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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.

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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 lefthanded according to the Standard Handedness Inventory (Briggs & Nebes, 1975) and had normal or corrected-to-normal visual acuity. All subjects gave their written informed consent prior to their inclusion in the study and were naïve as to its purpose. Specific information concerning the study was provided only after the subjects completed all the experimental sessions. The experimental procedures were approved by the ethics committee of the University of Bologna and were carried out in accordance with the principles of the 1964 Helsinki Declaration. None of the participants had a history of neurological, psychiatric, or other medical problems or any contraindication to TMS (Rossi, Hallett, Rossini, Pascual-Leone, Safety of TMS Consensus Group 2009). No discomfort or adverse effects during TMS were noticed or reported.

2.2. *Electromyographic (EMG) and TMS recording*

EMG recording was performed with a Biopac system MP 150 electromyograph. EMG signal was band filtered (20 Hz–2.5 kHz, sampling rate 10 kHz), digitalized, and stored for offline analysis. Pairs of Ag/AgCl surface electrodes (1 cm diameter) were placed over the muscle belly (active electrode) of the right Extensor Carpi Radialis (ECR) and over the associated joint or tendon (reference electrode) in a classical belly-tendon montage. The right ECR was chosen to minimize any possible contamination of prior motor activity associated with button press. Indeed, the gambling task required participants to flex the index or middle finger of the left hand and this minimal motor activity should not substantially influence the excitability of the non-homologous right ECR (van den Berg, Swinnen, & Wenderoth, 2011; Muellbacher, Facchini, Boroojerdi, & Hallett, 2000; Tinazzi & Zanette, 1998; see Discussion). The ground electrode was placed over the right elbow. TMS was performed using a 70 mm figure-of-eight coil connected to a Magstim Bistim^2 (The Magstim Company, Carmarthenshire, Wales, UK) placed over the left M1. The coil was held tangentially to the skull with the handle pointing 45° away from the nasion-inion line in a postero-lateral direction (Brasil-Neto et al., 1992; Mills, Boniface, & Schubert, 1992). To find individual optimal scalp positions (OSP, i.e., the stimulation position that induces MEPs of maximal amplitude) for each muscle, the coil was moved in steps of 1 cm over the motor cortex and the OSP was marked on the scalp of the subjects by using a make-up pencil. Once the OSP was found the resting Motor Threshold (rMT) was defined as the lowest intensity of stimulation that produced five MEPs with amplitude of at least 50 μV out of ten consecutive magnetic pulses. Mean rMT was 49.9% ± SD 7.6 of maximal stimulator output. During the experimental conditions single pulses TMS with 120% intensity of individual rMT were delivered over the OSP. EMG recording endured for the entire block duration in order to control for the absence of muscular pre-activation in each trial. Motor evoked potential (MEP) peak-to-peak amplitudes (in mV) were collected and stored on a computer for off-line analysis.

2.3. *Visual stimuli*

The experimental visual stimuli consisted of two pictures depicting banknote of five and ten Euros (regular banknote) subtending a 10.5 × 5.8 cm region plus a neutral control stimulus consisting in a scramble picture of the same dimension and form. The latter stimulus was obtained by combining the pictures depicting banknotes using a custom-made image segmentation software. Regular banknotes were framed by a black or white line, which indicated to participants that they earned or lost the displaced monetary amount. The association between colour of the frame (back or white) and the monetary outcome (gain or loss) was counterbalanced across subjects. The scramble picture (i.e., no win, no loss) was always framed by a grey line. The full set of experimental stimuli is shown in the Supplementary Material.

2.4. *Procedure*

During the experimental sessions, subjects were comfortably seated in a dimly lit room at a distance of 80 cm in front of a computer screen (P791 Dell computer monitor 17″, 60 Hz refresh rate). Each participant was randomly assigned to one of two groups (‘choice’, ‘follow’), and tested in a single experimental sessions lasting approximately one hour.

Participants in the *choice group* were asked to guess which one, among two keys of the keyboard, would lead them to earn a monetary amount. In order to make the game likely, participants were told that they could win up to 50 Euros or lose everything. In the latter case, participants would receive a refund of 10 Euros for having take part to the study.

At the beginning of each trial, subjects in the choice group were presented with a visual GO cue shown on the screen for 1500 msec and asked to press, in less than one second and with their left hand, one of two keys (G or H) on a computer keyboard. One second after their choice, a feedback stimulus (a bill) associated to a winning or losing outcome was displaced at the centre of the computer screen for 1500 msec.

The session consisted of 48 trials: 16 win trials presenting winning bills (a bill of 5 Euros presented 8 times and a bill of 10 Euros presented 8 times); 16 lose trials presenting losing bills (a bill of 5 Euros presented 8 times and a bill of 10 Euros presented 8 times); 16 neutral trials presenting scramble bills. Thus, 16 MEPs per condition were obtained. Winning, losing and neutral trials were presented randomly within each block. To be sure that participants recognize the outcome displayed on the screen, in 6 vigilance trials, subjects were asked to verbally refer if they won or lost the monetary outcome previously displaced or nothing happened (scramble trial). To avoid changes in excitability due to preparation of verbal responses (Meister et al., 2003; Tokimura, Tokimura, Oliviero, Asakura, & Rothwell, 1996), participants were asked to provide their response about two seconds after the release of the magnetic pulse (Fourkas, Ionta & Aglioti, 2006; Candidi, Vicario, Abreu, & Aglioti, 2010; Komeilipoor, Vicario, Daffertshofer, & Cesari, 2014). All participants successfully answered in all the vigilance trials. During the stimulus presentation, a single pulse of TMS was delivered over the subjects' muscle OSP at 120% of rMT. The magnetic stimulation was delivered at random times ranging between 1100 and 1400 m from onset of the picture to avoid any priming effects that might influence MEP amplitude (Vicario, Candidi, & Aglioti, 2013; Vicario, Komeilipoor, Cesari, Rafal, & Nitsche, 2014; Vicario, Kritikos, et al., 2013). The inter-stimulus interval was set at 7000 msec. The TMS frequency during experimental blocks was $< .1$ Hz to avoid that TMS per se would influence M1 excitability (Chen et al., 1997). Participants in the 'follow' group were asked to passively (i.e., without key selection) view outcome randomly selected by the computer program. All the other parameters were identical to that of the experiment 1 (See Fig. 1 for diagram).

At the end of the experimental session participants were asked to quantify the intensity of their affective involvement for some particular emotions (sadness, happiness, disgust, anger, fear, regret, disappointment) while submitted to monetary gain, monetary loss and for the control condition (i.e., the scramble configuration). The emotional involvement was quantified by using a visual analogue scale (VAS).

3. Data analysis

Peak-to-peak mean MEP amplitudes were measured in mV in each experimental condition. Amplitudes that fell above or below 2.5 standard deviations from each individual mean for each condition were excluded as outliers (less than 1%). Moreover, MEPs preceded by motor artefacts were removed from the analyses (less than 5%). Mean raw MEP amplitudes were not normally distributed (Shapiro–Wilks test: $p < .05$). Thus, to test whether the two groups showed similar level of motor excitability in a 'baseline' condition, a Mann–Whitney *U* test on raw MEP amplitudes computed in the neutral condition (scramble configuration) was performed. No significant difference were found ($Z = 1.58, p = .11$). Thus, MEP amplitudes recorded in the win and loss conditions were divided by the amplitude of MEPs recorded during presentation of the neutral control condition. This procedure was effective in normalising data distribution (Shapiro–Wilks test: $p > .3$). Normalized MEPs were entered in a 2 × 2 mixed-model ANOVA with Group (choice, follow) and Outcome (win, loss) as between-subjects and within-subject factors, respectively. Post-hoc pair-wise comparisons were performed with Tukey HSD tests. The significance level was always set at $p = .05$. To further analyse intragroup modulations, raw MEP amplitudes in the win, loss and neutral conditions were submitted to non-parametric Friedman ANOVA and planned Wilcoxon matched pairs signed ranks tests. Effect size for parametric post-hoc comparisons on MEPs were computed using the repeated measure Cohen's d (Cohen, 1977; Wolf, 1986). Cohen's (1992) interpretational guidelines suggest that d = .2, d = .5 and d = .8 correspond to small, medium and large effect sizes. For non-parametric comparisons, the r was computed based on the Wilcoxon test, with r = .1, r = .3 and r = .5 indicating small, medium and large magnitudes respectively. VAS scores were analysed with a mixed-model ANOVA with Group (choice, follow) as between-group factor and Outcome (win, loss, and scramble) and Emotions (Sadness, Happiness, fear, Disgust, Anger, Regret, and Disappointment) as within-subject factors.

4. Results

The Group × Outcome ANOVA on normalised MEP amplitudes showed no main effect of Group [$F(1,18) = .181, p = .676$], but the main effect of the Outcome [$F(1,18) = 6.795, p = .018$; greater amplitude for monetary loss than win: 1.076 ± SD .148 *vs* 1.00 ± SD .133] and, critically, the double interaction Group × Outcome [$F(1, 18) = 5.781, p = .027$, Fig. 2]. Post-hoc comparisons showed that the interaction derived from a significant difference between win and loss monetary outcome in the choice group (win: .953 ± SD .103; loss: 1.099 ± SD .170; $p = .011$; Cohen's d = 1.55), while no significant difference was found in the follow group (win: 1.047 ± SD .148; loss: 1.053 ± SD .128; $p = .999$; Cohen's d = .04). This difference in the MEP amplitude indicates a relative facilitation of the motor excitability when a loss outcome followed the participants choice (1.099 ± SD .170) with respect to the win outcome (.953 ± SD .103; see Fig. 2) and was associated with a quite large effect size.

To directly investigate changes in excitability relative to neutral condition a further analysis was performed for each group using Friedman ANOVA conducted on raw MEP amplitudes. The analysis showed a significant effect of the Outcome in the choice group [$\text{Chi}^2(2) = 10.40, p = .006$] and Wilcoxon tests confirmed that in the loss condition (1.24 mV ± SD .62) amplitudes were greater than in the win (1.08 mV ± SD .53; $p = .005$; r = .89) and neutral (1.12 mV ± .50; $p = .047$; r = .63) conditions, which in turn did not differ from one another ($p = .53$). The same Friedman ANOVA conducted in the follow group was not significant [$\text{Chi}^2(2) = .80, p = .67$], suggesting no change in excitability in the win, loss and neutral conditions.

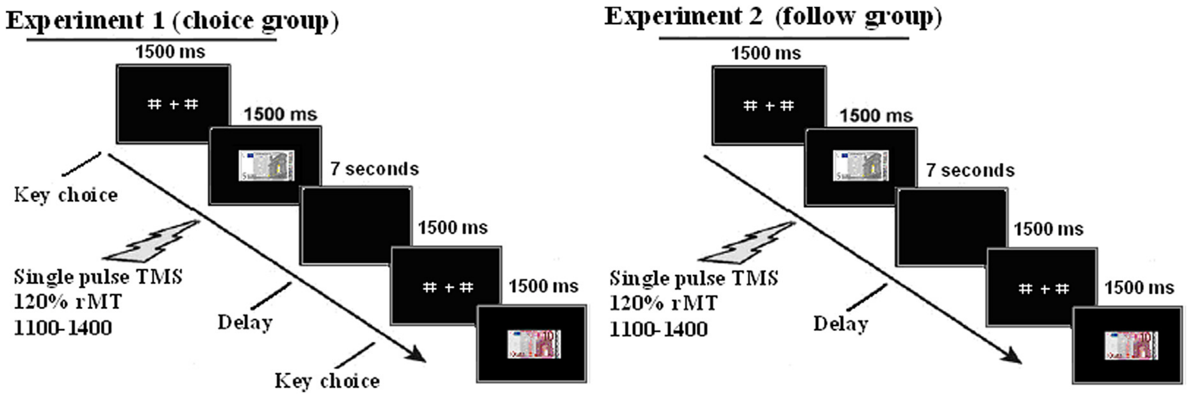

Fig. 1 – Examples of typical event trials for the 'choice' and 'follow' groups.

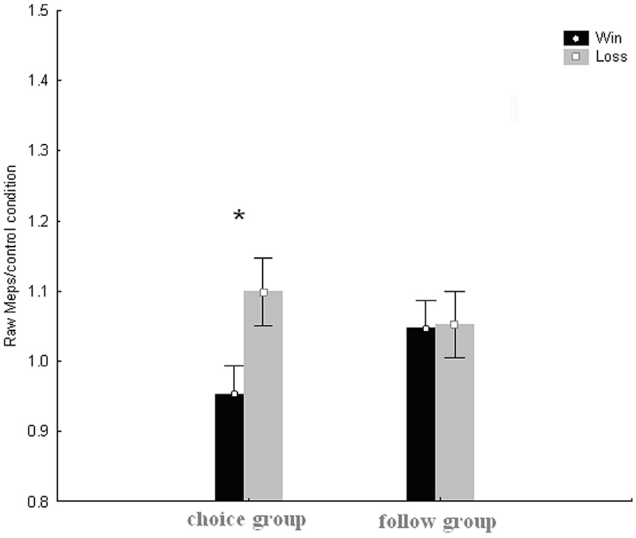

Fig. 2 – Interaction of Group and Outcome factors. Normalized MEPs' amplitude (mean ± standard error of mean) of MEPs recorded from arm (ECR). Histograms show that ECR was facilitated when a loss outcome follow the participant choice. * denote *p* values < .05.

In sum, relative to the neutral and win conditions, a selective and large increase in motor excitability for monetary loss was found in the choice group, whereas no significant modulation was found in the follow group.

Further analyses were performed on the VAS scores totalized in both experiments. No correlations were detected comparing amplitude changes of MEPs recorded from the ECR and the intensity of emotions reported by participants of both groups for winning and losing outcomes (See Supplemental Information). On the other hand, the Group × Outcome × Emotions ANOVA on VAS scores showed a main effect of the Group [$F(1, 18) = 15.38$, $p = .001$], which documents higher rating score for the choice group compared to the follow group. The factor Outcome [$F(1, 18) = 12.78$, $p = .002$] and Emotion [$F(6, 108) = 6.56$, $p < .001$] were also significant. Likewise we also detected significant results for the interaction factor Group × Outcome [$F(1, 18) = 8.91$, $p = .007$] and Outcome × Emotion [$F(6, 108) = 32.22$, $p < .001$], while no significant results were reported for the interaction factor Group × Emotion [$F(6, 108) = 1.37$, $p = .230$]. Crucially, we detected a significant Group × Outcome × Emotion interaction [$F(6, 108) = 4.97$, $p < .001$].

Focussing on the *choice group* post-hoc results show significant differences comparing the outcome conditions. In particular, VAS scores were higher comparing the monetary loss with respect to the monetary gain outcome for negative emotions such as *Sadness*, *Anger*, *Regret* and *Disappointment*; on the other hand, VAS score were higher comparing the monetary gain outcome with respect to monetary loss outcome for the *Happiness* emotion. This last result was also detected for the *follow group* in relation to a monetary gain (see Fig. 3 for details). The post-hoc comparisons are summarized in Table 1.

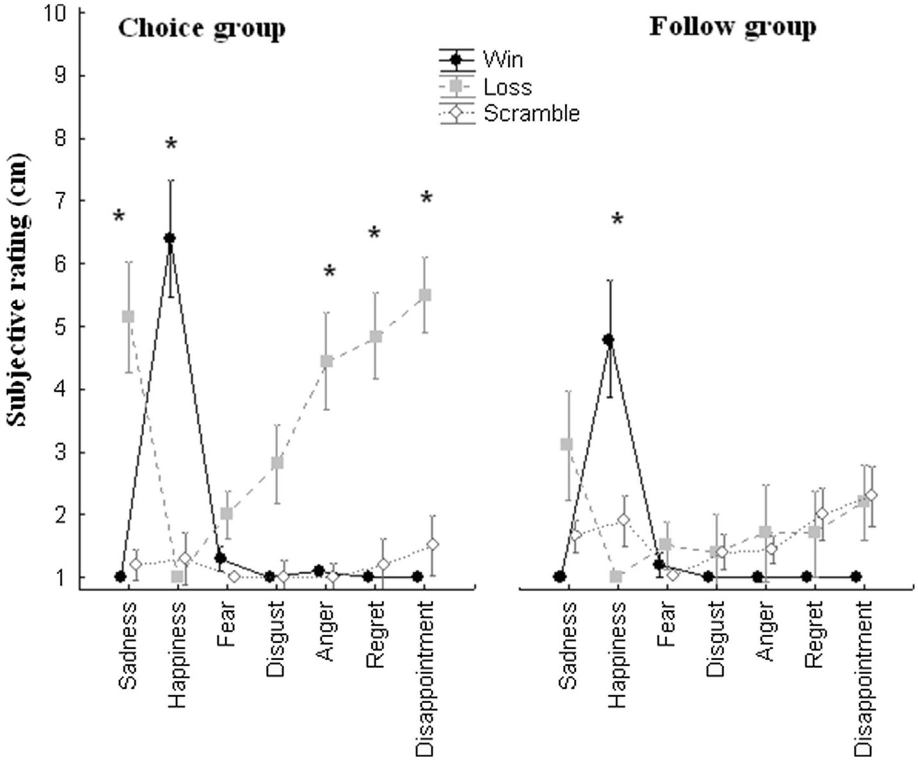

Fig. 3 – *Emotional arousal and monetary outcome*. The charts represent mean VAS ratings (mean in centimetres ± standard error of mean) provided for the examined affective states (Sadness, Happiness, Fear, Disgust, Anger, Regret, Disappointment) of both choice and follow groups submitted to win and loss outcomes. * denote *p* value < .05.

Table 1 – Tukey post-hoc pair-wise comparisons for the interaction factor Group × Outcome × Emotion. * indicate significant results.

Emotions	*Choice group*			*No choice group*		
	Post hoc comparisons			Post hoc comparisons		
	Win versus loss	Win versus neutral	Loss versus neutral	Win versus loss	Win versus neutral	Loss versus neutral
Sadness	*$p < .001$	$p > .050$	*$p < .001$	$p > .050$	$p > .050$	$p > .050$
Happiness	*$p < .001$	*$p < .001$	*$p < .001$	$p < .001$	$p > .050$	$p > .050$
Fear	$p > .050$	$p > .050$	$p > .050$	$p > .050$	$p > .050$	$p > .050$
Disgust	$p > .050$	$p > .050$	$p > .050$	$p > .050$	$p > .050$	$p > .050$
Anger	*$p < .001$	$p > .050$	*$p < .001$	$p > .050$	$p > .050$	$p > .050$
Regret	*$p < .001$	$p > .050$	*$p < .001$	$p > .050$	$p > .050$	$p > .050$
Disappointment	*$p < .001$	$p > .050$	*$p < .001$	$p > .050$	$p > .050$	$p > .050$

5. Discussion

The gambling task adopted in the current study was designed for exploring the effect of the monetary reward and counterfactual thinking on the human motor system. Thus, corticospinal excitability and emotional experience of two independent groups of participants were tested while manipulating the monetary outcomes (win/loss/no change) and the sense of responsibility (choice/follow) associated with a gambling task. The current study significantly expands upon previous investigations of the effect of reward on M1 excitability (e.g., Klein-Flügge & Bestmann, 2012; Suzuki et al., 2014; Thabit et al., 2011) by including monetary loss as possible outcome condition. This manipulation allowed us to examine the effect of the retrospective counterfactual thinking on motor excitability, when a monetary loss outcome was preceded by an action of key selection (i.e., in the choice group). In this case, the participant recognizes himself as agent for this negative event. We found that in context, participants felt strong negative emotions and showed increased motor excitability in the loss condition relative to the other conditions. No similar effects were found in the follow group that passively assisted the selection made by a computer.

In the study of Kapogiannis et al. (2008) it was shown that M1 excitability might be modulated by an upcoming potential reward. However, that study examined only the effect of passive viewing of a monetary gain. Moreover, the authors varied both reward value and the probability of getting reward, thus making it unclear whether the increased motor excitability relates to the urge in receiving the reinforcement per se, the level of arousal, or the experiences of expectancy/uncertainty. To address this issue, Gupta and Aron (2011) hypothesized that stimuli associated with stronger urges such as money would increase the excitability of those corticospinal circuits involved in making a relevant action, immediately before action execution. Accordingly, they found that MEPs were greater for larger monetary amounts, when participants knew that they had to make a choice through a motor response. They also showed that monetary amount does not modulate motor excitability when participants simply observe reward without having to take action. Similar effects by monetary reward on M1 excitability have been recently reported with other paradigms and experimental setups (Klein-Flügge & Bestmann, 2012; Suzuki et al., 2014; Thabit et al., 2011).

Whereas most of the previous studies have tested the effect of positive rewards versus neutral non-reward stimuli on the excitability of those segments of the motor system that were directly involved in making instrumental actions aimed at obtaining the reward, here we tested the influence of counterfactual thinking and monetary outcome on a segment of the motor system (ECR representation in the left M1) that was not directly involved in the motor task performed by the subjects (i.e., with the left hand) in the choice group. In this experimental context, in which win, lose and neutral monetary outcomes could be obtained, we did not detect an effect of the monetary gain outcome (compared to the baseline) on corticospinal excitability. This result could be explained by a possible greater saliency of monetary loss relative to gain outcomes in conditions in which a sense of responsibility is induced (see also Galea et al., 2013) and by several additional differences in the experimental design (e.g., the presentation of a monetary cue before versus after the TMS pulse stimulation; the onset between the monetary reward outcome and the single pulse TMS delivering) comparing the current work with respect to previous investigations (i.e., Gupta & Aron, 2011; Kapogiannis et al., 2008; Klein-Flügge & Bestmann, 2012; Suzuki et al., 2014; Thabit et al., 2011). Moreover, it should be mentioned that we did not study other parameters of motor excitability such as the intracortical inhibition or the short-latency afferent inhibition that may be more sensitive to monetary rewards (e.g., see Kapogiannis et al., 2008; Thabit et al., 2011) and emotional processing (Borgomaneri et al., 2015).

On the other hand, we found a change in motor excitability for monetary loss outcomes. In particular, a monetary loss preceded by a key selection action enhanced the excitability of the corticospinal system. No effect was found when participants were required to passively observe the monetary loss outcomes. This suggests that the motor excitability might be mainly modulated by the negative emotional experience associated with the selection of a ‘wrong’ action (which was possibly mediated by the sense of responsibility for that action and by backward counterfactual thinking), rather than by the monetary loss itself. Indeed, emotional ratings were higher in the choice than in the follow group, with greater self-report feelings of regret, but also disappointment, anger and sadness in the former compared to the latter group. These findings fit with the notion that activity in the motor system is enhanced when processing aversive stimuli and events (e.g., Borgomaneri et al., 2014a; Giovanelli et al., 2013; Oliveri et al., 2003; van Loon et al., 2010).

The increase in motor excitability for monetary loss and the notion that such emotionally negative events may be particularly salient when a sense of responsibility is induced fit also with the notion that making and detecting errors is associated to increased activity in motor areas (Amengual et al., 2013; van Schie, Mars, Coles, & Bekkering, 2004; Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013). In this vein, the evaluation of the one's own ‘erroneous’ decision (leading to monetary loss) may have activated neural processing associated to action monitoring.

The present research contributes to the current debate about the relationship between sensory and motor mechanisms in sensory-motor loops (e.g., see Perruchoud, Murray, Lefebvre, & Ionta, 2014 for a recent discussion), and suggests that a role of cognitive (i.e., counterfactual thinking) and emotional factors in mediating sensory-motor neural interactions. We propose that counterfactual thinking affects processing in the premotor cortex, which plays a key role in linking frontal regions involved in action monitoring, representation of action outcomes and cognitive reasoning, such as the dorsomedial prefrontal cortex, OFC and the dorsolateral prefrontal cortex, respectively, with M1. This account might be compatible with the late effect (i.e., between 1100 and 1400 msec after the monetary loss outcome) of counterfactual thinking on motor excitability that we observed. Future studies are needed to clarify the precise temporal dynamics and directly test the causal influence of premotor cortex in the effects we have documented here at the level of M1.

Different scholars have already evaluated the impact of emotions on corticospinal excitability (Borgomaneri et al., 2014a, 2014b, 2015; Coelho et al., 2010; Coombes et al., 2009; Hajcak et al. 2007; Oathes, Bruce, & Nitschke, 2008; Oliveri et al., 2003). For instance, using TMS, Oliveri et al. (2003) reported increased corticospinal excitability during the presentation of unpleasant, as compared with neutral images. In a following study (Hajcak et al., 2007), it was suggested that arousal rather than valence plays a role in modulating the corticospinal system. On the other hand, other studies have shown greater motor modulations when processing unpleasant, as compared with pleasant and neutral stimuli (Borgomaneri et al., 2014a, 2015; van Loon et al., 2010; Nogueira-Campos et al., 2014; see also Koganemaru, Domen, Fukuyama, & Mima, 2012). These findings have suggested that negative emotions are particularly adept to mobilize the body for action. Our results provide further support to this notion since we detected a modulation of corticospinal excitability only in relation to highly negative ratings associated with monetary loss in the choice group, while no effect has been observed for the positive event of winning that was associated with happiness.

One limit of the current protocol is that the follow group did not make any motor response. However, we believe that this lack of control for motor response does not pose a serious challenge to our interpretation of the results. The possible concern is that the motor task (pressing keys with the left hand) in the choose group may have changed the level of motor excitability as recorded in the right ECR muscle and this could have influenced the pattern of results. However, there are reasons to assume that the effect of motor activity on MEPs was minimal or negligible. Previous research (i.e., Muellbacher et al., 2000; Perez & Cohen, 2008; Stedman, Davey, & Ellaway, 1998; Tinazzi & Zanette, 1998; Ziemann & Hallett, 2001) documented an influence of hand movements on MEPs from homologous muscles in the other hand (ipsilateral M1) only during sustained isometric contraction, or while performing complex finger movements. Most of the studies have shown selective effects at the level of homologous muscles, although in a few cases the effects slightly extended to non-homologous muscles (cf van den Berg et al., 2011). However, several studies failed to show an influence of simple motor tasks (i.e., repetition of a single finger movement) even when motor excitability was tested simultaneously with motor performance and MEPs were recorded from the muscles homologous to those actively involved in the motor task (Tinazzi & Zanette, 1998; Ziemann & Hallett, 2001). Three aspects of our study are particularly relevant: i) On each trial, participants in the choose group performed a single and simple movement (i.e., key pressing); ii) such movement involved flexors of the left hand, whereas MEPs were recorded in non-homologue muscles i.e., the right ERC, which control the extension of the right wrist; and iii) moreover, the movements were executed at least 1100 msec (i.e., between 1100 and 1400 msec) before the TMS pulse, not during action execution. Taken together these three aspects suggest that the direct influence of participants' motor task on motor excitability may be very small or negligible in our study. This hypothesis is also directly supported by the absence of between groups difference when comparing MEP amplitude in the neutral (scramble) baseline condition (see Methods).

This suggests that the change in M1 excitability reported in the choice group is not substantially influenced by the key selection movement preceding the monetary outcome. In fact, if the motor response would have affected MEPs, a difference should have been detected comparing the baselines MEPs amplitude of these two groups (choice versus follow).

6. Conclusions

Counterfactual reasoning mediates the experience of regret when we recognize ourselves as responsible of a negative (i.e., punishing) outcome, such as a monetary loss. However, as suggested by the emotional rating scores collected in the current work, other negative emotional states (i.e., anger, disappointment, sadness) may spill out when thinking counterfactually after a wrong choice, thus suggesting that the reported pattern of corticospinal excitability might be the result of a complex spectrum of negative emotional feelings that contribute to making monetary loss a particularly negatively salient event.

A non-mutually alternative hypothesis is that the physiological effect detected in the current study following the monetary loss outcome might be due to processing of erroneous actions. In fact, one could speculate that the enhanced corticospinal excitability might reflect action monitoring processing associated to the appraisal in having made a wrong choice. This possibility fits with studies showing changes in motor excitability during error processing (Amengual et al., 2013; van Schie et al., 2004; Tidoni et al., 2013) and studies documenting a direct connectivity between the anterior cingulate cortex, which activity has been systematically linked to error detection (e.g., Carter et al., 1998) and M1 (Morecraft & Van Hoesen, al., 1992, 1993. See Paus, 2001 for a review). However, we did not provide a control for error detection, as this topic went over the goals of the current research. Moreover, we did not study the experience of counterfactual thinking in relation to the win and the loss of different (i.e., low versus big) monetary amounts (e.g., Kahneman & Tversky, 1982; Nicolle, Bach, Driver, & Dolan, 2011). In fact, although we used two different bank-note amounts (i.e., 5 *vs* 10 Euros), we did not provide a feedback about the alternative condition which could represent a monetary gain (low versus big), a monetary loss (low versus big) or a scramble configuration outcome.

Future works devoted to explore this issue might expand the current work by testing the experience of regret in relation to a monetary win (i.e., winning a monetary amount followed by the feedback that the alternative key choice would have provided a bigger monetary gain) and the experience of relief in relation to a monetary loss (i.e., losing a monetary amount followed by the feedback that the alternative key choice would have provided a bigger monetary loss). Moreover, and in the light of the sensory-motor loop model discussed above, future studies will have to investigate the issue of temporal dynamics by testing any change in the activity of M1 for earlier TMS onsets (e.g., 300–600 msec or 700–1000 msec with respect to the monetary loss outcome) and the possible influence of the premotor cortex in the observed effects.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.12.017.

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