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The plasticity of the mirror system: How reward learning modulates cortical motor simulation of others

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ABSTRACT

Cortical motor simulation supports the understanding of others' actions and intentions. This mechanism is thought to rely on the mirror neuron system (MNS), a brain network that is active both during action execution and observation. Indirect evidence suggests that (alpha/beta) mu suppression, an electroencephalographic (EEG) index of MNS activity, is modulated by reward. In this study we aimed to test the plasticity of the MNS by directly investigating the link between (alpha/beta) mu suppression and reward. 40 individuals from a general population sample took part in an evaluative conditioning experiment, where different neutral faces were associated with high or low reward values. In the test phase, EEG was recorded while participants viewed videoclips of happy expressions made by the conditioned faces. Alpha/beta mu suppression (identified using event-related desynchronisation of specific independent components) in response to rewarding faces was found to be greater than for non-rewarding faces. This result provides a mechanistic insight into the plasticity of the MNS and, more generally, into the role of reward in modulating physiological responses linked to empathy.

1. Introduction

According to simulation theories, cortical motor simulation is fundamental to interpret the actions and intentions of others (Gallese and Goldman, 1998). The mirror neuron system (MNS), which maps the correspondence between the perceived and executed actions, has been proposed as the neural substrate of cortical motor simulation (Rizzolatti and Sinigaglia, 2010). Alpha-mu (8–12 Hz) and beta-mu (12–25 Hz) rhythms generated over the sensorimotor cortex desynchronize (are suppressed) both during execution and observation of actions, and therefore have been proposed as an electroencephalographic (EEG) index of mirror-like activity (Arnstein et al., 2011; Braadbaart et al., 2013; Pineda, 2005). Importantly, mu suppression has been shown to occur during observation of facial gestures in infant monkeys (Ferrari et al., 2012), and when viewing emotional faces in humans (Moore et al., 2012). This neural mirroring of emotions has been hypothesized to facilitate the understanding of emotions experienced by others, which in turn might support the ability to empathize (Iacoboni, 2009; Niedenthal, 2007; Pfeifer et al., 2008). Consistent with this speculation, Woodruff et al. (2011) and Hoenen et al. (2013) found an association between mu suppression and empathic abilities.

An electrophysiological study by Caggiano et al. (2012) reported that the activity recorded from single mirror neurons was modulated by the reward value ascribed to the observed object on which the motor act was performed. This result was the first direct evidence for the role of reward in determining the plasticity of the mirror neuron response. There is substantial indirect evidence for the plasticity of the MNS response in humans using different task manipulations (e.g., group membership (Gutsell and Inzlicht, 2010), familiarity (Liew et al., 2011; Oberman et al., 2008)), which can be potentially argued to alter the reward value of the stimuli. E.g., in-group members are considered more rewarding than out-group members and are associated with greater reward response (Brewer, 1979; Chen et al., 2014), and greater familiarity is associated with greater liking and 'reward' (Hansen and Wänke, 2009). More specifically, MNS activation is enhanced in response to in-group members and familiar stimuli since these stimuli might be more rewarding to us than out-group, or unfamiliar stimuli. Based on these findings, it is reasonable to hypothesize that the extent of (alpha/beta) mu suppression will be modulated by the reward value of the observed stimuli.

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A link between empathy-related responses and reward has previously been demonstrated by Sims et al. (2012), who showed that spontaneous facial mimicry is modulated by the reward value associated with the imitated social stimuli. In this study, the reward value of neutral faces was manipulated using an evaluative conditioning paradigm before emotional facial expressions made by the same faces were presented to the participants in a passive viewing task. Participants showed greater spontaneous mimicry (measured using facial electromyography; EMG) in response to happy expressions performed by the faces associated with high reward as compared to those associated with low reward. Further evidence of the modulatory influence of reward value on mimicry comes from a recent neuroimaging study (Sims et al., 2014) that used the same paradigm as Sims et al. (2012). Results showed that functional connectivity between the ventral striatum, a region associated with reward processing, and the inferior frontal gyrus, a region involved in mimicry, was stronger when participants observed happy facial expressions of faces conditioned with high reward compared to those conditioned with low reward. Since spontaneous mimicry has been proposed to be a marker of empathy (Dimberg et al., 2011; Sonnby-borgström et al., 2003), this indicates the existence of a link between the reward and empathy systems.

The current study aimed at providing direct evidence of the relationship between motor cortical stimulation and reward by examining how reward modulates (alpha/beta) mu suppression. To this end, the reward value ascribed to neutral faces was experimentally manipulated using a paradigm similar to Sims et al. (2012, 2014). In light of previous results, we hypothesized that (alpha/beta) mu suppression would be more pronounced in response to happy expressions displayed by faces conditioned with high reward compared to those produced by faces conditioned with low reward.

2. Materials and methods

2.1. Participants

Forty adults (20 females) between 18 and 44 years of age (M=24.53; SD=5.73) were recruited from the University of Reading campus area. All participants had normal or corrected-to-normal vision and all but two were right-handed. None of the participants reported current neurological or psychiatric disorders, or history of regular drug/substance use. Four participants reported a history of depression and one participant had a history of eating disorder. From the original sample, 10 participants were excluded in the analysis due to regular cigarette consumption (n=2), low performance in the oddball task (i.e. score lower than 75%, see Section 3; n=3), and insufficient data after artifact removal (n=5). Regular smokers were excluded as smoking has been associated with alterations in reward processing (Martin-

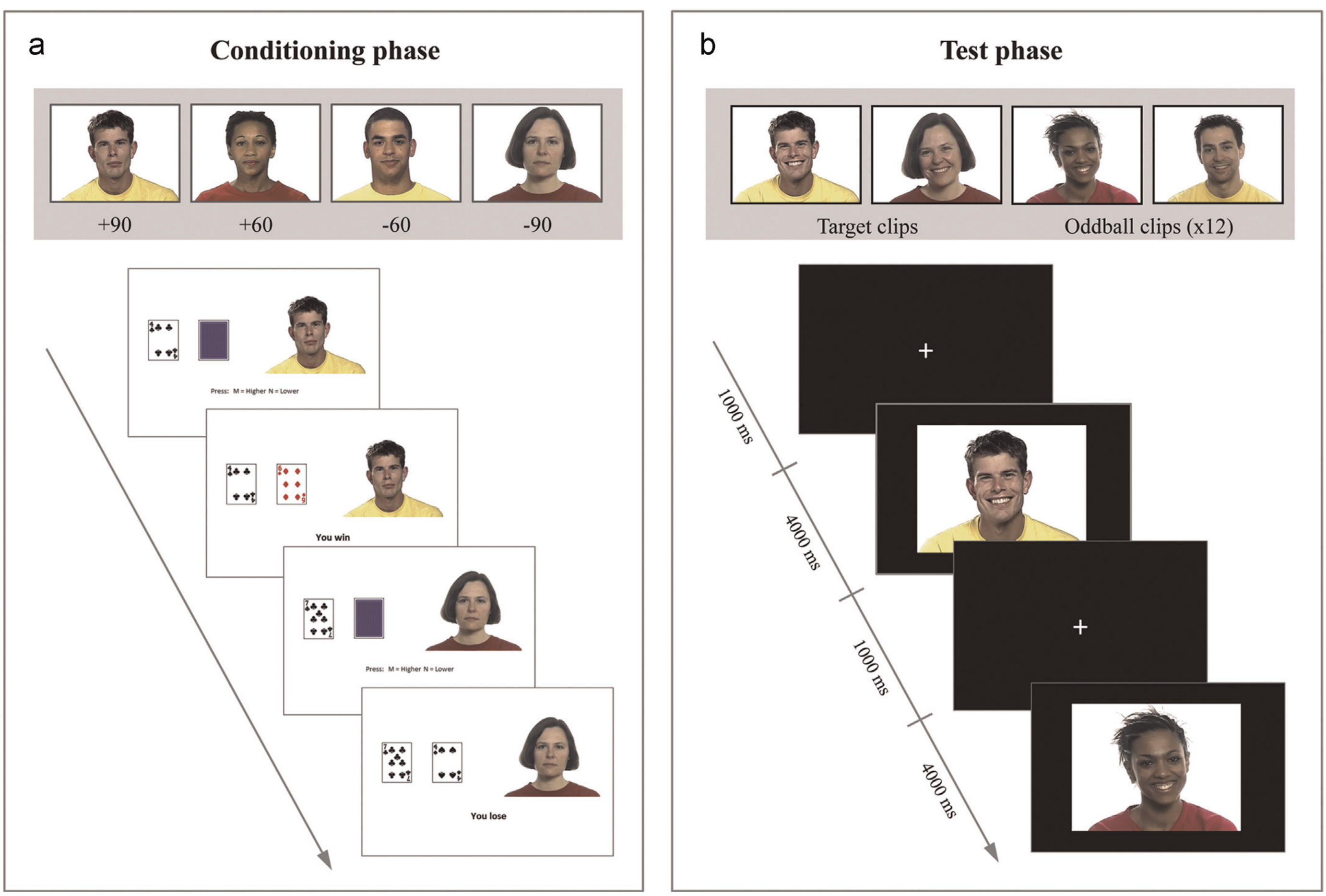

Fig. 1. (a) Top panel: example of the four neutral faces that were associated with different reward values (90% win, 60% win, 60% loss, 90% loss) during the conditioning phase. The first face corresponds to the High Reward condition, and the fourth face to the Low Reward condition. Bottom panel: example of two trials of the conditioning phase in which the participants had to predict whether the face down card would be of lower or higher value than the face up card. Following their key response, feedback was displayed. (b) Top panel: examples of the target clips (High Reward and Low Reward conditioned faces) and two of the oddball clips presented during the test phase. Bottom panel: example of two trials of the test phase. A fixation cross appeared during 1000 ms before the presentation of the 4000 ms clips of happy facial expressions made by the target or oddball faces. Participants had to make a keypress response every time an oddball clip was presented.