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When defeat leaves a bad taste in the mouth: Modulation of tongue corticobulbar output during monetary loss in a gambling task

The tongue is a crucial effector involved in most everyday behaviors. Due to its complex nature (i.e., as a muscle and somatosensory/gustatory organ) the tongue is endowed with a multifunctional integration capacity that makes it an unique and important actor for survival. Neurons of the cortical representation of the tongue within the primary motor cortex (tnM1) show a specific pattern of connectivity with cortical and subcortical regions involved in reward processing [1,2], suggesting a role of tnM1 neurons in processing reward-related stimuli/outcomes and internal (physiological and mental) states [3,4]. In line with this, we have previously shown that visual stimuli representing core disgust and social signs of disgust (i.e., rotten food and distasted faces) reduce corticobulbar excitability of the human tnM1, as measured via motor-evoked potentials (MEPs) induced by tnM1 transcranial magnetic stimulation (TMS) [5]. Similar findings of reduced tnM1 corticobulbar motor outputs were found when participants were exposed to social scenarios eliciting indignation for moral violations [6], suggesting shared mechanisms underly core, social and moral disgust [7]. Furthermore, we have recently shown that tnM1 downregulation via transcranial direct current stimulation (tDCS) reduces hunger in healthy humans [8]. All this work suggests a relevance of tnM1 for appetitive and defensive motivational systems. Yet, whether this role is generally relevant for experiences along the reward-punishing continuum, or rather exquisitely associated with oral dimensions, is still unclear.

To address this issue, we administered TMS of the tnM1 in healthy volunteers undergoing an established gambling protocol [9], to investigate whether reward-related experiences associated with monetary win and loss induce consistent modulations of tnM1 corticobulbar excitability (Fig. S1). Eleven participants (5 males, age mean 24.45 year, SD 3.74) performed 96 trials (48 trials per muscle) and were asked to guess which one of two keys on a keyboard would be rewarded with a monetary win. Upon key pression, participants were presented with one of the following outcomes: in 16 trials (win trials) banknotes associated with the sentence “You win” were presented; in 16 trials (lose trials) banknotes associated with the sentence “You lost” were presented; in 16 trials (neutral trials) scrambled banknotes without any win/loss outcome were presented. After the feedback presentation, we recorded MEPs from the tongue and the extensor carpi radialis (ERC) muscles. Thus, 16 MEPs per muscle and condition were obtained and stored for offline analysis (for details see the Supplemental Materials). The experimental procedures were approved by the local ethics committee at the University of Bologna and were carried out in accordance with the principles of the 1964 Helsinki Declaration.

MEPs were log-transformed to reduce skewness, averaged for each muscle and condition, and then submitted to an ANOVA with the within-subjects factors Monetary outcome (win, lose, neutral) and Muscle (tongue, ECR). In line with our previous findings [9] showing higher corticospinal excitability following a monetary loss, we found a significant main effect of Monetary outcome ($F_{2,20} = 9.35$, $p = 0.001$, $\eta_p^2 = 0.48$), with higher MEPs following a loss (mean raw MEP amplitude in mV ± standard deviation: 1.39 ± 0.48) compared to the win (1.25 ± 0.42; $p = 0.001$, Cohen's $d = 1.42$) and neutral (1.27 ± 0.43; $p = 0.023$, $d = 0.97$) outcomes, which in turn did not differ from one each other ($p = 0.40$). The main effect of the factor Muscle ($F_{1,10} = 2.44$, $p = 0.15$, $\eta_p^2 = 0.20$) or the Muscle x Monetary Outcome interaction ($F_{2,20} = 0.39$, $p = 0.69$, $\eta_p^2 = 0.04$) were not significant (Fig. 1).

Stepwise regression analyses between emotional (i.e., happiness, anger, fear, disgust, regret, disappointment) ratings (measured via visual analogue scale) associated with the three monetary outcomes (see caption to Fig. S1 for details on data collection) and the respective MEP amplitudes revealed a significant model for loss trials ($R^2_{adj} = 0.64$, $F_{1,9} = 18.64$, $p = 0.002$) showing a strong negative relation ($\beta = -0.82$, $p = 0.002$; $f^2 = 2.07$; Fig. S2) between regret rating and tongue MEP amplitudes. No further significant results were found (see Table S1) and the relation between regret and MEPs remained specific for tongue when contrasting tongue ($\beta = -0.79$, $p = 0.005$, $f^2 = 1.68$) and ECR MEPs ($\beta = -0.09$, $p = 0.67$, $f^2 < 0.01$).

The present findings support and expand our previous work [9] by showing that when participants are active agents of monetary loss in a gambling task (but not when they passively observe monetary outcomes [9]), corticospinal excitability (ECR) and corticobulbar excitability (tongue) are increased. This points to a link between negative emotions, sense of responsibility, and functional modulation of the motor cortex [9]. We also provide preliminary evidence that tnM1 excitability during loss trials predicts the experience of regret – an emotion arising from counterfactual thinking of what would have happened had participants made a different choice. The negative relation between regret ratings and tnM1 excitability suggests a mapping of specific aspects of the experience of monetary loss.

The increased excitability of tnM1 in response to monetary loss, which was independent of the specific muscle representation, might reflect generalized action monitoring processes activated by an “erroneous” decision carrying negative consequences in the gambling task and is associated with widespread activation of mediofrontal and motor cortices [10], leading to enhanced MEPs from the two target muscles. Motor response was variable across

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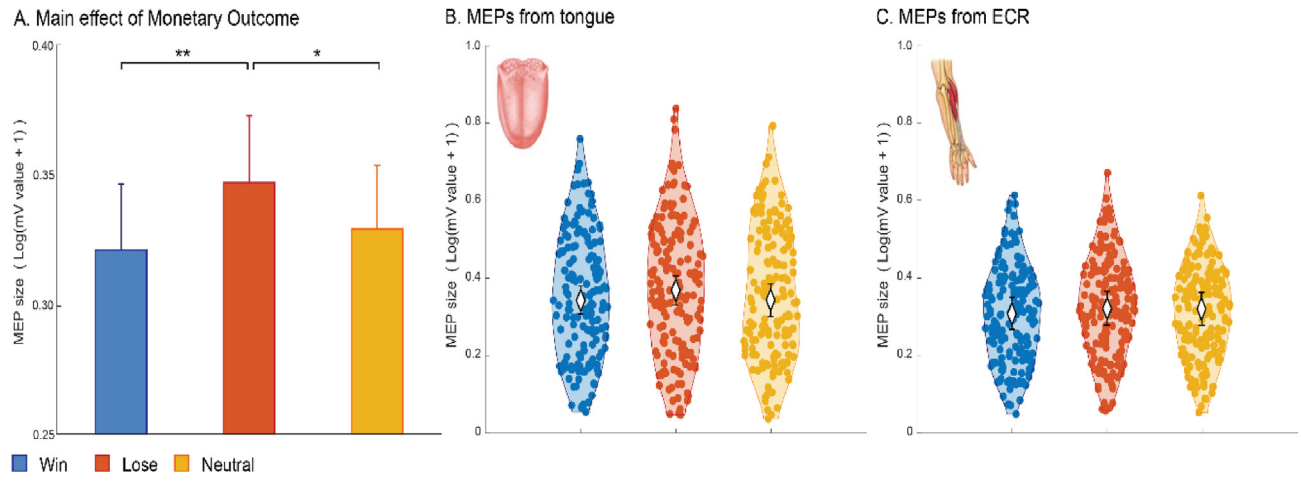

Fig. 1. A. The main effect of the gambling task monetary outcome showed an overall larger MEPs response when a loss outcome followed the choice, compared to the win and the neutral (no win/no loss) conditions. Asterisks indicate significant results of the pairwise comparisons: *p ≤ 0.05, **p ≤ 0.005. Vertical bars denote standard errors. **B./C.** Violin plots of single-trial MEPs from the tongue and ECR muscles across individuals.

individuals (Fig. 1B and C) and associated with affective self-reported ratings (Fig. S2). While our study cannot clarify directly whether aspects of the subjective experience of monetary loss contributed to enhanced corticospinal or corticobulbar excitability, our findings suggest nevertheless that the tnM1 excitability enhancement due to monetary loss tends to attenuate in participants who experience larger regret as a result of their choice. This tongue-specific attenuation might reflect aversion towards the negative monetary outcome associated with retrospective counterfactual thinking and might derive from a pattern of neural connectivity between tnM1 and the anterior cingulate-insular cortex network [1–3], which is known to be involved in aversion processing [7]. This interpretation is also in line with prior work [5,6] showing that perceiving aversion in response to pictures of rotten foods or moral violations was associated with reduction of tnM1 corticobulbar excitability. The expression "defeat leaves a bad taste in the mouth" may be more than a metaphor when describing the experience of regret, an aversive state perceived by individuals for their wrong choices or when they have failed to achieve a goal.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brs.2022.10.010.

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