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Reward anticipation modulates primary motor cortex excitability during task preparation

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ABSTRACT

Task preparation has been associated with a transient suppression of corticospinal excitability (CSE) before target onset, but it is an open question to what extent CSE suppression during task preparation is susceptible to motivational factors. Here, we examined whether CSE suppression is modulated by reward anticipation, and, if so, how this modulation develops over time. We administered a cue-target delay paradigm in which 1000 ms before target onset a cue was presented indicating whether or not reward could be obtained for fast and accurate responses in a Simon task. Single-pulse transcranial magnetic stimulation was applied over left primary motor cortex (M1) during the delay period (400, 600, or 800 ms after cue onset) or 200 ms after target onset, and electromyography was obtained from the right first dorsal interosseous muscle. Behaviorally, the anticipation of reward improved performance (i.e. faster reaction times). Most importantly, during reward anticipation we observed a linear decrease of motor evoked potential amplitudes that was absent when no reward was anticipated. This suggests that reward anticipation modulates CSE during task preparation.

Introduction

By anticipating what is to come, task preparation allows humans to rapidly and flexibly meet environmental demands and plan actions (Bode and Haynes, 2009; Brass and Von Cramon, 2002, 2004). For example, in waiting at a crossroad for the traffic light to turn green, we monitor both the light and ongoing traffic, and prepare ourselves to switch gears and hit the gas when appropriate. In general, this type of task preparation can be divided into at least two main components: Configuring the attentional set in order to attend to the relevant information in the environment (e.g., monitor the light), and activating the relevant stimulus-response mappings to respond rapidly to the selected information (e.g., hold the gear stick).

An increasing number of studies have demonstrated that task preparation is sensitive to the anticipation of reward (for recent reviews, see Botvinick and Braver, 2015; Notebaert and Braem, 2015). However, all these studies focused on the first component of task preparation, demonstrating how the anticipation of reward can modulate preparatory attentional processes by increasing perceptual sensitivity to identify targets (Engelmann et al., 2009; Engelmann and Pessoa, 2014) or by improving the suppression of task-irrelevant information (Padmala and Pessoa, 2011). In contrast, the present study set out to investigate to what extent the second component, preparing the motor system for what is to come, might also be sensitive to motivational factors.

Recent studies using transcranial magnetic stimulation (TMS) in combination with electromyography (EMG) implicate the primary motor cortex (M1) in the preparation of the motor system. Specifically, the preparation of motor responses has been associated with decreased corticospinal excitability (CSE) (Duque and Ivry, 2009; Duque et al., 2012; Duque et al., 2010; Greenhouse et al., 2015; Lebon et al., 2015). For example, after cueing which effector (i.e., hand) would be involved in the response, Duque and Ivry (2009) reported a most prominent prestimulus decrease in CSE for the hand involved in the forthcoming response execution. Furthermore, decreased CSE has also been found when participants could not anticipate the forthcoming response (Duque and Ivry, 2009), and for task-irrelevant and non-homologous muscles (Greenhouse et al., 2015). Consequently, it has been suggested that preparatory CSE suppression reflects a general mechanism that prepares for multiple potential actions by suppressing the whole motor output system during task preparation (Cisek, 2007; Cisek and Kalaska, 2005; Koch et al., 2006). Accordingly, a continuous tug-of-war between distinct action representations in the motor cortex is assumed to reflect the impact of multiple (cognitive) processes biasing the system towards an action alternative (i.e. preparation to act), implemented by a parallel flow of information between perceptual decision making systems and the motor system (Bestmann and Duque, 2015; Cisek, 2012; Servant et al., 2015; Thura and Cisek, 2014). Hence, CSE suppression might be an important aspect of action selection. If the

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latter is indeed the case, we expect it to be modulated by motivational factors.

Various studies have investigated the impact of motivation on CSE prior to action execution (e.g. Chiu et al., 2014; Gupta and Aron, 2011; Suzuki et al., 2014; Vassena et al., 2015). In these studies, however, (partial) information about which action to perform was provided before excitability was measured. These studies generally observed that higher states of motivation (e.g. after the anticipation of affective or reward predicting stimuli compared to aversive or no reward predicting stimuli) were associated with increased CSE. This approach certainly yields insight into the effects of motivation on CSE when preparing specific actions, but does not provide information about a general, task-preparatory effect at play when no information about the required response is provided. In the present study, we investigated whether task-preparatory, pre-target motor suppression is modulated by reward anticipation, and if so, how this motivational influence develops over time. Contrary to earlier studies investigating motivational effects on CSE, we measured motor evoked potentials (MEPs) before any information about the target was available. We presented reward cues 1 s before target onset. The cue indicated whether reward could be obtained or not after good performance (see below). Within the cue-target delay period, we applied single-pulse TMS over the left M1 to probe CSE during one of three different epochs (400, 600, or 800 ms after cue onset), while EMG was recorded from the right first dorsal interosseous (FDI). Besides the impact of reward anticipation on motor suppression, a secondary aim of the current study was to explore the relationship between reward anticipation and conflict behaviorally and at the neurophysiological level. To this end, targets consisted of lateralized, colored circles (i.e. Simon stimuli) and participants were instructed to respond to the color of the target by providing a left or right index finger response. We chose to administer a Simon task to investigate whether, much like the reduced interference effect in Stroop-like paradigms (Padmala and Pessoa, 2011), reward anticipation would also attenuate the well-known Simon effect (faster responses when stimulus location corresponds spatially with response location; Simon, 1969). Additionally, previous investigations have shown that at the neurophysiological level the task-irrelevant location of (incompatible) Simon stimuli evoked an early transient increase of CSE in the uninvolved hand, followed by a continuous CSE increase in the involved hand, suggesting that the canonical behavioral Simon effect could be traced back to alterations in CSE (van Campen et al., 2014). However, evidence that conflict in the Simon task may interact with reward anticipation at the level of M1 is limited (c.f. Herz et al., 2014). Correspondingly, a fourth potential stimulation epoch was added in which a TMS pulse over left M1 could be applied 200 ms after target onset to investigate the consequences of conflict and reward anticipation on CSE.

Materials and methods

Participants

Twenty right-handed participants (sixteen female, mean age = 22.6 years, SD = 2.3 years) were naïve to the real purpose of the study and prescreened for psychiatric and neurological disorders as well as for factors that may interfere with a safe application of TMS (Rossi et al., 2009). Participants provided written informed consent and were monetarily compensated (30€). Furthermore, prior to the experiment, they were informed that the best-performing participant would receive a voucher (25€) for a multimedia store. The study was approved by the ethical committee at the Ghent University Hospital.

TMS stimulation and EMG recordings

EMG was measured from the right FDI muscle that is crucial for abducing the right index finger away from the right middle finger. An ActiveTwo system (www.biosemi.com) was used to record EMG activity, while sintered 11 × 17 mm active Ag-AgCl electrodes were mounted on the right FDI and on the metacarpophalangeal joint, respectively. Two ground-electrodes were placed on the dorsum of the hand. The EMG signal was amplified via internal gain scaling, digitized at 2048 Hz and high-pass filtered at 3 Hz.

Primary motor cortex was stimulated using a 70 mm figure of eight coil connected to a biphasic stimulator (Rapid2; The Magstim Company Ltd.) (for recent reviews, see Bestmann and Duque, 2015; Bestmann and Krakauer, 2015). The stimulation coil was tangentially positioned over the right hand motor area (i.e. left M1) so that the handle pointed to the dorsocaudal part of the participant's head, thereby creating an angle of 45° with the sagittal plane. The coil was held by a mechanical arm throughout the experiment. The TMS stimulation location was determined by the scalp position that evoked the most reliable MEP. Throughout the whole experiment, participants wore a swimming cap where the optimal stimulation location was marked. Correspondingly, the experimenter could continuously monitor TMS stimulation location. The resting motor threshold (rMT) was dependent on the stimulation intensity that evoked MEPs larger than 50 μV in 50% of the cases (Rossini et al., 1994). Eventual stimulation intensity was adjusted to 110% of the rMT. On average, this led to a stimulation intensity of 62% (range 43%–78%) of the maximal stimulator output.

Stimuli and procedure

Participants were seated in a comfortable chair with an eye-monitor distance of approximately 50 cm. Participants were instructed to place their tips of their left and right index finger on a reversed QWERTY keyboard between the F4, F5 and F8, F9 buttons respectively (cf. Klein et al., 2012). Moreover, they were asked to respond with an abduction movement towards the medial response buttons (F5 and F8) to eventually perform a key press. Stimulus presentation was carried out by Presentation® software (Version 16.3, www.neurobs.com) on a 17-inch computer monitor (1024 × 768 pixels).

Individuals were able to accumulate points for fast and accurate responses on 50% of all trials. Fast and accurate responses were predefined as correct responses that occur within 700 ms after target onset. Thus, if individuals accurately responded within 700 ms after target onset on reward trials, they earned an additional point. However, if they responded slower than 700 ms they did not receive any points on that trial. Participants were told that they could win a voucher for a local multimedia store when they accumulated the highest amount of points across all participants.

Each trial began with the presentation of a fixation star for 500 ms. Thereafter, a cue was presented above the fixation that indicated whether subjects could obtain reward for fast and accurate responses or whether no reward could be obtained on the current trial (see Fig. 1 for a schematic illustration of the trial procedure). More specifically, a '+1' presented above fixation was indicative of potential reward, whereas a '+0' indicated no reward. Both the cue and fixation star were presented for 300 ms. This was followed by a fixation period for 700 ms. Within this interval, during 60% of the trials, CSE was assessed 400, 600 or 800 ms after cue onset (i.e. 100, 300, 500 ms after cue offset). Subsequently, a colored circle (i.e. Simon stimulus) was presented left or right of fixation for maximally 1000 ms. Depending on the color of the circle, participants were required to respond with a left/right FDI abduction movement towards and eventually press the response key. During another 20% of the trials, a TMS pulse was applied over the left M1 200 ms after target onset to examine CSE during task processing. Last, during the remaining 20% of the trials, no TMS stimulation was applied. If participants responded within the 1000 ms window of stimulus presentation a fixation period followed for 200 ms. Eventually, a feedback screen was shown for 1000 ms. Specifically, on reward trials, if participants provided a correct response within the allowed time window after target onset, this feedback screen consisted of either '+1' (if the response was provided within 700 ms after target onset) or