

# Faces in the mirror, from the neuroscience of mimicry to the emergence of mentalizing

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**Summary** - *In the current opinion paper, we provide a comparative perspective on specific aspects of primate empathic abilities, with particular emphasis on the mirror neuron system associated with mouth/face actions and expression. Mouth and faces can be very salient communicative classes of stimuli that allow an observer access to the emotional and physiological content of other individuals. We thus describe patterns of activations of neural populations related to observation and execution of specific mouth actions and emotional facial expressions in some species of monkeys and in humans. Particular attention is given to dynamics of face-to-face interactions in the early phases of development and to the differences in the anatomy of facial muscles among different species of primates. We hypothesize that increased complexity in social environments and patterns of social development have promoted specializations of facial musculature, behavioral repertoires related to production and recognition of facial emotional expression, and their neural correlates. In several primates, mirror circuits involving parietal-frontal regions, insular regions, cingulate cortices, and amygdala seem to support automatic forms of embodied empathy, which probably contribute to facial mimicry and behavioural synchrony. In humans these circuits interact with specific prefrontal and temporo-parietal cortical regions, which facilitates higher order cognitive functions such as cognitive empathy and mental state attribution. Our analysis thus suggests that the evolution of higher forms of empathy, such as mentalizing, is also linked to the coupling between the perceptual and motor system related to face processing, which may have undergone a process of exaptation during primate phylogeny.*

**Keywords** - *Mirror neurons, Facial mimicry, Mentalizing, Exaptation, Niche construction, Primate evolution.*

## Introduction

In the last decades, there have been an increasing number of studies that examine the phenomenon of empathy. Originally defined as “feeling into” (*Einfühlung*) other people’s emotions and feelings (Stein, 1989), empathy has been studied by social psychologists as a phenomenon causally involved in creating prosocial attitudes and behavior. Empathy has since acquired a central importance in understanding agency in the human sciences and human beings as social and moral agents (Stanford Encyclopedia of Philosophy).

Various levels of empathy that have been investigated among different animals, such as mammals and primates (Trivers, 1971; de Waal, 2009; Bekoff, 2004), make it clear that emotional understanding and prosocial attitudes are not human prerogatives; rather, they have quantifiable biological bases that emerged during evolution, likely because of the advantages they brought (and bring) at individual and group levels (Wilson, 2005; Hamilton, 1963; de Waal, 2009).

Empathy has been defined as a multi-layered and multifaceted phenomenon, encompassing mimicry and emotional contagion at

a low level of cognition, and sympathy, cognitive empathy and prosocial behavior at a higher level of cognitive computation (Tab. 1) (Preston & de Waal, 2000; Christov-Moore *et al.*, 2014). In particular, mimicry and emotional contagion appear to be shared by several mammalian species, such as mice (Langford *et al.* 2006), pigs (Reimert *et al.*, 2013), dolphins (Connor & Norris, 1982), elephants (Hamilton-Douglas, 2006), dogs (Haidt, 2001), monkeys (Schwartz, 2015), and apes (Preston & de Waal, 2002). On the other hand, the existence of higher forms of empathy, such as cognitive empathy and proper altruism has been proposed only in dolphin, elephant, great apes and humans (Preston & de Waal, 2002).

At the cerebral level, neural mechanisms of action-perception coupling are considered a crucial correlate of at least the most basic levels of empathy such as facial mimicry and emotional contagion (Hatfield & Cacioppo, 1994; Singer, 2006; Gallese, 2001; Christov-Moore *et al.*, 2014; Preston & de Waal, 2002). Such neural mechanisms have mainly been identified with the mirror neuron system, which has the key property of activating the same neuronal population during execution and perception of the same or similar actions and emotions (Gallese, 2001; Iacoboni, 2009). Consequently, a comparative perspective of this neural mechanism and the anatomical location in which it has been described serves to highlight certain aspects of empathy and the factors related to its emergence in different species.

In this review, we focus mainly on mirror mechanisms related to mouth actions and facial expression. Faces, which comprise two important regions, the eyes and mouth, are in fact very salient communicative classes of stimuli and are thought to allow observers access to the emotional and physiological status of other individuals (Darwin, 1872; Ekman *et al.*, 1993). In fact, mutual face recognition is crucial in different social conditions, such as conflict resolution, sexual signaling, parent-offspring interactions, social integration and communication (Bradbury & Vehrencamp, 1998; Regenbogen

& Habel, 2015). Further, in recent decades studies of primates' mirror mechanisms related to mouth and faces have provided very interesting results, both at the developmental and comparative level (Ferrari *et al.*, 2003; Ferrari *et al.*, 2012; De Waal & Ferrari, 2010).

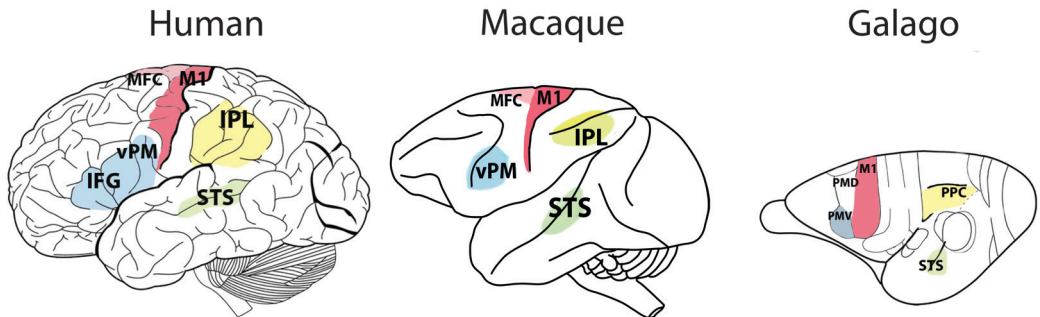
In light of these premises, we aim to provide a comparative perspective on primate face mirroring in an attempt to illustrate continuous and discontinuous aspects of empathic abilities that emerged during the evolution of primate sociality.

### Mirror mechanisms in facial perception

Below we describe patterns of activations of neural populations related to observation and execution of mouth actions and emotional facial expressions in four species of monkeys (*Macaca nemestrina*, *Macaca mulatta*, *Macaca fascicularia*, *Macaca fuscata*) and in humans (Fig. 1). Although these brain phenomena have been investigated using different techniques, the heterogeneity of the techniques prevents certainty about whether, in various brain regions of humans or monkeys, identical neurons induce these types of sensorimotor matching responses. Where appropriate, we distinguish between mirror neurons, mirror mechanisms, and a mirror neuron system (Tab. 1).

#### *Macaque*

Mirror neurons (MNs) have been localized in specific sections of premotor and parietal cortex of macaque monkeys and defined as neurons firing during both execution and perception of same or similar actions, for example grasping with hand or with mouth (Rizzolatti & Craghiero, 2004). Premotor MNs are connected with parietal MNs, which in turn are linked to the superior temporal sulcus (STS), a multisensory area that provides the main visual input to MNs and that possesses neurons visually coding a variety of behaviors (i.e. walking, face and hand movements), thus forming what is known as the mirror neuron system (MNS) (Keysers & Perrett, 2004). Subsequently, mirror neurons



**Fig. 1 - The mirror neuron system that is associated with facial processing in macaques and humans, and a similar circuit in an adult prosimian brain. The human MNS consists of specific sectors of the posterior parietal cortex, especially the inferior parietal lobule (IPL); ventral sector of premotor cortex (vPM); and part of the inferior frontal gyrus (IFG). Mirror activities have also been reported in the primary motor area (M1), and in pre- and supplementary motor areas (pre-SMA and SMA). Neurons in the walls of the superior temporal sulcus (STS) are activated during decoding of sensory information but have not been implicated in motor resonance. The macaque MNS involves a premotor area in ventral premotor cortex (vPM), the rostral part of posterior parietal cortex (IPL), part of the primary motor area (M1), and medial frontal cortex (MFC). The main visual input is provided by the region surrounding the superior temporal sulcus, which lacks motor properties but is considered part of the MNS. Similar temporoparieto-frontal circuits have also been identified in prosimians. It is possible to find both ventral and dorsal premotor (respectively PMV and PMD), motor (M1), sensory association (STS) and posterior parietal (PPC) regions in the galago brain. MNS in this species have not yet been investigated. In order to give a general idea of the structural similarities between the brains of these species, we depict the gross cortical regions involved in mirror responses related to the face, but not the other limbic and subcortical areas that participate in its mirror responses. The colour version of this figure is available at the JASs website.**

were also found in medial frontal cortex, which roughly comprises pre supplementary motor area (pre-SMA) and (SMA), and primary motor cortex (M1) (Yoshida *et al.*, 2011; Vigneswaran *et al.*, 2013), thus widening the possible regions involved in the MNS.

However, in the lateral sector of the ventral premotor cortex in both right and left hemispheres, two different types of MNs have been investigated. These are involved during both the observation and the execution of actions/gestures performed with the mouth. *Mouth ingestive MNs* discharge in presence of an interaction between mouth and an object, for example during ingestion, grasping and holding (with mouth), sucking, chewing and breaking (Ferrari *et al.*, 2003). *Mouth communicative MNs*, in contrast, discharge in response to non-directed intransitive actions such as lipsmacking or tongue protrusion (Ferrari *et al.*, 2003).

Lipsmacking is a typical macaque gesture related to affiliative behavior, which probably derived from a process of ritualization in which ingestive actions lost their original function to become involved in dyadic affiliative communication, thus assuming new meanings (van Hooff, 1967; Ferrari *et al.*, 2003). Lipsmacking gestures have specific features (cyclic opening-closing of the mouth) that, according to some scholars, could have played an important role in the evolution of primate vocalizations via their incorporation into basic motor-patterns (Partan, 2002; see also Shepherd *et al.*, 2012; Morrill *et al.*, 2012). If so, lipsmacking may have been a possible precursor of speech-like sounds (Morrill *et al.*, 2012; Bergman, 2013). *Communicative MNs* might therefore have emerged in the context of face-to-face interactions and could constitute a basic mechanism for mapping visual stimuli related to others' facial gestures into the observer's motor representation.

Tab. 1 – Glossary.

<b>Mirror neurons</b>	They were first discovered in macaque monkeys and are defined as neurons that fire during both execution and perception of the same or similar actions, such as grasping with the hand or mouth. They have been localized through single cell recording in the premotor cortex (F5), and in the inferior parietal lobule (IPL). Furthermore, a recent experiment suggests that mirror neurons might also be present in primary motor cortex, an area strongly connected with premotor regions.
<b>Mirror neuron system</b>	This system is a network of interconnected areas that simultaneously processes information about executed and observed mouth and hand actions. It is comprised of tissue in and around the superior temporal sulcus (STS), which contain no mirror neurons, and sections of premotor (F5), parietal cortex (IPL), medial frontal cortex (MFC), and primary motor cortex (M1).
<b>Mirror mechanism</b>	This refers to an action-perception brain mechanism, typically measured by fMRI and EEG, that facilitates same/similar patterns of activity in and outside of the brain's traditional mirror areas during the observation of specific actions in others and the execution of these same actions in observers.
<b>Facial mimicry</b>	Facial mimicry is an involuntary, rapid and automatic response in which an individual mimics the facial expression of another individual. This phenomenon is distinguished from other voluntary and cognitive forms of imitation because of the rapidity of the responses involving the face.
<b>Emotional contagion</b>	The transfer or communication of a certain mood among individuals. It can also be defined as the tendency for two individuals to converge emotionally, which may be expressed through automatic mimicry and synchronization of facial or gestural expressions, vocalizations and/or postures.
<b>Cognitive empathy or mentalizing</b>	This is often defined as "perspective taking" and it refers to the ability to understand through inferential evaluative processes the emotions, feelings, desires or beliefs of other individuals.

This finding is intriguing because the brain control of many monkey vocal communications has long been attributed to mesial and subcortical structures and is thought to be involuntary, due to emotional and motivational activation (Jurgens, 2002; Fogassi *et al.*, 2013; Fogassi & Ferrari 2007). *Communicative MNs* can thus be interpreted as neurons implicated in the control and perception of mouth gestures, which are dissociated from vocal communication in macaques. This is likely the reason why the investigation of MNs response to perception and execution of conditioned vocalization in macaque's premotor cortex has given negative results (Coude *et al.*, 2011; Hage *et al.*, 2013).

Interestingly, monkey newborns are able to imitate mouth actions, such as lipsmacking or tongue protrusion, in the very first period of life (Ferrari *et al.*, 2006, 2012). In neonates

between days 1 to 7, in fact, perception of different facial expressions produces a plethora of facial responses that can be interpreted as a form of dyadic communication in the context of parent-infant interactions (Ferrari *et al.*, 2006). This suggests that mother–infant interactions in monkeys may both rely on and refine action–perception coupling mechanisms related to face and mouth.

As a matter of confirmation, specific variations in alpha frequency during EEG studies have been recorded in the context of neonatal imitation (Ferrari *et al.*, 2012). The suppression of this rhythm, named the mu rhythm, during action execution and observation has been interpreted as the result of activation of sensorimotor cortex, an indirect marker of mirror neuron activity. More specifically, when adults and children view

others' goal-directed actions, electroencephalography activities recorded over the motor cortex are suppressed (Marshall & Meltzoff, 2011). A recent EEG study in newborn macaques has found suppression in the 5 – 6Hz frequency band in association with execution and observation of lipsmacking and tongue protrusion gestures (Ferrari *et al.*, 2012). These data are the first to show that sensorimotor structures are activated during early facial gesture observation in infant monkeys (Ferrari *et al.*, 2012), providing an important clue regarding the presence of a mirror mechanism at birth as a correlate of infant synchronous dyadic communication.

Pioneering studies are suggesting the existence of a mirror mechanism related to face coding in areas associated with emotional processing, such as insula, anterior cingulate cortex (ACC) and amygdala (Gothard *et al.*, 2007; Livneh *et al.*, 2012). During both the production and monitoring of facial gestures such as lip smacking or aggressive threats parts of dorsal ACC and amygdala are activated (Gothard *et al.*, 2007; Kuraoka *et al.*, 2007; Livneh *et al.*, 2012), which suggests that these regions are recruited during direct face-to-face interaction. It is, thus, highly plausible that the same neural populations are activated during perception of others' emotional facial expressions, as well as during integration of visceromotor signals while individuals experience the same emotional state. In addition, the rostral part of the insula, an olfactory and gustatory center that appears to integrate visceral sensations and the related autonomic motor responses, seems to be causally implicated in the facial expression of disgust and, more generally, in processing facial stimuli and responses to them (Wicker *et al.*, 2003; Kaada *et al.*, 1949; Showers & Lauer, 1961; see also the review Gallese *et al.*, 2001). Interestingly, electrical stimulation of this part of the insula in monkeys elicits different facial motor responses, such as disgust and lip smacking (Caruana *et al.*, 2011). However, more studies are necessary in order to clarify the behavior of specific neuronal populations in the insula during emotional face perception and to trace the boundaries between mirror and non-mirror areas of the brain.

Nevertheless, these findings are consistent with the hypothesis that observation of facial expressions in monkeys activates a subcortical circuit involving the thalamus, superior colliculus (SC), amygdala, and anterior insula, which may represent a fast and automatic encoding route for a rapid evaluation of facial expressions (Burrows, 2008). Basic visual information from the SC and thalamus feeds into the amygdala, which extracts emotional cues (Haxby, 2006). This subcortical pathway may then project to frontoparietal circuits through the insula and ACC, in association with more detailed processing of facial expression (Burrows, 2008). Within this pathway for facial processing, some regions are also strongly implicated in motor control. Amygdala and the dorsal ACC are, in fact, directly connected with the facial nucleus, which suggests they engage in the production of automatic facial movements (Livneh *et al.*, 2012).

In conclusion, the overlapping of specific subcortical and cortical regions that facilitate different levels of coordination between actions and perceptions supports the hypothesis that a mirror mechanism is instrumental in coordinating facial expressions within social contexts.

### *Human*

Activations of specific regions of premotor, parietal and sensory cortex during observation and execution of similar mouth actions has also been discovered in humans (Rizzolatti & Craghiero, 2004; Iacoboni, 2009). Using different brain techniques, mouth mirror mechanisms have been identified (Leslie *et al.*, 2004; Buccino *et al.*, 2001), which show that both observation and execution of different mouth configurations, such as those used in smiling or speaking, recruit activity in ventral premotor and the posterior parietal cortex (Leslie *et al.*, 2004; Buccino *et al.*, 2001). Consistent with these results, specific sections of premotor and parietal cortices, primary motor area (M1), and pre-supplementary motor area (pre-SMA) are activated during imitation and observation of a specific set of mouth actions that have been correlated with six main emotions (happiness, sad, angry, disgust, surprise and fear)

(Carr *et al.*, 2002). Further, MNs responding to the execution and perception of smiling have been recorded through extracellular recordings of neuronal ensembles in the supplementary motor area, SMA (Mukamel *et al.*, 2010). However, more studies at single cell levels are required to better elucidate whether other cortical motor areas of the classical mirror system have neuronal responses similar to those reported for SMA in monkeys' F5-IPL circuits.

Moreover, consistent with monkey studies, amygdala, ACC and anterior insula are active during observation of emotional facial expressions (Carr *et al.*, 2003; Wicker *et al.*, 2003; Singer *et al.*, 2004). In particular, the anterior sector of the insula is bilaterally activated when human subjects are exposed to disgusting odors or tastes. Interestingly, the insula activates anteriorly and posteriorly in relation to the observation of unpleasant and pleasant stimuli, respectively, suggesting that seeing someone else's emotional facial expressions triggers recruitment of activity in the same part of the observer's insula (Wicker *et al.*, 2003). Anterior insula is not only involved in the experience and observation of disgust, it also mediates empathy for pain (Singer *et al.*, 2004). Considering that this structure, together with ACC, is crucially involved in pain perception and pain-related visceromotor reactions, it is likely that empathy for pain is mediated by a mechanism similar to that postulated for disgust (Singer *et al.*, 2004). Additionally, the anterior part of the amygdala is involved in processing observed fear and happy or angry facial stimuli, strengthening the conclusion that we understand the feelings of others via a mechanism in which observation of their actions/responses shapes similar emotional experiences in observers. Thus, observers' empathic resonance is grounded in their own experiences, e.g., the emotions associated with producing specific facial movements (Carr *et al.*, 2003; Molenberghs *et al.*, 2012).

At the developmental level, different findings suggest that a neural system matching visual perception and executed actions may be active very early in human life, and may, in fact, be the primary means for mediating dyadic interactions

during nonverbal and other intersubjective communication. Similar to monkeys, human newborns are capable of being attentive and, within 36 hours of birth, recognize and reproduce up to six different emotional facial states expressed by the experimenter or caregiver (Nagy & Molnar, 2004; see also Simpson *et al.*, 2014). Neonates also tend to reproduce mouth opening and tongue protrusion during this developmental period (Meltzoff & Moore, 1983). As sensorimotor matching is considered one of the crucial components of neonatal imitation (Meltzoff & Borton, 1979; Simpson *et al.*, 2014), the discovery of populations of neurons in parietofrontal cortex that fire during observation and execution of mouth actions supports the idea that a mirror mechanism may be functional and involved in neonatal imitation from birth (Ferrari *et al.*, 2006).

In sum, investigations of macaques and humans indicate that they have neural mechanisms for coding perceptions and actions of mouths and faces that overlap, at least partly, at neurobiological and developmental levels. Although anatomical studies related to brain connectivity in humans can't be investigated as extensively as in monkeys, several findings suggest that both species share similar subcortical and cortical circuits for facial processing (Paus, 2005; Caria *et al.*, 2012). This opens the possibility that the two species may have performed the same biological functions, facial gesture processing and coordinating face-to-face dyadic interactions, with similar anatomical substrates and neural mechanisms.

#### *Emotional communication in prosimians*

In order to better understand the evolution and functional significance of mirror systems, comparative data from other species of primates would be helpful. Neural investigations aimed at assessing the existence of mirror responses have not been performed in strepsirrhine primates. However, since most of the parietofrontal circuits controlling hand and mouth movements have a similar pattern of connections in all primates (Kaas, 2008; Preuss & Goldman-Rakic, 1989), it is plausible that some communications based

on facial displays in strepsirrhines such as diurnal lemurs might rely on these circuits that operate through neuronal mirroring in similar ways to macaques and great apes. Although speculative, it is possible that dyadic communicative episodes, such as displays of a relaxed open mouth used as play signals in ring tailed lemurs (Palagi *et al.*, 2014), are grounded in frontoparietal circuits for facial and mouth movements (Wu *et al.*, 2000; Stepniewska *et al.*, 2005) that are coupled with temporal regions devoted to face and mouth perception (Preuss & Goldman-Rakic, 2004). If so, these circuits may also be in synergy with other subcortical regions (Burrows, 2008), thus coupling the mechanisms of perception of facial gestures with the mechanisms of motor control.

However, in lemurs complex communicative signals based on face-to-face exchanges have been observed preferentially during late adolescence and adulthood, when individuals show relatively high stereotyped frequencies of play, grooming, and reproductive behaviours (Doyle, 1979), but not during the early postnatal period. Indeed, parents of lemurs spend very little time with their infants, who are mostly born precociously, with eyes open and ready to face the life's challenges on branches from the first weeks of development (Klopfer & Boskoff, 1979). Further, given the nature of prosimian maternal behaviour, in which mothers of some species tend to carry their babies in their mouths, the number of face-to-face interactions during mother-infant relationships is relatively rare and based less on facial gestural exchanges than in monkeys, apes, and humans (Klopfer & Boskoff, 1979). These observations lead some scholars to propose that prosimian infants are much less attached to their parents compared to anthropoid primates (Highly & Suomi, 1986). Indeed, the extent of parental attachment is uncertain in these species and such attachment may represent a relatively recent adaptation among primates (Suomi, 1995).

Taken together these observations may have important implications for brain development and, more specifically, for how cortical and subcortical networks evolved to sustain complex social interactions based on facial gesturing. We

suppose it might be unlikely that some species of prosimians have mouth mirror mechanisms for communication in the first phases of postnatal development similar to those of macaques. We cannot exclude, however, that these prosimians might have developed mirror mechanisms for ingestive mouth actions, since this activity is highly social and coordinated among group members. Clearly, brain analyses (fMRI or EEG) in selected prosimian species, such as diurnal lemurs, would be very useful for exploring whether significant activation occurs in specific sensorimotor regions in response to observations of face and mouth actions in other individuals.

### **Niche construction for facial mirror mechanisms**

Neural mechanisms that couple executed with perceived facial gestures may not be restricted to anthropoid primates. Some prosimian species experience a sufficient level of facial interaction between adults, although such face-to-face interactions are absent in the infant phases of development (Klopfer & Boskoff, 1979; Kappeler & van Shaik, 2002). This suggests that, with increasing social demand during the transition to modern anthropoid primates about 40 million of years ago (Dunbar, 2010), mirror mechanisms related to face expression may have been selected and extended from the very first phases of development to adulthood. Changes in social niches, such as the birth of multilevel society and more complex dynamics of parental and social bonding (Dunbar, 2010), may have favored individuals who were more efficient in coordinating their facial and mouth movements in response to those of others, including caregivers, partners, and companions. If so, this likely produced a stronger selective pressure on facial recognition and the complexity of the neuroanatomical mechanisms controlling facial muscles. Indeed, strepsirrhine primates clearly differ from anthropoid primates in their facial expressions and gestures. Only a few facial expressions have been reported in aggressive/fearful contexts in ring-tailed lemurs

(Pereira & Kappeler, 1997) and during play (play-face) in sifakas. Further, neonatal face-to-face interactions seem to be absent in prosimians (Palagi, pers. communication), while anthropoid primates present a plethora of facial signals produced primarily within social contexts, and spend much more time in face-to-face interactions as evidenced by the fact that, during the neonatal phase, they show the most-intricate facial displays of all mammals (Burrows, 2008).

Because a link between social bonding and facial expression is suggested by the co-evolution of group size and facial motor control in anthropoid species (Dobson, 2012; Sherwood *et al.*, 2005), higher frequencies of face-to-face interactions may have tuned and coupled neural circuits for the production and recognition of facial expressions (i.e. cortical and subcortical mirror mechanisms) and increased the control of facial musculature related to eye and mouth movements.

Comparative analyses of facial muscles in the three groups of primates considered here (humans, macaques and lemurs) could be highly informative. Diurnal lemurs, similar to nocturnal prosimians, intensively use olfactory signatures as a means of individual identification, which is associated with a concentration of muscle attachments around the external ear and upper lip (Burrows, 2008). On the other hand, macaques, chimpanzee and humans rely more on visual identification of conspecifics and have developed more muscles in the nasolabial and eyebrow regions (Burrows, 2008). Further, anthropoid primates have *depressor anguli oris* and *labii inferioris* muscles localized around the mouth (Diogo *et al.*, 2009) that are responsible, respectively, for pulling the corner of the mouth downward and inward and pulling the lower lip downward and laterally (Kanade *et al.*, 2000), and, as such, are involved in the fine control of emotional facial expressions entailed in sad, happy and frowning faces (Waller *et al.*, 2008).

Interestingly, perception of socially relevant facial expressions in other humans (e.g. smiling) elicits differential muscular activity in the observer's zygomaticus major muscle (Schilbach *et al.*, 2007), which is strongly connected with

labial muscles that are absent in lemurs. This strengthens the conclusion that anthropoids may have evolved more complex *facial mimicry* as a side effect of their pervasive face-based emotional communications.

In sum, this scenario highlights the increased role played by facial expression in anthropoids, especially modern humans (Burrows, 2008), and we hypothesize that increased complexity in social environments has promoted specializations of facial musculature, the behavioral repertoire related to production and recognition of emotional facial expressions, and their neural correlates.

### Exaptation in face mirroring

The observation that mirror mechanisms and facial mimicry can be identified during the early postnatal period in humans and macaques, suggests that these species have evolved a system for prelinguistic emotional communicative exchanges that functions very early in life (Ferrari *et al.*, 2006; Mancini *et al.*, 2013). From this perspective, facial mimicry can be interpreted as a phenomenon that facilitates parent – infant affiliation and attachment (Mancini *et al.*, 2013), and that it is tightly linked to *emotional contagion* between individuals (Hatfield & Cacioppo, 1994). In anthropoid primates, in fact, mothers and infants often engage in intense emotional communication characterized by mutual gaze, facial expressions (e.g., smiles), and vocalizations (Ferrari *et al.*, 2009), which seem to be instrumental for the development of various social skills such as goal directed behaviors and the understanding of emotions and intentions in others (Steel *et al.*, 1999; Simpson *et al.*, 2014; Thomas *et al.*, 2007; Belsky & Fearon, 2002).

However, empathy is not limited to its fast and automatic brain/body responses. Rather, in its original meaning, it encompasses the capacity to experience the perspective of another, including what that individual knows, wants, feels or believes (Premack & Woodruff, 1978; Preston & de Waal, 2002). Higher forms of empathy in humans are, in fact, interpreted as a deliberative



process through which inferences can be made about others' bodily and affective states, beliefs, and intentions or *mentalizing* (Keysers & Fadiga, 2008; Zaki & Ochsner, 2012). From a neurobiological perspective, the human medial prefrontal cortex, temporoparietal junction (TPJ), and frontoparietal circuit interact to process information about self and others in abstract, evaluative terms (Mitchell *et al.*, 2005; Uddin *et al.*, 2005; Christov-Moore *et al.*, 2014). Indeed, medial prefrontal cortex and TPJ are activated when human subjects attribute mental states to others, suggesting these parts of the brain play a special role in theory of mind or social understanding (Jacoboni *et al.*, 2004; Saxe, 2006; Frith & Frith, 1999).

If specific sectors of the amygdala and insula plus the frontoparietal mirror system provide a simulative motor resonance mechanism that is connected to facial mimicry and emotional contagion (Jacoboni, 2009; Gallese, 2001; Carr *et al.*, 2003), the medial prefrontal cortex plus certain temporal areas might be involved in self-other representations at a more cognitive mental level that interacts with the frontoparietal mirror neuron system (Carmichael & Price, 1995; Iriki, 2006; Uddin *et al.*, 2005).

During primate phylogeny, neural circuits with mirror properties and other circuits involved in mentalizing might have been exapted to support more abstract cognitive functions, such as cognitive empathy. Indeed, increased activity in the anterior superior temporal gyrus and the medial prefrontal cortex are consistently reported in studies that involve some kind of social judgments such as attributing mental states and thinking about others' intentions (Castelli *et al.*, 2002; Frith & Frith, 2003; Gallagher & Frith, 2004). Thus, when watching an emotional face, observers might not only participate through synchronized mimicry, they might also understand the relevance of the agent's mental state for social interaction (Grosbras & Paus, 2006; Shulte-Rueter *et al.*, 2007).

It is not yet fully understood how the circuits implicated in mentalizing, or their connections with other functionally relevant areas, differ in monkeys and humans (Baron-Cohen *et al.*, 2013). However, their crucial involvement

in higher-level cognitive functions opens interesting experimental and conceptual perspectives that may be useful for understanding the selective pressures and mechanisms that played a key role in the emergence of an ability to attribute mental states to others via facial mimicry and other responses to their facial expressions.

## Conclusions

A full explanation of the complex neural and behavioral features associated with an ability to recognize the self and others, which arose during the evolutionary emergence of empathy and mentalizing, is beyond the purpose of this review.

Nonetheless, we hypothesize that the neonatal sensitivity to facial mimicry of anthropoid primates is connected to their highly communicative environmental niche. Accordingly, it is plausible that a progressively more demanding social niche increased selective pressures for individuals to be more efficient in intraspecific communication (Schultz & Dunbar, 2007), thus favoring the coordination of dyadic facial events during neonatal affiliative communications. This new selective environment may have been associated with increased complexity in facial musculature of the mouth and eyes, and in related sensorimotor neural structures with mirror properties. Indeed, anthropoid primates rely extensively on the production and processing of facial expressions during proximal communications (Burrows, 2008), which has been associated with a general *mirroring* process at a pre-conscious level that underlies and facilitates sharing of others' behaviors (Keysers & Fadiga, 2008). In contrast, lemurs and other mammals may have evolved tools for social communication and mutual understanding based on shared recognition of odors.

In humans, frontoparietal mirror circuits in connection with specific prefrontal and temporoparietal sections of cortex seem to be crucially implicated in higher order cognitive functions such as cognitive empathy and mental state attribution, suggesting that they may have undergone a process of exaptation during primate

evolution. Whether changes in mate choice and parental attachment (Miller, 1998), specialization of tool use in a social niche (Iriki & Taoka, 2008), or causes completely independent from the evolution of sociality (Shea, 1989) gave rise to the pronounced cognitive empathy in humans is unknown. However, this analysis suggests that the evolution of higher cognitive skills, such as mentalizing, is linked to the coupling between the perceptual and motor systems related to face processing and that it involves affective and emotional processes to a greater extent than previously believed.

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