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Review article

A neuroendocrine account of facial mimicry and its dynamic modulation

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ABSTRACT

Facial expressions are considered central in conveying information about one's emotional state. During social encounters, facial expressions of another individual are often automatically imitated by the observer, a process referred to as 'facial mimicry'. This process is assumed to facilitate prosocial behaviour and is thought to rely on the mirror neuron system, known for its involvement in both observation and execution of motor actions. However, recent studies have revealed mimicry to be a more dynamic process than previously conceptualized, leaving mere perception-action coupling insufficient to explain its behavioural flexibility. In the current review, we describe the consequences of these findings for the theoretical conceptualization of facial mimicry, and present a novel neuroendocrine model for the dynamic modulation of facial mimicry. Our model can guide research on the communicative function of facial expressions and can provide insight into the position of facial mimicry in theoretical models of empathy and social interaction.

Contents

1. Nonverbal facial communication and emotion understanding

During human social interactions, emotional facial expressions are considered one of the most important sources of nonverbal information, enabling mutual understanding of emotional states (Buck, 1994). Human facial expressions have evolved from signalling rudimentary emotional experiences, such as disgust and fear, to displaying a broad range more complex emotional motives which are often under cognitive control (Chapman et al., 2009; Du et al., 2014). An example is the non-Duchenne or 'social' smile, where a smile is displayed without the accompanying contraction of the eye-muscles (Frank et al., 1993). As such, the human face has gained an essential signalling function throughout evolution, thereby facilitating nonverbal communication in

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dyadic interactions. It has been suggested that this nonverbal facial communication most likely predated language as a means to communicate intentions to others, in order to cooperate in joint goal-directed behaviour (Tomasello, 2014). The increasing importance of facial communication during social interactions in the human lineage could therefore have served as selection pressure on the evolution of human facial expressions (Tramacere and Ferrari, 2016).

Over the last decades, research investigating facial interactions has demonstrated that humans often tend to imitate facial expressions of another individual during social encounters, a process termed 'facial mimicry'. This process is assumed to be rapid, unconscious, and unintentional, and is considered a precursor for more advanced empathic abilities such as perspective-taking and mindreading, as well as for moral reasoning (Decety and Svetlova, 2012; Preston and De Waal, 2002; Seibt et al., 2015). Such facial mimicry is thought to be the result of 'mirroring': a tight association between the perception of an emotional facial expression and the actual display of an emotional facial expression (Chartrand and Bargh, 1999). This process is thought to be facilitated by the activation of neurons involved in both observation and execution of actions, referred to as mirror neurons (di Pellegrino et al., 1992; Gallese et al., 1996). These mirror neurons predominantly reside in the inferior parietal lobule, the inferior frontal gyrus, the primary motor cortex, and in pre- and supplementary motor areas, together known as the classical Mirror Neuron System (MNS) (Cattaneo and Rizzolatti, 2009; Molenberghs et al., 2012; Pineda, 2008; Rizzolatti and Craighero, 2004; Tramacere and Ferrari, 2016). However, more recent investigations on facial mimicry demonstrate that, although facial mimicry is considered to be an automatic process, it appears to be context specific and can be modulated by several factors, including group membership (Bourgeois and Hess, 2008; Brown et al., 2006; van der Schalk et al., 2011; van Schaik and Hunnius, 2016; Yabar et al., 2006), group dynamics such as cooperation and competition (Lanzetta and Englis, 1989; Likowski et al., 2011; Seibt et al., 2013; Weyers et al., 2009), fairness (Hofman et al., 2012), and empathic concern (Bos et al., 2016b). There even is evidence that facial mimicry can occur in the absence of emotion-specific visual cues, showing that emotion-specific facial expressions can even be elicited when combining neutral facial displays with verbal information about the emotional state of another or when presenting one with emotion-specific auditory stimuli (Fischer et al., 2012; Hietanen et al., 1998). These results suggest that the process of facial mimicry is not solely based on mimicking the expressive facial muscle movements of the observed, but also includes the interpretation of emotional intentions and the influence of contextual modulators (Chartrand et al., 2012; Hess and Fischer, 2013)

Several studies have focused on the specific modulatory factors that influence the process of mimicry (for a recent review see Seibt et al., 2015). However, whereas these studies have focused on the behavioural modulation of mimicry, it is currently not known what neural mechanisms bring forth such behavioural modulation. Here, we propose a neuroendocrine model of the modulatory character of facial mimicry. We suggest that the process of context-dependent social evaluation of facial emotional expressions has driven the formation of higher-order cognitive control – a neural pathway that, while still under the influence of endocrine modulation, has gained importance throughout evolution by the increasing pressure on the communicative function of facial responses in social interactions.

2. The perception-action link underlying the automatic tendency to mimic

Human facial responses to emotional expressions of others can be divided into intentional and spontaneous facial expressions (Buck, 1994), often occurring in an interactive and simultaneous manner. Whereas the former refers to the highly-controlled and often learned instrumental facial expressions that can be manipulated for one's own goals (Hess and Fischer, 2013), spontaneous expressions refer to the nonintentional and almost reflex-like emotional displays (Buck, 1994). The automatic nature of spontaneous facial mimicry is demonstrated by observations that the facial muscular changes in response to emotional expressions largely occur outside of conscious awareness (Dimberg and Thunberg, 1998), for example in response to subliminal stimuli (Dimberg et al., 2000) or when participants are instructed to inhibit them (Dimberg et al., 2002; Korb et al., 2010). Moreover, these rapid muscular changes are also observed in non-human mammals (Davila Ross et al., 2011, 2008; Mancini et al., 2013; Palagi et al., 2015; Scopa and Palagi, 2016), as well as during early childhood in humans (Geangu et al., 2016; van Schaik and Hunnius, 2016) and neonatal non-human mammals (Myowa-Yamakoshi et al., 2004). These results strengthen the assumption that the rapid, nonconscious changes in facial muscular activity in response to emotional displays are an automatic and almost reflex-like reaction to environmental cues.

As such, facial mimicry has often been explained in the context of the perception-action model (PAM). This model proposes that the perception of the affective state of another individual automatically activates a corresponding state in the observer, which further activates associated somatic and autonomic responses (Preston and De Waal, 2002), a mechanism also referred to as the Chameleon effect (Chartrand and Bargh, 1999). It has been suggested that the predominant function of this automatic tendency to mimic is to unintentionally increase the feeling of similarity and understanding between interaction partners, thereby facilitating prosocial behaviour; ultimately increasing social cohesion and coordination (Chartrand and Bargh, 1999; Decety and Svetlova, 2012; Hess and Fischer, 2013; Preston and De Waal, 2002). The PAM model places empathic understanding in an evolutionary perspective, serving to facilitate social behaviour in group-living animals including humans. With regard to the underlying neural mechanisms behind state matching, the model proposes that the same neural structures are activated during observation and execution of motor actions (Preston and De Waal, 2002). This concept is now widely accepted and has also been referred to as the Matched Motor Hypothesis (Hess and Fischer, 2013).

3. Dynamic modulation of facial mimicry

The above conceptualizations of the function of facial mimicry partly rely on studies investigating behavioural imitation of posture, which are, in contrast to facial expressions, often without reflecting inherent emotional meaning (Hess and Fischer, 2013). In other words, the sole imitation of one's facial expression may reflect a matched motor response, similar to behavioural imitation such as foot tapping and adopting congruent postures. This, however, does not directly indicate the imitation of the associated emotion, which includes additional emotional and contextual components. For example, a frown has been empirically attributed to anger, but can also indicate an overall negative mood of the observer, a negative attitude towards the presented stimulus, empathic concern (Eisenberg and Fabes, 1990), or can even be subject to fluctuations in concentration (Hess and Fischer, 2013; Larsen et al., 2003). This is also true for a smile, which often signals happiness, but can also signal pity, embarrassment, or pride, dependent on the context (Niedenthal et al., 2010). These observations indicate that mimicry of facial expressions is not only dependent on the emotional facial display, but is also reliant on environmental or social contextual cues. This notion is funded by recent series of studies investigating the effect of context on the occurrence of facial mimicry (e.g. Bos