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Citation

Prochazkova, E. (2021, March 4). *Connecting minds and sharing emotions through human mimicry*. Retrieved from https://hdl.handle.net/1887/3147343

Author: Prochazkova, E.
Title: Connecting minds and sharing emotions through human mimicry
Issue Date: 2021-03-04

Chapter 2

Connecting Minds and Sharing Emotions through Mimicry

Based on: Procházková, E., & Kret, M. E. (2017). Connecting minds and sharing emotions through mimicry: A neurocognitive model of emotional contagion. *Neuroscience & Biobehavioral Reviews*, *80*, 99-114. – PART 1

Abstract

During social interactions, people tend to automatically mimic their interactor's facial expressions, vocalizations, postures, and bodily states. Automatic mimicry might be implicated in empathy and affiliation and is impaired in several pathologies. Despite a growing body of literature on its phenomenology, the function and underlying mechanisms of mimicry remain poorly understood. The current review puts forward a new Neurocognitive Model of Emotional Contagion (NMEC), demonstrating how basic automatic mimicry can give rise to emotional contagion. We combine neurological, developmental and evolutionary insights to argue that automatic mimicry is a precursor to healthy social development. We show that (i) strong synchronization exists between people, (ii) that this resonates on different levels of processing, and (iii) we demonstrate how mimicry translates into emotional contagion. We conclude that our synthesized model, built upon integrative knowledge from various fields, provides a promising avenue for future research investigating the role of mimicry in human mental health and social development.

Keywords: social neuroscience, empathy development, affect, autonomic mimicry, motor mimicry

Introduction

In environments with many rapidly changing elements, brains provide an evolutionary advantage for survival by allowing organisms to extract patterns of information that aid predictions (Adolphs, 2001). Humans, like many other social animals, live in groups. On the one hand, groups can offer better prospects for survival by communication and cooperation, but on the other hand, group members can also form a threat within a group as they can free-ride or exploit other group members (de Dreu et al., 2010, de Dreu et al., 2016). Furthermore, compared to the physical environment, the social environment is relatively unpredictable. Despite its complexity, humans are often readily able to intuit others' feelings and also understand and even anticipate others' actions. This is done seamlessly, without effort, and often without conscious awareness (Dimberg et al., 2000, Tamietto and de Gelder, 2010; Kret et al., 2013a, Kret et al., 2013b; Wood et al., 2016). The remarkable capacity to share others' affective states and empathize with others is the key characteristic of many of humanity's modern achievements. The development of social cognition is closely related to the development of emotional and affective communication between an infant and his or her mother (Adolphs, 2001, Francis et al., 1999, Simpson et al., 2014). Social capacities can be extremely sensitive to even small differences in the environment (Crabbe et al., 1999). When infants are born, their verbal and motor abilities are still very limited and their communication relies mainly on subtle social cues from their environment.

The current literature argues that a potential mechanism that allows humans to recognize (Neal and Chartrand, 2011, Stel and van Knippenberg, 2008, Wood et al., 2016) and share emotions is automatic mimicry (Decety and Lamm, 2006, Schuler et al., 2016, Singer and Lamm, 2009). Automatic mimicry is defined as the unconscious or automatic imitation of speech and movements, gestures, facial expressions, and eye gaze (for an extensive review see Chartrand and van Baaren, 2009). The tendency to automatically mimic and synchronize movements with those of another person has been suggested to consequently result in emotional contagion (Cacioppo et al., 2000). Although the focus in the literature has been predominantly on the mimicry of facial expressions or bodily postures (motor mimicry), evidence is accumulating that humans mimic on many more levels than muscle movements alone.

For example, automatic mimicry is demonstrated by the synchrony of heart-rate and pupil-diameter during social interactions, the tendency to blush when an interaction partner blushes, and the contagiousness of crying or yawning (for a review, see Kret, 2015, Palumbo et al., 2016). During the present review, we refer to the mimicry or synchronization on this more autonomic level as 'autonomic mimicry'. Even though autonomic mimicry might have important consequences for social behavior (i.e. Kret et al., 2015, Kret and de Dreu, 2017), it is an understudied topic in the field of social neuroscience and is therefore one of the key topics of this review.

In two different ways, this chapter aims to provide a new perspective on the role of automatic mimicry in the development of empathy. First, by building upon the perception-action model (PAM) of empathy (Preston and de Waal, 2002), the current review integrates mimicry studies coming from multiple scientific disciplines, ranging from developmental psychology, evolutionary biology and neuroscience in order to explain how automatic mimicry gives rise to complex social cognition. The second aim is to introduce a new Neurocognitive Model of Emotional Contagion (NMEC), which incorporates these additional autonomic pathways to explain how empathic abilities emerge from dynamic synchronous activity between two interacting brains. The NMEC is a multidisciplinary conceptual model explaining mimicry on different levels of processing through which affective information can be shared. This model has laid out how information passes from a sender's face or body to a receiver's brain and subsequently to their face or body, and how the transition of perceptual inputs builds emotional understanding. The purpose of this review is not to provide a complete literature overview of all the mimicry studies that have been conducted (for an extensive review, see Chartrand and Dalton, 2009, Chartrand and van Baaren, 2009, Chartrand and Lakin, 2013, Kret, 2015, Palumbo et al., 2016). Instead, through the integration of evidence from various fields, we aim to provide novel insights into the role of automatic mimicry in the development of human socio-cognitive functions.

Definitions and terminology

Different types of automatic mimicry

First, we define the mimicry terms that we will be using. Although we are fully aware of the fact that 'what is pure mimicry and what is not' is a matter of debate and there are some gray areas, the present review uses the term ‘automatic mimicry’ as an umbrella term for the different types of synchronous behaviors. A distinction in automatic mimicry will be made between ‘motor mimicry’ controlled by the motor muscles which are partly implicit but can also be consciously controlled, and ‘autonomic mimicry’ which relies on an unconscious signaling system that is controlled by the autonomic nervous system (ANS) (Fig. 1). For example, ‘motor mimicry’ occurs when two or more people engage in the same behavior within a short time window (typically between 3 and 5 s), and includes mimicry of motor movements such as facial expressions (Dimberg et al., 2000, Niedenthal et al., 2001), body postures (Tia et al., 2011), vocal characteristics (Gregory and Webster, 1996, Webb, 1969), contagious yawning (Helt et al., 2010), speech gestures (Goldin-Meadow and Alibali, 2013) and laughter (Estow et al., 2007). The second type of automatic mimicry, ‘autonomic mimicry’, involves any associative pattern in the physiologies of interacting partners, such as synchrony in heart rate (Feldman et al., 2011), breathing rhythm (Creaven et al., 2014, Van Puyvelde et al., 2015), pupil diameter (Fawcett et al., 2016, Kret et al., 2015, Kret and de Dreu, 2017) and hormonal level (Laurent et al., 2012, Saxbe et al., 2014).

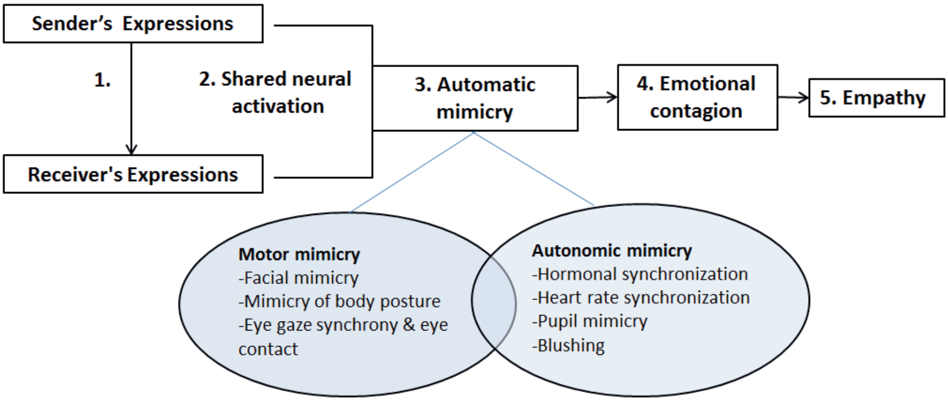

Fig. 1. Schematic Representation of Empathy Development: (1) The sender's (mother's) emotional state is reflected in her nonverbal motor movements (facial expressions, body postures, and eye-gaze) and physiological responses (heart rate, hormonal levels, sweating, facial color, pupil diameter). (2) The perception of a target's

state instantly activates the observer's (child's) neural representations that are also active during the first-hand experience of that same state (shared neural activation). (3) Shared neural activation in turn activates somatic and autonomic responses resulting in motor mimicry & autonomic mimicry. (4) Automatic mimicry facilitates physiological and motor feedback inducing emotion in the receiver (emotional contagion). (5) This helps observer to understand sender's mental state better (empathy).

Emotional contagion

Observation of emotional expressions has been shown to elicit not only motor and autonomic mimicry but also corresponding emotional responses (Hatfield et al., 1994). In the literature this type of emotional mimicry is referred to as to 'emotional contagion'. Emotional contagion is defined as the tendency to take on the sensory, motor, physiological and affective states of others (Hatfield et al., 1994). Hatfield et al. (1994) argued that one of the main mechanisms underlying emotional contagion is automatic mimicry (synchronization of expressions, vocalizations, postures and movements with those of another person). When people unconsciously mimic their partner's expressions of emotion, they come to feel reflections of those emotions as well. It is important to note that while emotional contagion is related to mimicry, it is not the same phenomenon. Emotional contagion is a multilevel phenomenon that can arise from several types of mimicries occurring at different levels of processing (sensory, motor, physiological and affective). For example, if someone mimics our facial expressions, it does not necessary mean that he or she is experiencing the same emotional state as we do. This is because the affective component from motor muscles alone may not always extend to full emotional experience – that is, the psychological feeling associated with the muscle movement. For example, while facial muscles' feedback may help an observer to correctly attribute emotional valence of an expression, a visceral arousal may be necessary to fully emotionally converge (Laird, 1974). In other words, emotional contagion is a higher cognitive/emotional construct that is not necessarily tied to one specific mimicry form.

The evolution of empathy

Many theories share common definitions of empathy. However a failure to agree on the specific psychological processes that constitute empathy has led to considerable disagreement in the field. We adapt the working definition of empathy based on the idea that empathy consists of two main processes:

1. Emotional contagion/hot empathy: the tendency to take on the sensory, motor, physiological, and affective states of others (Hatfield et al., 1994).
2. Mentalizing/Perspective-taking/cold empathy: a mental process that enables humans to take another's perspective and relate to other people's emotions, thoughts, and intentions (Decety and Svetlova, 2012).

The first process is a rather primitive, automatic, implicit, and uncontrollable form of empathy, and is the main focus of this review.

From mimicry to emotional contagion (Fig. 1)

According to Preston and de Waal's (2002) perception-action model, the most basic form of empathy is emotional contagion, which is the tendency to take on the sensory, motor, physiological and affective states of others. A theory developed by Hatfield et al. (1994) proposed that emotional contagion is a result of multiple psychological and behavioral phenomena. This is because emotional contagion can be produced by a complex social stimulation (e.g., a mother giving a verbal compliment/criticism to her child), or a more innate nonverbal stimulus (e.g., mother's positive/negative facial expressions towards her infant). In both cases, these expressions are likely to result in emotional contagion (an affective transfer between the mother and the infant). An example of a display of emotional contagion is an experiment where one mouse receives an electrical shock accompanied by a tone whilst being observed by another mouse. Eventually, the mouse that has been merely observing the scene also freezes in response to the tone, even though the mouse itself has never experienced the sensation of an electrical shock (Panksepp, 1998). The genetic background has an impact on the level of these responses (Chen et al., 2009). In animals, this phenomenon is also called 'observational learning of fear' (for a review, see Olsson and Phelps, 2007). Other evidence comes from studies in great apes in which the apes start yawning when they see conspecifics yawn (Anderson et al., 2004).

Contagious yawning has also been found in budgerigars (Miller et al., 2012). The basic idea is that by observing others, species vicariously learn from their conspecifics to readily adapt the same state as conspecifics, which in turn has survival benefits.

When infants are born, their verbal and motor abilities are still very limited and their communication relies mainly on subtle social cues from their environment. This is why during early development, emotional understanding is likely to take the 'bottom-up' route (de Waal and Ferrari, 2010). It has been suggested that humans have evolved communicative faces with a smooth skin, large eyes, and red lips which ease communication and therefore foster cooperation (Tomasello et al., 2005). During face to face interactions (Fig. 1), the mother's emotional state is reflected in her nonverbal motor movements (facial expressions, body postures, and eye-gaze) and her physiological responses (heart rate, hormonal levels, sweating, facial color, and pupil diameter). Infants, similarly to other animals, implicitly pick up these subtle social signals from caregivers' faces and bodies. This in turn has an impact on the infants' own physiology and cognition.

Research in social neuroscience suggests that the observation of another person's emotional state automatically activates the same neural representation of that affective state in the observer, along with related autonomic and somatic responses (Anders et al., 2011, Gallese and Goldman, 1998, Goldman and Sripada, 2005, Keysers and Gazzola, 2010). Scientists refer to this as 'neural resonance' or 'brain-to-brain coupling' and have documented it as a robust and consistent phenomenon in emotion perception studies (Anders et al., 2011, Jackson et al., 2005, Jackson et al., 2006b, Keysers and Gazzola, 2009, Lloyd et al., 2004, Prehn-Kristensen et al., 2009). Wood et al., (2016) explained that when people observe a facial expression of emotion, they themselves experience partial activation in the corresponding neural populations, which may (or may not) result in automatic mimicry of the emotional expression. According to the facial feedback theory, mimicking facial expressions of emotion helps to recognize the emotional expression of the observed person (Buck, 1980). Through the afferent feedback from one's own muscle movements and changes in arousal, automatic mimicry helps infants to feel what their caregiver is feeling and to better understand a caregiver's mental states. Moment by moment, subjective emotional experiences are affected from such mimicry (Hatfield et al., 1994). This suggests that mimicry might be a precursor to a more general mind-reading capacity. Whereas some have ascribed advanced social capacities observed in humans to the development of language (Astington and Baird, 2005, Astington and Jenkins, 1999), other authors propose that social cognition begins with earlier and more basic and nonverbal characteristics that precede language development (Asada et al., 2001, Preston and de Waal, 2002). In the current review, we argue that the development of empathy begins with the innate drive to implicitly mimic and emotionally align with others.

Fig. 1 shows that when people mimic a perceived facial expression, they partially activate the corresponding emotional systems in themselves. Automatic mimicry and shared neural activation reflect on the underlying sensorimotor simulation that supports the corresponding emotion. Since emotions involve behavioral, physiological, and cognitive components, activation of one component automatically activates other components (Wood et al., 2016). In return, mimicry provides a basis for inferring the underlying emotion of the expresser (Buck, 1980). Instead of the brain being a ‘stimulus–response’ system activated by a specific type of emotion (anger, happiness, fear), the brain rather functions as a generative system which constructs others’ emotions as affective information is gathered over time. While visual information (e.g. pupil size, facial redness) gives a description of visible affective components, it does not provide a full understanding of another individual’s emotional state. For that conjunction, a variety of autonomic input is essential in order to evaluate past experiences and use them as predictions about the state underlying the observed expression.

From emotional contagion to cognitive empathy

Theories of empathy make a distinction between emotional contagion (the primitive form of empathy) and the more cognitive, “sophisticated” processes such as cognitive empathy (Decety and Lamm, 2006, Preston and de Waal, 2002). The key argument for such a distinction is that if empathy is a purely bottom-up process without inhibitory processes (based on the perception-action loop), then emotional contagion could not be controlled. However, this is not the case, as emotional contagion is influenced by social context, for example, by the relationship between observer and expresser (Hess and Fischer, 2013). Emotional contagion is stronger among relatives and familiar others (Gonzalez-Liencres et al., 2014) and autonomic mimicry occurs more often between members of the same species (humans-to-human and chimpanzees-to-chimpanzee) (Kret et al., 2014). While emotional contagion is fast, automatic and is shared by most vertebrates, cognitive empathy has been related to primates and other intelligent animals living in social groups such as dolphins, elephants, and wolves (Sivaselvachandran et al., 2016). In humans, perspective taking does not develop before the age of four, which suggests that empathy is not a purely innate capacity, but that at least certain components develop later in life and probably through learning from interactions with the social environment (Adolphs, 2001, Selman, 1971, Walker, 1980).

Preston and de Waal (2002) posited that since emotional contagion is an ontogenetically and phylogenetically older mental process, cognitive empathy is likely to be an extension of emotional contagion or even an identical process with added functions. In theory, the trajectory of social cognitive development follows a progressive evolutionary/developmental slope. In early childhood, the brain is still very malleable and relies heavily on external inputs. Social schemas and verbal skills are yet to develop and the communication between the infant and its caregiver is largely symbolic. Based on basic reflex-like mimicry, a child continuously learns new associations and an individual's social abilities develop further. This is accompanied by the maturation of prefrontal regions and increased neural density in the anterior cingulate cortex (Gogtay et al., 2004). As the brain matures and becomes more complex and stabilized, accumulated knowledge starts to serve as predictors for further actions, which saves processing energy and the need for vicarious learning. This is why in adulthood, mimicry may become more cognitively redundant and play a rather affiliative function (e.g. serving more and more as a social function; Lakin and Chartrand, 2003, Lakin et al., 2003). However, in infancy, mimicry provides an implicit form of emotional communication and is a fundamental precursor for the development of higher cognitive abilities, including empathy.

The empirical dispute

In recent years the scientific community began to question the role of mimicry, shared neural activation and sensorimotor simulation (facial feedback) in facilitating empathy (Assogna et al., 2008, Hickok, 2009, Jacob and Jeannerod, 2005, Lamm and Majdandžić, 2015). These critiques were not directed at the actual empirical foundations of mimicry per se, but rather the methods of the studies behind the empirical findings. Most mimicry and functional magnetic resonance imaging (fMRI) studies rely on correlations (e.g., comparing mimicry levels with empathy measures from questionnaires/tasks or with neural activation), thus, determining the conceptual significance of mimicry is extremely difficult. In particular, on the one hand, it could be argued that mimicry is a form of emotional contagion that allows the sharing of affective states between species (Gallese and Goldman, 1998, Hatfield et al., 1994). On the other hand, it could be counter-argued that cognitive empathy precedes mimicry. In other words, people first psychologically appraise the social context before they “decide” to empathize and display mimicry. From this standpoint, mimicry could be seen as an epiphenomenon (e.g., of trust) that does not have a direct impact on the development of empathy.

To determine a causal link between mimicry and empathy, earlier research has both studied mimicry in clinical populations and tried to directly manipulate mimicry in healthy populations. For instance, Neal and Chartrand (2011) tested participants’ performance on the “Reading the Mind in the Eyes Test” (RMET; Baron-Cohen et al., 2001) before and after Botox treatment. In line with emotion contagion theories, this study revealed that Botox administration blocked automatic facial mimicry and impaired subjects’ ability to recognize other peoples’ emotions. A classical study by Strack et al. (1988) supports the facial feedback hypothesis by showing that peoples’ facial activity influenced their emotional responses. Another study by Niedenthal et al. (2001) found that blocking facial mimicry influenced participants’ emotional state and decreased their ability to recognize emotional expressions. Similarly, in Oberman et al.’s (2007) study, blocking facial muscle mimicry by biting on a pen or chewing gum selectively impaired recognition of emotional expressions, partially supporting the facial feedback theory stating that facial mimicry enhances emotion recognition. Goldman and Sripada (2005) reported studies showing that deficits in face-based recognition lead to reduced ability to produce the same emotion (fear, disgust, and anger). However, research in clinical populations with impaired facial feedback yield inconsistent findings. Specifically, Bogart’s and Matsumoto’s (2010) study revealed that subjects with Möbius syndrome (facial paralysis) did not significantly differ from the control group in emotion recognition, contradicting the view that facial mimicry is necessary for emotion recognition. Furthermore, research into Parkinson's disease and emotion recognition has yielded mixed reports (see Assogna et al., 2008, for review). Nevertheless, it can be argued that clinical populations have developed compensatory mechanisms to recognize emotional expressions in other people (Goldman and Sripada, 2005). Unfortunately, the variety of methods and population samples used in mimicry research makes it impossible to conduct a solid meta-analysis.

In summary, although mimicry research has been very informative, a careful test for a causal relationship between mimicry and emotion recognition is far from established and is an important issue to be addressed in future research. Despite a growing body of literature, the empirical support for the role of mimicry in emotion processing has remained controversial (Bogart and Matsumoto, 2010, Wagenmakers et al., 2016). We propose that this is partly because the underlying mechanisms of emotional contagion remain largely elusive and not very well integrated. While one line of research describes the neural correlates of face perception (Haxby et al., 2002) and empathy (Carr et al., 2003, Decety et al., 2016, Decety and Lamm, 2007, Decety, 2011, Fan et al., 2011, Mutschler et al., 2013, Singer and Lamm, 2009, Shamay-Tsoory et al., 2009, Shamay-Tsoory, 2011), others have described the non-verbal emotional signals that humans share and mimic (Chartrand and Dalton, 2009, Chartrand and van Baaren, 2009, Chartrand and Lakin, 2013, Kret, 2015). Moreover, very few studies have directly investigated the neural correlates of mimicry (Lee et al., 2006, Harrison et al., 2006). Thus far, no model has described a full cycle of emotional contagion. That is, no model has laid out how information passes from a sender's face or body to a receiver's brain and then to their face or body, and how the transition of perceptual inputs builds emotional understanding. The present review aims to provide such a conceptual model. In the Neurocognitive Model of Emotional Contagion (NMEC), we explain how empathic abilities emerge from a dynamic synchronous activity between two interacting brains. We argue that while shared neural activation and automatic mimicry reflect the degree to which people internally simulate perceived emotional states, importantly, it is the emotional signals – not the mimicry – that drive the common patterns of neural representations that underlie empathy. To provide an in-depth understanding of the behavioral mechanisms involved in emotional communication, in the next section, we propose different levels of mimicry in humans and explain how they may relate to the development of empathy.

Different levels of emotional contagion in humans

Kret's (2015) schematic representation of emotion processing (see Fig. 2) shows that emotions are expressed and experienced within three main communication compartments, namely, psychological (Feelings/Emotions), physiological (Arousal) and behavioral (Expressions). For example, during a social interaction, both person A and person B experience feelings and emotions and these emotions are expressed through physiological reactions and facial expressions. Consequently, emotional contagion is likely to take place through all of these three channels, although they are not always required simultaneously. In the next section, we will use this schematic model to discuss various types of automatic mimicry in infants and discuss their impact on affective and cognitive development. A distinction in automatic mimicry will be made between motor mimicry controlled by facial muscles which are partly implicit, but can also be consciously controlled, and autonomic mimicry which relies on an unconscious signaling system that is controlled by the ANS. In the next section (5.1), we will primarily focus on autonomic mimicry, which is an underexplored area in the emotional contagion literature. In addition, we will also review several studies on motor mimicry.

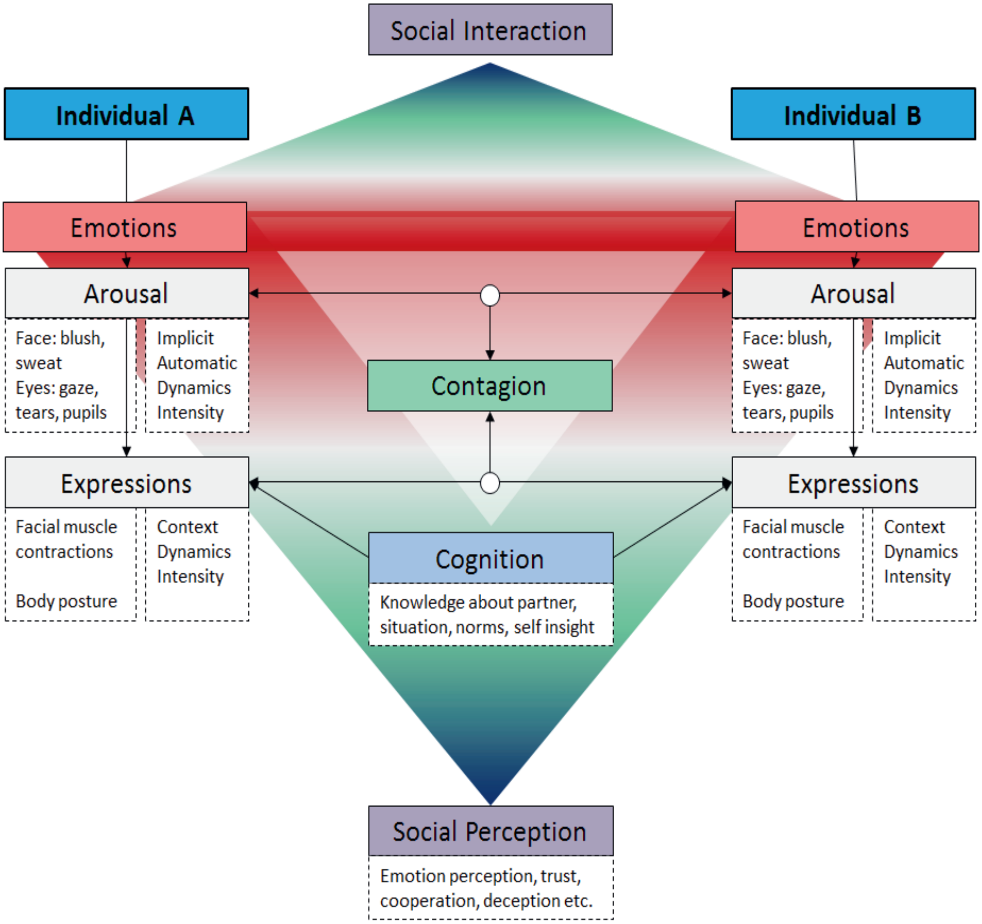

Fig. 2. Schematic representation of emotion processing during social interactions, adapted from (Kret, 2015; Fig. 1) shows how emotions that are expressed during a social interaction by Person A, through emotional contagion, influence the emotions and expressions of Person B. Person A and B not only mimic each other's facial expression, they also link on the physiological level and without being aware of it, synchronize on the level of arousal.

Motor mimicry

1. Facial muscle mimicry

One physical characteristic that distinguishes humans from any other species is the high level of expressiveness of the human face. Humans' closest relatives in the animal kingdom, namely chimpanzees, have strikingly similar underlying mimetic musculature in their faces (Parr and Waller, 2006). Still, humans have slightly more refined muscles, especially around the eyes, and also smoother skin, readily revealing muscle movement. Moreover, humans use a greater variety of facial expressions and also detect facial movements with more speed and precision (Vick et al., 2007). The emotions people experience are often automatically displayed in facial expressions without conscious awareness or voluntary intention. Infants generate, attend to and mimic facial expressions soon after birth (see Simpson et al., 2014, for a review). Several studies have demonstrated that when a researcher shows an infant a facial expression or gesture, such as the wiggling of a tongue, the infant repeats the gesture by wiggling its tongue back (Anisfeld, 1996, Field et al., 1982, Jones, 2006). This evidence has fostered the theory that the innate tendency to imitate precedes emotional understanding and empathy development in humans (de Waal and Ferrari, 2010, Meltzoff and Decety, 2003a).

A landmark study by Meltzoff and Moore (1983) provided evidence that very young infants ranging between 1 h and 3 days old already imitate the behavior of strangers. Psychophysiological research has found that facial mimicry is at times almost instantaneous as people seem to be able to track the most subtle moment-to-moment changes in their partners' faces (Dimberg et al., 2000). These micro-expressions are so subtle that they sometimes cannot be detected by the human eye and can only be measured through electromyography (EMG), i.e., with electrodes that are sensitive to micro-movements of the facial muscles (Dimberg and Thunberg, 1998, Tamietto et al., 2009). In line with the facial feedback theory, some evidence suggests that people do indeed recognize emotions from other peoples' faces by experiencing changes in their own physiological state. In the Ekman et al. (1983) study, participants were asked to produce the following six basic emotions; disgust, surprise, anger, fear, sadness and happiness. They were requested to either recall times when they experienced such emotions, or to arrange their facial muscles according to these emotions. This study revealed that both the act of recalling emotional experiences and the production of facial expressions produced the same skin conductance response. This finding suggests that facial expressions can generate ANS responses informing an observer about the partner's emotional experience. In another study, Dimberg et al. (2000) tested the implicit activity of facial muscles involved in smiling and frowning in response to emotional pictures of faces. They predicted that if distinct emotions can be automatically elicited by subliminal cues, then the unconscious exposure to happy or sad faces should differentially activate these muscles. In line with this hypothesis, the results revealed that participants' muscle responses were implicitly elicited and corresponded to the muscle movements that were generated during happy and sad facial expressions, even though participants reported not being aware of the stimuli presentation, nor of their own muscle movements. Similarly, Tamietto et al. (2009) found that facial and bodily expressions trigger fast emotionally congruent facial expressions in observers. Interestingly, this effect was enhanced when affective stimuli were presented subliminally. Niedenthal et al. (2012) showed that a pacifier disrupted facial mimicry in male children and was associated with compromised emotional development (lower perspective taking and emotional intelligence). The pacifier use did not predict these emotion processing skills in girls.

The above-reviewed findings suggest that people (a) are generally not consciously aware of subtle changes in a partner's facial characteristics and (b) do not voluntarily react to them, but still process these subtle signals as is demonstrated by mimicry. By doing so, they process information about a partner's emotional expressions via their own physiological feedback. Oostenbroek et al.'s (2016) recent longitudinal study of 106 infants between the ages of one and nine weeks, failed to replicate evidence for infants' imitation of any of the 9 observed gestures previously reported in the literature. With regards to this replication failure, the authors challenged the view that imitation is an innate capacity. However, as mentioned earlier, facial mimicry is only one type of mimicry. Motor mimicry can be implicit and without awareness, but can also, to some extent, be consciously inhibited and controlled. We refer to this type of mimicry as motor mimicry, as muscle movements are involved which rely on the activation of motor preparation areas. In the following section, we will review some other types of motor mimicry (eye-contact and contagious crying) in order to give examples of how motor muscles may have an impact on affective behavior and mental health later in life. We will then review research showing that in addition to motor movements, infants mimic the pupil sizes of observed others (Fawcett et al., 2016), cardiovascular responses (Feldman et al., 2011; Moore et al., 2007) and hormonal levels (Laurent et al., 2012). The broad variety of the different types of mimicry documented in the literature suggests that social information can be shared on many more levels than previously thought.

2. Eye contact

One of the earliest and most salient types of automatic mimicry is dyadic joint attention, or mutual eye-gaze. In our view, eye contact classifies as mimicry simply because in order to make eye contact, two people must be able to synchronize their eye movements. Research shows that direct eye contact is related to other forms of mimicries (e.g., Feldman, 2012, Wang et al., 2011) and it's abnormalities has been linked to problems with empathy (Charman et al., 1997) and autism (Senju and Johnson, 2009). During close interactions, both infants and adults focus on their interactive partner's eyes, grasp emotion signals from the eye whites and pupils, and follow eye gazes (Baron-Cohen et al., 1995, Kret and de Dreu, 2017, Haith et al., 1977). Research shows that the direct eye region captures more attention than an averted gaze (Farroni et al., 2002). By following gazes, people can follow the path of a partner's attention and get insight into his/her emotions to facilitate shared experiences (Baron-Cohen et al., 1995). Research has reported that direct eye contact increases autonomic mimicry in heart beat between a mother and a child (Feldman et al., 2011). Wang et al. (2011) found that direct eye gaze increases the speed of mimicking hand movements by 13 ms compared to an averted gaze. The authors proposed that this is possibly because direct eye gaze relies on an innate biological system that inevitably stimulates arousal levels in the observer, which in turn leads to faster processing of the social situation and fosters social understanding. Whether eye contact can be accounted for a type of mimicry might be disputable, however the fact that eye contact is a contagious communicative signal that transfers affective information is undeniable. Furthermore, similar to facial mimicry, eye contact is an innate reflexive human predisposition that is not always under our conscious control, which makes it a likely source of emotional contagion (Kret, 2015). Consistent with this, longer eye contact is positively correlated with trust, sexual attraction and openness, but also with aggression and fear (Kleinke, 1986). In light of this evidence, we conclude that eye contact is of the utmost importance and fosters emotional contagion.

3. Contagious crying

Most people who have visited a newborn ward will have noticed that crying is contagious. Martin and Clark (1982) played audio recordings to newborns and found that one-day-old babies were more likely to mimic crying when they heard a recording of another newborn crying than when they heard their own cries or those of a much older infant. The specificity of mimicking supports the view that crying mimicry is not merely the result of elevated noise but is a contagion mechanism. Geangu et al. (2010) tested infants at 1, 3, 6, and 9 months of age in response to different types of cries. Their emotional reactions were recorded in terms of vocal (presence of vocal distress, latency, and intensity) and facial expressions (anger and sadness). The results revealed that infants from all age categories mimicked crying, and distress was highest in response to cries of pain. The ability to distinguish between different types of crying and to respond in kind has been proposed as one of the first signs of empathy in humans.

In the previous section, we reviewed different levels of emotional contagion in humans. Kret's (2015) schematic representation of emotion processing during social interactions shows that mimicry is very broad and complex. People mimic not only motor expressions, but also autonomic signals, which is still an underexplored area in current emotion research. In the next section we will review such evidence demonstrating that apart from facial expressions, direct eye contact, and contagious crying, adults and young infants also tend to mimic autonomic responses which rely on an unconscious signaling system that is controlled by the ANS. Importantly, these autonomic signals are harder to control than facial muscles, they add to the perceived intensity of an expression, and can even over-ride the emotion that facial muscles try to reveal (Kret, 2015).

Autonomic mimicry

1. Physiological linkage

Mothers and their children share a deep physiological connection. This type of physiological linkage is shared by most mammals and represents the earliest form of emotional contagion that occurs between a mother and a child before the child is born

(Feldman, 2012). In 2010, a team of doctors at Sydney hospital witnessed the almost miraculous power of physiological connections. Kate Ogg put her prematurely-born son on her chest, whispering soothing words of comfort. Her doctors told her that her son Jamie would die soon, and that she should prepare to say goodbye. Then, unexpectedly, little Jamie moved. After two hours of skin-to-skin contact, Jamie, to the immense surprise of the medical staff, opened his eyes. He is now a healthy young boy living with his family and twin sister in Sydney (Crane, 2015).

The current literature posits that what saved little Jamie's life was a physiological synchrony between him and his mother (Feldman et al., 2014). Accumulating evidence reports that skin-to-skin contact between mother and infant can significantly reduce neonatal mortality (Feldman et al., 2014, Lawn et al., 2010). Researchers attest that this is because when infants are put into direct contact with the skin of their mothers, this has a positive impact on the child's physiological adaptation and behavior (for a systematic review and meta-analysis see Moore et al., 2007). Research shows that the mammalian's ANS develops through tactile, thermal, and nutritive stimuli provided by the mother's body (Hofer, 1987). Mother-infant synchrony in autonomic physiology is a well-documented phenomenon (for a systematic review, Palumbo et al., 2016). In psychology, this is also called "autonomic mimicry", "physiological linkage" or "physiological synchrony", and refers to any associative pattern in the physiologies of interacting partners. Because infants breathe irregularly and have a faster heart rate than adults, by feeling their mothers' heart palpations and breathing movements, they automatically mimic their mother's cardiovascular responses and temperature and more quickly reach homeostasis (Gray et al., 2000; Moore et al., 2007). The skin-to-skin contact early after birth is associated with reduced stress, an enhanced mother-infant bond, and cognitive development up to 25 years later (Charpak et al., 2005).

Interestingly, autonomic mimicry can also occur without any direct physical contact (Levenson and Gottman, 1983, Palumbo et al., 2016). This is a striking observation considering that physiological states are uncontrollable and (with the exception of the pupil) are invisible to an interaction partner. For instance, research suggests that during non-physical close interactions, mothers and infants synchronize their heart rhythms and breathing patterns (Feldman, 2011; Palumbo et al., 2016).

Interestingly, the heart rate synchrony significantly increases when the mother and child mimic each other's smiles and show vocal mimicry, which suggests a further link to affective communication. Although mother-infant ANS synchrony is generally a positive marker, the physiological linkage can also have a negative impact. Animal studies, mainly in rodents, have revealed that early maternal contact is related to physiological and behavioral processes that have an impact on the infant's system-level brain development. These regulatory systems are essential for the support of cognitive and social skills as well as the management of stress and homeostasis (Hofer, 1987, Meaney, 2001). For example, numerous studies have reported that maternal stress negatively impacts on the development of an infant’s Hypothalamic-Pituitary-Adrenal (HPA) axis and mental health (Van den Bergh et al., 2008, Weinstock, 2005).

Dysfunction of the HPA axis is expressed by elevated cortisol levels and is related to increased vulnerability to stress and depression (Shea et al., 2005, Heim et al., 2008). A recent longitudinal study by Van Puyvelde et al. (2015) assessed respiratory sinus arrhythmia (RSA) – synchrony of breathing rate and heart rate (a physiological marker of parasympathetic response). In this experiment, mothers breathed at varying paces while holding their infants. The testing was repeated every week for an eight-week-long period and then again in the twelfth week. This study showed that mother-infant dyads’ RSA synchronized across different breathing paces up until the infants were eight weeks old. A link between autonomic mimicry and parenting behavior was found in Creaven’s and colleagues’ (2014) experiment examining the effect of child maltreatment on heart rate and RSA synchrony in 104 mother-child dyads. Importantly, the researchers tested mother-child groups that exhibited child maltreatment as well as groups that exhibited no child maltreatment. The mother and child (3–5 years old) pairs were resting quietly in near proximity while watching an animated (low-action) video. A significant positive correspondence was found in the heart rates of non-maltreating mother-child groups, while negative heart rate synchrony was found between mothers and children in the maltreating groups. Apart from heart rate and RSA, a recent study reported triadic autonomic mimicry between 103 adolescents and their parents during a family conflict discussion task (Saxbe et al., 2014). Researchers sampled saliva before and after a conflict and found a positive correlation between cortisol levels of the parents and adolescents. Results showed that the mothers' cortisol levels were predicted by those of the adolescents, the fathers' cortisol levels were predicted by those of the mothers, and adolescents' cortisol levels were predicted by those of the fathers. The authors concluded that during family interactions, members displayed shared physiological reactions which reflected family dynamics. Papp et al. (2009) examined parent-adolescent cortisol synchrony in 45 families. Results indicated a significant covariation over time in mother-adolescent cortisol levels. In addition, mother-adolescent cortisol synchrony was strengthened among dyads in which mothers and adolescents spent more time together, and in families with high parent-adolescent shared activities and high parental supervision.

The evidence reviewed here shows that the physiological state of a mother can directly affect the physiological profile of a child, which is also translates into the psycho-emotional interaction between the pair. However, this physiological linkage is only beneficial if the mother is psychologically healthy and has normal HPA activity and if the infant exhibits normal attachment patterns to the mother (Van den Bergh et al., 2008, Weinstock, 2005). Only recently have researchers started to argue for a broader exploration of emotional signals from other autonomic sources. Specifically, the synchronization of pupil-diameter, blood profusion of the skin (i.e. redness), and temperature have all been proposed as potential autonomic pathways to emotional contagion (Kret, 2015). These signals are directly related to changes in the ANS and therefore are much harder to control than facial muscles. Yet, because at least some of these signals (for example pupillary changes) are principally visible to observers, they might add to the perceived intensity of facial expressions or even overrule the emotional signals that facial muscles try to communicate. For instance, a smile combined with red cheeks may be interpreted differently than a smile on a very pale face.

2. Pupil mimicry

Changes in pupil diameter are related to ANS activity (Partala and Surakka, 2003). While pupil dilation is a physiological marker of the sympathetic 'flight-or-fight response', the constriction of pupils is part of the parasympathetic 'rest and digest response'. What makes pupils especially interesting is that in contrast to most other physiological expressions of autonomic arousal such as GSRs (Galvanic Skin Responses), cardiovascular changes and neural activity, pupil-size changes are, consciously or unconsciously, in principle visible to others. Hess et al. (1965) presented heterosexual and homosexual groups pictures of males and females. They found that heterosexual males showed a greater pupil response when looking at pictures of women than when looking at pictures of men, while homosexual males showed a greater pupil response when looking at pictures of men than when looking at pictures of women. Hess (1975) was the first to argue that in addition to adaptations to changes in light in the environment, pupils may also fulfill a social function as they constitute an implicit form of communication between people. In one of the first experiments on the topic, Hess (1975) presented participants with pairs of pictures of the same young woman; the pictures were completely identical except for one small difference: in one of these pictures the woman had relatively large pupils, while in the other picture her pupils were made relatively small. Participants, unaware of this manipulation, perceived the woman with large pupils as friendlier, softer, and warmer than the woman with the small pupils. This evidence was the first to show that another's pupil size is processed and implicitly picked up by observers. Kret (2015) argues that this positive association is formed through pupil-mimicry, also dubbed 'pupillary contagion' (Harrison et al., 2007, Fawcett et al., 2016). Pupil mimicry is not uniquely human, but has also been observed in chimpanzees (Kret et al., 2014). In a study including both humans and chimpanzees, Kret and her colleagues found that pupil sizes synchronized between partners of the same species during social interactions, but not during cross-species interactions. In a second study including only humans, a link with behavior was observed: when participants synchronized their pupil size with the dilating pupils of their virtual partner, they established greater trust in their partner (Kret et al., 2015). Intriguingly, this only worked for interactions with partners from the same ethnic group. These findings have recently been replicated (Kret and de Dreu, 2017). Another recent study revealed that even 6 and 9-month-olds infants exhibit pupil mimicry (Fawcett et al., 2016). This evidence suggests that pupil mimicry is inborn or develops early in infancy, which is supportive of the view that pupil-mimicry might be an early contagious mechanism that constitutes affective transfer between individuals and in this way contributes to social behavior.

3. Blushing

An as of yet understudied form autonomic mimicry can take is blushing. Blushing occurs when individuals experience strong affect, which leads their skin to become perfused with oxygenated blood (Drummond and Lazaroo, 2012). Such a change is directly observable as increased redness of the face. People associate redness in the face with health, anger, or aggression; however, blushing may also signal shyness or embarrassment (Dijk et al., 2009, Dijk et al., 2011, Shearn et al., 1990). It is possible that blushing has evolved as a passive behavioral defense, confirming a lower status in the social hierarchy. Indeed, redness of the face has been shown to affect observers' social judgments. For example, Dijk et al. (2011) found that higher levels of redness were associated with greater trust. In their experiment, subjects played a prisoner's dilemma game on a computer screen with a photograph of an opponent who defected subjects during the game. A photograph of the opponent displayed either a blushing face or a face with a neutral color. The follow-up trust task showed that blushing opponents were trusted more as they were expected not to defect again. Another recent study by Drummond and Bailey (2013) demonstrated that direct eye contact evoked blushing independently of a participant's subjective negative affect. This finding implies that blushing is not necessarily related to conscious feelings of social awareness, but can be an unconscious bottom-up physiological response to nonverbal social cues. Even though no direct evidence presently exists for 'blushing mimicry', the literature reviewed here demonstrates that, like pupil size, blushing is an autonomic response that is difficult to control, and therefore may be another contagious mechanism that plays a social signaling role, providing an implicit form of communication between individuals.

In the previous section we reviewed evidence showing that during early life humans align their physiology with their caregivers. This, in turn, has an impact on their social behavior. The autonomic mimicry between the infant's and mother's moment-by-moment physiologic states suggests that infants possess a finely tuned physiological system that is sensitive to its caregivers' autonomic cues (Feldman et al., 2014). Furthermore, the evidence reviewed here supports the view that emotional contagion and social bonds operate both on the physiological and cognitive level. The fact that emotional contagion between a mother and a child can have both positive or negative impacts on a child's socio-emotional development, and that mimicry occurs at different levels of processing (behavioral/autonomic), complements this work's view that empathic abilities emerge from the physical-cognitive interaction during a child's development with its social surroundings. In the next section, we will explain how emotional contagion may work on a neurocognitive level.

The correspondence problem

Mimicry requires the mimicker to solve the correspondence problem; the ability to translate visual information from an observed action into matching motor output (Heyes, 2005). For more than three decades this has been a widely debated problem in developmental psychology and neuroscience. Meltzoff and Moore (1997) put forward an active intermodal matching model (AIM), arguing that the correspondence problem is solved by an innate cognitive mechanism or 'body scheme' that computes and detects similarities between observed and executed acts. Infants' own facial expressions are not directly visible to themselves, but they are still perceived/felt by them. For instance, when infants see facial movements, these movements are mapped onto the infant's own facial movements. This transition is reflected in mimicry. Meltzoff (2002) proposed that infants' imitation implicates 'an innate common code of human acts' or 'supramodal' representation that provides transformations of acts between the self and the other. In later work, Meltzoff and Decety (2003b) linked the neural basis for common coding to areas known to be involved in the mirror neuron system (premotor cortex and the superior and inferior parietal cortices, in particular, the right inferior parietal cortex is involved specifically in the intention to imitate). Some researchers have posited that infants begin to understand others' actions through a direct link between action observation and execution supported by the mirror neuron system (Gallese and Goldman, 1998). Nevertheless, further specifications of the code that would explain how understanding is formed through action observation are still under empirical debate. Rizzolatti and Craighero (2004, p.172) proposed that "Each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's *premotor cortex*. This automatically induced motor representation of the observed action corresponds to that which is spontaneously generated during the active action and whose outcome is known to the acting individual. Thus, the mirror system transforms visual information into knowledge". The central idea is that observing the same movement in others enables self-generated movements which induce inherent meaning of the observed action. From a developmental perspective, the AIM model suggests that a newborn infant receives information about others intentions based on sensorimotor resonance from its own motor neurons and muscle movements. The problem is that such a theory only works when one sensory input is associated with *one* cause (Hickok, 2009, Kilner et al., 2007). In real life, the same sensory input can have many causes. For example, one may cover one's eyes to protect them from the burning sun or hide them in embarrassment. Thus, an identical movement may have several causes and goals in executors and multiple possible interpretations in observers.

In contrast to the AIM view, more recent findings from cognitive neuroscience, artificial intelligence, and the evolution of cognition are suggestive of an alternative argument: 'a wealth of the stimulus' argument (Ray and Heyes, 2011). The 'wealth of the stimulus' argument suggests that the reciprocity between human social behaviors provides sufficient information to power associative learning and ontogenetically develop the capacity to imitate (Smith et al., 1999, Thelen, 2001). In contrast to the AIM model, Associative Sequence Learning (ASL) by Ray and Heyes (2011) proposes that infants can learn flexibly from their own environment and therefore are not dependent on a specialized 'innate cognitive mechanism'. The principle of associative learning is that in order to be able to mimic a perceived action, an infant first needs to see the action and perform the contingent action quickly after, such that the perception and action are close together in time. Indeed, observational studies in young children show that infants spend a large amount of time looking at their limbs and exploring sensorimotor changes produced by their movements (Rochat, 1998). But even more crucially, the experience of being imitated is fundamental for the development of imitation in humans (Ray and Heyes, 2011). Research shows that infants spend most of their waking time interacting face-to-face with their caregiver. Of this time, 65% consists of adults expressing salient emotions which are imitated by the infants

(Uzgiris et al., 1989). Imitation occurs very frequently; approximately once a minute in mother-infant face-to-face interactions, with most time consisting of the mother imitating the child (Pawlby, 1977). Hickok (2009) argues that perhaps just like unconscious reflexes, mirror neurons do not code for any particular meaning or goal-directed action. Instead, similarly to Pavlovian associations, the activity of mirror neurons simply reflects on associative learning via sensory–motor pairings. In support of this theory, evidence shows that mirror system activation can be recoded with training such that it becomes associated with a completely different action (Catmur et al., 2007). In summary, while the AIM model assumes an innate mechanism, which automatically converts the sensory signals related to the mother's behavioral states to the corresponding motor states of the receiver, without any prior experience (or training), the ASL model assumes extensive learning (or conditioning) experience.

Building upon previous influential neuroscientific reviews (Decety, 2010, Kret, 2015, Schuler et al., 2016, Tamietto and de Gelder, 2010), we here introduce a new Neurocognitive Model of Emotional Contagion (NMEC). In contrast to a detailed list of all neural substrates involved in each component of empathy that can be found in previous literature (Carr et al., 2003, Decety, 2011, Nummenmaa et al., 2008, Shamay-Tsoory, 2011), the NMEC describes how social signals dynamically pass from senders' facial displays to receivers' brains and bodies, and how the transition of perceptual inputs builds emotional understanding. In particular, we propose that the understanding of actions and emotions may rely on more general perception–action matching mechanisms. The NMEC shows that measurements of several types of mimicry at once will provide a more holistic physiological profile of the level to which people understand/process other people's social signals. This conceptual framework has practical implications for further clinical and developmental research (Kret and Ploeger, 2015). The concrete mapping of its mechanisms should be an important aim for future research.