Neuroscience and Biobehavioral Reviews 80 (2017) 99–114

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

Connecting minds and sharing emotions through mimicry: A neurocognitive model of emotional contagion

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ARTICLE INFO

Keywords:
Social neuroscience
Empathy development
Affect
Autonomic mimicry
Motor mimicry

ABSTRACT

During social interactions, people tend to automatically align with, or mimic their interactor's facial expressions, vocalizations, postures and other 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) 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.

1. 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). As a consequence of responsiveness to one's own behavior, 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 Castelli, 2009; Tamietto and de Gelder, 2010; Kret et al., 2013a,b; 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 the muscle movements alone. For example, this 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

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http://dx.doi.org/10.1016/j.neubiorev.2017.05.013
Received 27 October 2016; Received in revised form 25 April 2017; Accepted 11 May 2017
Available online 12 May 2017

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 article 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 a 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.

2. Definitions and terminology

2.1. 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).

2.2. 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). The literature refers to this type of emotional mimicry 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 it. 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.

3. The evolution of empathy

Many theories share common definitions of empathy. Much disagreement in the field is the result of scientists failing to agree on what specific psychological processes empathy encompasses. We adapt the working definition of empathy based on the idea that empathy consists of two main processes:

Emotional contagion/hot empathy: the tendency to take on the

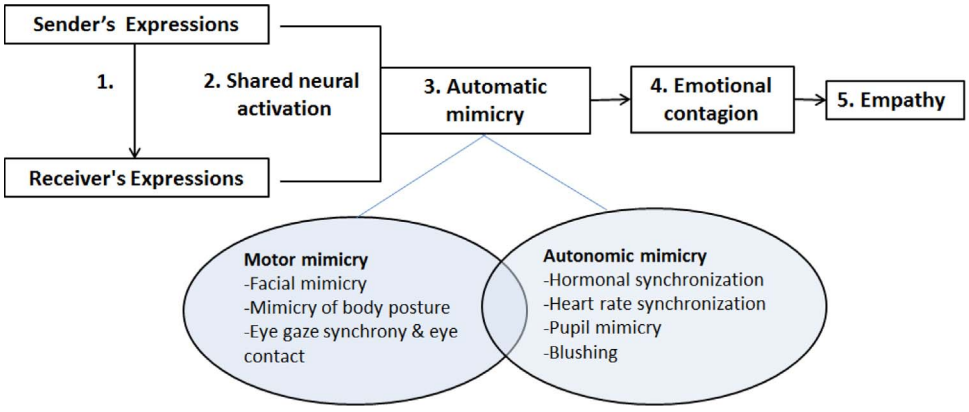

Fig. 1. Schematic Representation of Empathy Development: (1) The sender's (mother's) emotional state is reflected in her nonverbal motor movements (facial expressions, body postures, and eye-gaze) and physiological responses (heart rate, hormonal levels, sweating, facial color, pupil diameter). (2) The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

sensory, motor, physiological, and affective states of others (Hatfield et al., 1994).

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 one is rather primitive, automatic, implicit, and uncontrollable form of empathy which is also the main focus of this review.

3.1. 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, for example, comes from studies in great apes whereby 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 have 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 fostered 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 infants' own physiology and cognition.

Research in social neuroscience suggests that observation of another person's emotional state automatically activates the same neural representation of that affective state in the observer, along with autonomic and somatic responses related to them (Anders et al., 2011; Gallese and Goldman, 1998; Goldman and Sripada, 2005; Keysers and Gazzola, 2010). Scientists referred to this as 'neural resonance' or 'brain-to-brain coupling' and have documented that this is 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 inarousal, 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 gathered over time. While the visual information (e.g. pupil size, facial redness) gives a description of the visible affective components, it does not provide a full understanding of the other's emotional state. For that conjunction, a variety of autonomic input is essential to evaluate past experiences to predict the posterior probabilities that serve as a prediction about the observed expression.

3.2. 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.

4. 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. Instead, thus 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 tried to manipulate mimicry in humans and by studying mimicry in clinical 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 are coupled with problems to produce the same emotions (fear, disgust, and anger). However, research in clinical populations with impaired facial feedback yield contradictory 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). Of course, it can be argued that clinical populations have developed compensatory mechanisms to recognize emotional expressions in other people (Goldman and Sripada, 2005). The great 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 (Assogna and Pontieri, 2008; Bogart and Matsumoto, 2010; Wagenmakers et al., 2016). We propose that 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.

5. 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.

5.1. Motor mimicry

5.1.1. 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

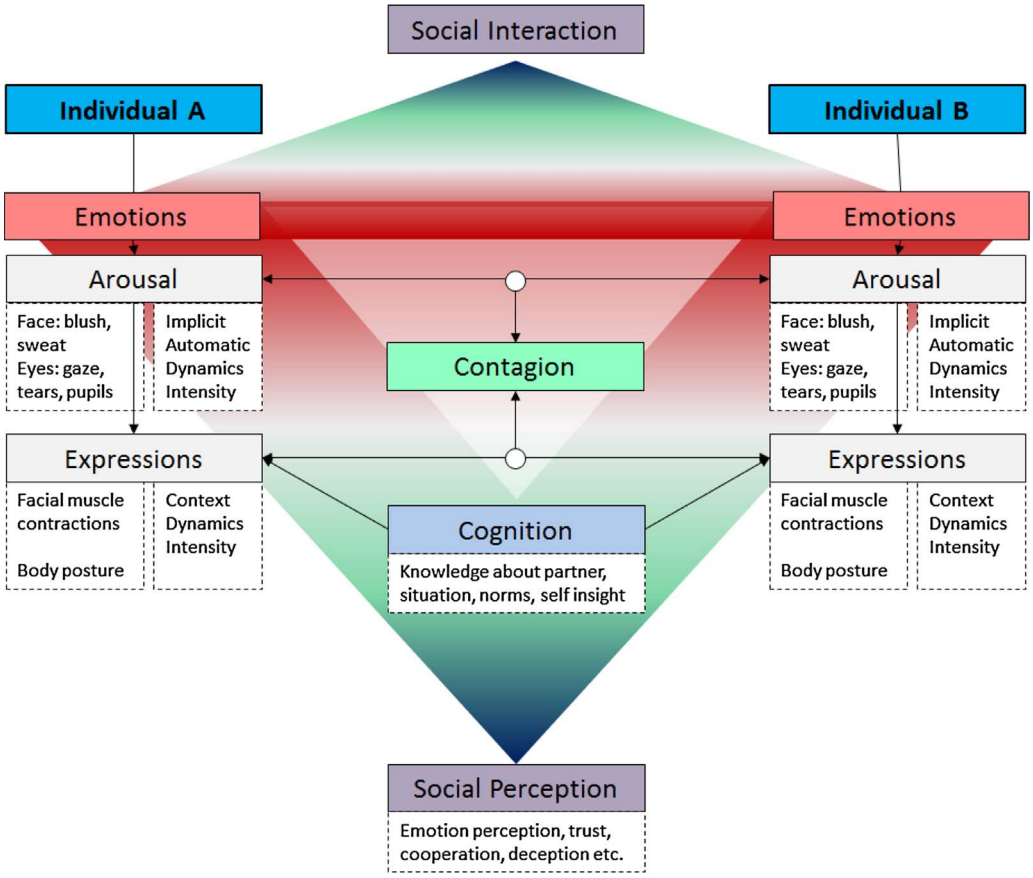

Fig. 2. Schematic representation of emotion processing during social interactions, adapted from Fig. 1, Kret (2015) shows how *emotions* that are expressed during a social interaction by Person A, through emotional *contagion*, influence the emotions and expressions of Person B. Person A and B not only 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.

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 imitated 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 be consciously inhibited and controlled, to some extent. We refer to these types of mimicries 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.

5.1.2. 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 also 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, get insight into his/her emotions and also share 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, nevertheless, the fact that eye contact is a contagious communicative signal that transfers affective information is undeniable. With the muscles attached to their eyeballs. Conceptually, we do not see any reason why certain muscles should be excluded from mimicry. 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.

5.1.3. Contagious crying

Most people who have visited a new-born ward will have noticed that crying is contagious. Martin and Clark (1982) played audio recordings to new-borns. They 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 heard a much older infant crying. 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, whereby the distress was highest in response to cries of pain. The ability to distinguish between different types of crying that is accompanied by the similar response of distress has been claimed to be 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 and they add to the perceived intensity of an expression, or even over-ride the emotion that facial muscles try to reveal (Kret, 2015).

5.2. Autonomic mimicry

5.2.1. 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 already before birth (Feldman, 2012). In 2010, a team of doctors at Sydney hospital witnessed nothing less than the miraculous power of this strong physiological connection. Kate Ogg has put her prematurely-born son on her chest, whispering words of comfort in soothing words. Doctors told her that he would die soon, and she was prepared to say her last goodbye. Then something unexpected happened, little Jamie moved. She cried for help, but doctors refused to come back, believing it was only a reflex; they didn't want to keep Kate in denial. After two hours of skin-to-skin contact, Jamie opened his eyes. Jamie is a healthy young boy today, he lives with his family and twin sister in Sydney (Crane, 2015).

The current literature agrees 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 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 controls heart beat and 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 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 except for the pupil size, 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 its 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 brain system development. These regulatory systems are essential for support of cognitive and social skills that manage stress and guide organisms in its environment (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 andis related to increased vulnerability to stress and depression (Shea et al., 2005; Heim et al., 2008). Field et al. (1989) tested the coherence and cross coherence in heart rate and behavioral states in mother–-infant dyads with depressed and non-depressed mothers while dyads were interacting face-to-face. The results showed that there was a synchrony in heart rate for both depressed and non-depressed dyads, showing no difference in autonomic mimicry between depressed and non-depressed dyads. 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. The autonomic synchrony was observed until infants were 8 weeks old, but dyads no longer synchronize at week 12. 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. 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. The RSA synchrony was negatively correlated in both 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. During this laboratory study, fathers', mothers', and adolescents' cortisol levels were positively correlated. Results showed that the mothers' cortisol level was predicted by that of the adolescents', the fathers' cortisol level was predicted by that of the mothers', and adolescents' cortisol level was predicted by that of the fathers'. The authors concluded that during family interactions, members displayed shared physiological reactions which reflect 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 here reviewed evidence shows that the physiological state of a mother can directly affect the physiological profile of a child, which is also translated in the psycho-emotional interaction between the pair. However, this physiological linkage is only beneficial if the mother is psychologically healthy and has a normal HPA activity and if the infant is normally attached to her (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.

5.2.2. 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 principal visible to others. Hess et al. (1965) presented heterosexual and homosexual groups pictures of males and females. They showed that heterosexual males showed a greater pupil response when looking at pictures of women than when looking at pictures of men. For the homosexual group, it was the other way around. 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 one 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 and has been observed in chimpanzees as well (Kret et al., 2014). In their study, which included 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 human study, 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 in a study (Kret and de Dreu, 2017). Another recent study revealed that also 6 and 9-month-olds infants show 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.

5.2.3. Blushing

Another form of autonomic mimicry may be found in blushing; although this has not been investigated substantially. What is known about blushing is that when people experience a strong affect, their skin gets perfused with oxygenated blood (Drummond and Lazaroo, 2012). Such a change is directly observable by increased redness of the face. People associate redness in the face with health, anger or aggression; however, blushing may also signal shyness or embarrassment (Dijket 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. Redness of the face has been shown to affect observers' social judgments. For example, Dijk et al. (2011) found that higher levels of redness are associated with greater trust. In this experiment, subjects played a prisoner's dilemma game on a

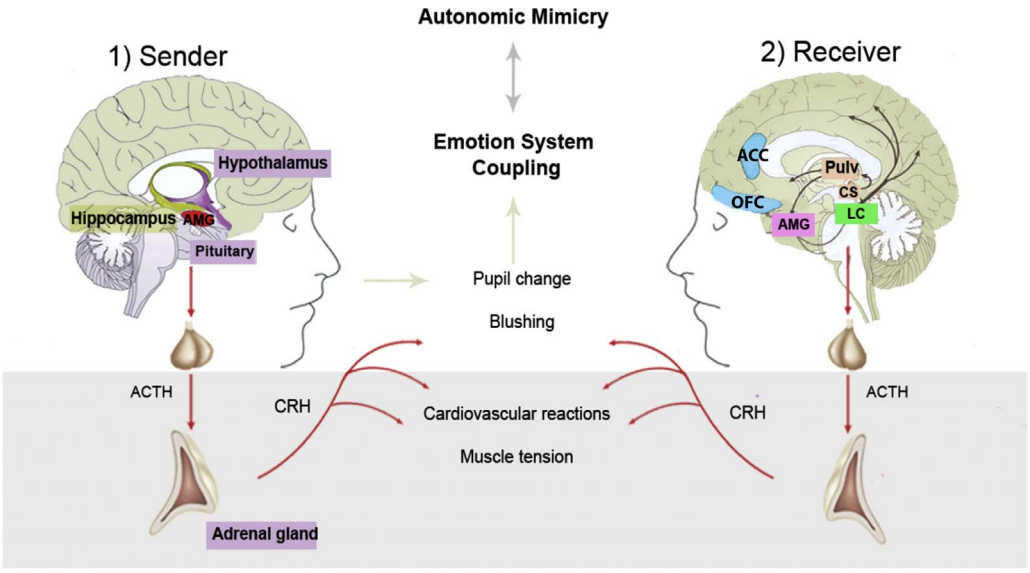

Fig. 3. Neurological Mechanisms of Autonomic Mimicry. **Sender**: (1) Sender's stress response is initiated by hypothalamus-pituitary-adrenal axis activation. (2) Adrenal gland secretes ACTH increasing the level of CRH in the bloodstream. (3) The neuroendocronological reactions are accompanied by cardiovascular changes, muscle tension, pupil dilation, blushing, and sweating. **Receiver**: (4) The affective information is implicitly registered by receivers' senses and passes through (5) the CS-Pulv pathway to the AMG. (6) The AMG and LC activate the HPA. (7) AMG and LC project to higher cortical networks such as OFC, ACC and VMPFC influencing social decisions. (8) Sender and receiver emotionally converge on *physiological* (gray) and *cognitive* (white) levels.

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 evokes 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 have reviewed evidence showing that at the beginning of life, people 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 system that is sensitive to its caregivers' autonomic cues (Feldman et al., 2014). Furthermore, the here reviewed evidence 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 a positive or a negative impact on a child's socio-emotional development. And also 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 surrounding. In the next section, we will explain how emotional contagion may work on a neurocognitive level.

6. 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 believe 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

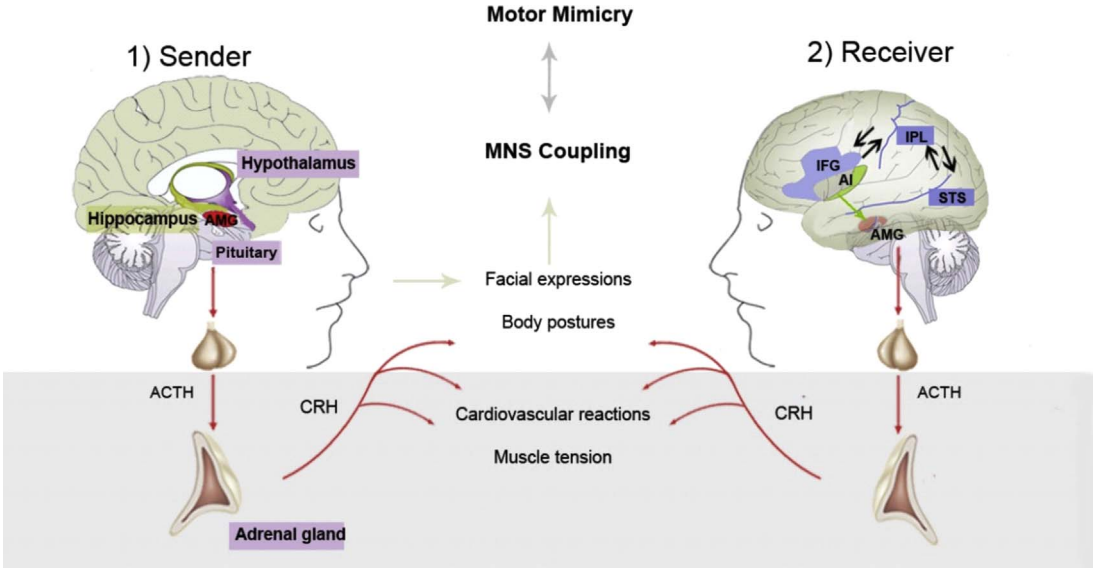

Fig. 4. Motor mimicry (1) Observation of bodily movements activates the STS which is involved in early visual description of actions. (2) The STS projects to the IPL with *mirror* neurons tracking precise kinaesthetic movements and (3) passes this information to the IFG coding for 'the goal of the action'. (4) The goal directed motor plans are sent from the IFG via the IPL back to the STS. (5) The MNS coupling initiates motor mimicry. The anterior insula AI (green) connects MNS with AMG and provides a possible neurological crossroad between these two independent, yet mutually interacting systems. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 contingently (close together in time). Indeed, observational studies in young children show that infants spend a large amount of time looking at their limbs and explore 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, from which 65% of this time the adult expresses salient emotions and they engage in imitation episodes (Uzgiris et al., 1989). Imitation occurs very frequently; approximately once a minute in mother-infant face-to-face interactions and most times the mother is 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/processes 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.

7. The neurocognitive model of emotional contagion (NMEC)

The core assumption of the perception action model of empathy proposed by Preston and de Waal (2002) is that perceiving a target's state automatically activates the corresponding representations of that state in the observer, which in turn activates somatic and autonomic responses. In line with the perception–action mechanism, a number of behavioral studies using EMG, demonstrated that viewing facial expressions triggers similar expressions on the observer's own face (Dimberg et al., 2000; Tamietto and Castelli, 2009; Kret et al., 2013a,b). This observation has been related to the discovery of the Mirror-neurons system (MNS) in the premotor area, F5, of the macaque monkey which discharges not only during action execution but also during action observation (Di Pellegrino et al., 1992). Further fMRI studies in humans have shown that the perception of a specific emotion activates similar neural systems in the observer that are responsible for the generation of that emotion. For instance, a similar neural response has been found following the perception of other's and own experience of pain (Jackson et al., 2006b), fear (de Gelder et al., 2004; Hadjikhani and de Gelder, 2003), disgust (Wicker et al., 2003), anxiety (Prehn-Kristensen et al., 2009), reward (Mobbs et al., 2009) and also higher order affects such as envy (Takahashi et al., 2009) and embarrassment (Krach et al., 2011). In 2011, Anders, Heinzle, Weiskopf, Ethofer, and Haynes used information-based fMRI to investigate the flow of affective information between two interactive brains of romantic partners. In this experiment, both partners were engaged in on-going face-to-face communication whilst inside the scanner. The sender (either male or female) was instructed to pose different emotional expressions to share his or her feelings with his or her partner (the receiver), while the

partner was trying to understand the affective experience of the sender. Apart from cerebral blood flow, skin conductance responses (SCR) were also measured to assess the partners' physiological arousal during each interaction period. The neuroimaging results revealed that the level of neural activity within the emotion-specific network predicted the neural activity in the same network in the perceiver's brain and the neural coupling was associated with synchrony of the autonomic system. Importantly, this was achieved with the same temporal resolution corresponding to the phase of partners' affective interactions. These findings are fundamental in the way they show that during face-to-face interactions, the movements in the partner's face are directly projected and can be decoded from the observer's neural activation. Scientists referred to this as 'neural resonance' or 'shared neural activation' and have documented this as a robust and consistent phenomenon in emotion perception studies. In modern neuroscience, this observation has transformed the way we think about neural architecture as it suggests that affective perception and its expression are not separate neurocognitive entities. These accounts provide empirical support for the hypothesis that neural resonance and automatic mimicry are directly involved in emotional contagion and empathy (Hatfield et al., 1994; Preston and de Waal, 2002).

In addition to this view, we propose that while mirror neuron activation and mimicry reflect on the degree to which people internally simulate perceived emotions, it is the perceptual input, not the neural/physiological resonance per se, that drives emotional contagion between species. Hasson et al. (2012) proposed that environmental stimuli, including faces, emit different forms of mechanical, chemical and electromagnetic energy. The sensory receptors convert these elements into electrical impulses that the brain then uses to gather environmental information and to coordinate an appropriate action. In this way, via the transmission of a signal through the environment, the neural processes in one brain can couple to the neural processes in another (Hasson et al., 2004; Stephens et al., 2010). To the best of our knowledge, at the time of writing this review, no neurocognitive model has incorporated different emotional signals into one neurocognitive framework. The present review therefore illustrates how affective information passes from one person's facial display to another's body and brain, and how the transition of perceptual input improves emotional understanding. The NMEC (Figs. 3 and 4) depicts a situation where a sender is experiencing a sudden feeling of anxiety while being observed by a receiver.

Imaging research has demonstrated that the anterior cingulate cortex (ACC), the medial prefrontal cortex (mPFC) and the temporoparietal junction (TPJ) play roles in perspective taking, self-awareness, and in more cognitive types of empathy (Carr et al., 2003; Decety and Lamm, 2007; Nummenmaa et al., 2008). The subcortical areas processing, among other things, emotions, and the regions that are known to be part of the MNS such as the inferior frontal gyrus (IFG, Brodmann area 44), are associated with more basic emotional contagion/emotional empathy (Carr et al., 2003; Shamay-Tsoory, Aharon-Peretz, and Perry, 2009). In the NMEC, we focus on these emotional contagion areas, which develop from early infancy onward.

7.1. NMEC: the autonomic mimicry pathway (Fig. 3)

One conceptual difficulty with mimicry is that it is hard to differentiate it from a response. For example, if one expresses fear following another's outburst of anger, this is an emotional reaction. But what if the result is an expression of anger? Is this still a reaction or should this be defined as mimicry? In our theoretical framework, we would like to conceptualize any type of interaction that results in corresponding autonomic levels between sender and receiver as autonomic mimicry. Accordingly, in the NMEC we argue that autonomic mimicry relies largely on the same neural substrates and pathways that are also involved in emotion responses and ANS activation. Aversive responses, including feelings of fear or anxiety, are modulated by hardwired neural circuits that share common neuroarchitectures among mammals (Le Doux, 2012; Parr and Waller, 2006). These basic evaluative systems are associated with the ANS and motor responses that together aid the adaptive responding of the organism (Decety, 2011). The feeling of fear is related to the activation of the sympathetic nervous system (Armony and Le Doux, 1997). Sympathetic nerves are located near the brainstem and the stress response is initiated by activation of the hypothalamic-pituitary-adrenal (HPA) axis (Herman et al., 2005). When the HPA axis is activated, the adrenal medulla secretes acetylcholine increasing (adrenaline) epinephrine and (noradrenaline) norepinephrine release. This, in turn, activates the cardio- vascular system and, as a result, heart and respiration rates increase and digestion slows down (Herman et al., 2005). Importantly, sympathetic nerves are directly connected to sensory channels on the surface of the body, such as the pupils, the skin and the muscles (Ekman et al., 1983). For this reason, arousal can lead to autonomic pupil dilation, blushing, skin conductance, as well as involuntary facial/bodily expressions (see Fig. 3, Sender).

In nature, organisms survive and thrive by detecting unconditioned arousal signals. In the case of both olfactory and visual unconditioned signals (such as a partner's pupil size), the signals are generally processed implicitly, passing through the superior colliculus (CS)- pulvinar (Pulv) pathway to the amygdala (AMG; Tamietto and de Gelder, 2010). The amygdala is a brain region located in the deep layers of the limbic cortex and is mainly associated with detecting biologically relevant cues including emotions expressed by peoples' faces and bodies (Adolphs, 2001; Atkinson and Adolphs, 2005). This area is also used to direct the appropriate action following threat detection (Armony and Le Doux, 1997) and is an important regulator of stress-related glucocorticoids in response to physical or psychological stressors (Dedovic et al., 2009). Research shows that monkeys, similar to humans, exhibit increased amygdala signaling in response to emotional faces (Gothard et al., 2007). When a receiver perceives a signal of a partner's increased arousal, the amygdala activates the locus coeruleus (LC) part of the noradrenergic system (Tamietto and de Gelder, 2010). The locus coeruleus has connections to the ventromedial hypothalamus, which in turn, outputs to motor control areas to promote adaptive behavioral responses to the event (Phillips and Le Doux, 1992). As a consequence, in response to the mother's autonomic signals, the infant automatically experiences a reflection of the mother's arousal in his or her own body and thus, both synchronize their ANS responses (Fig. 3, Receiver).

Apart from the LC in the brain-stem, the AMG also projects to temporal and frontal regions including the orbitofrontal cortex (OFC) and the anterior cingulate cortex (ACC). The amygdala and the OFC share reciprocal connections with the superior temporal sulcus (STS) that underlies rapid and prioritized processing of affective signals (Decety, 2011). These areas are involved in emotional control and higher forms of empathy such as perspective-taking (Adolphs, 2001; Mutschler et al., 2013). These higher-order regions fully develop relatively late in development (Gogtay et al., 2004). In early development, subcortical circuits including the amygdala, hypothalamus, hippocampus and OFC, are essential components of affective arousal.

7.1.1. How are the autonomic states of a sender mapped onto the receiver?

The NMEC (Fig. 3) shows that autonomic responses of the sender directly modulate neural activity in the emotion system of the receiver. In line with the AIM, we argue that this form of emotional contagion is fast, automatic, shared by most vertebrates and does not require extensive training. The mimicry of autonomic responses (such as pupil size change, facial redness, cardiovascular responses and hormonal level) detected by the receiver results in emotion system coupling between the infant and its caregiver. Human infants possess an innate mechanism which automatically converts the sensory signals related to senders' autonomic states to their own corresponding autonomic states. Yet, how are the autonomic states of a sender mapped onto the receiver?

Kilner et al's. (2007) predictive coding framework of the mirror

neuron system provides a promising account of its potential mechanisms. These predictive computations are not necessarily tied to one specific neural system but can take place at different forms of functional processing including the emotion system. Similar to PAM (Preston and de Waal, 2002), in the predictive coding framework, perception and action are tightly coupled (Barrett and Simmons, 2015). Through sensorimotor feedback, an organism's body receives essential information from its environment. For example, the receptors in the skin inform us about the angle of the surface we walk on, the temperature of the air and the taste of food. These highly specialized innate mechanisms transmit environmental stimuli to impulses in our brain, making us move and act adaptively in our environment. Similarly, the autonomic signals of an expresser, such as his or her pupil size, changes in facial redness, cardiovascular responses and hormonal levels are implicitly (unconditionally) detected by the receiver. As information arrives via receptors of the body (visual, olfactory, auditory, tactile receptors, among others), predictions are sent through the cortex. Limbic cortices, with their simple laminar structure, issue predictions within every sensory system with a well-developed laminar structure (Chanes and Barrett, 2016). These predictions induce the discharge of neurons in regions anticipating the trajectory of an emotional reaction, while receiving actual sensory input from the environment. Hence, predictions function as hypotheses about the world that can be tested against sensory signals that arrive in the brain (Barrett and Simmons, 2015). A mismatch between sensory input and prediction is registered as a prediction error. The brain tries to minimize 'prediction error' by reducing such a mismatch. One way to do this is via mimicry. By generating a response to mimic the observed sensory input, the prediction error is sent back along cortical connections to update predictions about the situation. A newly born's brain has strongly developed limbic structures but the neocortex is still underdeveloped. Since human behavior often fails to follow an anticipated pattern of action, coupled withinfants' lack of prior experiences, the model of the world is still to be established. During this process, autonomic mimicry can be beneficial to reduce prediction errors and to establish emotion system coupling between the infant and its caregiver. For a detailed description of computations, see Kilner et al. (2007) and Chanes and Barrett (2016).

The fact that arousing stimuli and others' reactions toward arousing stimuli induce arousal in the observer has obvious evolutionary benefits. However, it is important to note that we cannot just assume that perceived autonomic states of the sender must only elicit corresponding autonomic states because of the adaptive value. Just because default responses are in place, it does not mean that they determine human actions. Instead of the brain being a 'stimulus–response' organ stimulated by a specific type of emotion (e.g. fear, happiness or anger), the brain functions as a generative system which constructs others' emotions as affective information accumulates over time. While the visual information (i.e. pupil size, facial redness) gives a description of the visible affective components, it does not provide a full explanation critical for understanding the other's emotional state in all its complexity. For that conjunction, a variety of autonomic input is essential to estimate the prior probability (from past experiences) to create the posterior probabilities that serve as a prediction about the action.

Predictions guide our actions and perception by continually constructing possible representations relative to the present context. In other words, the organism has the opportunity to choose from the repertoire of actions based on past experience, yet does not require extensive training as innate "default processes" are already in place. This gives organisms greater flexibility and avoids single input–output relationship criticized in mirror neuron theories (Hickok, 2009; Kilner et al., 2007).

Kleckner et al. (2017) argued that ascending sensory inputs from the organs, such as autonomic visceral and vascular function, neuroendocrine fluctuations are similarly anticipated by the brain to anticipate bodily needs before they even arise. In support of NMEC, researchers began to identify analogous introspective mechanisms for representing sensations from within the body (Kleckner et al., 2017). With the use of tract-tracing experiments in macaque monkeys, followed by fMRI studies in humans, researchers were able to map the intrinsic allostatic/interoceptive system supported by subcortical, hippocampal, brainstem and cerebellar connectivity. In the follow-up fMRI experiment, subjects viewed arousing photos. The results showed that individuals with stronger functional connectivity within the allostatic/interoceptive system also reported greater arousal while viewing images and also demonstrated a greater sympathetic nervous system activity while viewing arousing images. This evidence suggests that these networks transfer emotional information across individuals and that connectivity of this network is essential for vicarious experiences (concordance between objective and subjective measures of bodily arousal). We propose that measures of autonomic mimicry, along with these system hubs, may provide an implicit index of interoceptive ability related to autonomic fluctuations.

In the first part of NMEC (Fig. 3), we have described how the intra-individual coupling between partners' amygdala and HPA axis underpins autonomic mimicry. Yet, the synchrony of autonomic signals (heart rate, skin conductance, pupil diameter and hormonal expression) is not sufficient for emotional contagion to occur. This is because emotions have at least two fundamental dimensions: the arousal level (intensity) and the valence level (Russell, 1978). In a recent review, Wood et al. (2016) argued that in order to recognize facial expressions, humans must integrate several perceptual and contextual inputs at once. This is because modalities of perceptual input (auditory, visual, tactile and olfactory) are often incomplete, and the brain needs to generate predictions by integrating information from other modalities (Driver and Noesselt, 2008). For example, increased facial redness and sweating may be interpreted as either positive or negative, depending on additional visual input (e.g., facial expression). In this way, visual input from one sensory modality can affect the perception of another modality (Wood et al., 2016). While autonomic mimicry communicates intensity (the arousal level) of observed emotion, the motor movement of facial expression and gestures provides visual input that helps observers to label the increase in physiological arousal with the appropriate emotional valence. In other words, by pairing physiological synchrony with motor synchrony, emotional meaning can be transferred from one individual to another.

7.2. NMEC: the motor mimicry pathway (Fig. 4)

Apart from synchrony of autonomic arousal, another mechanism that plays a fundamental role in emotional contagion is the mirror neuron system (Gallese, 2005; Iacoboni, 2009; Likowski et al., 2012; Nummenmaa et al., 2008). The second part of the NMEC (see Fig. 4) depicts neurological pathways of the MNS through which motor signals can be registered. In humans, the MNS system is a neural network connecting several brain areas including the inferior parietal lobe (IPL), the inferior frontal gyrus (IFG) and the superior temporal sulcus (STS; Dinstein et al., 2007; Iacoboni, 2009). The regions of the MNS are assumed to contain 'mirror' neurons similar to those studied in analogous regions in macaque monkeys (Rizzolatti et al., 1996). In the macaque monkey, the mirror neurons in the ventral premotor area (F5) responded both when the monkey executed a specific movement and when the monkey observed performing that same movement (Di Pellegrino et al., 1992; Rizzolatti et al., 1996). However, the MNS system is also activated when goal-directed hand movements are performed (Di et al., 1992). Interestingly, apart from one's own hand movements, the MNS is also activated when people observe others enacting object or non-object- related actions made with the mouth, hand or foot (Buccino et al., 2001; Grafton et al., 1996) or only imagine that someone is performing a motor action (Grafton et al., 1996).

Movements in a partner's face are registered in the superior temporal sulcus (STS), a multisensory area which activates when observing biological motion (Iacoboni, 2009). From the STS, motor information is

transferred to the inferior parietal lobe (IPL; BA 39,40) and then to the inferior frontal gyrus (IFG; Brodmann's Area 45/44/6); (Carr et al., 2003). The IFG region is an important region in social cognition as it codes for the 'goal of the action' (Gazzola et al., 2006). These goal-directed motor plans are then sent back to the IPL and the STS (Carr et al., 2003). Cattaneo et al. (2010) provided convincing neurobehavioral evidence for mirror neurons contribution to cognition by means of transcranial magnetic stimulation (TMS). In this experiment, blindfolded participants repeated an object- directed action (push or pull). When participants categorized others' actions, this resulted in visual after-effect, as a result of motor-to-visual adaptation (of mirror neurons). TMS over the ventral premotor cortex suppressed the after-effect. These data are consistent with the existence of premotor mirror neurones that have access to the action meaning in humans.

In the past decades, the MNS has attracted scientific attention as it has been suggested that, in addition to motor imitation, the MNS also supports social functions (Gallese and Goldman, 1998; Keysers and Gazzola, 2010; Rizzolatti et al., 2009). Specifically, since the same neural networks are involved in motor production and observation, it has been theorized that the MNS may play a critical role in empathy as it allows for feedback from facial and bodily actions that simulation reflects on the emotions of others.

7.3. Anterior insula connecting the MNS and the emotion systems

A key neural structure believed to connect the mirror neuron system with the emotion system is the anterior insula (Carr et al., 2003). The anterior insula has been implicated in playing a role in the perception and experience of pain (Jackson et al., 2006a; Mutschler et al., 2013). Apart from vicarious physical pain, the AI is also associated with feelings of embarrassment or social pain (Krach et al., 2011). The anterior insula is structurally and functionally coupled to limbic structures including the amygdala (Augustine, 1996). For this reason, the AI has been proposed to be the neural structure connecting the mirror neuron system with the emotion systems in empathy. Carr et al. (2003) showed in an fMRI study that activation of the AI correlated with activity in the premotor cortex, IFG and AMG and all areas associated with emotional contagion, as demonstrated in numerous empathy reviews (Decety, 2010; Gazzola et al., 2006; Iacoboni, 2009). Interestingly, in Jackson et al.'s (2006a,b) fMRI experiment, subjects were presented with people in a painful situation and instructed to imagine perceiving the pain from first and second person perspectives. The first perspective of pain led to increased pain ratings as well as increased activation in the somatosensory cortex, the ACC and the insula. Taking the perspective of others increased activation in the precuneus and the right TPJ, areas involved in theory of mind and mentalizing. These results indicate that perceptions of pain processed in the insula, as well as in the ACC, represent self-centered experiences, while the TPJ and the precuneus play a role in self-other discrimination, which are crucial aspects of human empathy.

The aforementioned reviewed literature suggests that empathy is, in part, based on shared brain-to-brain coupling of affective states. While previous reviews have clarified that neural pathways are involved in the detection of subtle emotional signals in a partner's face and body (Hasson et al., 2012; Kret, 2015; Tamietto and de Gelder, 2010) and that other reviews have addressed the neural underpinnings of motor imitation (Ferrari et al., 2005; Iacoboni, 2009; Rizzolatti et al., 2001), we here propose a new model that incorporates these neurological accounts into one interactive emotional contagion model. In addition, NMEC accounts for how the sender's nonverbal facial characteristics (movements/autonomic responses) lead to brain-to-brain coupling and mimicry between the partner's emotion system (limbic system and HPA axis) and the mirror neuron system (IFG, IPL, STS). Both motor mimicry and the autonomic mimicry indicate a high level of neural coupling between these areas, where autonomic mimicry contributes to the intensity of communicative signals and motor mimicry frames the expression with the appropriate emotional valence. Consequently, by combining autonomic and motor signals, people can extract affective meaning from a partner's face. Disrupted emotion processing has been related to a range of mental disorders and can possibly explain the high comorbidity between mental disorders. Kret and Ploeger (2015) reported evidence for disrupted emotion processing in anxiety disorders, mood disorders, schizophrenia, autism spectrum disorder, borderline personality disorder and eating disorders. Multiple measures of automatic autonomic mimicry, along with motor mimicry early after birth, could be used as developmental markers of social deficits. If true, pediatrics could intervene early to substantially reduce the adverse symptoms of these disorders.

8. Discussion

The current review provides an overreaching overview of studies spanning across developmental psychology, social sociology, evolutionary biology and neuroscience, supporting the notion that automatic mimicry is essential for the development of empathy. The literature indicates that people are generally not consciously aware of subtle changes in an interaction partner's face and do not voluntarily react to these changes (Dimberg et al., 2000; Tamietto and Castelli, 2009; Tamietto and de Gelder, 2010; Wood et al., 2016). Yet, infants, as well as adults, automatically mimic facial expressions as well as autonomic signals from their partner's face or body and by doing so enhance their understanding of the other's feelings, emotions, intentions and actions. Automatic mimicry has here been proposed as a potential mechanism that allows humans to recognize and empathize with other's emotions (Buck, 1980). In theory, automatic mimicry of the perceived affective signals, in turn, simulates further neural systems involved in the corresponding emotional state, which helps observers to implicitly infer the expresser's internal state (Wood et al., 2016). This is an evolutionary adaptive skill for organisms to survive and thrive by detecting unconditioned signals of emotionality or arousal. Nevertheless, causal evidence for this hypothesis remains controversial. The above reviewed literature provides a unique and novel inside the possible function and underlying mechanisms of mimicry.

Building upon Preston and de Waal's (2002) perception-action model, we showed that strong synchronization exists between two people. We argued that automatic mimicry provides a physical-cognitive link during an organism's development and is a precursor of healthy social development. To support this argument, we demonstrated that emotional contagion can occur at different levels of processing. We reviewed well established, as well as recent, studies introducing several physiological mechanisms of automatic mimicry through which affective information can be shared. The presently reviewed literature implies that people mimic both autonomic and motor expressions (Dimberg et al., 2000; Niedenthal et al., 2001; Tia et al., 2011; Gregory and Webster, 1996; Webb, 1969; Helt et al., 2010; Goldin-Meadow and Alibali, 2013; Estow et al., 2007). Special attention has been given to autonomic mimicry, which is an underexplored area of current emotional contagion research. The "autonomic mimicry" involves synchrony in heart rate (Feldman, 2011), breathing rhythms (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 levels (Laurent et al., 2012; Saxbe et al., 2014). Psychophysiological research indicates that strong autonomic mimicry exists between mothers and neonates and that this physiological association translates to psycho- emotional interactions between the pair. While autonomic mimicry is generally a positive marker promoting attachment, if the mother is in distress, physiological synchrony can actually have negative consequences on the child's social development. This supports the argument that physiological alignments allow for the direct transfer of affective information from one individual to another and thus facilitates implicit emotional communication.

Summarizing the newest discoveries in social neuroscience, we

explained that mimicry is likely to be a result of overlapping neural networks. We proposed a new "Neurocognitive Model of Emotional Contagion". At its core, NMEC illustrates how complex processes, such as empathy, might emerge from automatic mimicry of conspecifics. We argued that while shared neural activation and automatic mimicry reflect the degree to which people internally simulate perceived emotional states, it is the emotional signals – not the mimicry – that drive the common patterns of neural representations that underlie empathy. We proposed that emotions are communicated via various communicative channels (Figs. 1 and 2) and the degree of mimicry and brain-to-brain coupling (Figs. 3 and 4) corresponds to the level the receiver is able to "tune in" to one or more of these communicative channels. Therefore, measurements of several types of mimicries at once would provide a more holistic physiological profile of the level to which one individual understands/processes another individual's social signal. Especially useful, might be measures of autonomic signals that are not likely to be influenced by learning, social interactions or conscious control (Kret, 2015). In line with this hypothesis, there is an increasing interest in how mimicry may underlie social deficits in social disorders (Duffy and Chartrand, 2015). Still, to what extent mimicry is necessary for healthy social development remains inconclusive. Considering the potential role of automatic mimicry in social pathologies, we propose that future research should measure the mimicry of emotional signals on the different level of expression.

9. Future directions

The topics of motor mimicry and especially autonomic mimicry are very new and as of yet, still underexplored. Therefore, the first step in future studies is to conduct longitudinal studies whereby automatic mimicry will be continuously measured throughout a child's development (Feldman et al., 2014). While most previous studies measured automatic mimicry during virtual interactions, a study of mimicry during real-life interactions is highly recommended to provide real-life implications. Importantly, multiple measurements of emotional signals (e.g., facial muscles, eye gaze, pupil-size, blushing and body postures) are needed to measure several processes underpinning emotional contagion during social interactions. Apart from behavioral experiments, future studies may combine neurological techniques (EEG, fMRI) with physiological measures and try to block mimicry in order to shed light on how different forms of mimicries are represented in the brain. Neuroimaging analyses should be hypothesis driven and make use of functional connectivity analysis and dynamic neural network modeling in order to make sense of social cognition as an interactive system.

An alternative way to tackle the correspondence problem of mimicry is to study mimicry in robots. The possibility that empathy can be generated by sensorimotor processes in robots has already excited the cognitive science community. This is because artificial systems provide the benefit of a blank state in which neuroscientific theories of brain functions can be tested (de Kleijn et al., 2015). With robots, researchers can carefully manipulate parameters in a controlled way. There is evidence showing that if robots mimic another person's affective actions, this automatically activates a motor representation and affective experience in the human that is coherent with the robot's affective expression (Hofree et al., 2015; Li and Chignell, 2011; Mayer et al., 2010). Similarly, as in human-to-human interactions, research shows that during human-robot interactions, humans perceive robots that mimic as more positive and empathic (Fuente et al., 2015; Hofree et al., 2015). Hypothetically, if automatic mimicry would allow for affective representations to be manifested in a robot, it would confirm the theory that mimicry is sufficient for emotional contagion to emerge (Asada, 2015). By developing robots that can detect subtle social signals and exhibit mimicry, we could then test whether robots start to develop social behavior similar to humans. In the future, brain-inspired algorithms and computational models of neural networks (e.g., simulations of neural microcircuits, connectionist networks) could provide well-controlled mimicry parameters for social cognitive models (Asada et al., 2001; Watanabe et al., 2007). The application of the NMEC in robots in future studies may provide evidence to refute or support the hypothesis that automatic mimicry is necessary for empathy development.

10. Conclusion

In conclusion, the current review argues that automatic mimicry is essential for the development of healthy social cognition. The current review provided an interdisciplinary approach to the study of human cognitive developmental. Through the integration of information from social neuroscience evolutionary biology, this review provided a fresh view and new insight into the development of human cognitive functions utilizing synthetic and constructive approach.

Acknowledgements

Funding Research was supported by the Netherlands Science Foundation (VENI # 016-155- 082) to MK and (Talent Grant # 406-15-026) from NWO (Nederlandse Organisatie voor Wetenschappelijk Onderzoek) to MK and EP.

We would like thank to M. R. Giffin and B. Smith for providing critical feedback on the text.

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