after the completion of a tDCS safety screening questionnaire.

2.1.2. Procedure

Participants were seated in a semi-darkened room facing a visual display (19″ SyncMaster 940N, Samsung). Their right-hand rested beside a trigger switch on the table in front of them (aligned with body midline; 10 cm from participant, 45 cm from display). When prompted by on-screen instructions participants held down the trigger switch to commence each trial. A white fixation cross (0.9°) was presented alone in the centre of a black background for 1000 ms before being joined by three squares (3.8° × 3.8°) positioned at 12 o'clock, 4 o'clock or 8 o'clock around a circle (radius of 12.2°). Two of the squares (the distractors) were green ($u' = 0.11$, $v' = 0.24$, $L = 64.43$) and the other square (the target) was red ($u' = 0.46$, $v' = 1.03$, $L = 22.43$), or vice versa.

Participants were instructed to reach as quickly and as accurately as possible to the target square. To encourage participants to start their reaching movements as quickly as possible we included a tone at 400 ms after stimulus presentation on every trial. If participants failed to initiate their reach before the tone they were instructed to concentrate on doing so on the next trial by the experimenter. An initiation period of 400 ms was chosen based on previous studies within our laboratory that showed this to approximate the average latency. Trials that exceeded the 400 ms threshold were still included in the analysis (unless removed as outliers; see Section 2.2).

As well as commencing the onscreen trial procedure, the trigger switch also activated motion capture cameras (Qualisys ProReflex MCU240, 120 Hz). The cameras recorded the 3D position of a small (4 mm), passive reflective marker attached to the participant's right index fingernail from the point at which the trigger switch was