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Research report

Counterfactual thinking affects the excitability of the motor cortex

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ABSTRACT

Evidence suggests that monetary reward and affective experiences induce activity in the cortical motor system. Nevertheless, it is unclear whether counterfactual thinking related to wrong choices that lead to monetary loss and regret affects motor excitability. Using transcranial magnetic stimulation (TMS) of the motor cortex, we measured corticospinal excitability of 2 groups of healthy humans asked to actively guess the winning key among two possible alternatives (choice group); or passively assist to monetary outcomes randomly selected by the computer program (follow group). Results document a selective increment of the corticospinal excitability when a monetary loss outcome followed the key selection (i.e., in the choice group). On the other hand, no change in corticospinal excitability was found when participants passively assisted to a monetary loss randomly selected by the computer program (i.e., follow group). These findings suggest that counterfactual thinking and the negative emotional experiences arising from choices causing monetary loss – i.e., “I would have won instead of lost money if I'd made a different choice” – are mapped in the motor system.

1. Introduction

Reinforcement underpins behaviours, from basic ones of lower organisms such as fight/flight and approach/avoid reactions, to the complex such as economics (Vicario & Crescentini, 2012; Vicario, Kritikos, Avenanti & Rafal, 2013). In the context of human decision-making, representation of value of choices that are taken plays an essential role in guiding choice behaviour, but there is also a considerable adaptive advantage in representing the potential value of choices that are untaken (Boorman, Behrens, & Rushworth, 2011). When faced with mutually exclusive options, the choice we make is conditioned not only by what we hope to gain, but also by how we hope we will feel afterward (Camille et al., 2004). For instance, the subjective emotions experienced

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in a gambling task depend on the values of the obtained outcome: a missed economical opportunity, as a result of wrong choices, may result in the emotion of regret while a feeling of happiness is engendered by earning (Byrne, 2002; Camille et al., 2004). Regret is a cognitively mediated emotion triggered by our capacity to reason counterfactually (Kahneman & Miller, 1986; Kahneman & Tversky, 1982; Mellers Schwartz & Ritov, 1999). Therefore, counterfactual reasoning is intrinsically linked to the emotional experience arising in consequence of a wrong choice.

The experience of regret is thought to be underpinned by a complex cortical and sub-cortical neural network (Camille et al., 2004; Coricelli et al., 2005; Coricelli, Dolan, & Sirigu, 2007). One critical role played by medial prefrontal and orbitofrontal regions is thought to represent affective values of reinforcers and action outcomes. These regions are connected with the dorsolateral prefrontal regions active in reasoning and planning, and with limbic structures such as the amygdala, which is directly involved in the processing of emotions (Blair, 2007; Camille et al., 2004; Kiehl, 2006), striatum, and dopaminergic midbrain which play a role in reward processing (O'Doherty, 2004; Wächter, Lungu, Liu, Willingham, & Ashe, 2009). Notably, some of these midbrain regions share direct and indirect reciprocal connections with various segments of the motor system, and in particular, with the primary motor cortex (M1) (Haber, 2003; Morecraft & Van Hoesen, 1998). For instance, evidence indicates that ventral tegmental area dopaminergic neurons project directly to M1 in roughly equal numbers as to the ventral striatum (Gaspar Stepniewska & Kaas 1992; Williams & Goldman-Rakic, 1993). Moreover cortical dopaminergic projections that synapse on both pyramidal cells and GABAergic interneurons (Sesack, Hawrylak, Melchitzky, & Lewis, 1998) modulate M1 activity, along with other frontal areas.

Notably, transcranial magnetic stimulation (TMS) studies also indicate that various affective experiences linked to the processing of salient and emotional auditory or visual stimuli modulates excitability of M1 and its corticospinal projections (Avenanti, Annela, & Serino, 2012; Avenanti, Candidi, & Urgesi, 2013; Borgomaneri, Gazzola, & Avenanti, 2012; Hajcak et al., 2007; Makin, Holmes, Brozzoli, Rossetti, & Farnè, 2009; Oliveri et al., 2003; Serino, Annella, & Avenanti, 2009), in particular when emotional stimuli are negative and potentially threatening (Borgomaneri, Gazzola & Avenanti, 2014a, 2014b; Borgomaneri, Vitale, Gazzola, & Avenanti, 2015; Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Giovannelli et al., 2013; van Loon, van den Wildenberg, van Stegeren, Hajcak, & Ridderinkhof, 2010; Nogueira-Campos et al., 2014). Therefore, M1 may represent an important brain region to investigate in relation to better understand the neural mechanisms associated reward/affective experiences including the experience of regret contingent upon counterfactually reasoning.

Previous investigations have shown that processing reward-related information affects motor excitability prior, during or after the execution of a relevant action. Some studies have focused on the anticipatory processing of upcoming potential rewards that occurs immediately before and during the selection of an appropriate action aimed at getting the rewards (Klein-Flügge & Bestmann, 2012; Freeman, Razhas, & Aron, 2014; Gupta & Aron, 2011) or even in the absence of any motor requirement (e.g., slot machine paradigm; Kapogiannis, Campion, Grafman, & Wassermann, 2008). Other studies have explored the effect of seeing pictures of coins relative to abstract symbols presented soon after the execution of an action (Suzuki et al., 2014; Thabit et al., 2011).

While these studies have explored changes in motor excitability in rewarding and neutral conditions, more recently Galea Ruge, Buijink, Bestmann, & Rothwell (2013) investigated the effect of monetary punishment. In that study, participants performed an index finger movement and were instructed that monetary reward and punishment were based on its kinematics. Punishments led to increased movement variability (reflecting the exploration of kinematics parameters for less punishing and/or more rewarding outcomes) and this was parallelled by increased variability of motor excitability assessed early after the presentation of the action outcome.

While this latter study suggests that monetary loss may influence motor excitability, it is unclear whether cognitive-mediated negative emotions such as the experience of regret induced by counterfactual reasoning is associated with changes in motor excitability. To address this issue, in the current work we combined behavioural and neurophysiological assessment to investigate changes in affective experiences – including the feeling of regret and other negative and positive emotional feelings – and corticospinal excitability during a gambling task in which participants experienced both monetary gain and loss outcomes that were based on their own choice or a computer software selection. We administered single-pulse TMS over the left M1 to record TMS-induced motor-evoked potentials (MEPs) after participants were challenged to guess which key, between two possible alternative, would provide a monetary gain ('choose' condition), or asked to passively assist to monetary gain and loss outcomes randomly selected by a computer program ('follow' condition). The experience of regret originates from a comparison processes in which the outcome obtained is compared to the outcomes that might have occurred (Kahneman & Tversky, 1982; Zalla et al., 2014). As a sense of responsibility is critical to the experience of regret and this might be present in the 'choose' but absent in the 'follow' condition, our paradigm dissociated the effect of counterfactual reasoning and regret from that of mere disappointment for a loss occurring independently of participants' decision. Based on the notion that negative emotions may be particularly effective in priming the body for action (Borgomaneri et al., 2014a, 2015; Ekman & Davidson, 1994; Frijda, 2009; van Loon et al., 2010; Vicario & Newman, 2013) we predicted that negative outcomes would increase motor excitability more than the other conditions. Moreover, since in the choose condition participants should feel more regret and other negative emotions relative to the follow condition, we predict motor modulation for monetary loss to be more pronounced in the former condition.

2. Materials and methods

2.1. *Subjects*

Twenty healthy subjects (11 males, mean age 24.1 ± SD 3.8 years) participated in this experiment. Two subjects were left-