NeuroImage 122 (2015) 73–79

Contents lists available at ScienceDirect

NeuroImage

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

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

Eliana Vassena [a,b,*], Stephanie Cobbaert [a], Michael Andres [a,c], Wim Fias [a,b], Tom Verguts [a,b]

[a] Department of Experimental Psychology, Ghent University, Henri Dunantlaan 2, B-9000 Ghent, Belgium
[b] GIfMI, Ghent Institute for Functional and Metabolic Imaging, Ghent University Hospital, De Pintelaan 185B, B-9000 Ghent, Belgium
[c] Psychological Sciences Research Institute, Université Catholique, de Louvain, Place Cardinal Mercier 10, 1348 Louvain-la-Neuve, Belgium

ARTICLE INFO

Article history:
Received 20 February 2015
Accepted 29 July 2015
Available online 5 August 2015

Keywords:
Value
Prediction-error
Effort
Reward
TMS
MEP

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 an unsigned 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.

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 rely 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., 2004; 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 costs (Apps and Ramnani, 2014; Basten et al., 2010; Botvinick et al., 2009; Croxson et al., 2009; Prévost et al., 2010).

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

* Corresponding author at: Department of Experimental, Psychology, Ghent University, Henri Dunantlaan 2, B-9000, Ghent, Belgium.
E-mail address: Eliana.Vassena@UGent.be (E. Vassena).

http://dx.doi.org/10.1016/j.neuroimage.2015.07.081
1053-8119/

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 et al. (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 corticospinal 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., 2014a, 2014b; 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; Shipp 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 nor 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).

Materials and methods

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.

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 (Fig. 1b); each cue consisted of a gray 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 2×2 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 were 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, Fig. 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 1500 ms (stimulus onset asynchrony) the single TMS pulse was delivered. At this time point, MEPs were recorded. Five hundred milliseconds 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,