



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.

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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

et al., 2016b; for a recent review see Seibt et al., 2015), and is in line with studies demonstrating that the environment is routinely encoded during face perception (Barrett et al., 2015). Furthermore, a different line of studies investigating the endocrine underpinnings of human social interaction has revealed that facial mimicry is also affected by hormonal factors such as steroid hormones (Hermans et al., 2010), neuropeptides (Korb et al., 2016; Thompson et al., 2006, 2004), and opioids (Meier et al., 2016). Such data, combined with the current knowledge on the effect of such hormones on the brain, can provide more insight into the neural mechanisms that bring forth dynamic modulation of facial mimicry.

3.1. Modulation by social context

Context, with respect to facial mimicry, most often refers to one's social environment. Throughout evolution, belonging to a social group and acceptance by group members have proven to be fundamental needs in human life. The importance of social networks facilitated the evolution of the communicative role of facial mimicry into a highly dynamic process (Chartrand et al., 2005). This is illustrated by the tendency to show more (facial) mimicry towards an ingroup member than towards an outgroup member, called ingroup preference (Bourgeois and Hess, 2008; Brown et al., 2006; van der Schalk et al., 2011; Yabar et al., 2006). Ingroup membership refers to a shared social identity based upon ethnicity, gender, or fundamental values such as political affiliation or religion (Bourgeois and Hess, 2008). This phenomenon is already apparent during early childhood; 4–6-year-olds already exhibit more mimicry towards ingroup members than to outgroup members (van Schaik and Hunnius, 2016).

In addition, one often has to collaborate with and thus is dependent on another individual in order to reach individual goals (Seibt et al., 2015). Therefore, cooperation and competition are two basic concepts of social relationships that are well known to influence social-emotional behaviour within social interactions. Subliminal priming with cooperation has been shown to enhance facial mimicry, whereas subliminal priming with competition mostly leads to a decrease or absence of facial mimicry, and even incongruent facial expressions (Lanzetta and Englis, 1989; Likowski et al., 2011; Scopa and Palagi, 2016; Seibt et al., 2013; Weyers et al., 2009). It seems as in competitive relations the facial reactions are often antagonistic instead of agonistic to emotional expression observed in the other, as is the case with envy and schadenfreude (Hess and Fischer, 2013). Moreover, the decision to cooperate and also the decision with whom to cooperate is dependent on multiple factors, including the perceived trustworthiness of the interaction partner and the perceived fairness of the partner's behaviour. In particular the latter has shown to modulate facial mimicry (Hofman et al., 2012), reflecting the importance of perceived fairness of others in driving cooperative behaviour between individuals (Fehr and Fischbacher, 2004). This sensitivity and preference to comply with fairness norms can be explained by the fundamental need to belong and can be well fitted in the model proposed by the Preston and De Waal (2002), which stressed the influence of the increasing importance of social functioning within a group context for the evolution of facial mimicry. As such, fairness, and also cooperation, might serve as an important signal of acceptance, which is experienced as intrinsically rewarding (Rilling et al., 2002).

The above described studies clearly demonstrate that facial mimicry, although initially described as an automatic and unconscious process, can be modulated by social-environmental cues. This has led to recent adaptations of the classical Matched Motor Hypothesis, such as the Emotion in Context model (Hess and Fischer, 2013). This adapted model states that the process of facial mimicry can be considered the result of the affiliative intentions of the observer rather than the mere replication of the presented

emotional stimuli. This view is in line with the findings of increased mimicry of happy faces towards ingroup members and with attenuation of angry facial mimicry in competitive interactions (for a recent review see Seibt et al., 2015). However, since an angry facial expression can signal diverse underlying motives, affiliative intent is insufficient in explaining the context-modulations observed in angry facial responses. For example, a study by Hofman et al. (2012) showed increased expressions of anger towards opponents after unfair treatment. Such a response does not reflect a reduced affiliative intent but rather seems to be the result of normative motives serving as a corrective signal. Similarly, another recent study observed modulation of facial mimicry in adults toward children depending on contextual information about the children's behaviour and domestic situation (Bos et al., 2016b). Mimicry of angry facial expressions was enhanced towards children displaying negative behaviour, possibly indicating a corrective signal comparable to the study of Hofman et al. (2012). The study furthermore showed that mimicry was enhanced towards sad facial expressions of children that both displayed good behaviour and that had a difficult domestic situation, a response that might reflect increased empathic concern for such children (Eisenberg and Fabes, 1990). This demonstrates that contextual alterations are dependent on the facial expression of the sender. In the model presented here, we therefore stress the signalling function of emotional expressions in guiding cooperative behaviour, and incorporate it in a neuroendocrine network that can account for the modulation of facial mimicry.

3.2. Modulation by endocrine factors

Besides social context as an important factor in the modulation of facial mimicry, also endocrine factors have proven to be relevant. Increases and decreases in facial mimicry by administration of hormones have been repeatedly demonstrated. A testosterone administration study showed decreased facial mimicry towards both angry and happy facial expressions in women, compared to placebo (Hermans et al., 2010), which was interpreted as reduced empathic responsiveness. An administration study in which the neuropeptide oxytocin, known to promote social behaviour, was administered showed a positive influence of oxytocin on facial mimicry in males towards angry facial expressions in both children and adult faces (Korb et al., 2016). These findings are in line with the often opposite effects of testosterone and oxytocin seen in literature (Bos et al., 2012a). Also vasopressin, a neuropeptide related to oxytocin, has been shown to modulate facial mimicry. In a male sample, corrugator responses were strengthened towards neutral faces, whereas responses towards emotional facial expressions were unaffected (Thompson et al., 2004). In a follow-up study that included both males and females, a sex-specific effect of intranasal vasopressin administration was demonstrated (Thompson et al., 2006). Whereas the effects on the corrugator in males were replicated, an increased zygomaticus activation was observed in females towards neutral facial expressions of sex-matched stimuli, as well as reduced corrugator responses towards smiling angry females. According to the authors, such sex-specific effects can be brought forth by differential responses in males and females in stressful situations, during which vasopressin could lead to enhanced aggressive responding in males and to enhanced social bonding in females (Taylor et al., 2000). However, such effects could also be the result of sex-specific interactions of vasopressin with oxytocin activation (Carter, 2014). A recent paper by Meier et al. (2016) furthermore shows increased corrugator and depressor (indicative of sad facial expressions) responses towards smiling faces following administration of an opioid antagonist, which might reflect lowered interest in social interaction or affiliation brought forth by down-regulation of the neural reward circuitry. This is in line with studies

that demonstrate the importance of the opioid system in motivational and hedonic aspects of social reward behaviour (Chelnokova et al., 2014; Syal et al., 2015).

Thus, whereas research on the endocrine regulation of facial communication has only started to emerge in the last decade, and consist of only a limited number of studies, they clearly show that hormonal factors can alter facial mimicry.

4. Neural circuitry underlying facial mimicry and its dynamic modulation

4.1. The human Mirror Neuron System

As noted above, shared action-perception networks have been proposed to underlie the process of facial mimicry. The finding of neuronal populations responding to both observation and execution of the same behavioural response, currently well-known under the name of ‘mirror neurons’, has strengthened this assumption (Gallese et al., 1996; Harmon-Jones and Winkielman, 2007; Rizzolatti and Craighero, 2004). The human mirror neuron system and its function in automatic responses are thought to be a core mechanism underlying the broad range of human empathic behaviour (Decety and Svetlova, 2012; Keysers and Perrett, 2004; Lamm and Majdandžić, 2015; Preston and De Waal, 2002). Core empathic processes such as motor imitation, emotional contagion, and affect sharing can serve as a stepping stone in development of complex forms of empathy like perspective-taking and mindreading, as well as lead to increased feeling of similarity between interaction partners, which can result in prosocial behaviour (Betti and Aglioti, 2016; Decety and Svetlova, 2012; Hess and Fischer, 2013).

Abundant neuroimaging studies and non-invasive neurophysiological investigations have described the classical mirror neuron system in humans, which comprises the posterior parietal area in the rostral cortical convexity of the inferior parietal lobule (IPL) and the ventral premotor area of the inferior frontal gyrus (IFG) (Cattaneo and Rizzolatti, 2009; Molenberghs et al., 2012; Pineda, 2008; Rizzolatti and Craighero, 2004). Activity of mirror neurons have also been observed in the primary motor cortex (M1) and in pre- and supplementary motor areas (pre-SMA and SMA) (Rizzolatti and Craighero, 2004; Tramacere and Ferrari, 2016). Also, although the posterior superior temporal sulcus (pSTS) does not contain mirror neurons itself (Pineda, 2008), this area is strongly connected to, and shows similar neural activation in response to observed movement, as the regions described above (Gaag et al., 2007). It has been suggested that the pSTS functions as the main visual input not of the classical MNS (Hogeveen et al., 2015). Additionally, abundant neuroimaging studies show additional activation upon empathy-eliciting stimuli of limbic regions involved in emotional processing, including the amygdala, anterior cingulate cortex (ACC), and insula (Carr et al., 2003; Singer et al., 2004; Wicker et al., 2003). This indicates that the current MNS comprises not only the classically described brain structures, but can be extended with additional motor and limbic regions, which are connected via the pSTS.

Although the direct involvement of the MNS in facial mimicry has been suggested previously, only a few neuroimaging studies have tried to empirically test the neuronal structures involved in facial mimicry. Combining both facial electromyography (EMG) and blood oxygen level dependent (BOLD) responses upon passive viewing of facial motions of anthropomorphic virtual characters in two separate experiments, it was shown that the occurrence of facial mimicry correlated with neural activations in brain areas belonging to both the classic and extended MNS (Schilbach et al., 2008). Facial EMG and BOLD responses were, however, not mea-

sured simultaneously, and might thus reflect merely statistical dependencies. Therefore, Likowski et al. (2012) performed a simultaneous measurement of facial muscular activity using EEG and the BOLD response using fMRI, demonstrating significant correlations between facial mimicry and brain areas comprising and extending the classic MNS. This finding was supported by an electrophysiological study showing specific modulation of MNS activity as a function of facial mimicry by measuring mu-suppression – a validated EEG-index of mirror neuron activity (Arnstein et al., 2011; Hogeveen et al., 2015). This thus indicates that activation of the MNS is indeed directly involved in the process of facial mimicry within social encounters.

4.2. Beyond the human Mirror Neuron System

Along with the notion that facial mimicry cannot fully be explained by the imitation of facial expressions, the activation of the MNS alone is not sufficient to explain the highly dynamic and modulatory characteristics of facial mimicry. More important, the MNS alone does not code the goal-directed and strategic nature of observed actions. Therefore, other brain regions must be involved to establish those additional characteristics of facial mimicry, such as regions involved in more cognitive processes, including perspective-taking, mentalizing (Murata et al., 2016; Wang and Hamilton, 2012), and learning processes (Kavanagh and Winkielman, 2016). Interestingly, in a recent study it is suggested that the dynamic and flexible character of social mimicry can largely be retained without the involvement of higher-order mental representations (Carr and Winkielman, 2014). Instead, the authors suggest that the flexibility of facial mimicry can be established following the domain general learning principle, stating that the cortical connections involved in the mediation of motor activations upon action observation are formed by experience rather than being innate (Carr and Winkielman, 2014; Heyes, 2011). In other words, the flexible and highly dynamic communicative function of facial mimicry in social interactions is established and maintained by the selective strengthening of neural connections between perception- and action-related brain areas within a specific context. Although the latter, so-called non-representational framework, follows a completely different approach to explain the flexibility of facial mimicry, note that both concepts agree on the idea that social environmental cues are able to modify the occurrence of facial mimicry. However, whereas learning mechanisms undoubtedly play a critical role in development of imitative processes, gene-environment interactions shape the underlying neural circuitry in which such learning takes place. A recent model brought forth by Ferrari et al. (2013) shows how epigenetic alteration of gene expression could alter the ontogenetic developmental trajectory of perception-action networks, which over generations can tune parent-infant communication (Ferrari et al., 2013; Simpson et al., 2014). Such a view allows for both evolutionarily accounts of facial imitation, as well as the context-dependency that characterises the process of facial mimicry.

4.3. Modulation of neural activity by social context

Besides the role of mirror neurons and regions involved in emotion processing, other regions that could bring forth modulatory control over facial responses have been described. Neuroimaging studies focused on the effect of ingroup-preference in intergroup interactions showed that subjects exhibited more neural activation in the fusiform gyrus towards facial pictures of racial ingroup members compared to racial outgroup members (Golby et al., 2001; Kubota et al., 2012). This was consistent with another fMRI study, showing greater activation towards coalition members, regardless of ethnicity (Van Bavel et al., 2011). These results suggests that

group membership promotes enhanced visual encoding (Amodio, 2014), which was confirmed by another study using event-related potentials (ERPs) by showing increased processing of ingroup versus outgroup faces (Ratner and Amodio, 2013). Moreover, neural activation in the dorsolateral and ventro-medial prefrontal cortices, IPL, bilateral anterior insula, and mid-cingulate cortex has been observed upon presentation with outgroup pictures (Kubota et al., 2012; Rauchbauer et al., 2015). Regarding a more general concept, ethnic prejudice, a core neural network has been established for both the experience and expression of prejudice, comprising the amygdala, insula, ACC, striatum, and regions of the ventromedial and orbital frontal cortices – neural structures generally involved in emotion and motivation (Amodio, 2014; Kubota et al., 2012).

With respect to group dynamics, cooperation and competition stimuli both evoke neural activation in the frontoparietal network involved in executive functioning (Decety et al., 2004; McCabe et al., 2001), together with activation in the anterior insula and ACC (Decety et al., 2004; Gallagher et al., 2002; Rilling et al., 2002). Moreover, selective neural activation has been found specifically associated with either competition or cooperation. During competitive interaction, neural activation can be observed in the inferior parietal and medial prefrontal cortices, involved in self-other distinction and mentalizing processes (Decety et al., 2004; Rilling et al., 2002). Cooperation on the other hand elicits neural activation in the orbitofrontal cortex (OFC), which is thought to have a fundamental role in behavioural decision-making. Moreover, the OFC is known to be involved in the motivational control of goal-directed behaviour and in the signalling of relative values of reward (Decety et al., 2004; Elliott et al., 2003; Tabibnia and Lieberman, 2007). Furthermore, neuroimaging studies on cooperation and fairness – both significant aspects in the decision whether to cooperate with another – showed overlap in neural activation between the pleasure of being treated with fairness, and thus reward-value, and the intention to cooperate in the ACC and ventral striatum (Rilling et al., 2002; Tabibnia and Lieberman, 2007). These results thus suggest that fairness, mediated by neural activity in the anterior insula and medial prefrontal cortex (Corradi-Dell'Acqua et al., 2013; Singer et al., 2006), can function as motivational factor driving the decision to cooperate or not. Finally, empathic concern relies strongly on aforementioned neural regions including the anterior insula and ACC, involved in affective sharing and vicarious responses to pain in others (Betti and Aglioti, 2016; Lamm et al., 2011). In addition, empathic responses that result in prosocial behaviour have also been related to regions involved in emotion regulation, such as the medial prefrontal cortex (Masten et al., 2011).

4.4. Modulation of neural activity by endocrine factors

The neural regions involved in processing of social context largely overlap with the neural regions on which the abovementioned hormones and neurotransmitters act, thereby facilitating the endocrine modulation of facial mimicry. The attenuating effects of testosterone, for example, are most likely mediated by the actions of testosterone on subcortical structures or by altering connectivity of subcortical structures with the OFC (Bos et al., 2012a, 2012b). Testosterone robustly increases amygdala activation towards angry, fearful, and happy emotional expressions (Bos et al., 2013; Hermans et al., 2008) and decreases connectivity of the amygdala with the OFC in response to faces of others (Bos et al., 2012b; Wingen et al., 2010). Testosterone furthermore reduces the connectivity of the PFC with the ACC and premotor regions (Bos et al., 2016a). Especially this reduced connectivity of the IFG to the premotor cortex could explain the negative effect of testosterone on facial mimicry. The effects of oxytocin on the other hand are proposedly due to increased visual processing of the eye-region of the human face, since the eye-region is considered a critical

source of emotional information and it has been suggested that eye-contact functions as a trigger of facial mimicry (Korb et al., 2016; Niedenthal et al., 2010). Additionally, oxytocin has been shown to reduce amygdala activation towards emotional facial expressions and to increase amygdala connectivity to a broad emotion regulatory network, including the OFC, ACC, and temporal sulcus (Bethlehem et al., 2013). Data on the neural regions in humans on which vasopressin exerts its effects is scarce, but a few recent studies have shown vasopressin to elicit sex-specific effects on neural activation. The first studies executed only in males showed vasopressin to increase activation of the insula and ACC, as well as connectivity of the amygdala with these regions (Rilling et al., 2012; Zink et al., 2010). However, later studies including with much larger sample sizes including both sexes demonstrated differential activation patterns in both sexes. For example, while in males AVP enhanced activation in the bilateral insula, amygdala, and the striatum, in females this enhanced activation was absent, and in case of the amygdala and insula activity was even decreased (Feng et al., 2015; Rilling et al., 2014). Such sex-specificity of vasopressin action on the insula and amygdala might account for the selective effects of vasopressin administration on facial mimicry observed in males and females (Thompson et al., 2006, 2004). Finally, the increases in negatively valenced facial responses due to opioid blockade are expected to derive from the effect of administration on the ventral striatum, an area critically involved in reward processing (Meier et al., 2016).

5. The social evaluation model of facial mimicry

In addition to neural activation in brain regions attributed to the MNS, the multiple neuroimaging studies described above consistently show activation in brain regions involved in social evaluative and cognitive control processes. In addition, endocrine administration studies have demonstrated the dependency of mimicry on neural mechanisms other than the core MNS. Therefore, it might be so that facial mimicry is not merely established by the automatic co-activation of the MNS, the mentalizing system, and visual systems, but that it is rather the result of activation of a much broader network of brain areas involved in the evaluation of the social environment, thereby utilizing the unique characteristics of the individual neural systems. In line with broader involvement of cortical regions in facial mimicry, are previous demonstrations of the co-evolution of facial motor control and social group size, which suggests a link between facial emotional expressions and social bonding (Dobson, 2012; Sherwood et al., 2005). Relative neocortex size is correlated with relative facial nucleus size, indicating increased facial muscle control and thus enhanced emotional expressivity. In other words, the motor control of facial musculature has increased during evolution as an indirect consequence of the enlargement of the neocortex, due to increased cortical innervation of the facial motor nucleus (Dobson, 2012). This enlargement of the neocortex is supposedly due to the development of more complex cognitive functions, driven by an increasing communicative role of facial expressions during social interactions, to control the production, recognition, and regulation of facial mimicry (Tramacere and Ferrari, 2016).

Such an account of facial mimicry, and, more broadly, of dynamic facial communication, is depicted in Fig. 1. Visual and social information about a perceived facial emotional expression, which here serves as social signal within the social environment, enters the social evaluation network via the STS, the visual input node of the human MNS, and the IPL, involved in the perception of emotions in facial stimuli and the interpretation of sensory information. Subsequently, this neural input concerning social stimuli is projected towards areas belonging to the limbic system, the insula, striatum,

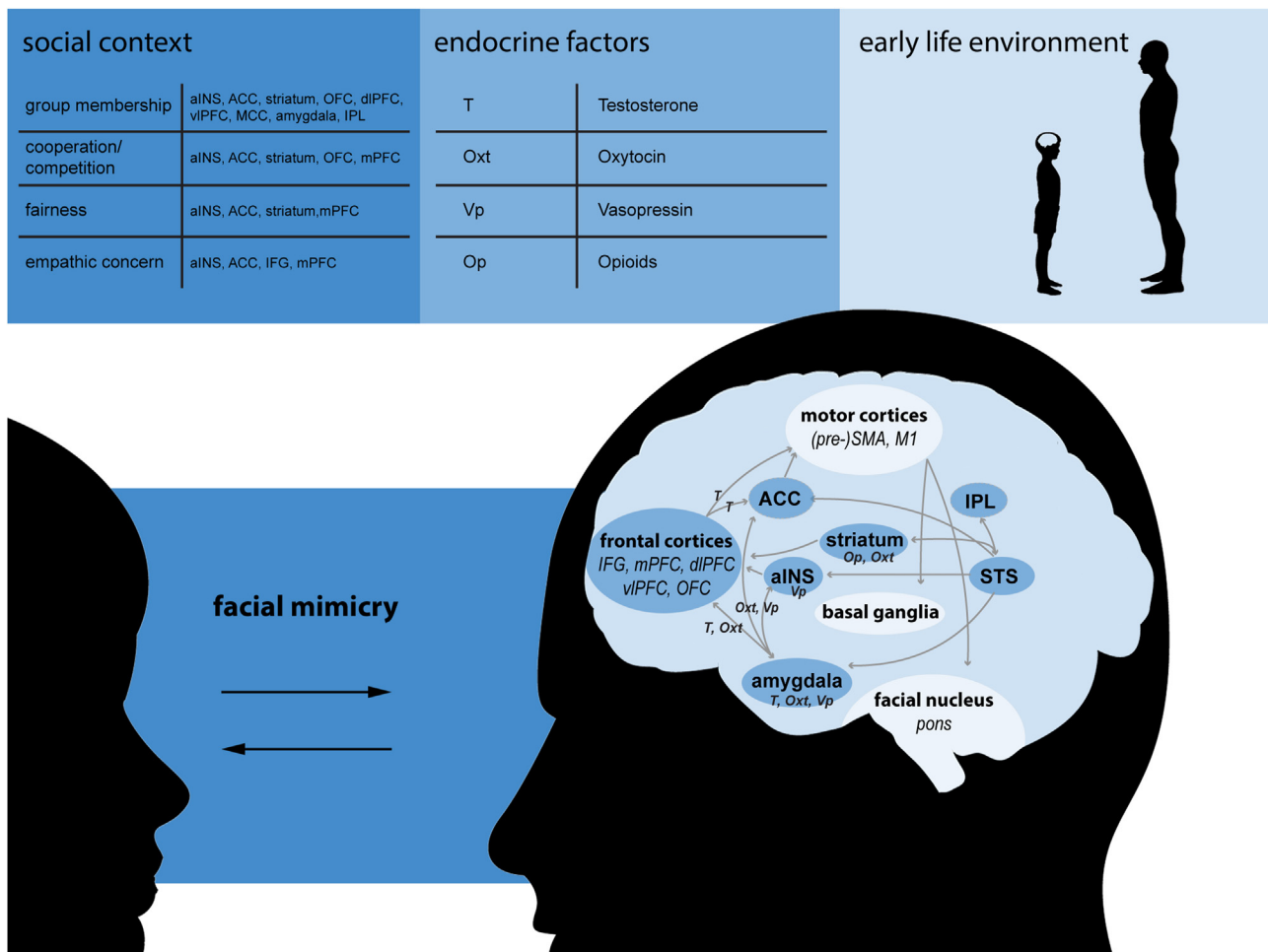


Fig. 1. Social Evaluation Model of facial mimicry.

This neuroendocrine model illustrates how a social stimulus consisting of a face with its environmental context (left upper panel) enters the brain via the STS and IPL, is projected to a network the regions involved in social evaluation, and is consecutively relayed to (pre)frontal, motor, and limbic brain areas, where endocrine factors such as levels of steroid hormones can influence neural processing (middle upper panel). The neural input eventuates in the facial nucleus of the pons, which is controlling the facial musculature to produce a responsive facial expression. Epigenetic shaping of perception-action networks throughout development is depicted in the right upper panel. (ACC, anterior cingulate cortex; aINS, anterior insula; dIPFC, dorsolateral prefrontal cortex; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; M1, primary motor cortex; mPFC, medial prefrontal cortex; OFC, orbitofrontal cortex; pre-SMA, pre-supplementary motor area; STS, superior temporal sulcus; vIPFC, ventrolateral prefrontal cortex).

ACC, and amygdala – brain regions which are involved in the processing of socially and emotionally relevant information about the stimulus, and are sensitive to endocrine factors. This neural information is then relayed towards the frontal cortices, including the mPFC, OFC, and IFG, and further towards the face area of the pre-SMA and M1, involved in the preparation of the appropriate motor program. From there on, the neural information about the prepared motor responses can either be directly relayed towards the facial nucleus localised in the pons (pyramidal system; responsible for voluntary facial expressions) or relayed towards the striatum, the input region of the basal ganglia (extrapyramidal system; responsible for spontaneous facial expressions). The basal ganglia can be considered as critical area in the modulation of the neural programs that originated in the cortex to produce the final motor response. Lastly, this motor response is relayed towards the facial nucleus in the pons, which controls the eventual facial musculature thereby producing a responsive facial emotional expression.

In our neural account of facial interaction, we emphasize that the dynamic character of facial mimicry is dependent on both the involvement of higher-order control processes, relying on the (sub)cortical structures described in Fig. 1, and the domain general learning principle, working together in a highly dependent and interactive manner. Hormones and neuropeptides can induce

state-dependent changes in neural activity and communication to alter the outcome of the processed social stimuli, most strongly acting on the amygdala insula, and striatum, as well as connections between these and other regions (see Fig. 1; Bos et al., 2012a, 2012b). Endocrine modulation of social-evaluative cortical structures can generate the characteristic flexibility of facial mimicry, and together with the principle of epigenetic shaping of perception-action networks throughout development (Ferrari et al., 2013), allow for unlimited temporal flexibility.

However, it is currently unknown which epigenetic alterations within the MNS or its connected networks involved in social evaluation could bring forth the developmental tuning to environmental variation. Although the exact mechanisms are unclear, alterations in the endocrine epigenome could hypothetically play a critical role. Recent studies have demonstrated that variation in the methylation of the genes coding for synthesis of oxytocin and expression of the oxytocin receptor predict neural responses in during tasks relevant to social and emotional behaviour (Haas et al., 2016; Puglia et al., 2015). Furthermore, increased methylation of the oxytocin receptor gene, which generally reflects reduced expression, has been observed in autism spectrum disorder (ASD) (Gregory et al., 2009), a condition characterised by impairment in social interaction, and in which abnormalities in mirror neuron activation and

connectivity have been repeatedly observed (Fishman et al., 2016; Hamilton, 2013). Critically, impairment of facial mimicry has also been observed in ASD (Forbes et al., 2016; McIntosh et al., 2006), as well as in a typical population scoring higher on traits of ASD (Hermans et al., 2009). Since oxytocin has an important function in the early development of cross-model integration of the visual system (Zheng et al., 2014), early life epigenetic modification of genes coding for synthesis and expression of oxytocin could result in later life changes in social behaviour that rely on perception-action networks, such as in the case of ASD. The above described finding of enhanced facial mimicry after oxytocin nasal spray (Korb et al., 2016) provides circumstantial evidence for the presence of such a mechanism. Besides a role in ASD, the same mechanisms might also apply to the positive relation between self-reported indexes of empathy and facial mimicry (Sonnby-Borgström, 2002), since oxytocin function has also been shown to relate to both cognitive and more affective aspects of empathy (Bos et al., 2012a). As such, the facilitating role of epigenetic variation leading to altered oxytocin sensitivity and subsequent facial mimicry might hold relevance to the pathways by which hormones regulate early parent-child interaction (Bos, 2016). Oxytocin has been ascribed a critical role in the onset of endocrine and behavioural synchronicity between parent and infant, which facilitates synchronising of social interactions, a mechanism whereby mutually dependent attachment relations are formed (Feldman, 2015). In line with the epigenetic perspective on the MNS brought forth by Ferrari et al. (2013), epigenetic alteration in the endocrine system in infancy could tune the brain for social interaction, and shape the dynamics of facial communication between caregiver and child over generations (Bos, 2016). Oxytocin has been ascribed a critical role in the onset of endocrine and behavioural synchronicity between parent and infant, which facilitates synchronising of social interactions, a mechanism whereby mutually dependent attachment relations are formed (Feldman, 2015). In line with the epigenetic perspective on the MNS brought forth by Ferrari et al. (2013), epigenetic alteration in the endocrine system in infancy could tune the brain for social interaction, and shape the dynamics of facial communication between caregiver and child over generations (Bos, 2016). Although derived from mother-infant bonding, such a mechanism in humans could have evolved to support romantic partner-bonding (Hurlemann and Scheele, 2016), as well as cross-species attachment. A study in dogs and their owners demonstrated a positive oxytocin-attachment loop which can be initiated by gazing behaviour of the dog (Nagasawa et al., 2015), relating to the facilitating effect of oxytocin on human eye-contact (Auyeung et al., 2015).

Taken together, the studies described above, together with neuro-evolutionary theoretical accounts of facial imitation and communication, give ground for the proposed neuroendocrine circuitries presented in Fig. 1 in bringing forth facial mimicry and its dynamic modulation.

6. Conclusion

In the more than 30 years since the seminal work by Dimberg on facial responses to emotional facial expressions (Dimberg, 1982; Dimberg et al., 2002, 2000; Dimberg and Thunberg, 1998), which laid the foundation for the research on facial mimicry, our knowledge of human facial communication has greatly increased. Whereas facial EMG studies have revealed the dynamic character of facial mimicry, the rise of neuroimaging research has given invaluable insight into the neuroendocrine mechanisms of human face processing and social-emotional behaviour. In this review, we base ourselves on those two sources of information to provide an informed current account on the neural underpinnings of facial mimicry. This account emphasizes the importance of social evaluation

during the process of facial mimicry, and thus also the neural circuitry involved in social evaluation, as well as the endocrine system, which can alter perception-action coupling as effectuated by the MNS. Although the model we present is coarse, and the proposed epigenetic-endocrine mechanisms for altered facial mimicry will prove simplistic in the face of future empirical findings, we think it can extend currently existing theoretical conceptualizations of facial mimicry (Bourgeois and Hess, 2008; Decety and Svetlova, 2012; Seibt et al., 2015). More broadly, our model can prove relevant to the discussion on the ontogenetic development of the MNS (Heyes, 2011; Simpson et al., 2014). Finally, it can also further inform research on the communicative function of facial expressions and provide insight into the position of facial mimicry in theoretical models of empathy and human social interaction. Affective and motor resonance does play an important role in several neuro-evolutionary models of the behavioural repertoire of empathy (Decety and Svetlova, 2012; Gonzalez-Liencrea et al., 2013; Panksepp and Panksepp, 2013; Preston and De Waal, 2002). Our current perspective can aid the discussion on how facial mimicry, and the role of motor resonance more generally, is related to the spectrum of cognitive and affective empathic abilities. Overall, we hope that our model can stimulate new research in which different research techniques can be combined to investigate exactly how the modulating factors described in this review alter facial mimicry. For example, combining endocrine administration with neuroimaging methods such as EEG or fMRI, together with indexes of facial mimicry would provide more insight compared to using these approaches separately. Another interesting avenue for further studies is to investigate how early life experiences, especially the quality of parental care, alters facial mimicry, and whether such a relation depends on epigenetic alterations of the oxytocin system. Attempts such as these will help to shed new light on the dynamics of facial communication and its neuroendocrine underpinnings.

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References

- Amodio, D.M., 2014. The neuroscience of prejudice and stereotyping. *Nat. Rev. Neurosci.* 15, 670–682. <http://dx.doi.org/10.1038/nrn3800>.
- Arnstein, D., Cui, F., Keyers, C., Maurits, N.M., Gazzola, V., 2011. Mu-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *J. Neurosci.* 31, 14243–14249. <http://dx.doi.org/10.1523/JNEUROSCI.0963-11.2011>.
- Auyeung, B., Lombardo, M., Heinrichs, M., Chakrabarti, B., Sule, A., Deakin, J., Bethlehem, R., Dickens, L., Mooney, N., Sipple, J., Thiemann, P., Baron-Cohen, S., 2015. Oxytocin increases eye contact during a real-time, naturalistic social interaction in males with and without autism. *Transl. Psychiatry* 5, e507. <http://dx.doi.org/10.1038/tp.2014.146>.
- Barrett, C.E., Arambula, S.E., Young, L.J., 2015. The oxytocin system promotes resilience to the effects of neonatal isolation on adult social attachment in female prairie voles. *Transl. Psychiatry* 5, e606. <http://dx.doi.org/10.1038/tp.2015.73>.
- Bethlehem, R., Honk, J., van Auyeung, B., Baron-Cohen, S., 2013. Oxytocin, brain physiology, and functional connectivity: a review of intranasal oxytocin fMRI studies. *Psychoneuroendocrinology* 38, 962–974.
- Betti, V., Aglioti, S., 2016. Dynamic construction of the neural networks underpinning empathy for pain. *Neurosci. Biobehav. Rev.* 63, 191–206.
- Bos, P.A., Panksepp, J., Bluthé, R.-M., van Honk, J., 2012a. Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: a review of single administration studies. *Front. Neuroendocrinol.* 33, 17–35. <http://dx.doi.org/10.1016/j.yfrne.2011.01.002>.
- Bos, P.A., Hermans, E., Ramsey, N., Van Honk, J., 2012b. The neural mechanisms by which testosterone acts on interpersonal trust. *Neuroimage* 61, 730–737.
- Bos, P.A., Honk, J., van Ramsey, N., Stein, D., Hermans, E., 2013. Testosterone administration in women increases amygdala responses to fearful and happy faces. *Psychoneuroendocrinology* 38, 808–817.

- Bos, P.A., Hofman, D., Hermans, E., Montoya, E., Baron-Cohen, S., van Honk, J., 2016a. Testosterone reduces functional connectivity during the reading the mind in the eyes test. *Psychoneuroendocrinology* 68, 194–201, <http://dx.doi.org/10.1016/j.psyneuen.2016.03.006>.
- Bos, P.A., Jap-Tjong, N., Spencer, H., Hofman, D., 2016b. Social context modulates facial imitation of children's emotional expressions. *PLoS One* 11, e0167991.
- Bos, P.A., 2016. The endocrinology of human caregiving and its intergenerational transmission. *Dev. Psychopathol.* 1–29, <http://dx.doi.org/10.1017/S0954579416000973>.
- Bourgeois, P., Hess, U., 2008. The impact of social context on mimicry. *Biol. Psychol.* 77, 343–352, <http://dx.doi.org/10.1016/j.biopsycho.2007.11.008>.
- Brown, L.M., Bradley, M.M., Lang, P.J., 2006. Affective reactions to pictures of ingroup and outgroup members. *Biol. Psychol.* 71, 303–311, <http://dx.doi.org/10.1016/j.biopsycho.2005.06.003>.
- Buck, R., 1994. Social and emotional functions in facial expression and communication: the readout hypothesis. *Biol. Psychol.* 38, 95–115.
- Carr, E.W., Winkielman, P., 2014. When mirroring is both simple and smart: how mimicry can be embodied, adaptive, and non-representational. *Front. Hum. Neurosci.* 8, 505, <http://dx.doi.org/10.3389/fnhum.2014.00505>.
- Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J.C., Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci. U. S. A.* 100, 5497–5502, <http://dx.doi.org/10.1073/pnas.0935845100>.
- Carter, C., 2014. Oxytocin pathways and the evolution of human behavior. *Annu. Rev. Psychol.* 65, 17–39.
- Cattaneo, L., Rizzolatti, G., 2009. The mirror neuron system. *Arch. Neurol.* 66, 557–560.
- Chapman, H., Kim, D., Susskind, J., Anderson, A., 2009. In bad taste: evidence for the oral origins of moral disgust. *Science* (80–) 323, 1222–1226.
- Chartrand, T.L., Bargh, J., 1999. The chameleon effect. *J. Pers. Soc. Psychol.* 76 (6), 893–910, <http://dx.doi.org/10.1037/0022-3514.76.6.893>.
- Chartrand, T.L., Maddux, W.W., Lakin, J.L., 2005. Beyond the perception-behavior link: the ubiquitous utility and motivational moderators of nonconscious mimicry. *The New Unconscious*, 334–361, <http://dx.doi.org/10.1093/acprof:oso/9780195307696.003.0014>.
- Chelnokova, O., Laeng, B., Eikemo, M., Riegels, J., Løseth, G., Maurud, H., Willoch, F., Leknes, S., 2014. Rewards of beauty: the opioid system mediates social motivation in humans. *Mol. Psychiatry* 19, 746–747, <http://dx.doi.org/10.1038/mp.2014.1>.
- Corradi-Dell'Acqua, C., Civi, C., Rumiati, R., Fink, G., 2013. Disentangling self-and fairness-related neural mechanisms involved in the ultimatum game: an fMRI study. *Soc. Cogn. Affect. Neurosci.* 8, 424–431.
- Davila Ross, M., Menzler, S., Zimmermann, E., 2008. Rapid facial mimicry in orangutan play. *Biol. Lett.* 4, 27–30, <http://dx.doi.org/10.1098/rsbl.2007.0535>.
- Davila Ross, M., Allcock, B., Thomas, C., Bard, K.A., 2011. Aping expressions? Chimpanzees produce distinct laugh types when responding to laughter of others. *Emotion* 11, 1013–1020, <http://dx.doi.org/10.1037/a0022594>.
- Decety, J., Svetlova, M., 2012. Putting together phylogenetic and ontogenetic perspectives on empathy. *Dev. Cogn. Neurosci.* 2 (1), 1–24, <http://dx.doi.org/10.1016/j.dcn.2011.05.003>.
- Decety, J., Jackson, P., Sommerville, J., Chaminade, T., Meltzoff, A., 2004. The neural bases of cooperation and competition: an fMRI investigation. *Neuroimage* 23, 744–751.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91, 176–180.
- Dimberg, U., Thunberg, M., 1998. Rapid facial reactions to emotional facial expressions. *Scand. J. Psychol.* 39, 39–45.
- Dimberg, U., Thunberg, M., Elmehe, K., 2000. Unconscious facial reactions to emotional facial expressions. *Psychol. Sci.* 11, 86–89.
- Dimberg, U., Thunberg, M., Grunedal, S., 2002. Facial reactions to emotional stimuli: automatically controlled emotional responses. *Cogn. Emot.* 16, 449–471.
- Dimberg, U., 1982. Facial reactions to facial expressions. *Psychophysiology* 19, 643–647, <http://dx.doi.org/10.1111/j.1469-8986.1982.tb02516.x>.
- Dobson, S., 2012. Face to face with the social brain. *Trans. R. Soc. London B Biol. Sci.* 367, 1901–1908.
- Du, S., Tao, Y., Martinez, A.M., 2014. Compound facial expressions of emotion. *Proc. Natl. Acad. Sci.* 111, 1454–1462, <http://dx.doi.org/10.1073/pnas.1322355111>.
- Eisenberg, N., Fabes, R.A., 1990. Empathy: conceptualization, measurement, and relation to prosocial behavior. *Motiv. Emot.* 14, 131–149, <http://dx.doi.org/10.1007/BF00991640>.
- Elliott, R., Newman, J., Longe, O., Deakin, J., 2003. Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. *J. Neurosci.* 23, 303–307.
- Fehr, E., Fischbacher, U., 2004. Social norms and human cooperation. *Trends Cogn. Sci.* 8, 185–190, <http://dx.doi.org/10.1016/j.tics.2004.02.007>.
- Feldman, R., 2015. Sensitive periods in human social development New insights from research on oxytocin, synchrony, and high-risk parenting. *Dev. Psychopathol.* 27, 369–395.
- Feng, C., Hackett, P., DeMarco, A., Chen, X., Stair, S., Haroon, E., Ditzgen, B., Pagnoni, G., Rilling, J., 2015. Oxytocin and vasopressin effects on the neural response to social cooperation are modulated by sex in humans. *Brain Imaging Behav.* 9, 754–764, <http://dx.doi.org/10.1007/s11682-014-9333-9>.
- Ferrari, P., Tramaccere, A., Simpson, E., Irlki, A., 2013. Mirror neurons through the lens of epigenetics. *Trends Cogn. Sci.* 17, 450–457.
- Fischer, A.H., Gillebaart, M., Rotteveel, M., Becker, D., Vliek, M., 2012. Veiled Emotions: the effect of covered faces on emotion perception and attitudes. *Soc. Psychol. Personal. Sci.* 3, 266–273, <http://dx.doi.org/10.1177/1948550611418534>.
- Fishman, I., Datko, M., Carbrera, Y., Carper, R., Müller, R., 2016. Reduced integration and differentiation of the imitation network in autism: a combined functional connectivity magnetic resonance imaging and diffusion-Weighted imaging study. *Ann. Neurol.* 116, 1477–1490, <http://dx.doi.org/10.1161/CIRCRESAHA.116.303790>.
- Forbes, P., Pan, X., Hamilton, A., 2016. Reduced mimicry to virtual reality avatars in Autism Spectrum Disorder. *J. Autism Dev. Disord.*, 1–10.
- Frank, M., Ekman, P., Friesen, W., 1993. Behavioral markers and recognizability of the smile of enjoyment. *J. Pers. Soc. Psychol.* 64, 83.
- Van der Gaag, C., Minderaa, R., Keyers, C., 2007. Facial expressions: what the mirror neuron system can and cannot tell us. *Soc. Neurosci.* 2, 179–222.
- Gallagher, H., Jack, A., Roepstorff, A., Frith, C., 2002. Imaging the intentional stance in a competitive game. *Neuroimage* 16, 814–821.
- Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. *Brain* 119, 593–609.
- Geangu, E., Quadrelli, E., Conte, S., Croci, E., Turati, C., 2016. Three-year-olds' rapid facial electromyographic responses to emotional facial expressions and body postures. *J. Exp. Child Psychol.* 144, 1–14.
- Golby, A.J., Gabrieli, J.D., Chiao, J.Y., Eberhardt, J.L., 2001. Differential responses in the fusiform region to same-race and other-race faces. *Nat. Neurosci.* 4, 845–850, <http://dx.doi.org/10.1038/90565>.
- Gonzalez-Liencre, C., Shamay-Tsoory, S., Brüne, M., 2013. Towards a neuroscience of empathy: ontogeny, phylogeny, brain mechanisms, context and psychopathology. *Neurosci. Biobehav. Rev.* 37, 1537–1548.
- Gregory, S.G., Connelly, J.J., Towers, A.J., Johnson, J., Biscocho, D., Markunas, C.A., Lintas, C., Abramson, R.K., Wright, H.H., Ellis, P., Langford, C.F., Worley, G., Delong, G.R., Murphy, S.K., Uccaro, M.L., Persico, A., Pericak-Vance, M.A., 2009. Genomic and epigenetic evidence for oxytocin receptor deficiency in autism. *BMC Med.* 7, 1, <http://dx.doi.org/10.1186/1741-7015-7-62>.
- Haas, B.W., Filkowski, M.M., Cochran, R.N., Denison, L., Ishak, A., Nishitani, S., Smith, A.K., 2016. Epigenetic modification of OXT and human sociability. *Proc. Natl. Acad. Sci. U. S. A.* 113, E3816–E3823.
- Hamilton, A., 2013. Reflecting on the mirror neuron system in autism: a systematic review of current theories. *Dev. Cogn. Neurosci.* 3, 91–105.
- Harmon-Jones, E., & Winkielman, P. (Eds.), 2007. Social neuroscience: integrating biological and psychological explanations of social behavior.
- Hermans, E., Ramsey, N., van Honk, J., 2008. Exogenous testosterone enhances responsiveness to social threat in the neural circuitry of social aggression in humans. *Biol. Psychiatry* 63, 263–270.
- Hermans, E., Wingen, G., van Bos, P., Putman, P., van Honk, J., 2009. Reduced spontaneous facial mimicry in women with autistic traits. *Biol. Psychol.* 80, 348–353.
- Hermans, E.J., Bos, P.A., Ossewaarde, L., Ramsey, N.F., Fernández, G., van Honk, J., 2010. Effects of exogenous testosterone on the ventral striatal BOLD response during reward anticipation in healthy women. *Neuroimage* 52, 277–283, <http://dx.doi.org/10.1016/j.neuroimage.2010.04.019>.
- Hess, U., Fischer, A., 2013. Emotional mimicry as social regulation. *Personal. Soc. Psychol. Rev.* 17, 142–157, <http://dx.doi.org/10.1177/1088868312472607>.
- Heyes, C., 2011. Automatic imitation. *Psychol. Bull.* 137, 463–483, <http://dx.doi.org/10.1037/A0022288>.
- Hietanen, J., Surakka, V., Linnankoski, I., 1998. Facial electromyographic responses to vocal affect expressions. *Psychophysiology* 35, 530–536.
- Hofman, D., Bos, P.A., Schutter, D.J.L.G., van Honk, J., 2012. Fairness modulates non-conscious facial mimicry in women. *Proc. R. Soc. London B Biol. Sci.* 279, 3535–3539, <http://dx.doi.org/10.1098/rspb.2012.0694>.
- Hogeveen, J., Chartrand, T.L., Obhi, S.S., 2015. Social mimicry enhances mu-suppression during action observation. *Cereb. Cortex* 25, 2076–2082, <http://dx.doi.org/10.1093/cercor/bhu016>.
- Hurlmann, R., Scheele, D., 2016. Dissecting the role of oxytocin in the formation and loss of social relationships. *Biol. Psychiatry* 79, 185–193.
- Kavanagh, L.C., Winkielman, P., 2016. The functionality of spontaneous mimicry and its influences on affiliation: an implicit socialization account. *Front. Psychol.* 7, 458, <http://dx.doi.org/10.3389/fpsyg.2016.00458>.
- Keyers, C., Perrett, D., 2004. Demystifying social cognition: a Hebbian perspective. *Trends Cogn. Sci.* 8, 501–507.
- Korb, S., Grandjean, D., Scherer, K., 2010. Timing and voluntary suppression of facial mimicry to smiling faces in a Go/NoGo task-An EMG study. *Biol. Psychol.* 85, 347–349, <http://dx.doi.org/10.1016/j.biopsycho.2010.07.012>.
- Korb, S., Malsert, J., Strathearn, L., Vuilleumier, P., Niedenthal, P., 2016. Sniff and mimic – intranasal oxytocin increases facial mimicry in a sample of men. *Horm. Behav.* 84, 64–74, <http://dx.doi.org/10.1016/j.yhbeh.2016.06.003>.
- Kubota, J.T., Banaji, M.R., Phelps, E.A., 2012. The neuroscience of race. *Nat. Neurosci.* 15, 940–948, <http://dx.doi.org/10.1038/nn.3136>.
- Lamm, C., Majdandžić, J., 2015. The role of shared neural activations, mirror neurons, and morality. *Neurosci. Res.* 90, 15–24.
- Lamm, C., Decety, J., Singer, T., 2011. Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage* 54, 2492–2502, <http://dx.doi.org/10.1016/j.neuroimage.2010.10.014>.
- Lanzetta, J., Englis, B., 1989. Expectations of cooperation and competition and their effects on observers' vicarious emotional responses. *J. Pers. Soc. Psychol.* 56, 543–554.

- Larsen, J., Norris, C., Cacioppo, J., 2003. Effects of positive and negative affect on electromyographic activity over zygomaticus major and corrugator supercilii. *Psychophysiology* 40, 776–785.
- Likowski, K.U., Mühlberger, A., Seibt, B., Pauli, P., Weyers, P., 2011. Processes underlying congruent and incongruent facial reactions to emotional facial expressions. *Emotion* 11, 457–467. <http://dx.doi.org/10.1037/a0023162>.
- Likowski, K.U., Mühlberger, A., Gerdes, A.B.M., Wieser, M.J., Pauli, P., Weyers, P., 2012. Facial mimicry and the mirror neuron system: simultaneous acquisition of facial electromyography and functional magnetic resonance imaging. *Front. Hum. Neurosci.* 6, 214. <http://dx.doi.org/10.3389/fnhum.2012.00214>.
- Mancini, G., Ferrari, P.F., Palagi, E., 2013. Rapid facial mimicry in geladas. *Sci. Rep.* 3, 1527. <http://dx.doi.org/10.1038/srep01527>.
- Masten, C., Morelli, S., Eisenberger, N., 2011. An fMRI investigation of empathy for social pain and subsequent prosocial behavior. *Neuroimage* 55, 381–388.
- McCabe, K., Houser, D., Ryan, L., Smith, V., Trouard, T., 2001. A functional imaging study of cooperation in two-person reciprocal exchange. *Proc. Natl. Acad. Sci.* 98, 11832–11835.
- McIntosh, D., Reichmann-Decker, A., Winkelman, P., Wilbarger, J., 2006. When the social mirror breaks: deficits in automatic, but not voluntary, mimicry of emotional facial expressions in autism. *Dev. Sci.* 9, 295–302.
- Meier, I.M., Bos, P.A., Hamilton, K., Stein, D.J., van Honk, J., Malcolm-Smith, S., 2016. Naltrexone increases negatively-valenced facial responses to happy faces in female participants. *Psychoneuroendocrinology* 74, 65–68. <http://dx.doi.org/10.1016/j.psyneuen.2016.08.022>.
- Molenberghs, P., Cunningham, R., Mattingley, J., 2012. Brain regions with mirror properties: a meta-analysis of 125 human fMRI studies. *Neurosci. Biobehav. Rev.* 36, 341–349.
- Murata, A., Saito, H., Schug, J., Ogawa, K., Kameda, T., 2016. Spontaneous facial mimicry is enhanced by the goal of inferring emotional states: evidence for moderation of automatic mimicry by higher cognitive. *PLoS One* 11, e0153128.
- Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., Matsuzawa, T., 2004. Imitation in neonatal chimpanzees (*Pan troglodytes*). *Dev. Sci.* 7, 437–442. <http://dx.doi.org/10.1111/j.1467-7687.2004.00364.x>.
- Nagasawa, M., Mitsui, S., En, S., Ohtani, N., Ohta, M., Sakuma, Y., Onaka, T., Mogi, K., Kikusui, T., 2015. Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science* (80-) 348, 333–336.
- Niedenthal, P., Mermillod, M., Maringer, M., Hess, U., 2010. The Simulation of Smiles (SIMS) model: embodied simulation and the meaning of facial expression. *Behav. Brain Sci.* 33, 417–433.
- Palagi, E., Nicotra, V., Cordoni, G., 2015. Rapid mimicry and emotional contagion in domestic dogs. *R. Soc. Open Sci.* 2, 150505. <http://dx.doi.org/10.1098/rsos.150505>.
- Panksepp, J., Panksepp, J., 2013. Toward a cross-species understanding of empathy. *Trends Neurosci.* 36, 489–496.
- Pineda, J., 2008. Sensorimotor cortex as a critical component of an extended mirror neuron system: does it solve the development, correspondence, and control problems in mirroring? *Behav. Brain Funct.* 4, 1.
- Preston, S., De Waal, F., 2002. Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25, 1–20.
- Puglia, M.H., Lillard, T.S., Morris, J.P., Connelly, J.J., 2015. Epigenetic modification of the oxytocin receptor gene influences the perception of anger and fear in the human brain. *Proc. Natl. Acad. Sci. U. S. A.* 112, 3308–3313. <http://dx.doi.org/10.1073/pnas.1422096112>.
- Ratner, K., Amodio, D., 2013. Seeing us vs. them: minimal group effects on the neural encoding of faces. *J. Exp. Soc. Psychol.* 49, 298–301.
- Rauchbauer, B., Majdandžić, J., Hummer, A., Windischberger, C., Lamm, C., 2015. Distinct neural processes are engaged in the modulation of mimicry by social group-membership and emotional expressions. *Cortex* 70, 49–67.
- Rilling, J., Gutman, D., Zeh, T., Pagnoni, G., Berns, G., Kilts, C., 2002. A neural basis for social cooperation. *Neuron* 35, 395–405.
- Rilling, J., DeMarco, A., Hackett, P., Thompson, R., Ditzgen, B., Patel, R., Pagnoni, G., 2012. Effects of intranasal oxytocin and vasopressin on cooperative behavior and associated brain activity in men. *Psychoneuroendocrinology* 37, 447–461.
- Rilling, J., DeMarco, A., Hackett, P., Chen, X., Gautam, P., Stair, S., Haroon, E., Thompson, R., Ditzgen, B., Patel, R., Pagnoni, G., 2014. Sex differences in the neural and behavioral response to intranasal oxytocin and vasopressin during human social interaction. *Psychoneuroendocrinology* 39, 237–248. <http://dx.doi.org/10.1016/j.psyneuen.2013.09.022>.
- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192. <http://dx.doi.org/10.1146/annurev.neuro.27.070203.144230>.
- Schilbach, L., Eickhoff, S.B., Mojzisch, A., Vogeley, K., 2008. What's in a smile? Neural correlates of facial embodiment during social interaction. *Soc. Neurosci.* 3, 37–50. <http://dx.doi.org/10.1080/17470910701563228>.
- Scopa, C., Palagi, E., 2016. Mimic me while playing! Social tolerance and rapid facial mimicry in macaques (*Macaca tonkeana* and *Macaca fuscata*). *J. Comp. Psychol.* 130, 153.
- Seibt, B., Weyers, P., Likowski, K.U., Pauli, P., Mühlberger, A., Hess, U., 2013. Subliminal interdependence priming modulates congruent and incongruent facial reactions to emotional displays. *Soc. Cogn.* 31, 613–631. <http://dx.doi.org/10.1521/soco.2013.31.613>.
- Seibt, B., Mühlberger, A., Likowski, K.U., Weyers, P., 2015. Facial mimicry in its social setting. *Front. Psychol.* 6 (1122). <http://dx.doi.org/10.3389/fpsyg.2015.01122>.
- Sherwood, C., Hof, P., Holloway, R., Semendeferi, K., Gannon, P., Frahm, H., Zilles, K., 2005. Evolution of the brainstem orofacial motor system in primates: a comparative study of trigeminal, facial, and hypoglossal nuclei. *J. Hum. Evol.* 48, 45–48.
- Simpson, E., Fox, N., Tramacere, A., Ferrari, P., 2014. Neonatal imitation and an epigenetic account of mirror neuron development. *Behav. Brain Sci.* 37, 220.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R., Frith, C., 2004. Empathy for pain involves the affective but not sensory components of pain. *Science* (80-) 303, 1157–1162.
- Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.J., Frith, C.D., 2006. Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439, 466–469. <http://dx.doi.org/10.1038/nature04271>.
- Sonnby-Borgström, M., 2002. Automatic mimicry reactions as related to differences in emotional empathy. *Scand. J. Psychol.* 43, 433–443.
- Syal, S., Ipser, J., Terburg, D., Solms, M., Panksepp, J., Malcolm-Smith, S., Bos, P., Montoya, E., Stein, D., van Honk, J., 2015. Improved memory for reward cues following acute buprenorphine administration in humans. *Psychoneuroendocrinology* 53, 10–15. <http://dx.doi.org/10.1016/j.psyneuen.2014.11.009>.
- Tabibnia, G., Lieberman, M., 2007. Fairness and cooperation are rewarding. *Ann. N. Y. Acad. Sci.* 1118, 90–101.
- Taylor, S., Klein, L., Lewis, B., Gruenewald, T., Gurung, R., Updegraff, J., 2000. Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. *Psychol. Rev.* 107, 411.
- Thompson, R., Gupta, S., Miller, K., Mills, S., Orr, S., 2004. The effects of vasopressin on human facial responses related to social communication. *Psychoneuroendocrinology* 29, 35–48. [http://dx.doi.org/10.1016/S0306-4530\(02\)00133-6](http://dx.doi.org/10.1016/S0306-4530(02)00133-6).
- Thompson, R., George, K., Walton, J., Orr, S., Benson, J., 2006. Sex-specific influences of vasopressin on human social communication. *Proc. Natl. Acad. Sci.* 103, 7889–7894.
- Tomasello, M., 2014. A Natural History of Human Thinking. Harvard University Press. <http://dx.doi.org/10.1007/s13398-014-0173-7.2>.
- Tramacere, A., Ferrari, P.F., 2016. Faces in the mirror, from the neuroscience of mimicry to the emergence of mentalizing. *J. Anthropol. Sci.* 94, 1–14. <http://dx.doi.org/10.4436/jass.94037>.
- Van Bavel, J.J., Packer, D.J., Cunningham, W.A., 2011. Modulation of the fusiform face area following minimal exposure to motivationally relevant faces: evidence of in-group enhancement (not out-group disregard). *J. Cogn. Neurosci.* 23, 3343–3354. <http://dx.doi.org/10.1162/jocn.a.00016>.
- van Schaik, J.E., Hunnius, S., 2016. Little chameleons: the development of social mimicry during early childhood. *J. Exp. Child Psychol.* 147, 71–81. <http://dx.doi.org/10.1016/j.jecp.2016.03.003>.
- van der Schalk, J., Fischer, A., Doosje, B., Wigboldus, D., Hawk, S., Rotteveel, M., Hess, U., 2011. Convergent and divergent responses to emotional displays of ingroup and outgroup. *Emotion* 11, 286–298. <http://dx.doi.org/10.1037/a0022582>.
- Wang, Y., Hamilton, A.F. de C., 2012. Social top-down response modulation (STORM): a model of the control of mimicry in social interaction. *Front. Hum. Neurosci.* 6, 160–169. <http://dx.doi.org/10.3389/fnhum.2012.00153>.
- Weyers, P., Mühlberger, A., Kund, A., Hess, U., Pauli, P., 2009. Modulation of facial reactions to avatar emotional faces by nonconscious competition priming. *Psychophysiology* 46, 328–335. <http://dx.doi.org/10.1111/j.1469-8986.2008.00771.x>.
- Wicker, B., Keysers, C., Plailly, J., Royet, J., Gallese, V., Rizzolatti, G., Deusinglaan, A., Gerland, U.C.L., Garnier, A.T., 2003. Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. *Neuron* 40, 655–664.
- Wingen, G., Van Mattern, C., Verkes, R., Buitelaar, J., Fernández, G., 2010. Testosterone reduces amygdala–orbitofrontal cortex coupling. *Psychoneuroendocrinology* 35, 105–113.
- Yabar, Y., Johnston, A.E.L., Miles, A.E.L., 2006. Implicit behavioral mimicry: investigating the impact of group membership. *J. Nonverbal Behav.* 30, 97–113. <http://dx.doi.org/10.1007/s10919-006-0010-6>.
- Zheng, J.-J., Li, S.-J., Zhang, X.-D., Miao, W.-Y., Zhang, D., Yao, H., Yu, X., 2014. Oxytocin mediates early experience-dependent cross-modal plasticity in the sensory cortices. *Nat. Neurosci.* 17, 391–399. <http://dx.doi.org/10.1038/nn.3634>.
- Zink, C., Stein, J., Kempf, L., Hakimi, S., Meyer-Lindenberg, A., 2010. Vasopressin modulates medial prefrontal cortex–amygdala circuitry during emotion processing in humans. *J. Neurosci.* 30, 7017–7022.