Neuropsychologia 65 (2014) 287–296

Contents lists available at ScienceDirect

Neuropsychologia

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

Research report

Dissociating the influence of response selection and task anticipation on corticospinal suppression during response preparation

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ARTICLE INFO

Available online 13 August 2014

Keywords:
Inhibition
Action selection
Competition resolution
Impulse control
Transcranial magnetic stimulation
Motor preparation
Movement

ABSTRACT

Motor behavior requires selecting between potential actions. The role of inhibition in response selection has frequently been examined in tasks in which participants are engaged in some advance preparation prior to the presentation of an imperative signal. Under such conditions, inhibition could be related to processes associated with response selection, or to more general inhibitory processes that are engaged in high states of anticipation. In Experiment 1, we manipulated the degree of anticipatory preparation. Participants performed a choice reaction time task that required choosing between a movement of the left or right index finger, and used transcranial magnetic stimulation (TMS) to elicit motor evoked potentials (MEPs) in the left hand agonist. In high anticipation blocks, a non-informative cue (e.g., fixation marker) preceded the imperative; in low anticipation blocks, there was no cue and participants were required to divide their attention between two tasks to further reduce anticipation. MEPs were substantially reduced before the imperative signal in high anticipation blocks. In contrast, in low anticipation blocks, MEPs remained unchanged before the imperative signal but showed a marked suppression right after the onset of the imperative. This effect occurred regardless of whether the imperative had signalled a left or right hand response. After this initial inhibition, left MEPs increased when the left hand was selected and remained suppressed when the right hand was selected. We obtained similar results in Experiment 2 except that the persistent left MEP suppression when the left hand was not selected was attenuated when the alternative response involved a non-homologous effector (right foot). These results indicate that, even in the absence of an anticipatory period, inhibitory mechanisms are engaged during response selection, possibly to prevent the occurrence of premature and inappropriate responses during a competitive selection process.

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1. Introduction

Most daily life situations require making decisions between several actions (Cisek, 2012; Oliveira, Diedrichsen, Verstynen, Duque, & Ivry, 2010). Computational and neurobiological approaches view decision making as a continuous process in which evidence simultaneously accumulates for different options, with selection occurring when the activity associated with a particular action reaches a threshold (Cisek, 2006; Cos, Duque, & Cisek, 2014; Domenech & Dreher, 2010; Kim & Basso, 2010; Klein-Flugge & Bestmann, 2012; Klein, Olivier, & Duque, 2012; Link & Heath, 1975; Mazurek, Roitman, Ditterich, & Shadlen, 2003; Tosoni, Galati, Romani, & Corbetta, 2008). Many variants of decision-making models assume that inhibitory mechanisms contribute to this accumulation process (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Usher & McClelland, 2004); but see also Brown & Heathcote (2008). In general, these inhibitory processes are assumed to help ensure that non-optimal actions are prevented from reaching threshold, although the manner in which they contribute to response preparation and initiation remains the subject of considerable debate (Aron, 2007; Munakata et al., 2011; Wiecki & Frank, 2013).

TMS applied over the primary motor cortex (M1) has been used to probe the dynamics of corticospinal (CS) excitability during response selection. When preparing a unimanual movement, CS excitability of selected hand muscles increases (Chen & Hallett, 1999). In contrast, nonselected hand muscles typically show a transient decrease in excitability (Duque et al., 2005, 2008; Leocani, Cohen, Wassermann, Ikoma, & Hallett, 2000), suggesting the existence of processes that not only promote activation of the selected action, but also inhibition of actions that have not been selected (Klein, Petitjean, Olivier, & Duque, 2014; Koch et al., 2006). This inhibition, or what we have called “inhibition for

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http://dx.doi.org/10.1016/j.neuropsychologia.2014.08.006
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competition resolution (CR)", can sharpen response selection in a competitive process (Duque, Olivier, & Rushworth, 2013; van Campen, Keuken, van den Wildenberg, & Ridderinkhof, 2014). Moreover, when both hands are potential responders, this inhibitory process might be essential to negate the likelihood of mirror movements that could result from bilateral planning (Davare, Duque, Vandermeeren, Thonnard, & Olivier, 2007; Duque et al., 2009; Swinnen, 2002).

However, it is also possible that CS suppression of a non-selected muscle reflects remnants of anticipatory inhibitory influences that are not directly related to selection processes (Duque & Ivry, 2009). That is, in most choice reaction time studies, the imperative signal is preceded by an alerting cue such as the onset of a fixation marker to initiate the trial. Such cues are included to allow participants to anticipate the task since the instructions generally encourage participants to respond as quickly as possible following the presentation of the imperative. Interestingly, this anticipation includes suppression of task-relevant muscles (Duque, Lew, Mazzocchio, Olivier, & Ivry, 2010; Fetz, Perlmutter, Prut, Seki, & Votaw, 2002; Hasbroucq, Kaneko, Akamatsu, & Possamai, 1999).

The aim of the present study was to re-examine the operation of inhibitory processes during response preparation, employing a design that can separate effects related to anticipation from those related to response selection. In all conditions, participants had to select between a left or right index finger movement. In a high anticipation condition, the imperative signal was preceded by two successive events, a fixation marker and an alerting cue. In a low anticipation condition, we eliminated these two events, precluding any explicit advance warning of the imperative signal. In the latter condition, we also included an unrelated secondary task, making it impossible for the participant to predict the task for the forthcoming trial. These manipulations were expected to greatly reduce the participants' ability to anticipate the imperative for the choice reaction time (RT) task in the low anticipation condition. While we did not include a direct measure of anticipation (e.g., EEG-based measure such as readiness potential), the RTs in the low and high anticipation conditions provided a proxy: we assumed RTs would be faster in the high anticipation condition.

We measured MEPs elicited in the left hand following TMS of right M1. The TMS pulses were administered either before or after the imperative signal. We predicted that, before the imperative signal, left MEPs would be attenuated relative to baseline in the high anticipation condition, consistent with previous results (Davranche et al., 2007; Duque & Ivry, 2009; Duque, Labruna, Verset, Olivier, & Ivry, 2012). In contrast, we predicted that MEPs would be unchanged in the low anticipation condition given that the participants could not anticipate the imperative.

Of greater interest was the dynamics of CS excitability changes following the imperative. In the high anticipation condition, left MEPs should remain inhibited when the imperative signals a right hand response, indicative of either anticipatory inhibition and/or the operation of inhibition related to response selection (CR). We considered three possible outcomes for the low anticipation condition. First, if the post-imperative inhibition reported in previous studies is related to selection processes, we would expect to observe a suppression of left MEPs after an imperative signalling a right hand response. Second, observing no post-imperative inhibition in the low anticipation condition would suggest that the inhibition observed in previous studies was due to anticipatory effects. Third, left MEP suppression following left and right hand cues would suggest the recruitment of a more generic inhibitory process during response selection and preparation. We conducted a second experiment in which we varied the relationship between the two response options to explore the generality of these preparatory dynamics.

2. Methods

2.1. Participants

A total of 25 right-handed healthy volunteers participated; 10 in Experiment 1 (5 women, 23 ± 1.7 years old) and 15 in Experiment 2 (6 women, 20 ± 0.6 years old). Participants were financially compensated and were naive to the purpose of the study. All participants gave written informed consent under a protocol approved by the Committee for the Protection of Human Subjects at UC, Berkeley.

2.2. Experiment 1

2.2.1. Experimental procedure

The participants sat in front of a computer screen with both hands resting on a pillow, palms down and the arms semi-flexed. Responses involved abductions of either the left or right index finger. We used a virtual *soccer* game task in which the required response was indicated by the position of the "ball" on the computer screen (Fig. 1A). The instructions emphasized that the participants should imagine shooting the ball with the index finger into the goal. In separate blocks of trials, the *soccer* game was performed under SINGLE or DUAL TASK conditions, designed to create conditions of high and low anticipation, respectively.

Trials in the SINGLE TASK blocks were similar to those used in Duque et al. (2010). Each trial began with the brief presentation (100 ms) of a fixation marker at the center of the screen. 900 ms later, an alerting cue appeared which consisted of two adjacent central brackets, the "goals", oriented to the left and right. After 900 ms, an informative imperative signal was added to the display. The imperative was a filled circle, the "ball" and was positioned on the left or right side of the goals. The participant was instructed to perform the specified abduction movement as quickly as possible. To emphasize reaction time, the imperative only remained visible for 350 ms. Note that with this design, response selection was only possible after the appearance of the imperative signal. However, participants could anticipate the imperative given that the fixation marker and alerting cue occurred at fixed intervals in advance of the imperative. The duration of the inter-trial interval was randomly selected to be between 2700 and 3150 ms.

The DUAL TASK condition was designed to minimize the role of inhibitory processes that operate during delay periods between a cue and an imperative signal (Duque & Ivry, 2009). In the DUAL TASK blocks, the *soccer* trials were randomly intermixed with a secondary task (see Fig. 1A). For the latter, the imperative was a *word* that appeared at the center of the screen. Participants responded with a left foot extension when the word denoted an animal and withheld responding when the word denoted an inanimate object. No fixation marker or alerting cue was provided during the DUAL TASK blocks. As a consequence, participants did not know which task (*soccer* or *word*) would be performed from trial to trial, nor were there any events to indicate the onset of the imperative. As such, we expected minimal anticipation and/or preparation of the manual responses. As in the SINGLE TASK blocks, the duration of the inter-trial interval was randomly selected to be between 2700 and 3150 ms.

The participants practiced the two block types for a few minutes to become familiar with the basic procedure. The main phase of the experiment consisted of six blocks, two SINGLE TASK blocks (high anticipation) and four DUAL TASK blocks (low anticipation). The blocks for a given condition were run successively, with the order of the two conditions counterbalanced. Each SINGLE TASK block consisted of 96 trials and each DUAL TASK block consisted of 84 trials (42 for each *soccer* or *word* task). Within each block, half of the soccer

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