



Added value of money on motor performance feedback: Increased left central beta-band power for rewards and fronto-central theta-band power for punishments



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ABSTRACT

Monetary rewards and punishments have been shown to respectively enhance retention of motor memories and short-term motor performance, but their underlying neural bases in the context of motor control tasks remain unclear. Using electroencephalography (EEG), the present study tested the hypothesis that monetary rewards and punishments are respectively reflected in post-feedback beta-band (20–30 Hz) and theta-band (3–8 Hz) oscillatory power. While participants performed upper limb reaching movements toward visual targets using their right hand, the delivery of monetary rewards and punishments was manipulated as well as their probability (i.e., by changing target size). Compared to unrewarded and unpunished trials, monetary rewards and the successful avoidance of punishments both entailed greater beta-band power at left central electrodes overlaying contralateral motor areas. In contrast, monetary punishments and reward omissions both entailed increased theta-band power at fronto-central scalp sites. Additional analyses revealed that beta-band power was further increased when rewards were lowly probable. In light of previous work demonstrating similar beta-band modulations in basal ganglia during reward processing, the present results may reflect functional communication of reward-related information between the basal ganglia and motor cortical regions. In turn, the increase in fronto-central theta-band power after monetary punishments may reflect an emphasized cognitive need for behavioral adjustments. Globally, the present work identifies possible neural substrates for the growing behavioral evidence showing beneficial effects of monetary feedback on motor learning and performance.

Introduction

Human motor performance and learning critically depends upon the processing of feedback. Beyond motor performance feedback, which informs of the accuracy of a movement (i.e., seeing oneself hitting or missing a target), external sources of feedback such as monetary rewards or punishments can provide additional guidance as to the behaviors to repeat or avoid. Support for this notion comes from converging lines of evidence showing that monetary feedback enhances short-term performance and retention of motor behaviors (Abe et al., 2011; Dayan et al.,

2014; Gajda et al., 2016; Galea et al., 2015; Hasson et al., 2015; Manley et al., 2014; Palminteri et al., 2011; Quattrocchi et al., 2017; Song and Smiley-Oyen, 2017; Steel et al., 2016; Wächter et al., 2009; Widmer et al., 2016). For instance, Galea et al. (2015) provided monetary rewards or punishments depending on task performance while participants acquired a novel upper limb reaching movement pattern. Compared to a control group receiving no monetary feedback, participants receiving monetary rewards following accurate performance showed improved retention of the new movement pattern. Furthermore, participants receiving monetary punishments following inaccurate performance

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presented more rapid performance adjustments. These results suggest that monetary feedback provides added value to motor performance feedback and acts as a catalyst to promote motor learning and performance. Yet, the neural bases of monetary feedback processing in the context of motor control tasks remain unclear.

Several electroencephalography (EEG) and magnetoencephalography (MEG) studies investigating non-motor tasks such as gambling have provided evidence for frequency-specific responses to monetary rewards and punishments in the high beta-band from 20 to 30 Hz (Andreou et al., 2017; Cohen et al., 2007; HajiHosseini and Holroyd, 2015a, 2015b; HajiHosseini et al., 2012; Marco-Pallarés et al., 2008, 2009; Mas-Herrero et al., 2015) and theta-band from 3 to 8 Hz (Andreou et al., 2017; Cohen et al., 2007; De Pascalis et al., 2012; Doñamayor et al., 2011, 2012; Hajihosseini and Holroyd, 2013; Marco-Pallarés et al., 2008), respectively. These power modulations have been shown to occur mainly over fronto-central regions in a time window ranging from about 200 to 600 ms post-feedback and to be enhanced when outcomes are lowly probable (Cohen et al., 2007; Doñamayor et al., 2012; HajiHosseini et al., 2012; Mas-Herrero and Marco-Pallarés, 2014). The role of fronto-central brain regions in monetary feedback processing is further supported by electrophysiological and functional magnetic resonance imaging (fMRI) studies which have reported activity in both the fronto-central cortex (Andreou et al., 2017; Balodis et al., 2012; FitzGerald et al., 2012; Hester et al., 2010; Jarbo and Verstynen, 2015; Mas-Herrero and Marco-Pallarés, 2014; Mas-Herrero et al., 2015; Noonan et al., 2012; Rogers et al., 2004; Wrase et al., 2007) and orbitofrontal cortex (Ablner et al., 2009; Camara Mancha et al., 2009; Kim et al., 2015; Klein-Flügge et al., 2013; Noonan et al., 2012; O'Doherty et al., 2001; Roesch and Olson, 2004; Rogers et al., 2004; Xue et al., 2013) following monetary feedback delivery.

Although the above-cited work argues for a frequency-specific signature for the processing of monetary rewards and punishments, it is unknown whether these oscillatory modulations also take place in the context of motor control tasks. In particular, unlike gambling paradigms, the delivery of monetary feedback in motor control tasks is contingent upon the accuracy of the movement and directly influences subsequent behavioral adjustments. Furthermore, to have an impact on motor learning and performance, monetary feedback would be expected to influence activity in brain regions in which movements are planned and executed, namely in functionally lateralized motor regions such as dorsal premotor cortex (PMd) and primary motor cortex (M1) (Fu et al., 1993, 1995; Mandelblat-Cerf et al., 2009, 2011; Overduin et al., 2009; Paz et al., 2003, 2005; Pearce and Moran, 2012; Richardson et al., 2012; Sosnik et al., 2014; Stark et al., 2007; Wise et al., 1998; Xiao, 2005; Xiao et al., 2006). Interestingly, recent studies have provided support for the notion that motor cortical regions are involved in reward processing (Marsh et al., 2015; Ramakrishnan et al., 2017; Ramkumar et al., 2016; Saiki et al., 2014; Suzuki et al., 2014). Indeed, neurons in monkey PMd, M1, and primary somatosensory cortex (S1) have been shown to respond differently when an upper limb reaching movement successfully achieves a target and is rewarded with juice as compared to when a target is missed (Ramakrishnan et al., 2017; Ramkumar et al., 2016). These findings thus open up the possibility that oscillatory modulations associated with monetary feedback processing in the context of motor control tasks would be lateralized over motor cortical regions.

In light of the preceding evidence, the objective of this study was to test the hypothesis that beta- and theta-band oscillations respectively reflect monetary rewards and punishments in a motor control task. Moreover, it was hypothesized that the use of monetary feedback would result in greater oscillatory activity than motor performance feedback alone. EEG was recorded while participants performed goal-directed reaching movements toward visual targets while the delivery of monetary feedback as well as its probability were manipulated based on behavioral performance. To investigate the possibility that monetary feedback processing entails lateralized responses, oscillatory activity was specifically assessed at electrodes overlaying the motor cortical regions bilaterally as well as over the fronto-central cortical regions.

Materials and methods

Participants

Twenty-three self-reported right-handed human participants (16 females; 22.3 ± 0.4 years old; all reported values are means \pm SEM) took part in the experiment. Participants were neurologically healthy with normal or corrected-to-normal vision. To ensure sufficient statistical power, the choice of the number of participants was based on an a priori power calculation (Button et al., 2013), which revealed that twenty-two participants were needed for analyses to be adequately powered (see below). Initially, data from twenty-four participants were collected, but due to a software malfunction, data of one participant were lost.

Participants were initially offered 20 \$ CAD for their participation and total earnings were adjusted according to their individual performance at the task. Upon completion of the experiment, participants received on average 19.3 ± 0.7 \$ CAD. Informed consent forms approved by the ethical committee of the Center Hospitalier de l'Université de Sherbrooke were signed prior to the start of the experiment.

The a priori power calculation analysis was conducted with G*Power 3 (version 3.1.9.2; Faul et al., 2007) using an alpha value of 0.05, power of 80%, within-factor design (two-way repeated measures ANOVAs) and effect sizes (partial eta-squared values) of 0.29 ± 0.05 for beta- and 0.42 ± 0.15 for theta-band power responses. Those values were calculated with the formulas provided by Fritz et al. (2012) based on recent EEG studies investigating reward and punishment processing (Cohen et al., 2007; HajiHosseini et al., 2012; HajiHosseini and Holroyd, 2015a, 2015b; Marco-Pallarés et al., 2008, 2009; Mas-Herrero et al., 2015), and the resulting values were averaged.

Apparatus

The experimental setup consisted of a table supporting a computer monitor which projected visual stimuli on a mirror positioned horizontally in front of participants (see Fig. 1a). The monitor (20-inch Dell P1130; resolution: 1024×768 ; refresh rate: 150 Hz) was mounted face down 29 cm above the horizontal mirror and the mirror was mounted 29 cm above the table. Thus, the visual stimuli appeared to be projected directly onto the surface of the table on the same plane as the hand. Because of the mirror, participants could not see their hand. A 2-joint planar manipulandum was placed on the table and was held by participants via a stylus located at its mobile end. The manipulandum was custom-built with 2 lightweight metal rods (48 and 45 cm for the distal and proximal rods, respectively), with the fixed end attached to the upper left corner of the table. A thin sheet of smooth plastic covered the table surface and foam pads were installed under the hinges allowing the manipulandum to be moved everywhere on the table with minimal inertia and friction. Two potentiometers positioned in the joints of the manipulandum allowed the measurement of the angle of each segment at 1000 Hz from which the 2D position of the stylus was calculated.

A 2 cm diameter grey circle served as the starting point for every trial. It was positioned at the center of the workspace 30 cm in front of participant's chest. The cursor representing hand position at movement end consisted of a 0.58 cm diameter circle. The target to be achieved consisted of a small inner circle surrounded by an outer annulus (see Fig. 1b and c). The color of the target and outer annulus informed of the reward/punishment contingency (green, red, and grey for rewards, punishments, and neutral, respectively; for details, see section 2.4). While the outer annulus had a consistent diameter of 2.47 cm, the diameter of the target was manipulated and ranged between ~ 0.8 and 1.5 cm across participants (for details, see section 2.5). Three targets were used, all located along a 10 cm radius semi-circular array in the upper quadrant of the workspace. Targets were separated by 4° and the middle target was located at 90° in line with participants' midline (only the middle target is shown in Fig. 1b). To assess if target location influenced kinematic variables, separate repeated measures ANOVAs (1×3 targets) were

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