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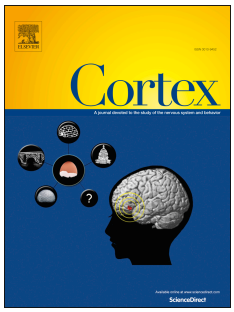

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PII: S0010-9452(19)30232-1

DOI: https://doi.org/10.1016/j.cortex.2019.05.020

Reference: CORTEX 2664

To appear in: *Cortex*

Received Date: 20 September 2018

Revised Date: 12 March 2019

Accepted Date: 27 May 2019

Please cite this article as: Bundt C, Bardi L, Verbruggen F, Boehler CN, Brass M, Notebaert W, Reward anticipation changes corticospinal excitability during task preparation depending on response requirements and time pressure, *CORTEX*, https://doi.org/10.1016/j.cortex.2019.05.020.

Reward anticipation changes corticospinal excitability during task preparation depending on response requirements and time pressure.

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Abstract

The preparation of an action is accompanied by transient corticospinal (CS) excitability changes. Motivation can modulate these changes. Specifically, when a cue indicates that a reward can be obtained, CS excitability initially increases, followed by a pronounced decrease. This dynamic could reflect processes related to reward expectancy, processes related to action preparation, or a combination of both. Here we set up two experiments to dissociate these accounts. A rewarded choice reaction time task was used in which individuals were cued at the beginning of each trial whether or not a response would be required at target onset and whether or not a reward could be obtained. We used single-pulse transcranial magnetic stimulation (spTMS) over the left primary motor cortex (M1) early (shortly after cue onset) or late (shortly before target onset) preceding target onset to examine CS excitability during motivated action preparation. Electromyography (EMG) was obtained from the right first dorsal interosseous (FDI) muscle. In the first experiment, we used a lenient response deadline, whereas a strict response time-out procedure was employed in the second experiment. Reward modulated CS excitability differentially only in the second experiment: CS excitability was highest during reward anticipation for the early stimulation epoch and was reduced for the late stimulation epoch when individuals were required to prepare a response, while CS excitability remained unchanged during non-reward anticipation. Our findings suggest that the reward effect on CS excitability is dependent on the actual implementation of effort to attain reward (i.e., the preparation of an actual action), as well as on temporal requirements (i.e., time pressure) invoked by the task.

Keywords: reward, response preparation, primary motor cortex, corticospinal excitability, transcranial magnetic stimulation.

Introduction

Our ability to prepare for specific tasks and actions allows us to respond rapidly to changing environmental demands (Bode & Haynes, 2009; Brass & Von Cramon, 2002, 2004). Changes in corticospinal (CS) excitability have been observed during action preparation using transcranial magnetic stimulation (TMS) with concurrent electromyography (EMG) (Duque & Ivry, 2009; Greenhouse, Sias, Labruna, & Ivry, 2015; Lebon et al., 2015). To assess action preparation, TMS over the primary motor cortex (M1) can be combined with a cue-target delay paradigm in which a cue specifies which action must be prepared before onset of a target (Duque & Ivry, 2009). After the presentation of such preparatory cue, CS excitability generally decreases within the cue-target delay period for effectors that are involved in task execution as well as for anatomically or functionally related effectors (Duque & Ivry, 2009; Greenhouse, Sias, et al., 2015). Such CS excitability changes during action preparation have been interpreted as reflecting a "tug-of-war" between distinct action representations that are modulated by decision-related factors (Bestmann & Duque, 2016). Examples for such decision-related factors are the estimation of biomechanical costs (Cos, Duque, & Cisek, 2014) and the subjective value (Klein-Flügge & Bestmann, 2012) associated with a particular action alternative. For instance, if an action would require the individual to exert more effort than an alternative action, such difference would be reflected by motor system state changes. Specifically, Cos et al. (2014) reported that as early as 150 ms after target onset, CS excitability is increased for a biomechanically easier response compared with a biomechanically more difficult response. These findings show that decision-related factors strongly influence our actions in a continuous manner. One of the major factors that drives our actions, however, is the potential reward that is associated with a particular action. To that end, the current study investigates the effect of reward prospect on CS excitability and how such effect is dependent on action preparation and engagement in the task.

Reward has been found to dynamically modulate CS excitability during action preparation (Chiu, Cools, & Aron, 2014; Suzuki et al., 2014; Vassena, Cobbaert, Andres, Fias, & Verguts, 2015). However, the dynamic of reward modulation remains unclear. Some studies found that increased motivation was accompanied by increased CS excitability prior to target onset. In other words, the preparation of a potentially rewarded response was associated with higher CS excitability compared with a response where no reward was available. In contrast, we recently found that CS excitability decreased throughout the delay period after a reward-promising cue, whereas CS excitability did not change significantly for no-reward cues (Bundt, Abrahamse, Braem, Brass, & Notebaert, 2016). Compared to no-reward cues, reward cues initially increased CS excitability, followed by a decrease during the later preparation stages (Fig. 1). The reward-related decrease of CS excitability at late stages during the delay period is consistent with other studies (Duque & Ivry, 2009; Greenhouse, Saks, Hoang, & Ivry, 2015; Greenhouse, Sias, et al., 2015; Lebon et al., 2015), whereas the initial increase of CS excitability was unexpected.

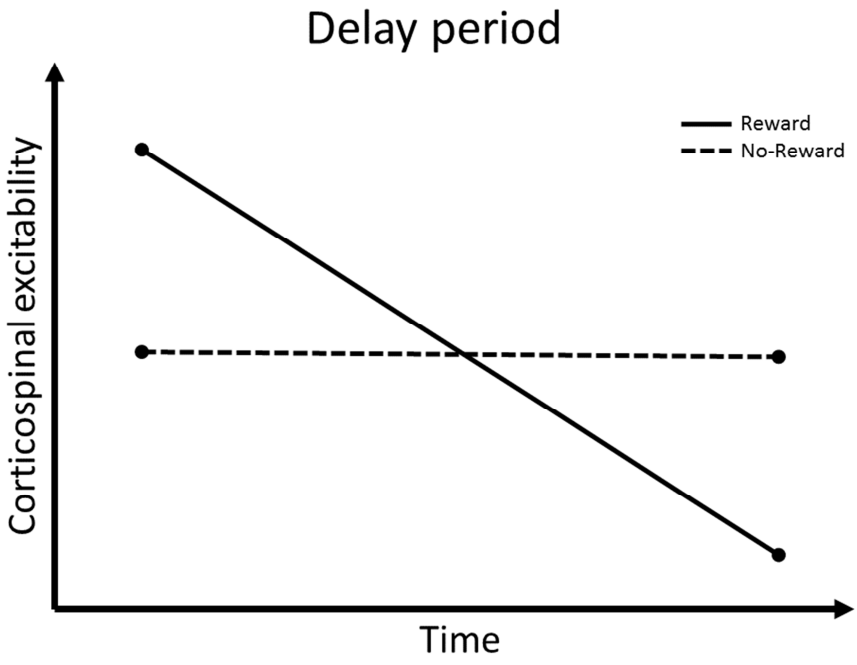

Fig. 1 Schematic illustration of reward-related modulation of CS excitability during the preparatory delay period as reported in (Bundt et al., 2016). For reward compared to no-

reward cues CS excitability increased early in the delay period, which was followed by a decrease closer to target onset.

The current study aimed to investigate two alternative accounts for this reward-related modulation. One possible explanation is that reward activates the motor system in a fast and automatic fashion, similar to the idea of incentive salience or reward 'wanting' (Berridge & Robinson, 2003). We will refer to this explanation as the 'wanting-account'. An alternative explanation of our findings is that the effect of reward on CS excitability is not fast and automatic, but is a reflection of the control (or effort) that is exerted at a specific moment. We will refer to this alternative explanation as the 'control-account'. Goal-directed behavior such as response preparation is dependent on various controlled processes that ensure successful task performance. Such control over task-related processes, however, is intrinsically costly due to limited capacity of the control system and individuals may be reluctant to employ all available cognitive resources at a time (Shenhav et al., 2017). Incentivizing behavior, however, has been found to improve performance. In contrast to the wanting-account, the control-account would predict that the effect of reward on CS excitability would be absent when no response is prepared and no control over task-relevant processes is required.

To dissociate both accounts, we designed a task in which two advance cues were presented in rapid succession (see Fig. 2). The first cue (the 'action cue') indicated whether the upcoming target would require a response or not. The second cue (the 'motivational cue') informed individuals whether they could accumulate an extra point for fast and accurate performance or not. After a delay, a small circle (i.e., the target) appeared left or right from fixation, and participants were required to either withhold or execute a response to the location (depending on the action cue presented at the beginning of the trial). Before target onset, single-pulse TMS (spTMS) was applied over the left M1 and EMG was obtained from

the right first dorsal interosseous (FDI). We assessed CS excitability during three stimulation epochs: a) within the inter-trial-interval (ITI; 200 ms before the onset of the action cue) to examine baseline CS excitability; b) 400 ms after the motivational cue onset to examine CS excitability during early stages of action preparation; and c) 800 ms after the motivational cue onset to examine CS excitability during late stages of action preparation.

At the neurophysiological level, both accounts make distinct predictions. The wanting-account predicts that the mere perception of a reward cue leads to increased CS excitability for reward compared to no-reward cues during the early stimulation epoch (i.e., 400 ms after motivational cue onset) irrespective of whether a response must be prepared or not. In contrast, the control-account predicts that the reward-related modulation of CS excitability is response-dependent: we should observe modulation when individuals need to prepare a response, but no modulation when no response is required as control over task-relevant processes would be redundant. Behaviorally, we hypothesized that both accounts make similar predictions such that reward compared to no-reward cues would speed up responses on preparation trials.

Experiment 1

In the first experiment we examined the influence of reward on CS excitability during the preparation of an action (preparation condition) compared to when individuals did not need to prepare any action (no-preparation condition) under no pronounced time pressure. We hypothesized that if the effect of reward on CS excitability was dependent on the preparation of a response (i.e., control-account), reward would only affect CS excitability in the preparation condition. However, if reward had a non-specific effect on CS excitability (i.e., wanting-account), reward should equally modulate CS excitability on preparation and no-preparation trials.

Methods

Participants

Twenty-five participants took part in the first experiment. One subject was excluded because of a technical error that resulted in no analyzable neurophysiological data. The statistical analyses reported below were based on the data of the remaining twenty-four individuals (17 female; *mean age*= 22.13 ± *SD*=2.23 years of age). Participants were screened for psychiatric and neurological disorders, as well as for factors that could interfere with a safe application of TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). All participants gave written informed consent and were monetarily compensated (25€) for their participation in the study. Moreover, participants were informed that the best-performing individual would receive an extra bonus in the form of a 25€ voucher for a local multimedia store. The study was in agreement with the Declaration of Helsinki (World Medical Association, 2013) and was approved by the local ethical committee at Ghent University Hospital.

Stimuli and apparatus

Participants were seated in a comfortable chair in front of a computer screen with an eye-to-screen distance of approximately 50 cm. Responses were provided via a QWERTY keyboard that was turned 180° horizontally with the function keys facing the participant (c.f., Bundt et al., 2016; Klein, Olivier, & Duque, 2012; Klein, Petitjean, Olivier, & Duque, 2014). Participants were required to place their left and right index finger tips on the keyboard between the F8 and F9, and F4 and F5 buttons, respectively. A response was executed by performing an index finger abduction movement towards the medial response key (i.e., either an abduction movement with the left index finger towards the F8 key, or an abduction movement with the right index finger towards the F5 key) and to eventually press the respective button.

TMS stimulation and EMG recordings

TMS stimulation and EMG recording were identical to our previous study (Bundt et al., 2016). Sintered 11 × 17 mm active Ag-AgCl electrodes were placed onto the right first dorsal interosseous (FDI) and the metacarpophalangeal joint, respectively and two ground electrodes were placed onto the right hand's dorsum. The EMG signal was recorded by an ActiveTwo system (www.biosemi.com), amplified via internal gain scaling, high-pass filtered at 3 Hz and digitized at 2048 Hz.

The left primary motor cortex was stimulated using a 70 mm figure-of-eight coil, which was connected to a biphasic stimulator (Rapid2; The Magstim Company Ltd.). The coil was positioned tangentially over the right hand's motor area in left M1 (posterior-anterior induced current flow) and held by a mechanical arm during the experiment. TMS coil positioning was defined as the scalp location at which the most reliable MEPs were evoked. This location was marked and enabled the experimenter to monitor accurate coil positioning throughout the experiment. The average resting motor threshold (rMT) of all individuals was M=60.75% ± SD=6.6% of the maximal stimulator output. The eventual TMS pulse intensity was set to 110% of the rMT.

Procedure

Each trial started with an asterisk presented in the center of the screen for 500 ms (see Fig. 2 for a schematic illustration of the trial procedure). On some trials, baseline CS excitability was assessed during this fixation period (see below). Subsequently, either a ")(" or "X" was presented for 300 ms above fixation (i.e., action cue). These action cues indicated if an action had to be prepared (i.e., preparation condition, indicated by ")(") or not (i.e., no-preparation condition, indicated by "X"). The preparation condition required individuals to provide a response at target onset, while in the no-preparation condition, individuals were

required not to respond at target onset. The presentation of an action cue was followed by another 600 ms fixation period. After this, the motivational cue was shown for 300 ms above fixation. Specifically, "+1" and "+0" indicated that reward (R) or no-reward (N) could be obtained for fast and accurate performance on the current trial, respectively. Note that participants received reward on no-preparation trials as well, but only if they managed to withhold a manual response. To ensure that participants attended the reward information even after they were informed that they did not need to respond (i.e., during no-preparation trials), the motivational cue was occasionally presented in blue ink color (i.e., catch trial). On these trials, participants were asked to provide a verbal response (i.e., they were required to say "blue") as soon as they detected a blue-colored reward cue (c.f., Gupta & Aron, 2011). Prior to the experiment, participants were told that if they failed to detect a sufficient amount of blue-colored motivational cues, their accumulated reward would be withheld (Gupta & Aron, 2011). After the presentation of the motivational cue, another fixation period of 600 ms (i.e., delay period) followed. On some trials, CS excitability was examined during this delay period (see below). If the motivational cue was presented in blue ink color and indicated a catch trial, the trial was terminated after this delay period and a new trial was initiated. If the motivational cue did not indicate a catch-trial, the action-cue reappeared above fixation and was accompanied by a circle presented left or right from it (i.e., target stimulus). On preparation trials, participants were required to provide a left or right index finger response when the target appeared left or right of fixation, respectively. The duration of the presentation of the target (and simultaneously the duration of the response deadline) was determined by the mean reaction time during a preceding practice phase (see below). After individuals provided a response or the deadline had passed, a fixation period followed (200 ms) and subsequent feedback was provided (1000 ms). If the response was correct and timely, the feedback indicated whether or not reward has been obtained on current trial (i.e., "+1" or

"+0" appeared above fixation), and the total reward amount accumulated throughout the course of the experiment was presented below fixation. Note that the correct 'response' on no-preparation trials was no key press. If the response was incorrect or too late, "fout" (Dutch for "wrong") or "te laat" (Dutch for "too late") was presented above fixation. Each trial was separated by a jittered inter-trial-interval (ITI) fixation period (900-1100 ms).

On a proportion of trials (352 trials; 57.5% of all trials), TMS was applied over the left M1 during three different stimulation epochs. TMS pulses were applied during the ITI fixation period 200 ms prior to the presentation of the action cue to examine CS baseline excitability ($TMS_{baseline}$; 32 trials). To test both, the wanting- and the control-account, CS excitability was examined at early and late time epochs in the delay period following the presentation of the motivational cue (i.e., during the motivational cue-target delay period). More specifically, TMS pulses were applied either 100 ms (TMS_{early}; 160 trials) or 500 ms after the motivational cue offset (TMS_{late}; 160 trials).

In total, the experiment consisted of 612 trials divided into five blocks. The first block (68 trials; thereof four catch-trials) served as practice phase where individuals were able to familiarize themselves with the experimental task. The mean reaction time of participants on correct preparation trials during this practice phase (M=426 ms ± SD=53.47 ms) was eventually used as the (individualized) target response deadline during the subsequent experimental blocks. No TMS was applied during the practice phase and trials were balanced across action cues (preparation/no-preparation), motivational cues (N/R), and responses (right/left).

The practice phase was followed by four experimental blocks (136 trials each; experimental phase), which did include TMS application. In total, the test phase comprised 32 $TMS_{baseline}$ trials, 160 TMS_{early} trials, 160 TMS_{late} trials, 160 trials not including any TMS, as well as 32 catch-trials (i.e., blue cue trials). Each block consisted of randomized trials that

were balanced across action cues (preparation/no-preparation), motivational cues (N/R), TMS epoch (early/late) and responses (right/left). Each experimental condition (i.e., action cues, motivational cues, TMS epoch) consisted of 40 trials.

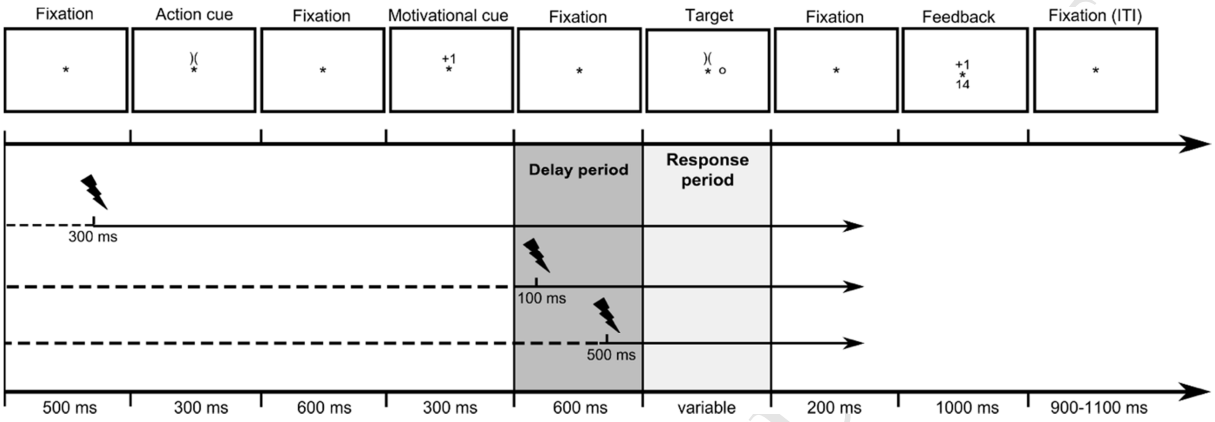

Fig. 2 Schematic trial procedure. Please refer to the main text for a detailed description of the trial procedure.

Data analysis: behavior

To exclude the possibility that the magnetic stimulation of M1 could interfere with behavioral measures (Hasbroucq, Kaneko, Akamatsu, & Possamaï, 1997), the behavioral analysis was based on trials that did not include any TMS pulse. In the RT, we included only correct responses that were not defined as premature (RT < 100 ms) or as too late (i.e., RT < individual mean RT in practice block). Furthermore, we excluded trials if the previous trial met one of the following criteria: the response was wrong, the response was too late, or the previous trial was a catch-trial.

For the preparation condition, the dependent variables RT and the percentage of late responses were then submitted to a paired-samples *t*-test (N vs. R), respectively. For the preparation and no-preparation condition, percentage correct responses were submitted to a paired-samples *t*-test (N vs. R), respectively. For paired-samples *t*-tests Cohen's d_z was

estimated by dividing the mean difference between samples by the standard deviation of the difference scores (Lakens, 2013).

Data analysis: CS excitability

CS excitability changes were analyzed offline using custom software in MATLAB (MATLAB and Statistics Toolbox Release 2012b, The MathWorks, Inc., Natick, Massachusetts, United States). One-second EMG epochs surrounding the TMS pulse (interval from 500 ms before the TMS pulse to 500 ms after the TMS pulse) were extracted. An automated search-algorithm identified the peak-to-peak motor-evoked-potential (MEP) amplitude during a window of 20-40 ms succeeding the TMS pulse. Prior to data collection had started, we decided to discard MEPs that were affected by pre-contraction (root mean square of background activity exceeding 0.1 mV during the 500 ms interval prior to the TMS pulse) or that were identified as outliers (i.e. values above or below three standard deviations from the mean calculated for baseline and delay-period TMS separately). Table 1 shows the average MEP size and the absolute number of trials that were included in the CS excitability analysis per experimentally manipulated level. MEP amplitudes were normalized relative to baseline and expressed as a percentage change score: (Condition/Baseline-1) × 100 (Lebon et al., 2015). Accordingly, positive values indicate activation, whereas negative values indicate suppression of CS activity. MEPs of valid trials were submitted to a repeated-measures ANOVA (rmANOVA) with action cue (preparation, no-preparation) × motivational cue (N, R) × stimulation epoch (early, late) as within-subjects factors. The alpha level for the rmANOVA was set at .05. Two-tailed one-sample *t* tests were used to examine whether CS excitability during the delay period was significantly suppressed relative to baseline (Duque & Ivry, 2009; Greenhouse, Sias, et al., 2015; Lebon et al., 2015) in which the alpha level was set at .00625 to Bonferroni correct for the number of tests against baseline (action cue (2) ×

motivational cue (2) × stimulation epoch (2)). For one-sample *t*-tests Cohen's d_z was calculated to estimate effect sizes (Lakens, 2013).

Table 1. Average MEP size in millivolt (mV±SD) and the absolute number (n±SD) of trials included in the CS excitability analysis for each experimental condition in Exp 1.

	No-Reward				Reward			
	Early		Late		Early		Late	
	mV±SD	n±SD	mV±SD	n±SD	mV±SD	n±SD	mV±SD	n±SD
No-Preparation	1.44±0.72	30±7	1.43±0.71	30±6	1.58±0.85	29±7	1.38±0.71	29±7
Preparation	1.54±0.87	31±5	1.30±0.77	28±6	1.58±0.79	30±5	1.28±0.69	28±6

Results

Behavior

In the preparation condition, RTs were significantly shorter during reward compared to no-reward trials (**Fig. 3**; 410 ms vs. 427 ms; $t(23)=-4.629$, $p<.001$, $d_z=-.945$). Percentages correct responses were not significantly different for reward and no-reward trials in the preparation condition (99.6% vs. 99.5%; $t<1$). In the no-preparation condition, percentages correct responses (i.e., correctly withholding a response) were not significantly different during reward compared to no-reward trials (99.6% vs. 100%; $t(23)=1.812$, $p=.083$). In the preparation condition, the percentage of late responses (i.e., responses that were not provided within the response deadline) was not statistically different between reward and no-reward trials (1.14% vs. 1.10%; $t<1$).

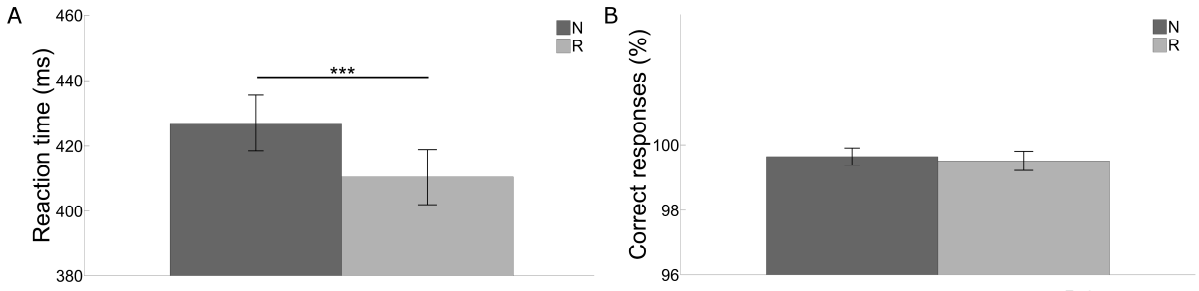

Fig. 3 Mean reaction time (A) and percentage correct responses (B) for no-reward (N) and reward (R) in Exp. 1. Error bars represent one standard error. ***p<.001.

CS excitability

Mean raw baseline MEP amplitudes were 1.55 mV (± 0.77 SD). The rmANOVA revealed that there was no main effect of action cue (no-preparation=-4.08% vs. preparation=-5.27%; F<1), nor a main effect of motivational cue (no-reward=-5.57% vs. reward=-3.79%; $F(1,23)=1.301$, $p=.266$, $\eta_p^2=.054$). However, there was a main effect of stimulation epoch: relative to baseline, CS excitability was significantly higher during early compared to late stimulation epochs (0.05% vs. -9.87%; $F(1,23)=13.658$, $p=.001$, $\eta_p^2=.373$). There was also a significant interaction between action cue and stimulation epoch ($F(1,23)=6.503$, $p=.018$, $\eta_p^2=.220$). This two-way interaction was due to a significant difference of CS excitability between early compared to late stimulation epochs for preparation trials (2.81% vs. -13.35%; $F(1,23)=14.334$, $p<.001$, $\eta_p^2=.384$), but not for no-preparation trials (-1.78% vs. -6.38%; $F(1,23)=2.702$, $p=.114$, $\eta_p^2=.105$), indicating a preparatory CS excitability decrease only when an actual action had to be prepared. No other two-way (ps>.225) or three-way (p=.162) interaction effects were observed.

CS excitability did not significantly differ from baseline for any condition (ps>.016).

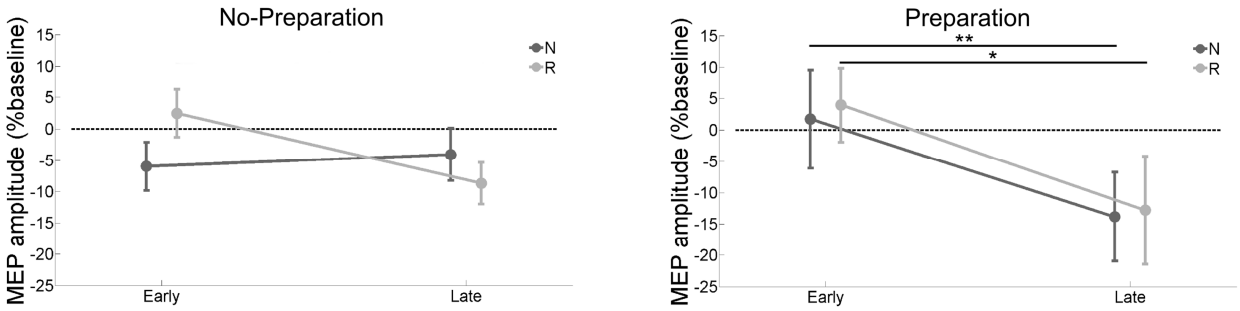

Fig. 4 CS excitability changes for Exp. 1. The figure shows the averaged CS excitability changes relative to baseline (horizontal dashed line) for the no-preparation (left panel) and preparation (right panel) condition during no-reward (N) and reward (R) for both (early and late) stimulation epochs. Error bars represent one standard error. *p<.05, **p<.001.

Discussion

The first experiment examined the influence of reward on CS excitability. We observed a reduction of CS excitability from early to late stimulation epochs during preparation trials, which suggests that action preparation is associated with time-dependent CS excitability changes (Bestmann & Duque, 2016; Duque, Greenhouse, Labruna, & Ivry, 2017). No such changes in excitability were observed on no-preparation trials. Importantly, this overall pattern of CS excitability was not modulated by the motivational cue.

These results do not replicate our previous findings (c.f., Bundt et al. 2016), and are in contrast with our initial hypothesis that reward compared to no-reward information differentially affects CS excitability. One possible reason for these findings may be the fact that there was only little time pressure on the participants. Specifically, a short initial practice phase determined the time participants had to respond to the target (i.e., response deadline) throughout the rest of the experiment. Given the low amount of late responses (around 1%), the chosen response deadline turned out to be very lenient. Such a lenient response deadline may result in low task demands where goal-directed behavior is achieved without (much) effort or engagement of the individual. In this context, incentivizing behavior may not

improve performance above non-incentivized behavior as goal-directed behavior is preserved in both situations. To put it differently, if there is enough time (and resources) available to prepare for both reward and no-reward trials equally well, one may not prioritize reward over no-reward information to attain goal-directed behavior (c.f., Verbruggen, McAndrew, Weidemann, Stevens, & McLaren, 2016). However, in situations of high task demand (e.g., under time pressure) prioritization of task-relevant over task-irrelevant information becomes critical for successful goal-directed behavior and the differentiation between incentives and no-incentives may become more pronounced.

Experiment 2

In order to examine whether increased task demands would result in differential processing of reward and no-reward information at the motor level, we employed a stricter response deadline in Exp. 2, which encouraged faster responding and therefore tighter control over task preparatory processes and prepotency of responding (Elchlepp & Verbruggen, 2017; Leiva, Parmentier, Elchlepp, & Verbruggen, 2015).

Methods

Twenty-three individuals participated (13 female; *mean age*=21.4 ± *SD*=1.8 years of age). Stimuli and trial procedure, TMS and EMG parameters, as well as data analyses were identical to Exp. 1 except for the following changes. First, the duration of the target presentation (and therefore the target response deadline) was determined by an adaptive tracking procedure (3-down/1-up) that allowed for the continuous adjustment of the response deadline. Specifically (and irrespective of the reward condition), on preparation trials, the adaptive tracking procedure subtracted 25 ms from the response deadline when the participant was able to provide three correct responses within the allowed time in a row, and added 25 ms

to the response deadline when the participant made an erroneous or late response (c.f., Elchlepp & Verbruggen, 2017; Leiva et al., 2015). Table 2 shows the average MEP size and the absolute number of trials that were included in the CS excitability analysis for each experimental condition for Exp. 2.

Furthermore, the number of trials of some conditions was adjusted to reduce the duration of the experiment. In total, the initial practice block consisted of 68 trials (i.e. the same number as in Exp. 1). The four experimental blocks (112 trials each, experimental phase) were comprised of 32 $TMS_{baseline}$ trials and catch-trials, respectively. Moreover, 128 TMS_{early} trials, TMS_{late} trials, and non-stimulation trials were included, respectively. Equivalent to Exp. 1, each block consisted of randomized trials that were balanced across action cues (preparation/no-preparation), motivational cues (N/R), TMS epoch (early/late) and responses (right/left). Each experimental condition (i.e., action cues, motivational cues, TMS epoch) consisted of 32 trials.

The average rMT was *M*=60.3% ± *SD*=7.3% of the maximal stimulator output (note that the rMT data was not archived for one subject, such that the rMT mean and SD reported here are based on all other individuals).

Table 2. Average MEP size in millivolt (mV ±SD) and the absolute number (n±SD) of trials included in the CS excitability analysis for each experimental condition in Exp 2.

	No-Reward				Reward			
	Early		Late		Early		Late	
	mV ±SD	n±SD	mV±SD	n±SD	mV±SD	n±SD	mV±SD	n±SD
No-preparation	1.42±0.91	20±6	1.39±0.92	20±6	1.37±0.83	20±5	1.41±0.82	20±6
Preparation	1.50±0.87	16±5	1.42±0.84	16±5	1.67±0.93	18±5	1.34±0.80	17±5

Results

Behavior

In the preparation condition, responses were significantly faster for reward compared to no-reward trials (366 ms vs. 381 ms; $t(22)=3.279$, $p=.003$, $d_z=.684$) (Fig. 5). The percentage of correct responses in the preparation condition was not significantly different between reward and no-reward trials (99.46 vs. 98.91%; $t(23)=-1.279$, $p=.214$, $d_z=-.267$). Neither were percentage correct responses (i.e., correctly withholding a response) in the no-preparation condition different between reward and no-reward trials (99.56% vs. 99.56%; $t<1$). In the preparation condition, the percentage of late responses (i.e., responses that were not provided within the response deadline; Fig. 6) was significantly lower for reward compared to no-reward trials (15.2% vs. 25.4%; $t(22)=-3.934$, $p=.001$, $d_z=-.820$).

The overall shorter RT and higher percentage of missed responses in Exp. 2 compared to Exp. 1 indicates that our tracking procedure encouraged faster responding and suggests that task demands are increased.

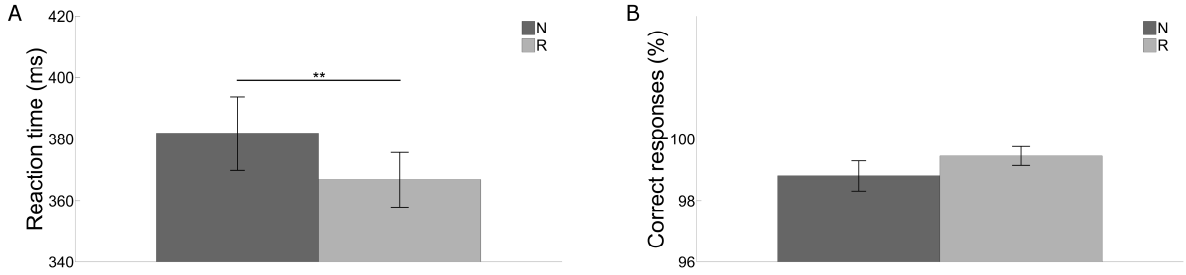

Fig. 5 Mean reaction time (A) and percentage correct responses (B) for no-reward (N) and reward (R) in Exp. 2. Error bars represent one standard error. **$p<.01$.

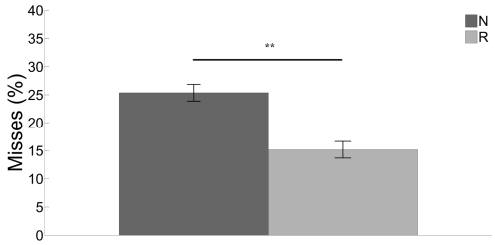

Fig. 6 Mean percentage of missed responses for no-reward (N) and reward (R) in Exp. 2. Error bars represent one standard error. **$p<.01$.

CS excitability

Mean raw baseline MEP amplitudes were 1.55 mV (± 0.92 SD). Fig. 7 depicts CS excitability changes for Exp. 2. There was no significant main effect of action cue (no-preparation=-6.7% vs. preparation=5.8%; $F(1,22)=1.650$, $p=.212$, $\eta_p^2=.70$) or motivational cue (no-reward=-2.0% vs. reward=1.1%; $F<1$). However, CS excitability was significantly higher during early compared to late stages within the delay period (3.7% vs. -4.7%; $F(1,22)=7.130$, $p=.014$, $\eta_p^2=.245$). Moreover, a significant interaction between action cue and stimulation epoch was obtained ($F(1,22)=5.254$, $p=.032$, $\eta_p^2=.193$). Most interestingly, results indicated a significant three-way interaction between action cue, motivational cue and stimulation epoch ($F(1,22)=7.417$, $p=.012$, $\eta_p^2=.252$). Further analysis of this three-way interaction revealed that while there were no significant main or interaction effects in the no-preparation condition (Fs <1), in the preparation condition, CS excitability across both stimulation epochs was significantly altered by the motivational cue ($F(1,22)=6.594$, $p=.018$, $\eta_p^2=.231$). This was due to significantly higher CS excitability during the early compared to the late stimulation epoch for reward trials (23.36% vs. -5.62%; $F(1,22)=11.161$, $p=.003$, $\eta_p^2=.337$), but not for no-reward trials (4.62% vs. 0.75%; $F<1$). Furthermore, we observed significantly higher CS excitability for reward compared to no-reward trials during the early stimulation epoch (23.36% vs. 4.62%;$F(1,22)=4.805$, $p=.039$, $\eta_p^2=.179$), but not the late epoch, (-5.61% vs. 0.75%; $F(1,22)=1.469$, $p=.238$, $\eta_p^2=.063$.

CS excitability did not significantly differ from baseline for any condition (ps>.098).

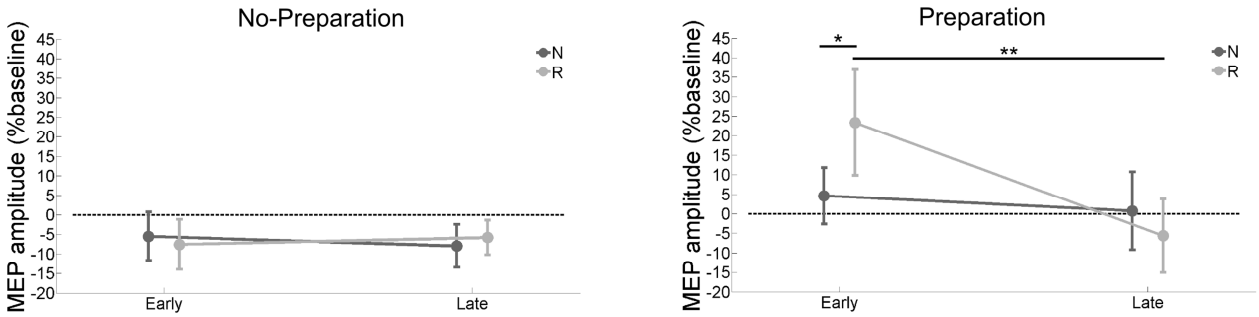

Fig. 7 CS excitability changes for Exp. 2. The figure shows the averaged CS excitability changes relative to baseline (dashed horizontal line) for the no-preparation (left panel) and preparation (right panel) condition during no-reward (N) and reward (R) for both (early and late) stimulation epochs. Error bars represent one standard error. *p<.05, **p<.01.

Discussion

In Exp. 2 faster responding was encouraged by the employment of a stricter response deadline using a trial-by-trial adjustment algorithm (Elchlepp & Verbruggen, 2017; Leiva et al., 2015). Behaviorally, reward again sped up reaction times. Most interestingly, reward was associated with increased CS excitability in the preparation condition during the early stimulation epoch and was then followed by a CS excitability decrease.

General discussion

In two experiments, the effect of reward on CS excitability during response preparation was examined. It was hypothesized that if reward activates the motor system in a fast and automatic fashion, such activation would be present irrespective of whether an actual response must be prepared or not (i.e., wanting-account). In contrast, the effect of reward on the motor system may reflect the amount of exerted control that is increased when incentivized (i.e., control-account). In this case, reward should only affect CS excitability during actual response preparation but not when no response is being prepared as there is no

(or significantly less) need to exert control to attain goal-directed behavior. It was expected that CS excitability is higher for reward compared to no-reward trials in early stages in the preparatory interval, while this pattern may reverse in late stages (Bundt et al., 2016). When employing a lenient response threshold in Exp. 1, CS excitability was not modulated by motivational cues. In fact, no-reward and reward were both associated with higher CS excitability early in the delay period and relatively lower CS excitability late in the delay period. Employing a strict response threshold in Exp. 2 resulted in no CS excitability changes in the no-preparation condition during the delay period. However, in the preparation condition, reward was associated with higher CS excitability early, and lower CS excitability late in the delay period, whereas such decrease of CS excitability was not observed for no-reward. Most importantly, CS excitability was higher in the preparation condition for reward compared to no-reward early in the delay period.

The main implications of the present study are twofold: First, our findings do not support the wanting-account. In both experiments, reward did not have any effect on CS excitability when response preparation was not required (no-preparation condition). To support the wanting-account, however, such reward effect would have been necessary to emerge even in conditions where no response was prepared. Such a pattern has been described earlier. Chiu and colleagues (2014) observed increased CS excitability after appetitive compared to aversive cues, irrespective of a response being required. Specifically, at the time CS excitability was measured, participants did not know whether a response was required or not and they probably prepared in both conditions.

The findings of the present study are in line with the control-account as reward did affect CS excitability only when response preparation was crucial for goal-directed behavior (preparation condition). Importantly, however, this effect appeared under increased task demands only (Exp. 2) and was absent under low task demands (Exp. 1). The finding that

reward did affect CS excitability only under increased task demands and only when a response was prepared could be explained by the concept of cognitive effort (Shenhav et al., 2017). More specifically, goal-directed behavior necessitates control over task-relevant processes to ensure successful task performance. These controlled processes, however, are inherently costly and individuals who need to exert cognitive effort to attain goal-directed behavior are reluctant to utilize all available resources at a time. The absence of any reward-related modulation of CS excitability in Experiment 1 may reflect cognitive resource preservation. Such preservation is only worthwhile, however, if goal-directed behavior can be retained and if task demands allow for it. Under increased task demands (Exp. 2), goal-directed behavior becomes more difficult and control over task-related processes increases. At the same time, the individual may become more susceptible to reward-promising cues in the environment that can 'pay' for increased cognitive effort.

One may wonder why, in Experiment 2, we did not observe lower CS excitability for reward compared to no-reward at late stages in the delay period when preparing a response. These findings are in contrast to our previous findings (Bundt et al., 2016). However, we did observe that CS excitability decreased from the early to the late stimulation epoch for reward trials, while such a decrease was not observed for no-reward trials. This relative pattern is similar to the findings of our previous study (Bundt et al., 2016). For the present purposes, the most important finding is that reward-based modulation is only observed when preparing for a response, in line with a control account. Future studies aiming at this late decrease more specifically should also consider the effect of the baseline. To control for task-related differences when assessing baseline CS excitability, future studies could incorporate pre-block baseline measures to avoid the experimental task biasing baseline CS excitability (Labruna, Fernandez-del-Olmo, & Ivry, 2011).

In conclusion, the present results show that during action preparation CS excitability is modulated by motivation (reward versus no-reward) only if the task demand – invoked by increased time pressure – is high. This modulatory influence of motivation on CS excitability may be a reflection of exerted control over task-relevant processes that is increased when incentivized. In contrast, when no action is prepared, motivation does not modulate CS excitability, which suggests that reward does not have an automatic effect on CS excitability in the present task.

Data statement

The present study is based on Bundt et al. (2016) and aimed for a similar sample size for comparison purposes. To that effect, we did not calculate sample sizes using power analyses a-priori for the present study. However, a post-hoc sensitivity analysis (two-tailed, alpha error probability: .05, power: .8) revealed effect sizes of .51 and .52 for Exp. 1 and Exp. 2, respectively. We confirm that all data exclusions, all inclusion/exclusion criteria, all manipulations, and all measures in the study are reported in the manuscript. Inclusion/exclusion criteria, all manipulations, and all measures were established prior to data analysis. No part of the study procedures or analyses was preregistered prior to the research being undertaken. Study data, digital study materials, and the analysis code can be found at https://osf.io/atx26/.

Declaration of interest

None

Acknowledgements

This work was supported by the Ghent University BOF initiative (BOF13/24j/080). MB is supported by Belgian Science Policy Office (Interuniversity Poles of Attraction Program; grant number P7/33). FV is currently supported by an ERC Consolidator grant (European Union's 362 Horizon 2020 research and innovation programme, grant agreement No 769595).

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Title: Reward anticipation changes corticospinal excitability during task preparation depending on response requirements and time pressure.

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Bundt, Notebaert: Formal analysis

Bundt, Verbruggen, Notebaert: Methodology

Bundt, Bardi: Project administration

Notebaert: Supervision

Bundt – Visualization

Bundt, Bardi, Verbruggen, Boehler, Brass, Notebaert: Writing – original draft

Bundt, Bardi, Verbruggen, Boehler, Brass, Notebaert: Writing – review & editing