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How mimicry influences the neural correlates of reward: An fMRI study

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ABSTRACT

Mimicry has been suggested to function as a "social glue", a key mechanism that helps to build social rapport. It leads to increased feeling of closeness toward the mimicker as well as greater liking, suggesting close bidirectional links with reward. In recent work using eye-gaze tracking, we have demonstrated that the reward value of being mimicked, measured using a preferential looking paradigm, is directly proportional to trait empathy (Neufeld and Chakrabarti, 2016). In the current manuscript, we investigated the reward value of the act of mimicking, using a simple task manipulation that involved allowing or inhibiting spontaneous facial mimicry in response to dynamic expressions of positive emotion. We found greater reward-related neural activity in response to the condition where mimicry was allowed compared to that where mimicry was inhibited. The magnitude of this link from mimicry to reward response was positively correlated to trait empathy.

1. Introduction

Mimicry is a facilitator of social bonds in humans. Spontaneous mimicry of facial expressions of emotion is seen in humans from an early stage in development, and contributes to the affective response to another person's emotion state, i.e. affective empathy (Meltzoff, 2007; Meltzoff and Decety, 2003; Meltzoff and Moore, 2002). Social psychological studies have suggested a bidirectional link between mimicry and liking. Human adults like those who mimic them, and mimic others more who they like (Kühn et al., 2010; Likowski et al., 2008; McIntosh, 2006; Stel and Vonk, 2010; Lakin et al., 2003). Liking and affiliation goals can be regarded as complex social processes that effectively alter the reward value of social stimuli. Consistently, experimentally manipulating the reward value associated with a face influences the extent of its spontaneous mimicry (Sims et al., 2012). At a neural level, functional connectivity between brain areas involved in reward processing (ventral striatum, VS) and facial mimicry (inferior frontal gyrus, IFG) was found to be higher when observing faces conditioned with high vs. low reward (Sims et al., 2014). Using an identical paradigm in an EEG experiment, greater mu-suppression (related to mimicry-relevant sensorimotor coupling/ mirror system activity) was noted in response to faces associated with high vs. low reward (Trilla-Gros et al., 2015).

The link from reward to mimicry is relevant to understand social communication in individuals who score low on measures of trait empathy, such as those with Autism Spectrum Disorder (ASD). Individuals with ASD display reduced spontaneous mimicry for the emotional facial expressions of others (Beall et al., 2008; McIntosh et al., 2006; Oberman et al., 2009). One hypothesis suggests that such reduced spontaneous facial mimicry is driven, in part, by the low reward value ascribed to faces and other social stimuli in individuals with ASD (Dawson et al., 2002; Chevallier et al., 2012). Consistent with this hypothesis, the link from reward to mimicry has been shown to be weak in individuals with high autism-related traits (Sims et al., 2014, 2012). Crucially however, the link between reward and mimicry is bidirectional. It is important to study these links in both directions, since mimicry is a key component of human behaviour from early development, and such bidirectional links with reward provides a potential mechanism through which mimicry facilitates social bonds.

If mimicry is rewarding by nature, two possibilities arise. First, the act of being mimicked is rewarding. Behavioural studies support this possibility by demonstrating that individuals find being mimicked to be more rewarding (Neufeld and Chakrabarti, 2016; van Baaren et al., 2004). Greater self-reported liking and reward-response (indexed by preferential gaze duration) was associated with faces that show greater mimicry vs. those that show lower mimicry (Neufeld and Chakrabarti, 2016). Importantly, the strength of this link from mimicry to reward was greater in individuals with high trait empathy. Second, that the act of mimicking *itself* is rewarding to the mimicker, as suggested from observations in non-human primates (de Waal and Bonnie, 2009). There is little or no empirical investigation of this second possibility. In order to fill this gap in the literature, we investigated the effect of

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inhibiting spontaneous facial mimicry on the extent of reward processing.

A commonly used technique to restrict spontaneous mimicry of happy facial expressions is to interfere with a participant's capacity to smile, by having him/her hold a pen between their lips. This action contracts the orbicularis oris muscle complex that surrounds the mouth and is incompatible with the contraction of the zygomaticus major muscle group in the cheek that is needed for smiling (Strack et al., 1988). Niedenthal (2007) and colleagues showed that happy faces were rated as less positive when participants' ability to spontaneously mimic was restricted using the procedure described above. We sought to use this manipulation as a potential method to restrict spontaneous mimicry of happy expressions. For the task to be suitable for use in the MRI scanner, we modified the task to instruct the participants to hold their tongue between their lips for half of the trials. This condition is referred to as the "Tongue" condition. In the remaining trials participants were merely instructed to observe the stimuli that were presented. This condition is referred to as the "NoTongue" condition. We performed a pilot study using facial EMG in order to validate the effectiveness of the method to restrict facial mimicry (described in Section 2). Notably, this 'Tongue' vs. 'NoTongue' manipulation does not have any impact on the mimicry of angry faces, which needs the free movement of the corrugator supercilii muscle.

The aim of the main study was to measure the response of two key brain regions involved in processing rewards - (ventral striatum [VS] and orbitofrontal cortex [OFC]) - as participants observed happy and angry facial expressions under two conditions, that either allowed or restricted spontaneous facial mimicry of happy faces.

The VS receives cortical input from the OFC and anterior cingulate cortex, as well as mesolimbic dopaminergic afferents. It projects back to the ventral tegmental area and substantia nigra, which, in turn, have projections to the prefrontal cortex, via the medial dorsal nucleus of the thalamus (Haber and Knutson, 2010). This circuit is an integral part of the cortico-basal ganglia system and plays a central role in reward processing in humans and other mammals. The OFC is another key node of this circuit, and is believed to encode the subjective value of stimuli, as suggested by multiple studies in humans and nonhuman primates (Rolls, 2000; Wallis, 2011). OFC neurons in primates have been shown to be involved in social context-dependent coding of reward value (Azzi et al., 2012). Activity in VS has been suggested to be related to the anticipation of both primary and secondary rewards, while OFC potentially serves to encode a variety of stimuli into a common currency in terms of their reward values (Haber and Knutson, 2010; Liu et al., 2011; O'Doherty, 2004; O'Doherty et al., 2002; Schultz et al., 2000).

We hypothesised that spontaneous mimicry of happy facial expressions would evoke greater activity in the VS and OFC compared to the condition where spontaneous mimicry is restricted. This hypothesis relies on the assumption of a feedforward signal from the brain areas involved in the act of mimicry to those involved in the reward response. This assumption is supported by a previous fMRI study, where activity in the parietofrontal network involved in mimicry in response to observing another human making an action toward an object was found to modulate the reward-related neural response to the object, as well as the self-reported desirability of the object (Lebreton et al., 2012). Increased striatal activity has also been shown whilst participants intentionally mimic, as opposed to merely observe, emotional facial expressions (Carr et al., 2003). Activity in the VS and the OFC during mimicry of hand signals has been shown to be modulated by "similarity biases" such as gender (Losin et al., 2012). However, the impact that spontaneous facial mimicry has on brain regions involved in reward processing has not been directly tested.

In order to test the effectiveness of the proposed mimicry manipulation, it is necessary to measure the IFG response, while spontaneous mimicry was allowed or restricted. IFG activity has been repeatedly associated with mimicry, as demonstrated in a meta-analysis (Caspers et al., 2010). The control condition involved participants' viewing angry facial expressions. As the spontaneous mimicry of angry faces requires sets of muscles that should not be inhibited during the Tongue condition (e.g. the corrugator supercilii) we would not expect to see any difference in IFG activity between the NoTongue and Tongue conditions in response to angry faces. We predicted that

i) a significant Tongue × Emotion interaction will be observed in the VS and the OFC response. Specifically, greater BOLD activity was predicted in the VS and OFC in response to NoTongue (High Spontaneous Mimicry) Happy vs. Tongue (Low Spontaneous Mimicry) Happy faces, but not in response to NoTongue Angry vs. Tongue Angry faces;
ii) a significant Tongue × Emotion interaction will be observed in IFG. Specifically, greater BOLD activity was predicted in the IFG in response to NoTongue Happy vs. Tongue Happy faces, but no difference in response to NoTongue Angry vs. Tongue Angry faces.

Individual differences in the strength of the link from mimicry to reward are of particular interest, in light of a previous study which demonstrated that individuals high in trait empathy showed a greater liking and preferential looking for faces who mimicked them more (Neufeld and Chakrabarti, 2016). Accordingly, a widely used and well-characterised trait measure of empathy, the Interpersonal Reactivity Index was used in the current study (IRI: Davis, 1980, 1983). Of specific interest was the correlation between individual differences in empathy and reward response to [free vs restricted-mimicry] happy faces in reward-related brain regions (VS and OFC). Based on previous human studies, we predicted that participants' IRI score would correlate positively with the Tongue x Emotion interaction term of the BOLD response in the reward-related regions.

2. Material and methods

Ethical approval for the pilot validation study and the main fMRI study was obtained from the University Research Ethics Committee of the University of Reading and all participants provided informed consent.

2.1. Pilot study: Validation of the manipulation to restrict facial mimicry

Six participants (4 female) with normal or corrected-to-normal vision were recruited from the University of Reading campus. Participants viewed movie clips of actors making either happy or angry facial expressions in two conditions ("Tongue" and "NoTongue"). The visual presentation and the EMG measurement were the same as in Sims et al. (2012). However, sensors were placed only over the zygomaticus major muscle. As in Sims et al. (2012), EMG data was rectified, screened for movement artefacts, and logarithmically transformed. The baseline for each trial was defined as the mean magnitude in activity for the period 500 ms prior to stimulus onset. The mean EMG magnitude for the period 2000–4000 of stimulus presentation was then calculated, and then divided by the pre-stimulus baseline (De Wied et al., 2009). A 2 (emotion: happy, angry) × 2 (mimicry conditions: Tongue, No Tongue) repeated measures ANOVA was performed. Of interest were specific pairwise comparisons, namely [NoTongue Happy vs. Tongue Happy], [NoTongue Angry vs. Tongue Angry], [Tongue Happy vs. Tongue Angry] and [NoTongue Happy vs. NoTongue Angry] to detect if the Tongue/NoTongue manipulation significantly and specifically restricts spontaneous mimicry of happy faces.

2.2. Main fMRI study

2.2.1. Participants

Twenty-nine neurotypical participants (17 females) aged between 20 and 36 years (mean age ± SD = 22.96 ± 4.17) were recruited from the University of Reading campus. Participants received an anatomical