"Unsigned value prediction-error modulates the motor system in absence of choice"

Vassena, Eliana ; Cobbaert, Stephanie ; Andres, Michael ; Fias, Wim ; Verguts, Tom

ABSTRACT

Human actions are driven by the pursuit of goals, especially when achieving these goals entails a reward. Accordingly, recent work showed that anticipating a reward in a motor task influences the motor system, boosting motor excitability and increasing overall readiness. Attaining a reward typically requires some mental or physical effort. Recent neuroimaging evidence suggested that both reward expectation and effort requirements are encoded by a partially overlapping brain network. Moreover, reward and effort information are combined in an integrative value signal. However, whether and how mental effort is integrated with reward at the motor level during task preparation remains unclear. To address these issues, we implemented a mental effort task where reward expectation and effort requirements were manipulated. During task preparation, TMS was delivered on the motor cortex and motor-evoked potentials (MEPs) were recorded on the right hand muscles to probe motor excitability. The r...

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**Title:** Unsigned value prediction-error modulates the motor system in absence of choice

**Abbreviated title:** Effort and reward influence the motor system

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Abstract

Human actions are driven by the pursuit of goals, especially when achieving these goals entails a reward. Accordingly, recent work showed that anticipating a reward in a motor task influences the motor system, boosting motor excitability and increasing overall readiness. Attaining a reward typically requires some mental or physical effort. Recent neuroimaging evidence suggested that both reward expectation and effort requirements are encoded by a partially overlapping brain network. Moreover, reward and effort information are combined in an integrative value signal. However, whether and how mental effort is integrated with reward at the motor level during task preparation remains unclear. To address these issues, we implemented a mental effort task where reward expectation and effort requirements were manipulated. During task preparation, TMS was delivered on the motor cortex and motor-evoked potentials (MEPs) were recorded on the right hand muscles to probe motor excitability. The results showed an interaction of effort and reward in modulating the motor system, reflecting a value prediction-error signal. Crucially, this was observed in the motor system in absence of a value-based decision or value-driven action selection. This suggests a high-level cognitive factor such as unsigned value prediction-error can modulate the motor system. Interestingly, effort-related motor excitability was also modulated by individual differences in tendency to engage in (and enjoy) mental effort, as measured by the Need for Cognition questionnaire, underlining a role of subjective effort experience in value-driven preparation for action.

Keywords: value, prediction error, effort, reward, TMS, MEP

1. Introduction
In a complex environment, identifying actions leading to a rewarding outcome is a core skill in adaptive behavior. The expected reward associated with the outcome is often termed value, and encompasses both intrinsic value (primary reinforcers like food and sex, Berridge et al., 2010), as well as learned value (secondary reinforcers like money). Considering their evolutionary relevance, it is not surprising that value signals are traceable in several brain regions (Haber and Knutson, 2010; Liu et al., 2011; Vickery et al., 2011). Predicting value and comparing the prediction with the actual outcome relies on a network including subcortical dopaminergic nuclei, the striatum, and the Anterior Cingulate Cortex (ACC, Haber and Knutson, 2010; Liu et al., 2011; Silvetti et al., 2011; Vassena et al., 2014a). Discrepancies between predicted and actual rewards lead to what is called value prediction-error, which drives decision-making as well as learning (Den Ouden et al., 2009; O'Doherty 2004; Schultz et al., 1997; Seymour et al., 2006; Silvetti et al. 2014; Sutton and Barto, 1998).

In a natural environment, pursuing valuable outcomes often entails mental or physical effort, which tends to be perceived as aversive and avoided if possible (Kool et al., 2010). Recent studies showed that upcoming mental effort is encoded by a network that partially overlaps with reward activation (Vassena et al., 2014b), in line with several theoretical accounts of prefrontal cortex function (Holroyd and Yeung, 2012; Shenhav et al., 2013; Sterling, 2012; Verguts et al., 2015; Weston, 2012). Moreover, reward value is discounted (decreased) by the required effort, resulting in an integrative signal termed net-value, which embodies both task-related benefits and
How reward and effort expectations influence task preparation remains however debated. Recent theories state that (net-)value influences the motor system during action selection. Cognitive variables such as value can contribute to determining the winning action plan in a competitive action selection process (Cisek and Kalaska, 2010). This influence might be mediated via top-down modulation of the value network on primary motor cortex (M1). In fact, ACC and striatum are involved in heterogeneous functions ranging from value coding and prediction-error, to motor learning and motor control (Beckmann et al., 2009; Cools, 2011; Humphries and Prescott, 2010; Paus, 2001; Silvetti et al., 2014). Both ACC and striatum project (indirectly) to motor areas and might provide a suitable pathway for a value modulation on the motor system. Hare and colleagues (2011) provided functional evidence of the value network contributing to value translation to M1, showing increased functional coupling between areas encoding stimulus value, ACC and M1 at the time of choice in a decision-making task.

This evidence suggests that value processing might be detectable by measuring the excitability of the motor system. More precisely, the value signals computed by the value network might influence M1 in preparation for action. Recent studies confirmed this hypothesis by measuring the amplitude of motor-evoked potentials (MEPs) induced by Transcranial Magnetic Stimulation (TMS) of M1 to estimate cortico-spinal excitability (CSE) during task preparation. These studies showed that expecting a reward modulates motor readiness and biases action selection (Klein et al., 2012; Klein-Flügge and Bestmann, 2012). An influence of value on CSE was also
reported during reward delivery (Kapogiannis et al., 2008; Thabit et al., 2011).

Finally, Gupta and Aron (2011) showed increased CSE during presentation of pictures of food items to which participants assigned higher value.

Despite such demonstrations of value modulation on motor excitability many questions remain open, which our study was designed to tackle. A first one is whether changes in CSE can trace the effect of value in a cognitive task, with no value-based decision (and related motor action) involved. We test whether value signals computed in higher-level areas can influence the readiness of the motor system, even in absence of action selection or planning. Second, the influence of upcoming (mental or physical) effort requirements on the motor system was never addressed in earlier literature. The partial neural overlap of reward and effort representations (Vassena et al. 2014, Krebs et al. 2012) suggests that effort expectation might modulate motor excitability as reward does. Alternatively, effort and reward signals may be computed by different networks, and yet both exert influence on the motor system during task preparation. Incorporating both reward and effort prospect in a single design allows addressing a crucial third question, namely how reward and effort expectations interact in modulating the motor system. Previous literature suggests two hypotheses. On the one hand, effort and reward information might be integrated in motor cortex in a net-value signal (as in other brain areas coding for value such as ACC and striatum; Croxson et al., 2009). This would predict increased motor excitability as a function of the net-value of the offered option, thus leading to a main effect of both reward and effort. On the other hand, motor excitability might reflect not net-value, but a net-value prediction-error signal. Such signal would encode the discrepancy between expected and actually obtained net-value. This hypothesis would be in line with the
predictive coding framework (Friston, 2012; Friston and Kiebel, 2009; Summerfield and Egner, 2009, Shipps et al., 2013), according to which predictive signals can also be traced in perceptual and motor cortices. This account would predict increased motor excitability for unexpected events, including net-value prediction-errors. Computationally, prediction error signals allow online estimation of parameters such as value, probability, and volatility (Alexander and Brown 2011; Silvetti et al. 2011). Behaviorally, such signals contribute in online performance adaptation, possibly by modulating learning rates (Bryden et al., 2011; Nassar et al., 2012). This account would predict neither main effects of reward or effort but an interaction between the two factors. In particular, both the best (high reward, low effort) and worst (low reward, high effort) options should generate the largest unsigned value prediction-error.

To test these predictions, we implemented an experiment where MEPs were recorded during task preparation while TMS was delivered to M1. During task preparation, participants passively viewed a cue, indicating the upcoming effort and potential reward. This allowed us to investigate the excitability of the motor system as a function of predicted effort and reward. Additionally, to test for any modulatory influence of individuals’ tendency to engage in and enjoy cognitively demanding tasks, we administered the Need for Cognition questionnaire (Cacioppo et al., 1984).

2. Materials and methods

2.1 Participants

Twenty-two healthy subjects participated in this study (age range 20-40, average age 25). All participants were right-handed males, with no history of
neurological or psychiatric disorders. The experimental protocol was approved by the ethical committee of the Ghent University Hospital. Each participant signed an informed consent prior to participation.

2.2 Experimental procedure

A mental effort task was implemented, adapting a previous version used for investigating anticipation of mental effort (Vassena et al., 2014b). Visual stimuli were introduced as cues (Figure 1b); each cue consisted of a grey circle with a superimposed grid. The horizontal lines represented the effort level, which could be low (lower black line) or high (higher black line). The vertical lines represented the potential reward, which could be low (left black line) or high (right black line). Such cues have been successfully used to convey combined reward and effort information (Croxson et al., 2009). Moreover, despite being task-irrelevant, such cues are correctly attended to by participants, as revealed by substantial differences in brain activity across conditions (Croxson et al., 2009; Krebs et al., 2012; Vassena et al., 2014b). In the current study, we opted for a $2 \times 2$ design, with effort (easy/hard) and reward (low/high) as factor, resulting in four possible cues (low effort/low reward, low effort/high reward, high effort/low reward, high effort high reward). One additional cue was used, where only the gray circle with no black lines was presented. This cue represented the baseline condition, in which a series of letters was presented on the screen, with the same timing as the other conditions. In this condition, participants did not perform any task, and they were aware that the final response would not matter. Each cue was presented 21 times, for a total of 105 trials. Every trial consisted of a mental calculation (except for the baseline condition trials). Each
calculation consisted of 5 single-digit numbers flashing on the screen (4 subsequent operations, Figure 1a). The last digit was followed by a display showing two possible results. Participants had to select the correct result. The incorrect result was bigger or smaller than the correct result, with distances 1 and 2 randomly varying. The easy task consisted of calculations with no carrying or borrowing, while in the hard task each operation required carrying or borrowing. This manipulation has proved effective in earlier work (Imbo et al. 2007; Vassena et al., 2014b). Reward could be 20 cents (low) or 40 cents (high). Participants were instructed to be fast and accurate. The time limit for responding was 1500 ms. In case of a late or wrong response, participants would lose the same amount they were playing for (to be subtracted from their accumulated budget). The possibility of a loss in case of wrong response was introduced to make sure participants would stay focused on the task. Following our previous work (Vassena et al. 2014b), and from further piloting of the current paradigm, this is not problematic as participants typically show very high accuracy in this task.

Each trial started with the cue for 500 ms. After 1500ms (stimulus onset asynchrony) the single TMS pulse was delivered. At this time point, MEPs were recorded. 500 ms after the pulse, a screen appeared displaying the word “READY” and participants were asked to press the right-hand key as fast as possible within 500 ms. Afterwards, the task started. If the response to this ready display was too slow, they were told that the current trial would not be considered. TMS and key press timing were based on Gupta and Aron (2011). Importantly, this key press was the same in every trial and was unrelated to the task, as we aimed at testing CSE modulation in absence of action selection. Crucially, pulse delivery was far apart in
time from the motor response to the calculation result, to avoid interference with the final motor response.

Participants first underwent a training phase to get familiar with the task. This phase consisted of a short version of the task (9 trials), with no TMS applied. Only in this training phase, each trial was followed by two questions, asking subjects to rate difficulty and pleasantness experienced during the trial (scale 1 to 7).

After the experiment, participants filled in the Need for Cognition questionnaire, measuring individual attitudes toward cognitive effort (Cacioppo et al., 1984). The goal was to explore the potential influence of individual differences in effort perception (Treadway et al., 2012; Westbrook et al., 2013) on CSE during task preparation.
Figure 1: a. Task structure and timing. Every trial starts with one of the five possible cues. The TMS pulse is delivered with a stimulus onset asynchrony (SOA) of 1500 ms from cue onset, and 500 ms before the ready display. At the ready display, participants have to press the right key as fast as possible to start the trial, with a maximum response time limit of 500 ms. Each presented number is followed by an inter-number 500 ms blank. The last number before the result display is followed by a 50ms blank. b. Visual cues. c. Accuracy. The plot reports the average accuracy in each of the four conditions (% of correct responses). The bars represent one standard
error of the mean. d. Difficulty ratings given during training per each trial type. The bars represent one standard error of the mean. e. Pleasantness ratings given during training per each trial type. The bars represent one standard error of the mean.

2.3 TMS and Electromyography

Single-pulse TMS was delivered through a biphasic magnetic stimulator (Rapid² Magstim, Whitland, UK) connected to a polymeruthane-coated figure-of-eight coil (5.4-cm inner diameter windings). The coil was held tangentially over the left hand motor area, with the handle pointing backwards and forming an angle of 45° with the sagittal plane. Electromyographical (EMG) activity was recorded with the ActiveTwo system (BioSemi, Amsterdam, The Netherlands). Sintered 11 × 17-mm active Ag–AgCl electrodes were placed over the right First Dorsal Interosseus muscle (FDI) in a belly–tendon arrangement. The FDI contributes to flex or abduct the index away from the middle finger.

The hot spot in the hand motor area was established by locating a stimulation site where TMS elicited reliable motor-evoked potentials (MEP) in the FDI. This position was marked on a closely fitting cap. TMS intensity was set at 110 % of the resting motor threshold, i.e. the minimum intensity to induce an MEP ≥ 50 µV peak to peak in more than 4 out of 10 trials. The average intensity (± S.D.) was 65.2 ± 8.11 % of the maximal stimulator output. EMG signal was amplified (internal gain scaling), digitized at 2 kHz, high-pass filtered at 3 Hz, and stored on a PC for off-line analysis. The peak-to-peak amplitude of the MEPs was computed using Matlab. In order to control for noise and fluctuations in the signal, EMG data were trimmed according to three criteria. Trials were excluded when the root mean square of the background
EMG signal recorded 500 ms before TMS was higher than 50 mV (1.45 %). Very similar results were obtained when this criterion was applied to the root mean square of the background EMG signal recorded 100 ms before TMS. Trials where the MEP amplitude was below 50 µV (3.47 %) or more than 3 standard deviations above or below the individual mean (1.35 %) were also excluded.

2.4 Data analysis

First, the behavioral data from the training phase were analyzed. Two repeated-measures analyses of variance (rANOVA) were performed on difficulty and pleasantness ratings as dependent variables, with effort (low/high) and reward (low/high) as factors. The goal was to test if high effort trials were perceived as more difficult and less pleasant (Kool et al., 2010).

Subsequently, behavioral data from the main task were analyzed. Two rANOVA were performed, with accuracy and reaction times to the “Ready” display as dependent variables. Two rANOVA were also performed with accuracy and reaction times to the calculation task as dependent variables. In all four models, the factors were effort (low/high) and reward (low/high).

In the main task, the TMS-MEP data were considered next. MEP amplitudes in the five conditions were computed. For each participant the average MEP amplitude in the baseline was subtracted from the average MEP amplitude in each of the four experimental conditions. The goal was to control for inter-individual variability in MEPs. A rANOVA was performed on this data, with effort (low/high) and reward (low/high) as factors.
Finally, a correlation was computed between NfC and effort-related CSE (high effort – low effort), to explore the relationship between the effort-related CSE and NfC. Spearman’s rank correlation coefficient was calculated, to control for the possible influence of outliers.

3. Results

3.1 Behavioral data

Ratings. Participants perceived high-effort trials as more difficult (main effect of effort $F_{(1,18)}=22.92, p<.001, \eta^2_p = .56$, low effort $M= 2.59 \pm 0.24$, high effort $M=3.86 \pm 0.3$, see Figure 1d), confirming the effectiveness of the manipulation. No significant effect of reward on perceived difficulty ($F_{(1,18)}=3.24, p=.089$), nor effort × reward interaction were obtained ($F_{(1,18)}=1.29, p=.27$). The pleasantness ratings did not show any significant effect (main effect of effort $F_{(1,18)}=1.455, p=.24$, main effect of reward $F_{(1,18)}=3.17, p=.092$, effort × reward interaction $F_{(1,18)}=1.12, p=.30$), although showing a plausible pattern (see Figure 1e). Moreover, also earlier literature confirms that high-effort stimuli are perceived as less pleasant (Vassena et al. 2014, Kool et al. 2010).

Main task, ready display. No significant effect was reported of effort or reward on the accuracy at the “Ready” display button press (i.e. responding within the time limit, effort $F_{(1,18)}=.25 p=.62$, reward $F_{(1,18)}=.02, p=.89$, interaction $F_{(1,18)}=.41, p=.53$), nor in the reaction times (effort $F_{(1,18)}=.31, p=.59$, reward $F_{(1,18)}=.02, p=.88$, interaction $F_{(1,18)}=.08, p=.78$). Note that the key press was identical in every trial and unrelated to the task itself. This feature of the design was crucial to exclude action selection effects on MEP, targeting purely cognitive preparation instead. Importantly,
the reliability of such cues eliciting a motivational effect in terms of task preparation
(despite being task-irrelevant) was consistently shown in previous neuroimaging
studies (Croxson et al., 2009; Krebs et al., 2012; Vassena et al., 2014b) and in our
own results (see below). Although the possibility persists that participants did not
attend to the cues, given previous research and current results this seems unlikely.

**Main task, calculations.** Accuracy in the calculation task was 81.2% (±7%). The
rANOVA showed a main effect of effort ($F_{(1,18)}=8.57, p<.01, \eta_p^2=.32$, low effort
81% ± 2.42, high effort 87% ± 2.21), and no effect of reward ($F_{(1,18)}=.199, p=.66$
nor effort × reward interaction ($F_{(1,18)}=.36, p=.56$, Figure 1c). No significant effect
was reported in the reaction times (main effect of effort, $F_{(1,18)}=2.42, p=.14$, main
effect of reward, $F_{(1,18)}=2.31, p=.15$, effort × reward interaction, $F_{(1,18)}=.297, p=.59$).
The effect of effort on accuracy confirmed that the effort manipulation was
successful. The absence of effect on reaction times could be attributed to the very
strict response time limit, making the effect of effort evident in the accuracy data
only. A further Spearman’s rank correlation analysis was performed on the accuracy
data and the difficulty ratings during the training. This analysis showed that accuracy
at the task correlated negatively with perceived difficulty (computed as difference
between difficulty ratings of high effort trials and low effort trials, $r = -.53, p=.019$).

### 3.2 TMS-MEP data

Two participants were excluded from further analyses due to technical issues
during the experiment. Two more exclusion criteria were applied to MEPs. Trials
were excluded where the final response to the calculation was incorrect (14.7%).
Cognitive processes that lead to errors differ from those in successful trials, and this
was not the target of the current experiment. Finally, trials were excluded where participants did not press the key at ready display within time limit (16,4%). The reason was that they were told that the trial would not count anymore and this might interact with MEPs. Data from one participant were excluded because less than 10 trials per condition were left after applying these criteria. The main analysis was run both with and without this participant, leading to similar results. For the remaining participants, there were on average 14.4 ± 3.35 trials in the low effort/low reward condition, 13.75 ± 3.07 trials in the low effort/high reward condition, 12.8 ± 3.21 trials in the high effort/low reward condition, and 13.4 ± 3.41 trials in the high effort/high reward condition.

Crucially, this MEP analysis showed a significant effort \( \times \) reward interaction (\( F_{(1,18)} = 6.63, p = .019, \eta_p^2 = .27 \)). No main effect of effort (\( F_{(1,18)} = 1.988, p = .18, \eta_p^2 = .099 \)) or reward (\( F_{(1,18)} = .575, p = .46, \eta_p^2 = .03 \)) was reported. This result is shown in Figure 2a, reporting the average MEP difference (baseline MEP per every participant is subtracted from each condition) across participants.

Planned comparisons (two-sided) showed significantly higher CSE for low effort/high reward as compared to low effort/low reward (\( t_{(18)} = -2.40, p = .027 \)); the difference between high effort/low reward condition and high effort/high reward did not reach significance (though showing a trend, \( t_{(18)} = 1.46, p = .16 \)).
Figure 2. a. MEP data. The plot shows the average difference in MEP signal (mV) in the four experimental conditions with respect to the baseline condition (per every participant, MEP to baseline cue is subtracted out to all four conditions). The bars represent one standard error of the mean. b. Individual differences analysis. Need for Cognition (x-axis) predicts effort-related increase in MEP (high effort – low effort). c. MEP data in the high Need for Cognition group. d. MEP data in the low Need for Cognition group.

The significant effort × reward interaction suggests an influence of value prediction on motor excitability, where higher CSE is recorded for the options carrying an unsigned value prediction-error. On the one hand, the low effort / high
reward option carries a positive prediction-error, being the best possible available option (receiving this cue is a positive surprise). On the other hand, the high effort / low reward option is the worst possible option, resulting in a negative value prediction-error (receiving this cue is a negative surprise).

3.3 Need for Cognition analyses

The NfC scale measures individuals’ attitudes towards engaging in mentally demanding activities. Participants who score high on this questionnaire tend to engage more often in cognitively effortful activities and to enjoy it (Cacioppo et al., 1984). We found a significant negative correlation between NfC and effort-related CSE (high effort – low effort, \( r = -0.55, p = 0.015 \), Figure 2b). Higher NfC scores were associated with a decrease in effort-related CSE. To test the selectivity of this effect, we performed the same analysis on the reward-related CSE (high reward – low reward), where no significant correlation was reported (\( r = -0.10, p = 0.68 \)).

To further characterize the relationship between effort-related CSE and NfC, some exploratory analyses were conducted. Participants were split in two groups (low NfC and high NfC), as in previous NfC research (Smith and Levin, 1996; Verplanken, 1993). The factor group was introduced in the previous analysis, resulting in a rANOVA with effort, reward and NfC group as factors. Crucially, the effort \( \times \) reward interaction from the original rANOVA analysis was preserved (\( F(1,17) = 6.25, p = 0.023, \eta^2_p = 0.27 \)). The interaction effort \( \times \) group was also significant (\( F(1,17) = 17.8, p = 0.001, \eta^2_p = 0.51 \)). No significant three-way interaction was reported (effort \( \times \) reward \( \times \) group \( F(1,17) = 0.54, p = 0.47 \)).
When the rANOVA was fit for each group separately, the high NfC group showed a main effect of effort (increased CSE for low vs high effort, \( F_{(1,9)}=12.7, p=.006, \eta^2_p=.59 \), low effort \( M=137 \pm 83.56 \), high effort \( M=-44.6 \pm 69.47 \), Figure 2c), a trend for the interaction (\( F_{(1,9)}=3.63, p=.089, \eta^2_p=.29 \)), and no effect of reward (\( F_{(1,9)}=.006, p=.94 \)). The low NfC group showed a main effect of effort in the opposite direction (increased CSE for high vs. low effort, \( F_{(1,8)}=6.26, p=.037, \eta^2_p=.44 \), low effort \( M=-18 \pm 84.77 \), high effort \( M=57.72 \pm 63.94 \)), a trend for the interaction (\( F_{(1,8)}=3.58, p=.095, \eta^2_p=.31 \)), and no effect of reward (\( F_{(1,8)}=1.25, p=.295 \), Figure 2d).

4. Discussion

The current study used TMS on M1 to investigate the influence of reward expectation and mental effort requirements on motor excitability during task preparation. The results revealed that motor excitability varies as a function of unsigned value prediction-error in a cognitive task, in absence of choice or action selection. Moreover, effort-related CSE was modulated by individual differences in Need for Cognition.

Traditional theories posited a serial decision process, where goals are set, the optimal motor program identified, and transmitted to lower level motor areas (e.g., Broadbent, 1958; Flash and Hogans, 1985, Sternberg, 1969). The assumption of a motor time separate from decision remains explicit in current models of cognition (e.g., Mulder et al. 2012; Ulrich et al., 2015). Here, M1 occupies the lowest level of the hierarchy, merely translating the received programs into action. Recent accounts postulated instead that action selection is a parallel and competitive process, where multiple action programs are simultaneously evaluated (Cisek, 2006; Cisek and
Kalaska, 2010). The selection of the winning program happens across all levels of the hierarchy, and cognitive factors can influence this selection also at the motor level. Supporting evidence has been provided by a few studies, showing that motor excitability can be modulated by the value of a given action (Klein et al., 2012; Klein-Flügge and Bestmann, 2012) or urge for action during decision-making (Gupta and Aron, 2011). Furthermore, neuroimaging studies reported an effect of value during task preparation, with no action selection nor value-based decision required (Croxson et al., 2009; Krebs et al., 2012; Vassena et al., 2014b). To our knowledge, the current result is the first to demonstrate that the influence of value (prediction error) on task preparation spreads to the motor cortex in a cognitive task, even in absence of value-based choice or action selection.

Another key factor affecting motivated behavior is the effort entailed in attaining a goal. The anticipation of an effortful task is associated with increased activation of cortico-limbic regions, overlapping in striatum and ACC with reward expectation (Krebs et al., 2012; Vassena et al., 2014b). These regions are also implicated in value-based decision-making and value-prediction (Rangel and Hare, 2010; Rushworth et al., 2011; Vassena et al., 2014a). In fact, effort and reward are combined in the ACC in an integrative net-value signal (Croxson et al., 2009; Kennerley et al., 2009). In the framework of competitive action selection, this leads to the prediction that anticipating effort might influence motor excitability as well. Our results provide the first evidence that effort information is combined with reward and influences motor excitability accordingly, showing a modulation of a value-prediction signal. This emerges from the interaction effect, showing how motor excitability is increased when the cue carries an unsigned value prediction-error. In
our data, this was clearer for the low effort / high reward cue (the best possible option), which carries a positive prediction-error (better value than expected when considering all the possible cues; Silvetti et al., 2011) than for the high effort / low reward cue (the worst possible option). As noted before, such prediction-errors can be used for online value estimation. An unsigned value prediction-error that modulates the motor system is also consistent with the predictive coding framework (Friston and Kiebel 2009; Summerfield and Egner, 2009). This account posits cascading prediction and prediction-error signals across higher-level cognitive and lower-level sensorimotor areas, including the motor cortex. In our data, this value prediction-error signal originating in the value network might affect motor excitability directly, driving the top-down modulation on M1 for subsequent behavioral adaptation. Crucially, in our study the prediction-error signal derives from a combined evaluation of effort and reward cues, suggesting that both effort and reward expectation are computed and integrated. Together, they contribute to a net-value computation, whose (unsigned) prediction-error component directly modulates motor excitability. This may be an evolutionarily adaptive process where deviations from the expected value boost motor excitability, speeding up action preparation to face unexpected circumstances. Alternatively, a brainstem arousal signal might be the mediator of the influence of unsigned value prediction-error on motor cortex. Typically, unexpected events (with either positive or negative valence) produce an arousal response (Aston-Jones and Cohen 2005, Sara and Bouret 2012), mediated by noradrenalin release in the brainstem. In our data, the increased arousal associated with the experienced prediction-error might drive the modulation on the motor system as a potential trigger.
for increased required engagement. This hypothesis is in line with a previous TMS-MEP study, also showing increased CSE for highly arousing pictures (both positive and negative, Hajcak et al. 2007). Identifying the neural mechanisms underlying the reported modulation is interesting ground for further research.

A crucial aspect of the current result is that the modulation occurs in absence of choice or value-related action. Klein-Flügge and Bestmann (2012) reported a modulation of value on action-selective increase in motor excitability in a free choice setting instead. Our result extends this finding in a context where no value-based decision is required. In our task, only one option is presented in every trial and our participants make no value-based decisions on the cues. The cue instead provides information on the upcoming task, which might trigger value-driven engagement. In fact, level of engagement can alter performance, and specifically in this task it can lead to a final smaller or larger win. In this sense, net-value might influence participants’ willingness to exert effort in the task. Convergently, our previous fMRI work showed how the cues currently used induce reward- and effort-dependent motivational effects to task performance (Vassena et al., 2014b). The intriguing hypothesis that value drives engagement, potentially correlating with accuracy in performance should be tested in further research. Moreover, a wider range of difficulty levels should be included, as the current experiment was piloted to achieve high accuracy only. One limitation of this result is that the unsigned value prediction-error effect seems to be mainly driven by the positive prediction error component. Despite the evidence that positive prediction error signals are more reliably reported, as compared to negative prediction error signals (Vassena et al., 2014a), future studies
should also focus on testing systematically the effect of negative prediction error on CSE.

The individual differences analysis revealed an effect of the Need for Cognition (Cacioppo et al., 1984). People with higher NfC tend to engage more in cognitively demanding tasks, and tend to find effortful tasks simpler (Baugh and Mason, 1986; Dornic et al., 1991). In our data NfC correlated with effort-related CSE. The subsequent exploratory analysis revealed that NfC interacted with effort. Although the crucial reward × effort interaction still showed the same direction and trend-level significance when tested in the two groups separately, the effect of effort was opposite in the two groups. Higher effort was associated with higher CSE in low-NfC participants, and with lower CSE in high-NfC participants. In a value prediction framework, low-NfC people might experience increased negative prediction-error when confronted with high effort, as they tend to avoid engaging in effortful tasks. Moreover, when they do engage, they experience greater distress (Cacioppo et al. 1996), and negative emotional arousal has been shown to increase CSE (Oathes et al., 2008; van Loon et al., 2010). These two factors may modulate the unsigned value prediction-error effect. Conversely, high-NfC people tend to engage more often in cognitively demanding task, and would therefore experience high effort as a smaller prediction error (and less arousing), as compared to low-NfC. In fact, in Figure 2c and 2d one can see that the trend-level interaction supporting the unsigned value prediction-error interpretation is mainly driven by negative prediction error in low-NfC (where effort might be more arousing), and by positive prediction error in high-NfC (where effort might be less arousing, potentially resulting in increased sensitivity to the reward component). One should also note that high-NfC profile only mimics
the overall group level result. Of course, this splitup between groups was only posthoc
and these conclusions speculative. Moreover, the sample size in the groups was rather
small; these hypotheses need to be tested more definitely with a larger sample size in
both groups, and more extensive subjective ratings.

To sum up, our results provide support for the influence of high-level cognitive
factors on the motor system, by showing for the first time a combined influence of
reward and effort anticipation (in an unsigned value prediction-error signal) on motor
excitability during cognitive task preparation, in absence of value-based choices or
action selection. Further, effort-related motor excitability was also modulated by the
tendency of each participant to engage in effortful tasks, underlining the importance
of individual differences in motivation.

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