Connecting minds and sharing emotions through human mimicry

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Connecting minds and sharing emotions through human mimicry

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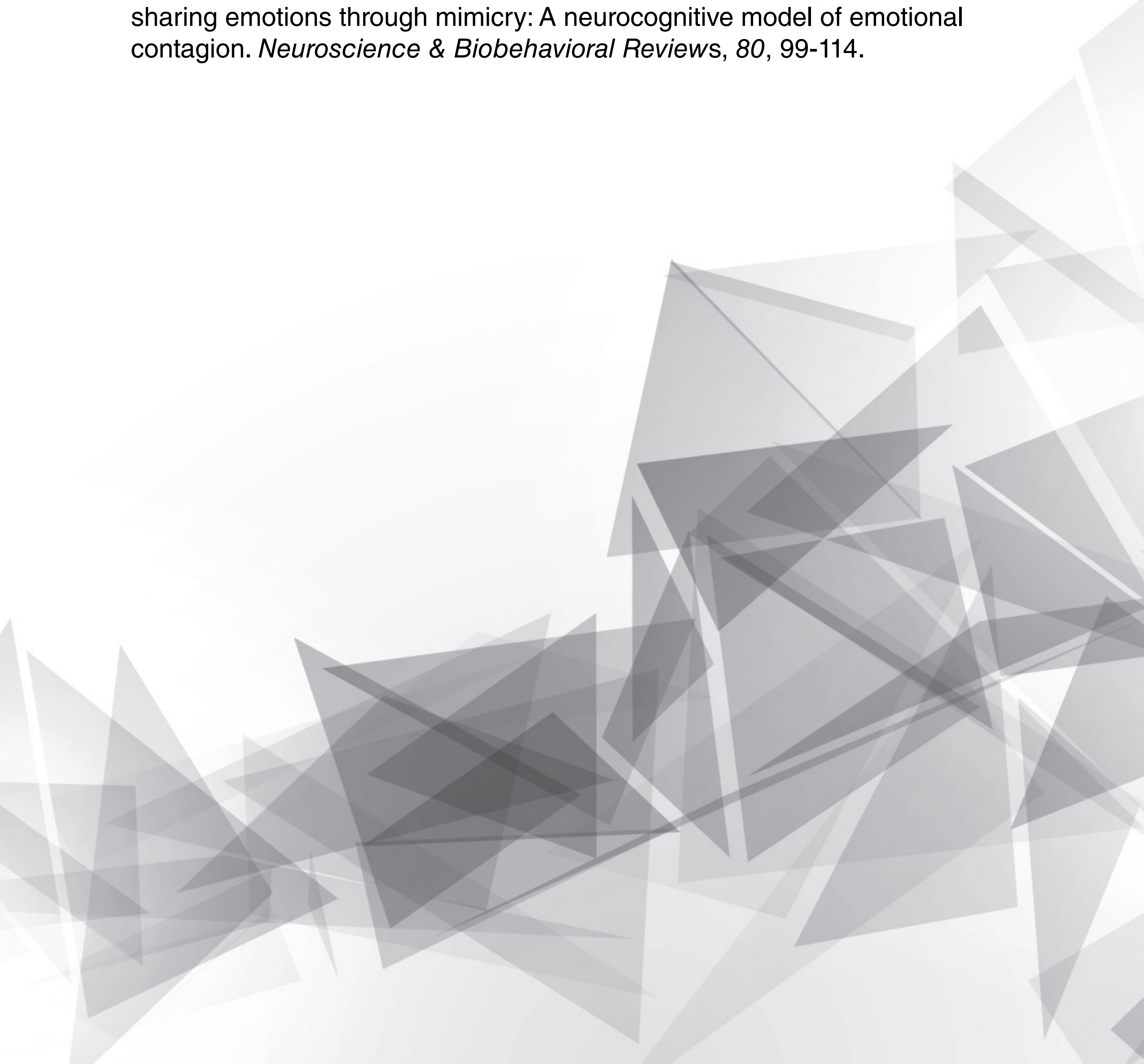
Chapter 1

General introduction

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



General introduction

Facial movements and bodily sensations play a fundamental role in social interactions, as demonstrated by our spontaneous inclination to synchronize emotional expressions with those of another person. The tendency to automatically mimic and synchronize with others has been suggested to result in emotional contagion – the ability to 'catch' another person's emotion (Cacioppo et al., 2000). Contemporary theories propose that emotional contagion may give rise to advanced human social capacities such as empathy, trust, and the ability to bond with each other (Preston and de Waal, 2002). Decades of neuropsychological research have been devoted to understanding the way human emotions are constructed in the brain, how they are influenced by internal and external factors, and the role they play in social interactions. However, while most research has been dedicated to motor mimicry (e.g., the mirroring of facial expressions and body postures), very little is known about the function of autonomic mimicry that is unconscious and difficult to regulate. To illustrate, imagine the following scenario:

A friend of yours has an important presentation. She is standing on a big stage, introducing the topic, while you are sitting in the first row. Suddenly, you notice the blush on her cheeks, the sweat on her forehead, the dilation of her pupils, and the tremble in her voice. As you take note of these details, you recognize changes in your own body: your heart rate is rising, your hands are perspiring, and despite your best efforts you are beginning to feel extremely anxious.

This scene describes emotional contagion - the most primal form of empathy (Preston and de Waal, 2002). Compared to our closest relative, the chimpanzee and bonobo, homo sapiens evolved expressive faces with smooth skin, large eyes and red lips that make our internal states more transparent (Tomasello et al., 2005). Partly because of these exaggerated features, humans are hardwired to share and communicate emotional states freely and without effort. People are able to adapt to others' emotions to the point where we can feel other peoples' pain, feel sadness in response to others' tears, and predict someone's surprise before the surprising event even happens. If you notice that a friend is in a stressful situation, it's adaptive to be on guard as well. However, there is a mismatch between how this contagion system evolved and how it is often activated in contemporary human life. From an evolutionary perspective, experiencing a stress response by witnessing a friend struggle through a presentation does not appear to have any adaptive value. In fact, if you feel highly stressed this reduces your ability to put your friend at ease and provide needed support, which could increase the stress of your friend (Bloom, 2016). Therefore, one may argue that such emotional transparency could put humans in a vulnerable position by increasing the risk of predation and exploitation. On the other hand, it has been proposed that emotional contagion may provide a much greater benefit: because humans' bodies mirror what we perceive, we can feel what others feel. This makes us care for each other deeply, and cooperate on a greater scale than any other species (Preston and de Waal, 2002).

In this thesis, I will explore the questions: what is the function of mimicry in human interactions? And furthermore, what underlies this remarkable capacity? Whereas most studies have focused on mimicry of facial expressions or body postures, I take a broader perspective and review evidence showing that people mimic each other on many more levels than previously thought. Special attention is given to autonomic mimicry (synchrony in heart rate, skin conductance, and pupil diameter), which is an underexplored area of research (for a review, see Kret, 2015; Palumbo et al., 2016). Overall, the aim of this thesis is two-fold: the **1st aim** is to explore different types of mimicry with respect to pro-social behavior. The **2nd aim** is to understand the underlying mechanisms of this mimicry. To reach these goals and sustain the ecological validity of our findings, we used a variety of tools measuring eye-tracking, skin conductance, heart-rate, and also employed brain stimulation, optical illusions, and neuroimaging. We furthermore conducted research both inside and outside of controlled laboratory settings.

Chapter Overview

This dissertation is based on one literature review and four empirical research articles. The whole thesis can be divided into three overarching topics: The first section (Chapters 2-3) presents a literature review summarizing evidence suggesting different types of mimicry that emerge early after birth. In Chapter 3, this review is extended to examine the neurocognitive mechanism of emotional contagion, introducing two distinct neurological pathways: the autonomic pathway and the motor pathway that give rise to two distinct types of mimicry. The second section (Chapters 4-5) provides empirical evidence for the theory that autonomic is liked to pro-social behavior (trust and attraction). Lastly, the third section (Chapter 6-7) shifts away from the previous correlational approach with experimental manipulations.

Chapter 2 provides foundations for the view that mimicry is a primitive, automatic and implicit form of empathy that plays a crucial role in the development of human social abilities. A distinction is made between two separate branches of mimicry - autonomic (physiological) and motor (facial) mimicry. Evidence is summarized implying that autonomic and motor mimicry are related to various pro-social abilities such as bonding, trust, and empathy.

Chapter 3 looks deeper into the underlying mechanisms of autonomic (physiological) and facial (motor) mimicry. The Neurocognitive Model of Emotional Contagion (NMEC, Procházková & Kret, 2017) proposes two neurological mechanisms by which mimicry shapes social behavior: autonomic mimicry is linked to a subcortical pathway involved in nonconscious affective processing. Motor mimicry, on the other hand, is reliant on the mirror neuron system (MNS) in the cortex that is involved in conscious imitation. Thus, whereas chapter 2 and 3 introduce different types of mimicry along with possible neurological mechanisms, Chapters 4 - 7 scrutinize this neurological model with the use of a variety of tools including eye-tracking, physiological measures, brain stimulation, optical illusions and fMRI.

Chapter 4 describes an fMRI experiment in which we looked into the underlying mechanisms of pupil mimicry and it's link to trust formation. Pupil mimicry is a particularly useful phenomenon to study because in contrast to most other types of autonomic mimicry (e.g., skin conductance, heart rate synchrony), pupils can be visible to others and therefore can be used as a visual stimulus to induce an autonomic response. In this experiment, participants played a series of one-person trust games inside of the MRI scanner. During each trial, the pupils of virtual partners dilated, constricted, or remained static, while subjects decided how much money they wanted to invest in the partner whose eyes they perceived. This set-up allowed us to track participants' brain activity and social behavior on a trial-by-trial basis. We were particularly interested in neural areas that became active during pupil mimicry and how these pupil mimicry-related regions modulated participants' trust decisions.

The highly controlled experimental setting presented in Chapter 4 has an intrinsic advantage in reducing confounding variables. Yet, studies in social neuroscience frequently face criticism for overly artificial tasks and the presentation of un-naturalistic stimuli. In real-life social interactions, there is not only one type of affective cue but a whole variety of signals that are being dynamically exchanged between partners. Thus, to improve the ecological validity of our findings, in **Chapter 5**, we measure the physiological dynamics between couples during real-life dating interactions outside the laboratory. A first date provides an excellent scenario in which to test if physiological synchrony promotes pro-social behavior. During dating interactions people are likely to exchange a broad variety of facial expressions and gestures and to experience concomitant changes in attraction to their dating partner. Participants wore eye-tracking glasses with embedded cameras as well as devices to measure physiological signals. Here the main focus was on signals that are difficult to perceive such as heart rate (HR) and skin conductance levels (SCL). We hypothesized that mutual synchrony in HR and SCL would boost attraction between newly met partners, an effect consistent with the observation that pupil mimicry promotes trust between strangers.

In **Chapter 6,** we test the NMEC proposal that autonomic signals (pupil sizes) are processed subconsciously. In support of this theory, an increasing number of studies have shown that affective displays can be perceived outside of perceivers' awareness (Skuse, 2003; Tamietto et al., 2009; Tamietto & De Gelder, 2010). We, therefore, returned back to the laboratory and took a more controlled approach. Participants played trust games as their pupil size and facial expressions were measured. They would either see their partner's face with a neutral, happy, or fearful expression, or partner's eye region in which the pupils were large, medium or small in size. Crucially, in half of the trials, we used continuous flash suppression (CFS; Tsuchiya & Koch, 2005) to render the stimuli they saw invisible. The main interest was to test whether facial expressions and pupils of partners were mimicked and influenced trust decisions even during the non-conscious (suppressed) condition. If true, this result would support the theory that autonomic signals can be processed without visual awareness of the perceiver.

Chapter 7 presents a study where we manipulate autonomic mimicry with brain stimulation. In this experiment, we used transcutaneous vagus nerve stimulation (tVNS); a method that has been proposed to increase norepinephrine concentrations in the brain and which we expected would induce pupil dilation. Participants' pupil sizes and investments were measured as subjects played trust games with partners whose pupils changed in size. We hypothesize that tVNS would modulate pupil mimicry and pupil-contingent trust. If true, this finding would provide causal evidence for the role of the noradrenaline system in pupil mimicry-promoted trust development.

Finally, **Chapter 8** closes the thesis with a general discussion, where I highlight and integrate the key findings from the different chapters. I also pose new questions that this dissertation yields.

Chapter 2

Connecting Minds and Sharing Emotions through Mimicry

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

Abstract

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

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

Introduction

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

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

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

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

Definitions and terminology

Different types of automatic mimicry

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

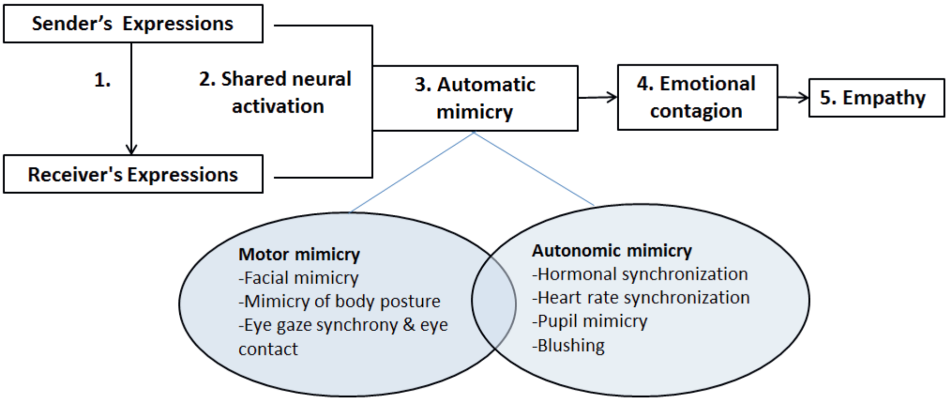


Fig. 1. Schematic Representation of Empathy Development: (1) The sender's (mother's) emotional state is reflected in her nonverbal motor movements (facial expressions, body postures, and eye-gaze) and physiological responses (heart rate, hormonal levels, sweating, facial color, pupil diameter). (2) The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

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

Emotional contagion

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

The evolution of empathy

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

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

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

From mimicry to emotional contagion (Fig. 1)

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

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

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

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

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

From emotional contagion to cognitive empathy

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

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

The empirical dispute

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

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

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

Different levels of emotional contagion in humans

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

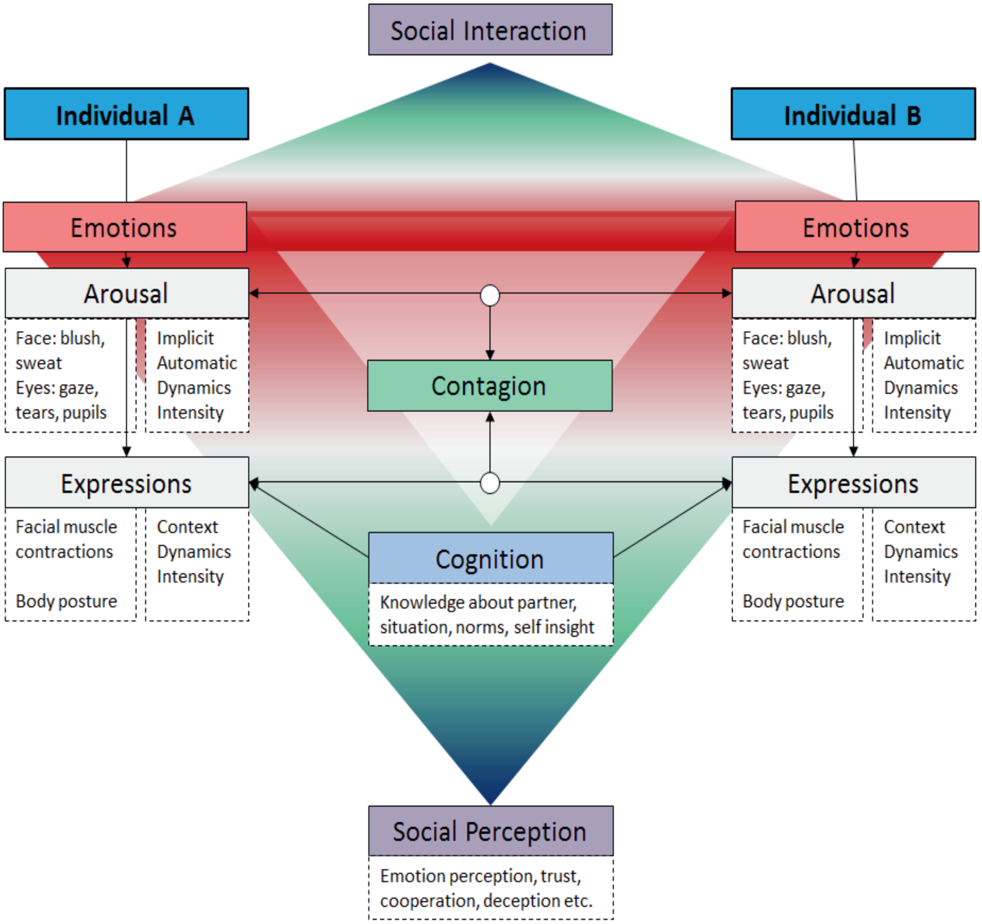


Fig. 2. Schematic representation of emotion processing during social interactions, adapted from (Kret, 2015; Fig. 1) shows how emotions that are expressed during a social interaction by Person A, through emotional contagion, influence the emotions and expressions of Person B. Person A and B not only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

Motor mimicry

1. Facial muscle mimicry

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

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

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

2. Eye contact

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

3. Contagious crying

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

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

Autonomic mimicry

1. Physiological linkage

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

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

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

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

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

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

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

2. Pupil mimicry

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

3. Blushing

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

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

The correspondence problem

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

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

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

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

Chapter 3

The neurocognitive model of emotional contagion (NMEC)

Based on: Procházková, E., & Kret, M. E. (2017). Connecting minds and sharing emotions through mimicry: A neurocognitive model of emotional contagion. *Neuroscience & Biobehavioral Reviews*, *80*, 99-114. – PART 2

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, Kret et al., 2013a, Kret et al., 2013b). 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 affective state activates similar neural systems in the observer that are responsible for the generation of that state. This has been observed in the domains 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), as well as 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 this 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 fundamentally showed that during face-to-face interactions, the movements in the partner's face are directly projected to and can be decoded from the observer’s neural activation. This has been dubbed ‘neural resonance’ or ‘shared neural activation’ and has been demonstrated to be a robust and consistent phenomenon in emotion perception studies. 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 is illustrated in Fig. 3 and Fig. 4, which 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 associated with, 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.

NMEC: the autonomic mimicry pathway (Fig. 3)

One conceptual challenge mimicry poses is that it is difficult to determine when exactly a response qualifies as mimicry. 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 muscles, and the skin (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).

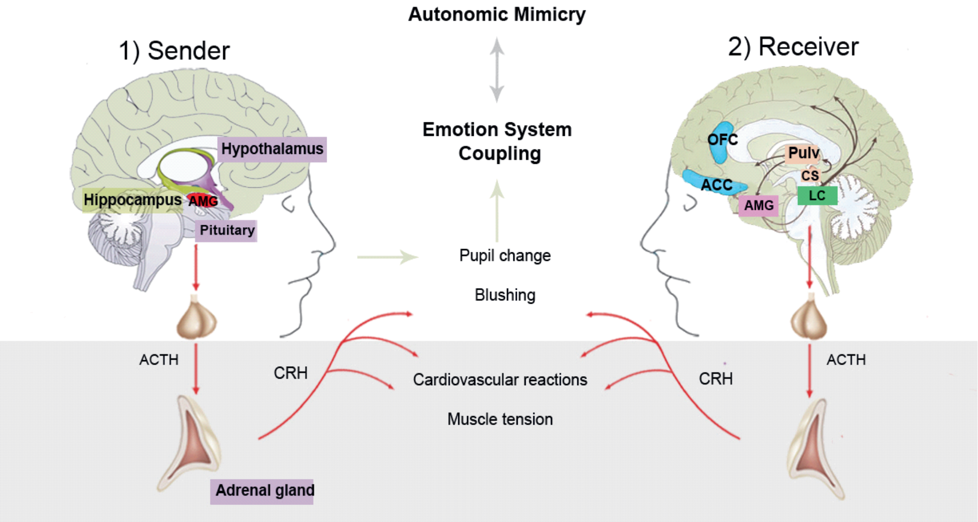


Fig. 3. Neurological Mechanisms of Autonomic Mimicry. Sender: (1) Sender's stress response is initiated by hypothalamus-pituitary-adrenal axis activation. (2) Adrenal gland secretes ACTH increasing the level of CRH in the bloodstream. (3) The neuroendocronological reactions are accompanied by cardiovascular 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.

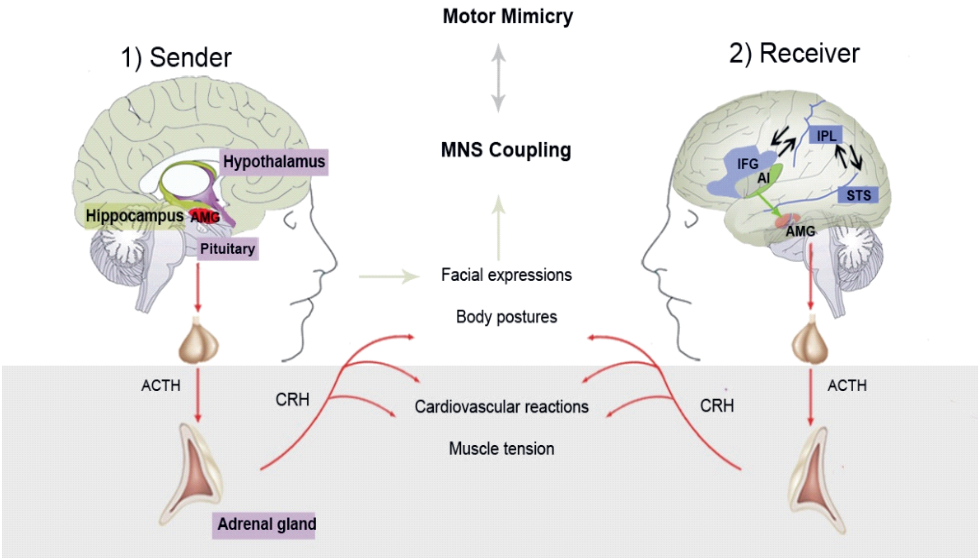


Fig. 4. Motor mimicry (1) Observation of bodily movements activates the STS which is involved in early visual description of actions. (2) The STS projects to the IPL with mirror neurons tracking precise kinaesthetic movements and (3) passes this information to the IFG coding for 'the goal of the action'. (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.

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). 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).

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. 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. For example, human infants possess an innate mechanism which automatically converts the sensory signals related to senders' autonomic states to their own corresponding autonomic states. 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. 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 rather to a network of regions that also include 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 newborn's brain has strongly developed limbic structures but underdeveloped neocortex. Because human behavior often fails to follow an anticipated pattern of action, and because infants lack prior experience, the model of the world is yet to be established. During this process of establishment, 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 visual information (i.e. pupil size, facial redness) gives a description of the visible affective components, it does not provide a full explanation sufficient for understanding the other's emotional state in all its complexity. 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 the 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 a 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: arousal (intensity) and valence (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.

NMEC: the motor mimicry pathway (Fig. 4)

In addition to synchrony of autonomic arousal, a 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 another individual 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). In addition to hand movements, the MNS is 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 even when individuals 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, being associated with coding 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 a 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 neurons associated with 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.

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 – all areas associated with emotional contagion, as demonstrated in numerous empathy reviews (Decety, 2010, Gazzola et al., 2006, Iacoboni, 2009). Interestingly, in several fMRI experiments (Jackson et al., 2006a, Jackson et al., 2006b), 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.

Discussion

The current review provides an overreaching overview of studies spanning 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 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 evolutionarily adaptive skill, allowing 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 insight into 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 (Fig. 1, Fig. 2) and the degree of mimicry and brain-to-brain coupling (Fig. 3, Fig. 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 different levels of expression.

Future directions

The topics of motor mimicry and especially autonomic mimicry are very new and as of yet, still underexplored. A valuable step in future studies could be to conduct longitudinal studies whereby automatic mimicry is 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.

Conclusion

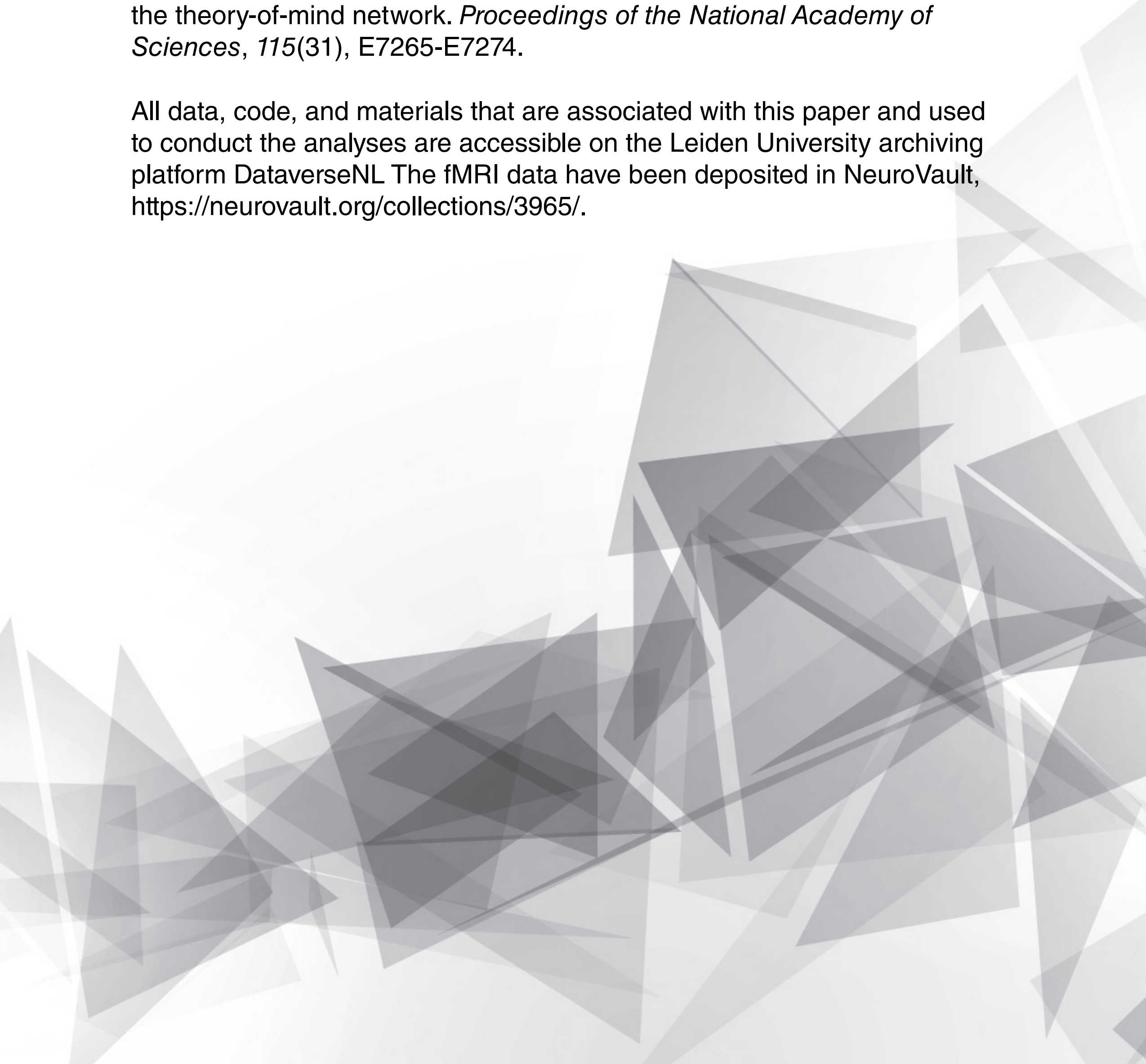
In conclusion, the current review argues that automatic mimicry is essential for the development of healthy social cognition. The current review provided an interdisciplinary approach to the study of human cognitive developmental. Through the integration of information from social neuroscience and evolutionary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

Chapter 4

Pupil mimicry promotes trust through the theory-of-mind network

Based on: Procházková, E., Procházková, L., Giffin, M. R., Scholte, H. S., De Dreu, C. K., & Kret, M. E. (2018). Pupil mimicry promotes trust through the theory-of-mind network. *Proceedings of the National Academy of Sciences*, *115*(31), E7265-E7274.

All data, code, and materials that are associated with this paper and used to conduct the analyses are accessible on the Leiden University archiving platform DataverseNL The fMRI data have been deposited in NeuroVault, https://neurovault.org/collections/3965/.



Abstract

The human eye can provide powerful insights into the emotions and intentions of others; however, how pupillary changes influence observers' behavior remains largely unknown. The present fMRI–pupillometry study revealed that when the pupils of interacting partners synchronously dilate, trust is promoted, which suggests that pupil mimicry affiliates people. Here we provide evidence that pupil mimicry modulates trust decisions through the activation of the theory-of-mind network (precuneus, temporo-parietal junction, superior temporal sulcus, and medial prefrontal cortex). This network was recruited during pupil-dilation mimicry compared with interactions without mimicry or compared with pupil-constriction mimicry. Furthermore, the level of theory-of-mind engagement was proportional to individual's susceptibility to pupil-dilation mimicry. These data reveal a fundamental mechanism by which an individual's pupils trigger neurophysiological responses within an observer: when interacting partners synchronously dilate their pupils, humans come to feel reflections of the inner states of others, which fosters trust formation.

Keywords: trust game; physiological linkage; neuroimaging; social cognition; affect.

Introduction

The propensity to trust is essential for individuals to cooperate and for societies to prosper (Fehr and Gächter, 2002; Rand et al., 2012). Nevertheless, individuals also need to be equipped with decoding machinery in the brain, which allows them to quickly detect signals of danger (Tamietto and De Gelder, 2010), refrain from cooperation, and withhold trust (de Dreu et al., 2016). Among the many implicit cues that may inform assessments of someone's trustworthiness, the human eye region stands out as particularly salient and powerful. By contracting the muscles around their eyes and pupils, people communicate messages with affective meanings, such as friendliness or threat (Hess, 1975; Kleinke, 1986; Kobayashi and Kohshima, 1997; Kret, 2017). Intriguingly, in our earlier research, we observed that if partner's pupils synchronously dilate, trust is promoted (Kret, Fischer, & De Dreu, 2015; Mariska E. Kret & De Dreu, 2017; Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018). Apart from human adults, pupil mimicry has been reported in chimpanzees (Kret, Tomonaga, & Matsuzawa, 2014) and young infants (Fawcett et al., 2016a, 2017), which suggests that pupil mimicry may have evolved as a social mechanism to promote empathic bonding with kith and kin. Nevertheless, how pupil mimicry works on a mechanistic level and how it influences decisions of trust remains unclear. Revealing the mechanisms will clarify how pupil mimicry modulates brain-wide neural interactions involved in trust formation.

In the literature, two core mechanisms have been proposed that facilitate pupil mimicry. One view suggests that pupil mimicry is controlled by a general "low-level" subcortical mechanism (Fawcett et al., 2016a, 2017; Harrison et al., 2007), possibly a direct amygdala-brainstem physiological response which can help people to quickly recognize socially arousing or threatening situations (Amemiya and Ohtomo, 2012; K E Demos et al., 2008; Procházková and Kret, 2017; Tamietto and De Gelder, 2010). In support of this hypothesis, observed pupil sizes are often processed non-consciously (Harrison et al., 2009, 2007, 2006), and perceived pupil dilation has been associated with increased amygdala activity (Amemiya and Ohtomo, 2012; K E Demos et al., 2008). Pupil mimicry might be involved in "high-level" mechanisms. Previous fMRI research in humans and electrophysiological studies in rodents indicate that the norepinephrine/acetylcholine systems associated with changes in own pupil size extend beyond functions exclusively mediated by the autonomic nervous system (Aston-Jones and Cohen, 2005; Eldar et al., 2013; Joshi, S., Li, Y., Kalwani, R. M. & Gold, 2016; Reimer et al., 2016). Furthermore, neural regions supporting social cognition have been reported to be associated with mimicry of affective cues (Likowski et al., 2012; Schulte-Rüther et al., 2007), including subtle changes in pupil size (Harrison et al., 2009, 2006). The intertwined neural circuitry between social cognition and pupillary processes implies that pupil mimicry has a potential social function. During pupil mimicry, the feedback from the visceral afferent fibers mapped hierarchically in the brain possibly influence cortical areas engaged in subjective feelings and social decisions (Critchley, 2009). Another possibility, therefore, is that the mimicry of pupil size shapes trust decisions via activation of the theory-of-mind (ToM) network (expanding above subcortical circuits), which is implicated in prosocial behavior and trust formation. However, to date there is no evidence that directly investigates the engagement of either of these neural mechanisms during pupil mimicry and trust formation.

The present study investigates the neurocognitive link between pupil mimicry and trust; we performed a combined fMRI and pupillometry study during which participants made trust decisions (Fig. 1). During each trial, the pupils of virtual partners dilated, constricted, or remained static over stimulus presentation time, while subjects decided how much money they wanted to invest in their partner, whose eye region was shown. Based on our earlier research (Kret et al., 2015; Kret & De Dreu, 2017; Wehebrink et al., 2018), we predicted that observed pupil dilation would increase participants' (*i*) trust and (*ii*) pupil size and that (*iii*) pupil mimicry would modulate the effect of the partner's pupil on trust. Crucially, we hypothesized that if pupil mimicry activates a "threat-related" mechanism, it should engage the amygdala, the frontal pole, and the brainstem nuclei, which orient behavior toward basic survival needs (Tamietto and De Gelder, 2010). In contrast, if pupil mimicry operates a function similar to more overt emotional expressions, such as body postures or facial expressions, pupil mimicry should activate ToM areas involved in social cognition [precuneus, superior temporal sulcus (STS), temporo-parietal junction (TPJ), and medial prefrontal cortex (MFPC)](Saxe & Wexler, 2005; Schaafsma, Pfaff, Spunt, & Adolphs, 2015; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). Accordingly, to disentangle these two possible neural pathways underlying pupil mimicry and trust formation, we included two independent localizer tasks to map threat-related and ToM-related neural networks and compared these to the pupil-mimicry pattern. In region-of-interest (ROI) analyses we investigated how pupil-dilation mimicry and pupil-constriction mimicry independently modulate ToM activity and tested which parts of the ToM network most closely associated with participants' level of trust.

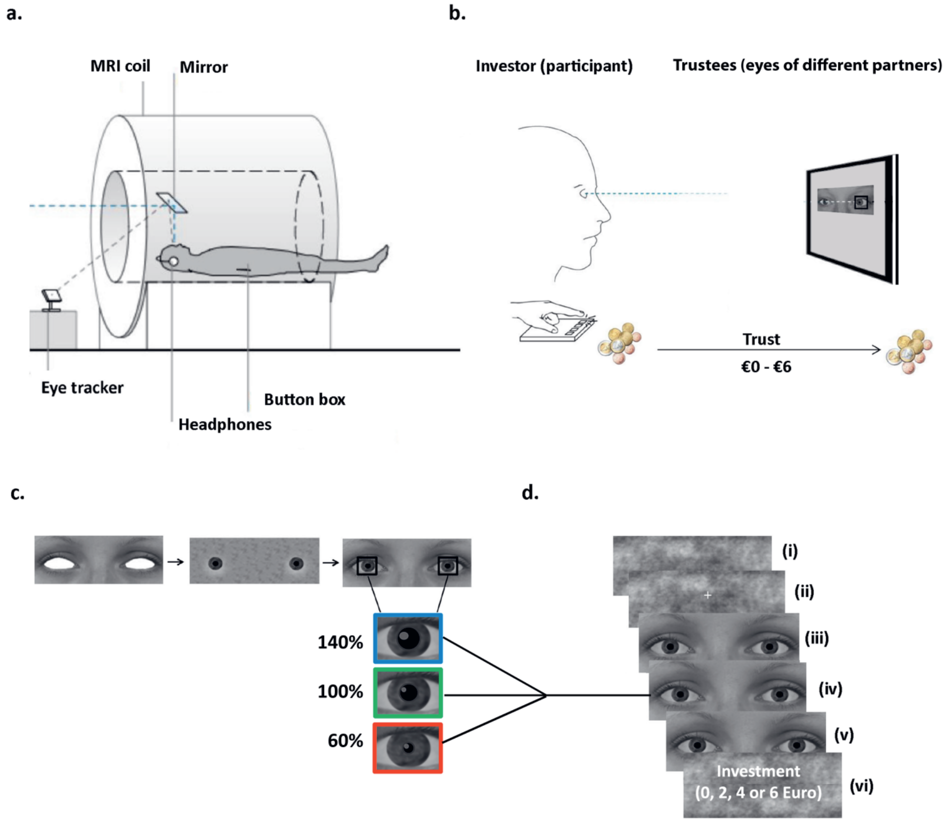


Figure 1 | Experimental set-up, stimuli and task. (a) Inside the MRI scanner, the participants played one-player trust-games while their investment-decisions and pupil diameter were measured with a button box and eye-tracker, respectively. **(b)** Subjects (investors) watched short video clips showing the eye region of different virtual partners (trustees) whose pupils were manipulated to change in size. In each trial, subjects were asked to transfer between €0 and €6 to their partner. Investments were then tripled and the virtual trustee was asked to transfer between 0% -100% of the tripled amount back to the investor. No feedback was provided so that subject's investments indicating trust were based on information from partners' eye-region only. **(c)** The stimulus material consisted of 18 photos with neutral expressions (9 males). The eyes were then filled with eye whites and irises, and an artificial pupil was added. The partner's pupil dilated (140% of the original size), constricted (60%) or remained static (range of 3-7mm). **(d)** Stimuli presentation. (i) A Fourier scrambled image was presented for 4,000 ms, (ii) fixation followed for 500 ms, (iii) the eye stimulus remained static for the first 1,500 ms, then (iv) in the dilation and constriction conditions, the pupils gradually changed in size over 1,500 ms and then (v) remained static at that size during the final 1,000 ms (in the static condition, pupils remained at the same size throughout the trial (vi) a screen appeared asking participants to make an investment decision.

Results

Behavioral & pupillary results

First, we conducted a series of multilevel models (*Methods*) to test our behavioral predictions. In the first model, we replicated previous findings (Kret et al., 2015; Kret & De Dreu, 2017; Wehebrink et al., 2018), by showing that partners with dilating pupils were trusted more than partners with static pupils [$\beta = 0.19$, SE = 0.05, CI (0.08, 0.30), $P < 0.001$] and partners with constricting pupils were trusted less than partners with static pupils [$\beta = -0.28$, SE = 0.05, CI (–0.38, –0.17), $P < 0.001$], [$F(2, 5{,}933) = 37.897$, $P < 0.001$] (Fig. 2*A* and *SI Appendix*, Table S1). Second, we found support for pupil mimicry. Fig. 2*B* shows that participants' pupil sizes dilated fastest when observing partners' pupils that dilated compared with partners' pupils that constricted or remained static: linear trend × partner pupil size [$F(2, 153{,}987) = 8{,}276$, $P < 0.001$]. Specifically, during trials where partners' pupils dilated, participants' pupils dilated faster compared with trials when partners' pupils remained static [$\beta = -0.55$, SE = 0.02, CI (–0.01, –0.02), $P = 0.005$] or constricted [$\beta = -0.77$, SE = 0.02, CI (–0.12, –0.04), $P < 0.001$] (*SI Appendix*, Table S2). Third, consistent with prior evidence (Kret et al., 2015; Kret & De Dreu, 2017), pupil mimicry modulated trust. Specifically, the interaction between partner pupil size × participant's own pupil size had a significant effect on trust [$F(2, 5{,}750) = 5.847$, $P = 0.003$]. Pair-wise post hoc comparisons confirmed that when participants mimicked dilating pupils, they trusted their partner more compared with when they did not mimic their partner [β = 0.175, SE = 0.08, CI (0.02, 0.33), *P* = 0.027]. Conversely, pupil-constriction mimicry decreased trust levels compared with when constricting pupils were not mimicked [β = –0.173, SE = 0.08, CI (–0.33, –0.02), *P* = 0.028]. Importantly, there was no significant difference in trust when participants' own pupils dilated compared with constricted during trials where partners' pupils remained static (*P* > 0.05) (**Fig. 2*C*** and *SI Appendix*, Table S3). Collectively, these behavioral analyses demonstrate that pupil mimicry enhances the effect that partners' pupils have on trust and support the notion that trust decisions are evaluated through integrating information from partners' pupils combined with own pupillary responses.

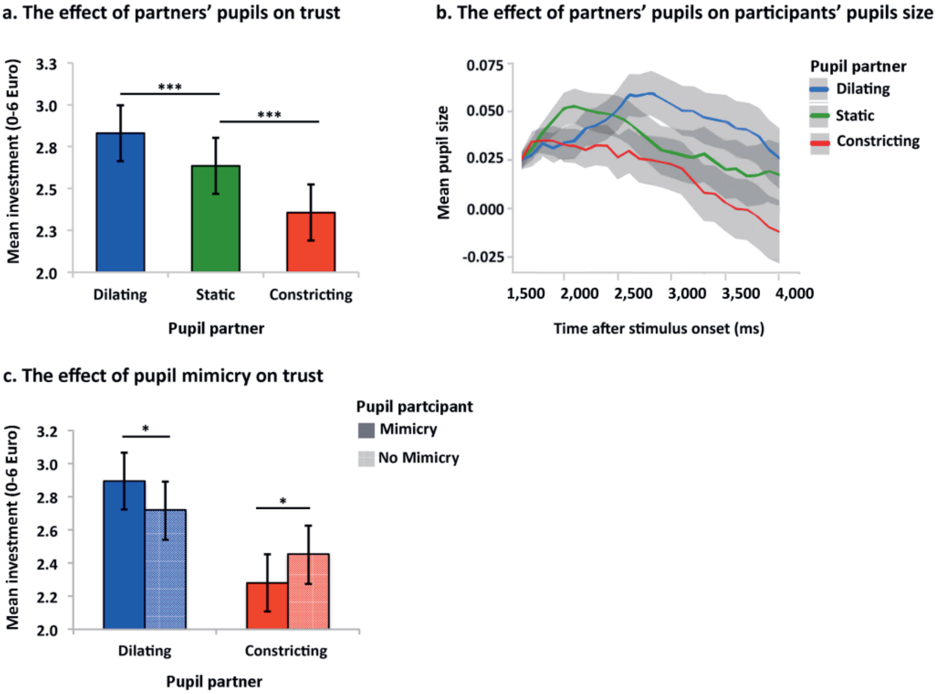


Figure 2 I Behavioral & pupillometry results (a) The bar plot shows that mean trust-related investments (€) increased in response to partners' dilating pupil size (n = 40 participants. Error bars indicate ±1SE. ****P* < 0.001 for each factor, pairwise contrasts: dilating pupils vs. static pupils (*B* = 0.19, *CI* (0.08, 0.30)) and constricting pupils vs. static pupils (*B* = -0.28, *CI* (-0.38, -0.17)). **(b)** Participants mimicked partner's pupil

sizes: the curves correspond to participants' mean pupil response from baseline over the remainder of stimulus presentation time (ms), in response to partner's dilating, static, and constricting pupils. Mean pupil size is depicted in arbitrary values. Shaded areas indicate the 99% confidence interval. **(c)** The bar plot shows mean investments (€) as a function of partners' and participants' pupil size. Error bars indicate ±1SE. *$P < 0.01$. Mean investment increases when participants' own pupils dilate in response to their partners' dilating pupils. Pairwise contrast: pupil dilation mimicry vs. no pupil dilation mimicry *(B* = 0.175, *CI* (0.02, 0.33)). Mean investment decreases when participants' pupil constricts in response to their partners' constricting pupils. Pairwise contrast: pupil constriction mimicry vs. pupil constriction no mimicry (*B* = -0.173, *CI* (-0.33, -0.02)).

fMRI Results

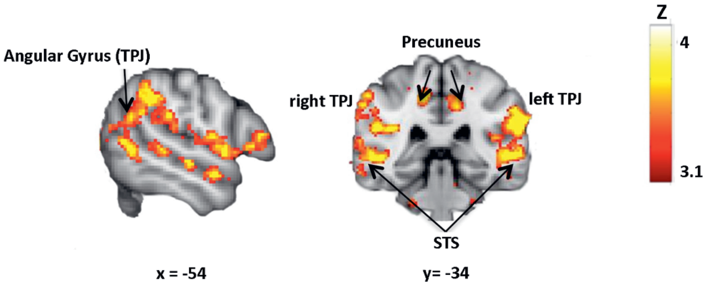
Neural correlates of pupil mimicry

Having established that the mimicry of subtle affective cues, such as pupil size, influences in part subjective evaluations of others' trustworthiness, we set out to investigate the neural regions that play a role in pupil mimicry, using the general linear model (GLM). The neural data were extracted 3,000 ms after the onset of the stimuli. This was the time point at which partners' pupils were maximally dilated or constricted (unless they had remained static) and participants' own pupils had had sufficient time to adjust to the presentation of the stimulus (Kret et al., 2015; Kret & De Dreu, 2017). The aim of the first analysis was to detect regions that are highly active during pupil mimicry. To test this, partners' and participants' pupillary responses were used as explanatory variables, resulting in the following conditions: pupil-dilation mimicry, pupil-constriction mimicry, no pupil-dilation mimicry, and no pupil-constriction mimicry (***Methods***). Of key interest was the whole-brain contrast comparing mimicry versus no mimicry trials.

Consistent with our hypothesis, the results showed that during pupil mimicry, participants displayed enhanced activation in all key regions of the ToM network: bilateral TPJ [60, –54, 18/–58, –54, 18], bilateral STS [52, –34, 2/–52, –34, 2], right MPFC [6, 46, 8] and bilateral precuneus cortex [8, –40, 48/–8, –40, 48] (Fig. 3*A* and *SI Appendix*, Table S4). Overlapping activation patterns during constriction mimicry and dilation mimicry were observed in the right lateral occipital cortex and in the precentral gyrus (*SI Appendix*, Tables S5 and S6). For a closer examination of the pupil mimicry fMRI pattern, Fig. 3 *B* and *C* depicts the neural overlap between the pupil mimicry-activation and ToM and threat-related brain-activation masks, which we obtained by conducting a metaanalysis via Neurosynth (27) (*SI Appendix*, Table S7). Specifically, the masks are derived from a metaanalysis we conducted on previous studies displaying brain regions that are consistently active in studies that include the name "theory of mind" or "threat" in the abstract ($n = 140$ and $n = 170$, respectively). These neural overlaps clearly indicate that pupil mimicry extends beyond the threat-related areas to neocortical regions involved in 'mindreading' (right temporoparietal junction) (Saxe & Wexler, 2005) and social judgment formation (medial prefrontal cortex) (Amodio and Frith, 2006). These results provide supporting evidence for the relationship between pupil mimicry and higher-level ToM processes.

The whole-brain analysis confirmed that the brain decodes pupils in a similar manner as more overt facial expressions of emotion (Critchley, 2009; H. Critchley et al., 2000; Mitchell & Phillips, 2015; Prochnow et al., 2013; Senju & Johnson, 2009). Assuming that morphological expressions of primates evolved as biological adaptations to transfer social information, changes in pupil size are likely used as social cues by observers. What remains unknown is whether—and to what extent—pupil mimicry is required for the brain to detect pupillary cues as socially relevant. To answer this question, one alternative needed to be ruled out. Participants' pupils may employ ToM activation, regardless of mimicry. For example, observed partners' pupillary changes may result in a similar ToM activation pattern as seen during pupil mimicry. If true, this would suggest that pupil mimicry is not a prerequisite for enhanced level of ToM activity. We ruled this out in a control analysis. In the control analysis we compared participants' neural activity when they saw partners' pupils dilate or constrict as opposed to staying static. The control analysis showed that without accounting for mimicry, the change in partners' pupil sizes (both dilation and constriction) was associated with enhanced activity in brain areas known to be involved in biological motion [movement of the eyes, mouth, or hand (Pelphrey et al., 2005)] and face processing (Rossion et al., 2003), but not in ToM processes (*SI Appendix*, Fig. S1 and Tables S8–S10). This shows that changes in a partner's pupil size, as a subtle form of autonomic expression, do not directly govern neural regions involved in implicit social evaluations. Instead, pupil mimicry is conditional for the engagement of social networks.

a. Mimicry > No mimicry



b. Mimicry and ToM mask (blue)

c. Mimicry and Threat mask (green)

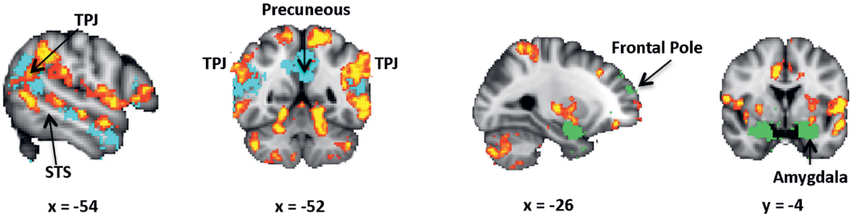


Figure 3 I Neural correlates of pupil mimicry. *STS = Superior Temporal Sulcus. *TPJ = Temporo-parietal Junction. **(a)** During mimicry, subjects displayed enhanced ToM activation. Peak voxels MNI x, y, z coordinates TPJ [60, -54, 18, /-58, -54, 18], bilateral STS [52, -34, 2/52, -34, 2], left medial prefrontal cortex [6, 46, 8] (not displayed in the image), Precuneous cortex [8, -40, 48/-8, -40, 40]; threshold at $P < 0.05$ (cluster-level FWE correction with multiple comparisons at 2.3, (n = 34 participants). For visualization, the threshold was set at Z = 3.1 – 4. **(b)** Shows additional overlaps between pupil mimicry pattern and ToM network (blue) and Threat network (green). The background images reflect MNI 2mm template (0.05 voxel size smoothing kernel), the right side of the image corresponds to the left side of the brain. Location coordinates are in stereotactic MNI space with a 2x2x2 voxel size. The source of anatomical labels: FSL Atlas tools.

ToM ROI selection

For a more quantitative examination of the effect of pupil mimicry on ToM activation, we incorporated a well-established independent ToM localizer task into our study's design (Dufour et al., 2013). The task consisted of 20 stories of two different types presented in two different blocks (for examples, see *SI Appendix*, Table S12). This functional localizer helped us to identify brain regions involved in ToM in individual participants. One subject was excluded from the ROI analysis due to excessive head motion during the ToM localizer task (*n* = 33 participants). After we defined ToM regions in the individual space (with the use of the ToM localizer), we standardized each participant's functional ToM image by multiplying the dichotomized masks with the average activation ToM mask that we obtained by conducting a metaanalysis on previous ToM/fMRI studies via Neurosynth (Yarkoni et al., 2011) (Supplementary Table 7). (*SI Appendix*, Table S7). Therefore, the final standardized ToM masks included only those voxels that were activated in the subjects of the present study as well as in the subjects that took part in the previous studies that were included in our metaanalysis (see Fig. 4*A* for an example of one subject's ToM mask).

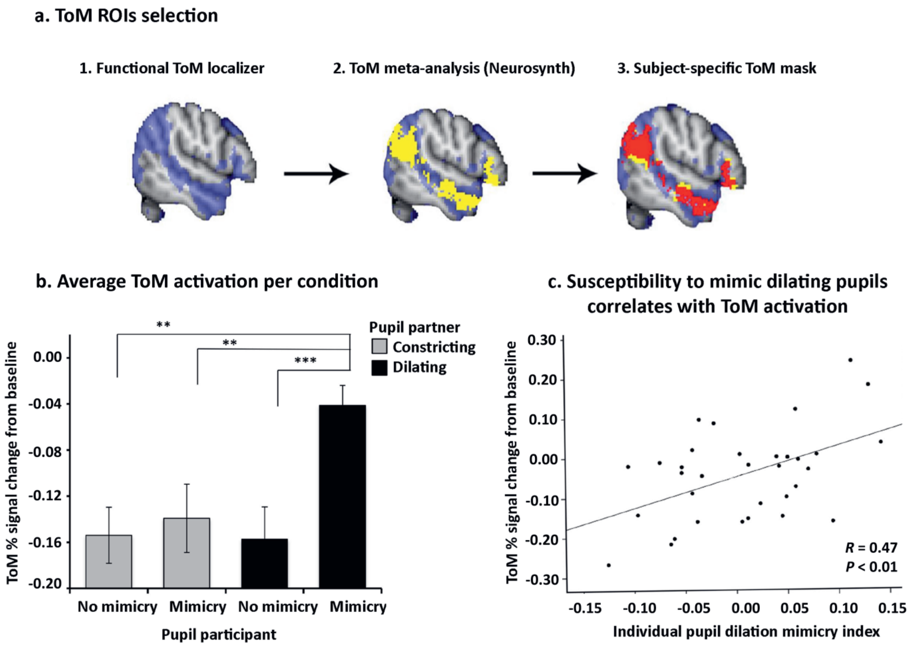


Figure 4 I ROI analyses. (a) Example of one subject's Theory of Mind Network (ToM)

mask selection. The ROIs were classified by an independent TOM localizer (blue) as well as by the additional inclusion of ToM masks (yellow), derived from our meta-analyses on previous studies**.** The overlapping voxels were used as the final mask (red). **(b)** The bar plot displays the mean parameter estimates averaged across all subjects (n = 33 participants) of the neural activation extracted from the individual ToM masks during four experimental conditions. During pupil dilation mimicry the ToM percentage signal increase was significantly greater as compared to all the other conditions including pupil constriction mimicry (*Mean difference* = -0.098, *SE* = 0.03, *CI* (0.02, 0.18), *P* = 0.005), no constricting mimicry (*Mean difference* = -0.113, *SE* = 0.03, *CI* (0.03, 0.19), *P* = 0.005), and no dilation mimicry conditions (*Mean difference* = -0.116, *SE* = 0.02, *CI* (0.05, 0.18), *P* < 0.001). ***P* < 0.01, ****P* < 0.001. Error bars indicate ±1 SE. **(c)** The scatter plot shows that the same subjects that displayed larger increases in pupil size during trials where partners' pupils were dilating (pupil dilation mimicry index) also displayed the greatest increase in ToM percentage signal during pupil dilation mimicry (*R =* 0.47, *P* < 0.01).

Pupil Mimicry and ToM activation

Growing evidence suggests that social signals, such as emotional expressions and gaze direction, are automatically encoded in social brain networks (Mitchell and Phillips, 2015; Senju and Johnson, 2009). Here we build upon these findings by investigating whether pupil mimicry modulates ToM activity, which further impacts on trust. To test this hypothesis, we extracted the parameter estimates of the neural activation from the individualized ToM masks and averaged ToM activation across subjects. A one-way repeated-measures ANOVA revealed that there was a significant difference in ToM activation across our four experimental conditions [*F*(1, 33) = 9.821, *P* = 0.004] (**Fig. 4*B***). As expected, the activation was higher when subjects mimicked partners' pupil size compared with when they did not. Interestingly, this was only the case when subjects mimicked dilating pupils. Follow-up pairwise comparison tests (with Bonferroni correction) revealed that the mimicry of dilating pupils was associated with a significantly greater activation in ToM regions compared with all of the other conditions, including pupil-constriction mimicry [mean difference = –0.098, SE = 0.03, CI (0.02, 0.18), *P* = 0.005]. This result suggests that the increase of activity in the ToM network observed on the whole-brain level (**Fig. 3**) was driven mainly by the mimicry of dilating pupils. These results imply that the ToM activation might be selectively sensitive to a partner's pupil dilation compared with pupil constriction.

One could think of this as supporting the view that pupil dilation correlates with physiological arousal (Fawcett et al., 2016a, 2017). Considering that pupil dilation is paired with norepinephrine release, accompanied by heightened activity in other brainstem areas (Eldar et al., 2013), it is possible that a participant's own pupil dilation explained the heightened activity in ToM areas, regardless of whether participants mimicked their partner or not. However, our analysis ruled out this alternative interpretation. Instead, we show that during trials where participants' own pupils dilated but their partners' constricted, ToM activity was significantly lower compared with when participants' mimicked partners' dilating pupils [mean difference = –0.113, SE = 0.03, CI (0.03, 0.19), $P = 0.005$]. Together, these results imply that the mirroring response is conditional for pupil dilation to activate ToM regions.

The second potential issue is regarding individuals' neural differences in social processing. That is, although ToM has been identified as a key system underlying social cognition, whether all of our subjects' engaged ToM areas during mentalizing about other's intentions is unclear. Therefore, we conducted an additional ROI analysis, indeed showing that pupil mimicry with dilating and constricting pupils modulates subject-specific ToM areas. Finally, a ROI analysis was conducted to investigate whether these social areas relate to trust. We elaborate on these analyses in the sections below.

Individual Differences in Pupil-Dilation Mimicry Correlate with ToM Activation.

Given that the group analysis revealed that the mimicry of a partner's dilating pupils is associated with greater ToM activation, we next determined whether a similar relationship was evident across all individuals. That is, we investigated whether an individual's susceptibility to mimic their partner's dilating pupils correlated with the average ToM percentage signal increase during pupil-dilation trials. We subtracted each subject's average pupil size on trials showing a partner with dilating pupils from his/her mean pupil size during trials where their partner's pupils remained static (**Fig. 4*C***). This difference represented an individual index of pupil-dilation mimicry susceptibility. As expected, the result shows a positive relationship between the pupil-dilation mimicry index and increases in the ToM signal during those trials (Pearson's *R* = 0.473, *P* = 0.005). Importantly, there was no direct association found between an individual's average pupil size (regardless of partner's pupil size) and activity in this network (Pearson's *R* = 0.029, *P* = 0.870). This suggests that the susceptibility to mimic a partner's dilating pupils discriminates people on the basis of their social network engagement.

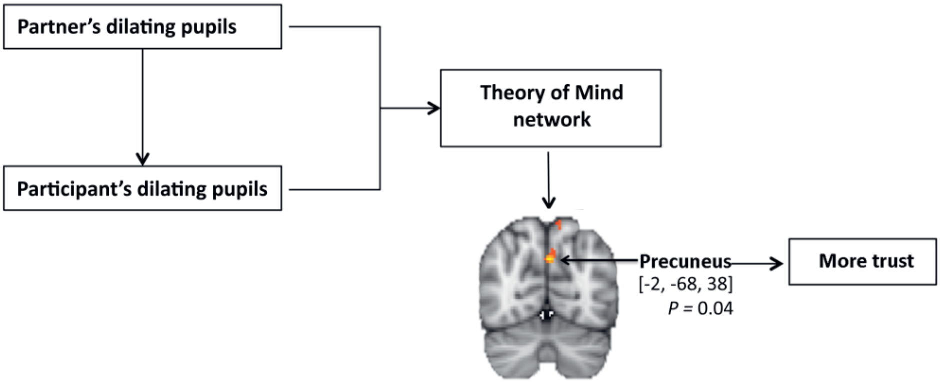


Figure 5 l ToM and trust. The diagram shows that the ToM network is modulated by pupil dilation mimicry. Within the ToM network, investment rates predicted precuneus BOLD signal changes, confirming ToM involvement in trust decisions. Peak voxel MNI x, y, z coordinates: [-2, -68, 38], corrected for ToM network with Threshold Free Cluster Enhancement (Smith & Nichols, 2009) (Threshold Z = 3.1, P < 0.05, FWE-corrected *P*-value from the minimum voxels in the cluster).

Trust and ToM Network.

The final goal of the fMRI experiment was to determine which neural mechanisms were engaged in the pupil mimicry–trust linkage. To that end, we investigated whether ToM regions that were associated with pupil mimicry were also modulated by trust decisions. To test this prediction, on each trial we used the participant's level of investment as a regression parameter convolved with the hemodynamic response function to identify the ToM voxels that were most closely correlated with trust (the level of the investment). The higher-level analysis and group-level analysis were performed by averaging the mean activation within and between subjects, without any additional contrasts. We compared the ToM signal against baseline and tested for significance with permutation testing (Methods) (36). As predicted, the results revealed that the level of trust modulated ToM activation, with peak activation in the precuneus [–2, –68, 38] threshold-free cluster enhancement P = 0.04 (Fig. 5), confirming the involvement of the ToM network in the development of trust. This analysis supported the hypothesis that a partner's pupil dilation drives trust through pupil mimicry and associated neural activation in brain areas related to social cognition.

Discussion

In this study, the combination of psychophysiological, behavioral, and neuroimaging data allowed us to disentangle the elusive link between pupil mimicry and trust. Behaviorally, we replicated previous findings by showing that trust is increased when looking into the eyes of a partner with dilating pupils and lowered when looking into the eyes of a partner with constricting pupils (Kret et al., 2015; Kret & De Dreu, 2017; Wehebrink et al., 2018). We further demonstrated that peoples' pupil sizes mimic those of observed partners and if pupil-dilation mimicry occurs, trust is promoted. These unprecedented findings already suggested a fundamental link between autonomic pupil-mimicry and social-cohesion. However, whereas pupil mimicry has now been well-documented (Fawcett et al., 2016a, 2017; Kret et al., 2014, 2015; Kret and De Dreu, 2017; Wehebrink et al., 2018), its function and underlying mechanisms remained largely unknown (Harrison et al., 2009, 2006). To test which neural organization facilitates this autonomic form of mimicry, we compared participants' neural activity when they mimicked versus did not mimic their partner's pupil size. A whole-brain analysis revealed that the mimicry of pupillary changes was associated with increased activation in the precuneus, TPJ, STS, and MPFC, all of which are key regions of the ToM network (Schaafsma et al., 2015). Neuroimaging research in humans has identified the ToM network as the basic system that facilitates social understanding (Dufour et al., 2013; Saxe and Wexler, 2005a; Schaafsma et al., 2015; Schurz et al., 2014).

ToM areas can be well dissociated from similar, but not entirely overlapping areas involved in empathy (Kanske et al., 2015). Kanske et al. (2015) define empathy and ToM as being “affective” and “cognitive” routes to understanding others. The central distinction between empathy and ToM is that empathy refers to the sharing of a sensory, affective, or bodily state (Singer, 2006), while ToM involves both affective states and the cognitive reasoning about others. On the neural level, empathy and ToM networks largely overlap (e.g., in the precuneus, STS, left TPJ). Nevertheless, empathy is more closely related to activity in the anterior insula and middle anterior cingulate cortex (Decety and Lamm, 2006; Fan et al., 2011), while ToM is associated with activity in the TPJ (Kanske et al., 2015).

It is important to note that areas involved in ToM appear often in the literature on mirror neurons or more broadly on motor theories of social cognition (Gallese et al., 2004; Rizzolatti et al., 2009). For example, the inferior frontal gyrus, parietal areas, and STS are active during grasping and the observation of grasping (Caspers et al., 2010). The current fMRI findings further contribute to this body of research by showing that pupil mimicry induces a neural pattern similar to those found during more explicit forms of mirroring (e.g., motor movement). According to its location in the brain, this evidence fosters the view that mimicry, even on a subtle autonomic level, may enable a route to interpret others’ behavior. An additional control analysis revealed that the ToM areas were active only when participants mimicked partners’ pupil sizes, but not in response to partners’ pupillary changes alone. This finding supports the hypothesis that pupil mimicry is involved in higher-level, social functions as opposed to being a lower-level mechanism restricted to subcortical structures. Although we did not find strong evidence for the involvement of subcortical structures during mimicry, this does not mean that these structures are not involved at all (Harrison et al., 2006). Instead, the current data provide supporting evidence for the view that pupil mimicry extends beyond physiological responses, such as arousal (Aston-Jones and Cohen, 2005; Eldar et al., 2013; Joshi, S., Li, Y., Kalwani, R. M. & Gold, 2016), as it also triggers higher neural areas involved in social processing.

To provide more direct evidence for the “social” hypothesis of pupil mimicry, we have built upon previous findings by including a ToM localizer task. This allowed us to map subject-specific ToM regions involved in social processing (the ability to attribute mental states to others). Within subject-specific ToM masks, we examined how pupillary responses to partners’ pupils modulated these neural areas. Intriguingly, our

ROI analysis demonstrated that the ToM network was significantly more active during pupil-dilation mimicry, compared with pupil-constriction mimicry. This effect was also evident on the individual level, whereby individuals' susceptibility to mimic dilating pupils was proportional to participants' ToM level of engagement. The fact that the ToM network is recruited significantly more during pupil-dilation mimicry compared with pupil-constriction mimicry suggests that the mimicry of dilating pupils is more socially relevant, at least in a relatively nonthreatening interaction, as in the current study. According to Tylén and colleagues (Tylén et al., 2012), the ToM network activation represents an adaptive neural system for rapid alerting in response to mutual social interest. If we consider that pupil dilation is tied to sympathetic nervous system activation, another person's pupil dilation as a form of affective expression is likely to trigger a spontaneous attribution of mental states (e.g., "interest in me") in the observer's brain. When a partner's pupils constrict, an observer can infer that the partner is not—or no longer—motivated to pursue social exchange and that such mental state attribution may be reduced or be absent during pupil-constriction mimicry. From this perspective, it could be argued that social brain activation during pupil dilation is more socially/evolutionary relevant. Importantly, our data demonstrate that ToM activation could not be fully explained by participants' or partners' pupil dilation alone. Instead, the mirroring response was conditional for pupillary cues to become reflected in a ToM signal (**Fig. 4**). Taken together, these fMRI data illustrate that only seeing a partner's pupils dilate, as a sign of arousal, is not sufficient for the brain to recognize this information as socially meaningful. In other words, there is need for mimicry—the autonomic alignment between interacting partners—to render another's autonomic expression as socially relevant.

Our findings go beyond previous studies (Harrison et al., 2009, 2007) by linking the engagement of neural mechanisms during pupil mimicry to social behavior. Here we demonstrate that within the ToM network, activation within the precuneus significantly correlated with participants' level of trust. The precuneus involvement in trust has been documented in previous studies (Baumgartner et al., 2008; Emonds et al., 2014; Krueger et al., 2007), yet the present study reveals that a partner's pupils' dilation drives trust through pupil mimicry and associated neural activation in brain areas related to social cognition. In parallel to this evidence, the empirical literature has implied that others' actions can be decoded by activating our own somatic and autonomic systems (Procházková and Kret, 2017; Tamietto and De Gelder, 2010). For instance, Harrison and colleagues (Harrison et al., 2007) found that individual sensitivity to another's pupil size predicted scores of emotional empathy. Furthermore, previous behavioral research has shown that pupil mimicry occurs within two members of the same species (human–human and chimpanzee–chimpanzee) but not across species (human–chimpanzee) (Kret et al., 2014). Kret and colleagues (2015; 2017) found that the pupil-dilation mimicry–trust linkage is bound to interactions between members of the same ethnic group and breaks in cross-ethnical group interactions. These studies are in line with other work showing increased trust with partners that are more familiar compared with partners who are unfamiliar, creating an in-group bias (de Dreu and Giffin, 2017). Although we did not manipulate familiarity in the present study, the neural mechanism that we observed during pupil mimicry, especially the activations in the temporal areas, suggest this factor might be of importance (Negro et al., 2015). Future studies might therefore want to investigate whether pupil mimicry is strengthened between closely bonded partners, such as parents and their children (Levenson and Gottman, 1983). Such evidence would further support our view that pupil mimicry is a social phenomenon, which possibly evolved in and because of group life.

To conclude, by examining the neural mechanisms of pupil mimicry in the context of an economic game, the present study provides support for the social hypothesis of pupil mimicry. We demonstrated that the neural regions involved in social decision-making are modulated by the subtle expression of pupil size and that mimicry is the target mechanism underlying this process. This is important because by knowing that pupil mimicry is involved in healthy social cognition, these data reveal a fundamental mechanism by which an individual's pupils trigger neurophysiological responses within an observer. We propose that pupil-dilation mimicry seems to bring interacting partners' neural activity into mutual alignment, creating a joint-pupillary state that may facilitate communicative success. In the future, pupil mimicry might be an especially useful measure for early social deficits because autonomic cues are not likely to be influenced by learning, social norms, or conscious control compared with facial expressions and other overt affective signals. Given that fMRI measures are of a correlational nature, further research using real-life interactions and pupil-mimicry manipulations will be highly valuable to determine the putative causal link between pupil mimicry and trust formation.

Methods

Participants. Forty-one healthy, right-handed, Dutch participants without a neurological or psychiatric history and normal or corrected-to-normal vision were recruited for the current experiment. One participant had symptoms of mild depression. We have excluded this participant, leaving a total of forty participants for behavioral analysis (mean age [± SD] 23.40 [± 2.91] years, 21 females, range: 19.5-32.7). Six participants (3 males and 3 females) were excluded from the fMRI data analysis due to excessive head-movements (more than 1.5 mm displacement), leaving thirty-four subjects for the fMRI data analyses (mean age [± SD] 23.5 [± 2.78] years, 18 females, range: 19.5- 32.7). For two participants, activation was averaged over two instead of three runs because of insufficient eye-tracking data with which to measure mimicry. Our sample size was motivated by those used in previous studies (Harrison et al., 2009, 2007). The experimental procedures were in accordance with the Declaration of Helsinki and approved by the Ethical Committee of the Faculty of Behavioral and Social Sciences of the University of Amsterdam.

Stimuli. The stimulus material consisted of nine female and nine male photos with neutral expressions derived from the validated Amsterdam Dynamic Facial Expression Set (van der Schalk et al., 2011). Pictures were standardized in Adobe Photoshop (Adobe Systems), converted to gray scale, and cropped to reveal only the eye region. Average luminance and contrast were calculated for each picture and then adjusted to the mean. The eyes were then filled with new eye whites and irises, and an artificial pupil was added in Adobe After Effects. After a static presentation of 1,500ms, the partner's pupil increased (140% of the original size), decreased (60% of the original size) or remained static within the physiological range of 3-7mm. In the last second of the stimulus presentation, the pupils were static again. This way, 54 unique stimuli (3 pupil types x 18 eye-regions) were created. In addition, in Matlab R2013b, Fourier scrambled images were created from the first frame of each video. These images contained the same low-level features including contrast and luminance of the original ones and were presented prior to the stimulus to reduce the light reflex. Stimuli were viewed on a back-projection screen via a mirror system attached to the MRI head coil.

Trust-game task. The trust-game was first practiced outside of the scanner. When participants correctly answered three practice questions, we moved on to the real experiment. The trust game experiment used a randomized event-related design. In each of the three runs, all 54 videos were presented in random order. The pupils inside the eyes of the virtual partners dilated, constricted, or remained static over stimulus presentation time; these were the three experimental conditions. A scrambled picture appeared for 4,000 ms and then a fixation cross was presented on top for 500 ms after which a video showing eyes appeared. One video showed one eye pair with dilating, constricting, or static pupils. After observing each stimulus, the participant was prompted to make an "investment decision (€0 or €6)". The participants then had 2,000 ms to choose 0, 2, 4 or 6 Euros; no feedback was provided. The inter-trial-interval (lasting between 9,300 to 12,300 ms) was sufficient for the hemodynamic response to return to the baseline.

Localizer Tasks. Two localizer tasks were performed using a randomized block design to map ToM and threat-related networks. Both localizers lasted 8,6 minutes and their order was counter-balanced across participants.

The ToM localizer task was taken from a widely used task to identify brain regions involved in social cognition (for more details, see (Dufour et al., 2013)). The task consisted of twenty stories, in which ten of them described a situation in which someone held a false belief (for example, see Supplementary Table 12). Participants had to indicate whether the suggestions referring to the stories were true or false. The other ten stories were false-photograph stories, which described situations with a false or outdated representation of the world. The False-belief localizer was presented in a block design and counterbalanced, starting with either the False-belief or the False-photograph story. These types of stories required the participant to deal with incorrect representations about the world and were therefore matched in their difficulty, logical complexity, and inhibitory demands, but differed in the need to think about someone's thoughts. Crucially, they differ in building a representation of someone else's mental state. The amount of words was matched over the two conditions. One story started with 12 seconds fixation cross, followed by 10 seconds story. After the presentation of the story, the participant had 4 seconds decide whether the story was true or false.

Threat-localizer task was designed to be as similar as possible to the ToM localizer and also included twenty stories; however, presenting ten threatening versus ten neutral sentences (for example, see Supplementary Table 12). The Threat localizer was presented in a block design counterbalanced starting with either the threatening or the neutral story. One story started with a 12 second fixation cross, followed by a 10 second long story. After presentation of the story, the participant had 4 seconds to make the decision whether the story was true or false. The threat and ToM localizers were matched in terms of the number of words they contained. The threat-localizer has been validated prior to usage so that only stories that were very threatening and very neutral were included. The stories were rated for threat sensation on a scale from 0 to 10 (0 being non-threatening, 10 being very threatening) and selected by 14 people out of a list of 15 threating and 15 non-threatening stories. Furthermore, only situations that participants could imagine or were rated as probable were selected. The 10 most threatening stories had an average threatening value of 8.75 ± 0.73 with a probability of 6.04 ± 0.083. The 10 non-threatening stories had an average of 0.86 ± 0.68, with a probability of 6.94 ± 0.57.

Procedure. The participants were instructed about the procedure, practiced the trust game, and completed the medical screening two days prior to scanning. Participants filled out a series of questionnaires as a control so that our sample did not deviate from the normal population on following scales: Interpersonal Reactivity Index measuring empathy (IRI; with Empathic Concern (EC) and Perspective Taking (PT) scales; (Davis, 1983)), the Liebowitz Social Anxiety Scale, to test social anxiety disorders (LSAS; (*Psychological medicine.*, n.d.); Supplementary Table 11). After participants signed the informed consent, they were reminded about the rules of the games whilst inside a 3 Tesla MRI scanner. Next, two electrodes were attached to participants' left ring and index fingers. After entering the room, a pulse oxidation signal (PO) was recorded from the middle finger. The breathing rate was measured with a band around the participants' chest (Philips Achieva). They were instructed to watch short video clips showing the eye region of different partners and decide how much money they would want to invest in the partner of whom the eye region was shown. Presentation 16.4 was used to present stimuli and acquire behavioral responses. Participants viewed stimuli on the projector screen over a mirror, which was mounted on the MRI head coil. They responded via a button box held in the right hand. First, a sham scan was implemented to ensure that the magnetic field was homogeneous. Subsequently, we obtained the T1 anatomical during which the participants performed a nine-point calibration of the eye-tracking system. Between the runs, two localizer tasks were performed to map ToM and threat-related networks (**Supplementary Table 12)**. The scan settings were the same as for the trust-game task (Methods, fMRI data acquisition). The total scanning session lasted between 60 and 80 minutes. After the scan session, participants filled out the State-Trait Anxiety Inventory for mental disorders (STAI; (Spielberger, 2010)), rated the eyes they had seen in the scanner on attractiveness, trustworthiness and arousal and performed the reading the mind in the eyes test (Baron-Cohen et al., 2001), and were instructed to draw pupils in a happy and angry face (Hess, 1975). Two weeks after the scanning session, participants received the Beck Depression Inventory (BDI, ("Psychometric properties of the Beck Depression Inventory: Twenty-five years of evaluation," 1988).

*Eye-tracking data acquisition***.** Pupil data acquisition was collected concurrently with the fMRI measurements and sampled at 1000 Hz with an average spatial resolution of 15 to 30 min arc. The MRI-compatible EyeLink 1000 Long Range Mount system (SR Research, Osgoode, Ontario, Canada) was placed outside the scanner bore and subjects' pupils were tracked via the mirror attached to the head coil. For optimal measuring with the eye-tracker, participants did not wear eye-make up. The eye tracker was calibrated prior to the start of each run. Pupil preprocessing was done in 5 steps. (1) Each participants' pupillary response were measured on a trial-by-trial basis, if a participants' pupil sizes across two time-samples exceeded 2 SD, the data were identified as outliers and removed from the analysis. (2) The gaps smaller than 250 ms were interpolated. (3) We smoothed the data with a 10th-order low-pass Butterworth filter. (4) The average pupil size 500 ms prior partner's pupils began to change (i.e., 1,000–1,500 ms after stimulus onset) served as the baseline and was subtracted from the pupil size during the remaining stimulus presentation (1,500–4,000 ms). Only the final 2.5 seconds of stimulus presentation was included in the analysis, as from that point on, partners' pupils started to change in size. (5). Analyses of pupil-related measures included those participants who had less than 50% signal loss during less than half of the trials.

*Behavioral & Pupil Analysis***.** Because of the nested structure of the data, multilevel modelling was the most appropriate method to analyze the data. All behavioral and pupillary data were analyzed using a Generalized Mixed Multilevel Models in IBM SPSS Statistics (Version 20). This allowed for the estimation of individual differences by modelling random slopes and intercepts. The multilevel structure was defined by trials (Level 1), nested in runs (Level 2), nested in participants (Level 3). As is common, non-significant factors were dropped one by one, starting with the higher-order interactions. Via log-likelihood tests, we determined whether dropping non-significant factors improved model fit or significantly worsened it, in which case the non-significant factor was kept. After specifying the fixed effects, model building proceeded with statistical tests of the variances of the random effects.

Trust investment decisions. Trusting behavior was analyzed with a series of two-level models defined by the different trials that were nested in runs and within participants. To test the effect of partners' pupils on trust, the partners' pupil size coded as –1 (constrict), 0 (static), and 1 (dilate) was used as a fixed factor, with investment level being the dependent variable.

Pupil mimicry. To investigate the effect of partners' pupils on the participant's own pupils, we kept the three-level structure but this time we added time (100-ms time slots) as a repeated factor with a First-Order Autoregressive covariance structure (AR1) to control for auto-correlation. The factors partners' pupil size in the 3 conditions, constricting, static, dilating (coded as -1, 0, and 1), served as predictors. The participants' own baseline corrected pupil sizes were used as target variables. Furthermore, three orthogonal polynomials were included to account for linear, quadratic, and cubic trends in the growth curves. A random intercept and random linear, quadratic and cubic terms accounted for individual differences.

Defining pupil mimicry. To further investigate the source of trust, participants' pupil responses were separated based on a median split into dilation mimicry trials or constriction mimicry trials. For example, a trial was categorized as a "dilation mimicry trial" or a "constriction mimicry trial" when the mean pupil size of the trial was higher than the median pupil size of a participant when viewing a partner with dilating pupils or when viewing a partner with constricting pupils. This way, we had an approximately equal number of trials in each condition: (i) dilation mimicry, (ii) constriction mimicry, (iii) dilation no mimicry, (iv) constriction no mimicry and (v) static pupils.

Pupil mimicry and trust. To test whether pupil mimicry modulates trust, we labelled each trial as a mimicry trial or a no mimicry trial depending on the participants' pupillary behavior. The fixed effects were Partners' pupil size (dilate, constrict, static), Mimicry (mimicry, no mimicry), Partners' pupil size x Mimicry. The target was the level of investment.

fMRI data acquisition. We collected the fMRI data on a 3.0-T Philips Achieva XT MRI scanner equipped with a standard 32-channel head coil. Structural images were obtained with a gradient echo-planar T1 sequence (T1 turbo field echo, 240*188 mm2 field of view (FOV), comprising a full brain volume of 220 slices (1mm slice thickness). Volumes were acquired continuously with a repetition time (TR) of 2s and an echo time (TE) of 3.73ms (8° flip angle (FA), sagittal orientation). Next, functional data were collected with T2*-weighted echo planar imaging sequence (2.0s TR, 27.63ms TE, 192*141.24 mm2 FOV, 39 slices, 3.3 mm slice thickness, 76.1° FA, sagittal orientation) covering the whole brain. The fMRI data were analyzed and pre-processed using the fMRI Expert Analysis Tool (FEAT) in FSL version 6.0 (Oxford Centre for Functional MRI of the Brain Software Library (www.fmrib.ox.ac.uk/fsl) on a MacBook Pro (Retina, 15-inch, mid-2015; Mac OS X 10.11.6). Data collection and analysis were not performed blind to the conditions of the experiments.

fMRI data Pre-processing. Preprocessing steps were run ahead of the first-level analysis and included motion correction, spatial smoothing using a Gaussian kernel of full width at half-maximum (5 mm), and high-pass temporal filtering with a cut-off of 100 seconds. Voxels belonging to brain tissue were extracted from non-brain tissue voxels using the Brain Extraction Tool (BET). Data from all runs were realigned to the mean volume of the middle run using a least squares approach with 6-degree rigid spatial transformation.

fMRI analysis. Functional MRI data were analysed using the GLM for event-related designs in FEAT tool in FSL 5.6 (Smith et al., 2004). All fMRI data was pre-whitened, slice-time corrected, spatially smoothed, motion corrected, and high-pass filtered. In the first level analysis, the hemodynamic response to events of each condition was modeled as the main effect by the hemodynamic response function (HRF). To correct for motion artefacts, subject-specific realignment parameters were modelled as covariates of no interest. Linear contrasts of regression coefficients (β values) were computed at the run level, averaged at the subject level and taken to a group-level random effect analysis, using one-sample *t*-tests. The same steps applied for ROI analysis. Our primary goal was to determine if the ToM network is modulated by pupil mimicry. We analyzed the fMRI data using two main GLMs of BOLD responses with first-order auto-regression.

GLM 1: Pupil mimicry. The GLM contained regressors including: (1) pupil dilation mimicry, (2) pupil constriction mimicry, (3) pupil dilation no mimicry, (4) pupil constriction no mimicry (5) static pupil trials. For this GLM, we calculated the following first-level single-subject contrasts: pupil dilation mimicry vs. baseline, pupil constriction mimicry vs. baseline, pupil dilation no mimicry vs. baseline, pupil constriction no mimicry vs. baseline, pupil mimicry > no mimicry (pooling over constriction and dilation mimicry), no mimicry > pupil mimicry.

GLM 2: Partner's pupil change. In a control analysis, we looked for regions that show significant increase in activation in response to changes in partners' pupil size irrespective of mimicry. The following repressors were used: (1) partners' pupils dilate (2) partners' pupils constrict (3) partners' pupils stay static. The analysis of main interest was in the whole brain contrast comparing trials when partners' pupil change (dilate /constrict) > stay static. In addition, the following contrasts were examined: partners' pupils dilate > partners' pupils stay static; partners' pupil constrict > partners' pupil stay static; partners' pupils dilate > partners' pupils constrict.

Whole-brain analysis. We pooled the fMRI data for each condition across three runs using a second-level (within-subject) fixed effects analysis. A third-level (across-subject) analysis was performed within mixed-effects (FLAME 1 + 2) analysis in FSL, treating subjects as a random effect. The effect for each experimental condition was calculated with FEAT. Unless otherwise specified, all cortical regions with a height threshold of $Z = 2.3$ and a cluster probability of $p < 0.05$ were reported. The resulting contrast images were linearly registered to the anatomical structure using FMRIB's Linear Registration Tool (FLIRT) with 7° of freedom and the full search space, then spatially normalized to the T1- weighted MNI-152 stereotaxic space template (2 mm) using FMRIB's Non-Linear Registration Tool (FNIRT) with 12 degrees of freedom and the full search space. Activation maps were overlaid on the MNI-2mm brain and regions were determined using the Harvard-Oxford Cortical Structural Atlas that accompanies FSL.

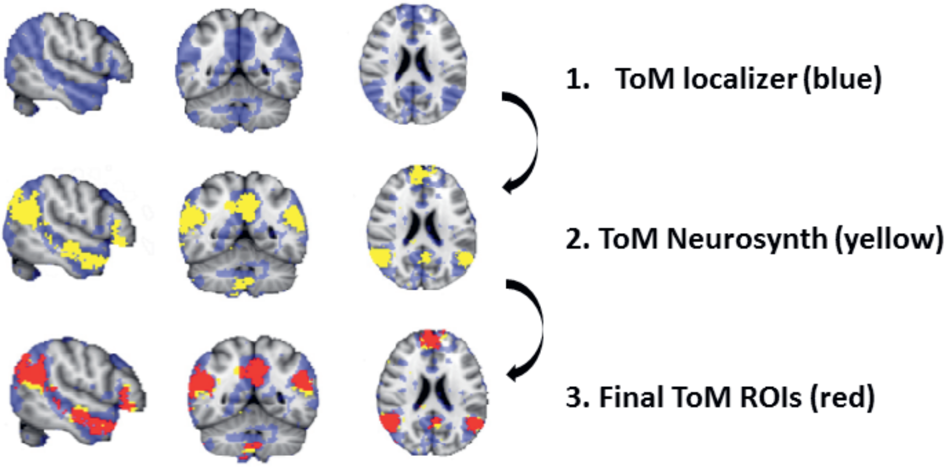


Figure 6 I ROIs selection example from one subject: The final ToM mask included MNI coordinates mentioned by Saxe and Kanwisher (R Saxe & Kanwisher, 2003). These were [-54 -60 21] for the left TPJ, [51 -54 27] for the right TPJ, [-9 -51 33] for the precuneus, [-57 -27 -12] for the left anterior STS and [66 -18 -15] for the right anterior STS. All subjects shared activation in threat ROIs: Amygdala [24, 2, -20/-22, 0, -22], Frontal Pole: [-24, 58, 16], Brainstem [2, -24, -14]. The background image reflects MNI 2mm template (0.05 voxel size smoothing kernel).

ROI Analysis. An additional region of interest (ROI) analysis was performed using Featquery within FSL within subject-specific ToM masks. First, we functionally defined regions of interest (ROIs). In the False-belief localizer, the GLM conditions were (1) the false belief (Theory of Mind) and (2) false photograph contrast (Neutral). A group analysis was conducted on the false belief > false photograph contrast providing threshold maps ($Z = 2.3$, $P = 0.05$). By contrasting those conditions, we have localized regions that subject's recruited when they were processing others' mental states**.** Within the Threat-localizer GLM contained regressors: (1) Threat and (2) Neutral. A group analysis was conducted on the very threatening > non-threatening contrast providing t-maps ($Z = 2.3$, $P = 0.05$). Contrasting those conditions localizes regions that are recruited during threat**.** The final ROIs were determined by additional inclusion masks obtained from Neurosynth (Yarkoni et al., 2011) where they are freely available for downloading. The masks were derived from meta-analyses of previous studies displaying brain regions that are *consistently* active in studies that include the name 'Theory of Mind' and 'threat' in the abstract. The final ToM regions were defined in the individual space by multiplying the binarized masks acquired by the localizers (liberal threshold $Z = 1.5$, $P = 0.05$) with the average activation mask downloaded from Neurosynth (Yarkoni et al., 2011), in each participant separately. As a result, we created subject-specific ToM inclusion masks in the individual space, which were used for the further ROI analysis.

The parameter estimates of the neural activation were extracted from the ROIs for each subject, and averaged across four experimental conditions: (1) pupil dilation mimicry, (2) pupil constriction mimicry, (3) pupil dilation no mimicry, (4) pupil constriction no mimicry. One-way repeated measures ANOVA was conducted to compare the ToM activation across conditions with zero determined by the implicit baseline (i.e., whatever is not included in the model). This was followed by pairwise comparisons with Bonferroni correction for multiple comparisons.

ToM and trust. To link ToM activation back to trusting behavior, the level of investment on each trial was taken as a regression parameter convolved with the HRF to identify the regions that most closely correlated with the level of investment. The higher-level analysis and group level analysis were performed within the ToM mask by averaging the mean activation within and between subjects, without any additional contrasts. Based on recent work showing parametric neuroimaging analyses to be susceptible to inflated false positive rates (Eklund et al., 2015), we corrected for multiple comparisons with FSL's randomise threshold-free cluster enhancement (TFCE; (Smith and Nichols, 2009)) with non-parametric permutation testing (5,000 permutations) and a variance smoothing kernel of 5 mm. This method enhances the signal of contiguous voxels that form clusters, but returns voxel-wise *P*-values family-wise error corrected (FWE-corrected) for the multiple voxels within a ROI. The *P*-value reported in the text is FWE-corrected *P*-values from the minimum voxels in the cluster.

Overview of the statistical tests used in the present study. Parametric tests were used with the assumption of normality (the normality of the data was not formally tested). This approach is typical in the analysis approaches used for neuroimaging. It is worth noting that, for some key results, we also conducted permutation tests, which do not require normality assumptions regarding the data.

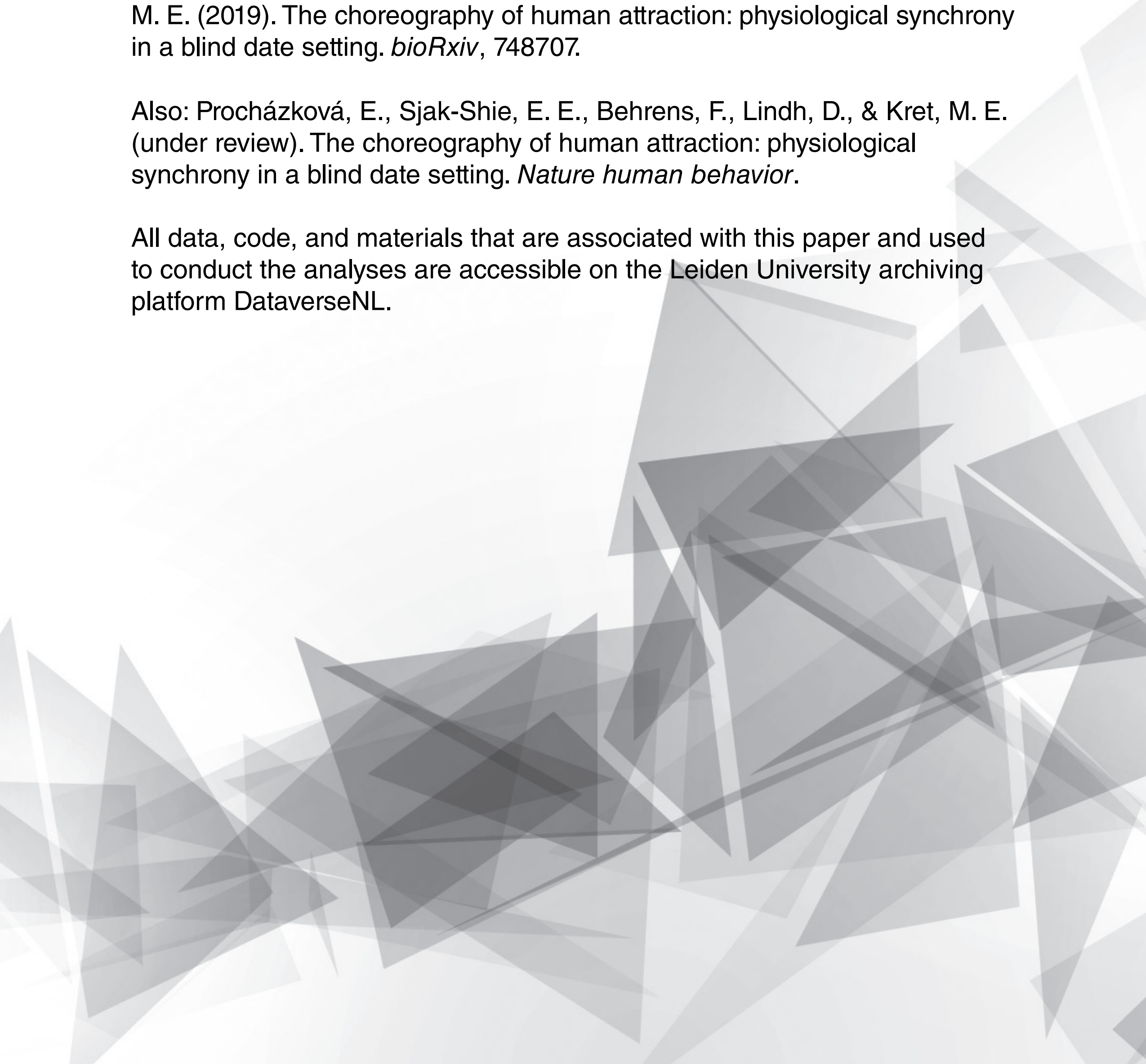
Chapter 5

Physiological synchrony predicts attraction in a blind date setting

Based on: Procházková, E., Sjak-Shie, E. E., Behrens, F., Lindh, D., & Kret, M. E. (2019). The choreography of human attraction: physiological synchrony in a blind date setting. *bioRxiv*, 748707.

Also: Procházková, E., Sjak-Shie, E. E., Behrens, F., Lindh, D., & Kret, M. E. (under review). The choreography of human attraction: physiological synchrony in a blind date setting. *Nature human behavior*.

All data, code, and materials that are associated with this paper and used to conduct the analyses are accessible on the Leiden University archiving platform DataverseNL.



Abstract

Humans are social animals whose well-being is shaped by the ability to attract one another and connect with each other. In a dating world in which success can be determined by brief interactions, apart from physical features, there is a choreography of movements, physical reactions, and subtle expressions that promote attraction. To determine what drives attraction between people, we measured the physiological dynamics between couples during real-life dating interactions outside the laboratory, where dating is most relevant. Participants wore eye-tracking glasses with embedded cameras, and devices to measure physiological signals including heart rate and skin conductance. We demonstrate that overt signals such as smiles, laughter, eye contact, or the mimicry of those signals, did not predict attraction. Instead, attraction was predicted by synchrony in heart rate and skin conductance between partners. Our findings suggest that when interacting partners' subconscious arousal levels rise and fall in synchrony, mutual attraction emerges. We conclude that physiological synchrony possibly provides a medium which translates subtle visible expressions into embodied emotions that influence attraction via somatosensory simulation.

Keywords: physiological linkage, nonverbal communication, mimicry, emotion, interpersonal coupling

Introduction

In our modern world where millions of people meet online before interacting face-to-face, the question “what defines attraction” has never been more relevant. Physical attractiveness is often valued as one of the most important characteristics of a potential partner (Walster et al., 1966). Yet, research demonstrates that judging a potential romantic partner based on written or visual stimuli (e.g., personal ads, photos) does not predict attraction during a first date (Eastwick and Finkel, 2008). This is because during a social situation, aside from static facial features and the conversation, nonverbal dynamics such as eye gaze, facial expression, and body posture play a key role. Importantly, research has begun to acknowledge that what people really seek in a partner is a “gut feeling of connection” expressed as a sensation in the body (Tahhan, 2013; Wheatley et al., 2012). This type of attraction is difficult to regulate, fake, or put in words, yet seems to be a major force that often overrides rational decisions when it comes to partner selection. Despite its importance, what sparks this feeling between people remains one of the unsolved mysteries of science. To understand how this romantic spark between people develops, we developed a blind date experiment utilizing state of the art technology including eye-tracking glasses linked to physiological measures in order to elucidate the nonverbal and physiological signals that predict attraction between strangers.

Early-stage romantic attraction is sometimes referred to as passionate love (Berscheid and Wastler, 1974). A first date provides an excellent scenario in which to test how attraction develops. This is because during dating interactions people are likely to exchange a broad variety of facial expressions and gestures, and during this process, their attraction towards a partner also transforms (Eastwick and Finkel, 2008; Grammer, 1990). For instance, both smiling and laughing have been reported to reflect the degree of attraction one person feels for another, and furthermore to lead to reciprocal attraction (Givens, 1978; Hall and Xing, 2015; Moore, 1985; Tickle-Degnen and Rosenthal, 1990). Similarly, friends and lovers implicitly mimic each other’s nonverbal behavior such as eye gaze and facial expressions, and this type of matching behavior has been proposed to be a key ingredient fostering liking and attraction (Chartrand and Bargh, 1999; Chartrand and van Baaren, 2009; Farley, 2014; Guéguen, 2009; Lakin and Chartrand, 2003; Stel and Vonk, 2010; Van Baaren et al., 2009). Nevertheless, while smiling is considered to signal affiliation, it *can* have different meanings. Research demonstrates that people smile to show subordination (Hecht and LaFrance, 1998), to gain approval (Cashdan, 1998), or to express embarrassment (Goldenthal et al., 1981). Likewise, prolonged gazing (Givens, 1978; Hall and Xing, 2015; Montoya et al., 2018) or the tendency to look away has both been reported as signs of affection (Goffman, 1977). Perhaps this is why research has been unable to reliably detect non-verbal signals of attraction (for review see Montoya et al., 2018). Nevertheless, if a “gut feeling of connection” truly exists (beyond perceiver’s projection of infatuation by perceiver onto the other), there must be a physical manifestation of interpersonal attraction in the real world of behavior.

One possibility is that the feeling of attraction between people is achieved on a physiological level not easily observed or detected. According to the Somatic Marker Hypothesis, emotional reactions have strong somatic components (Damasio, 1996). These somatic components mark the occurrence of important events through a parallel somatic/visceral response. In return, bodily information provides feedback perceived as a “gut feeling” that shapes a perceiver’s cognition and behavior. In this way, physiological responses can potentially contribute to social perception and provide input for romantic decisions. In line with this hypothesis, recent advances in methodologies have begun to uncover that during social encounters, partners tend to synchronize on physiological levels (Palumbo et al., 2017; Reed et al., 2013). This type of subconscious synchrony is reflected in the correlation between people's continuous measures of autonomic nervous system such as heart rate and skin conductance (Palumbo et al., 2017). Crucially, in established couples the level of synchrony has been associated with the amount of time couples have spent together (Papp et al., 2013), the ability to identify the emotions of one's partner (Levenson and Ruef, 1992), and their romantic satisfaction (Helm, Sbarra, & Ferrer, 2014; J. Helm, Sbarra, & Ferrer, 2012; Levenson & Gottman, 1983). The *function* of physiological synchrony is not well understood, but similar to motor mimicry (e.g. facial expression mimicry), it may help people to emotionally align (de Waal and Preston, 2017; Procházková and Kret, 2017). Specifically, physiological synchrony might be a result of the biologically mediated tendency to adapt to incoming social information (Hasson et al., 2012; Procházková and Kret, 2017). Through subtle changes in the face and body, changes in physiological arousal can become visible to others, allowing physiological synchrony to emerge. Physiological synchrony also seems to increase with familiarity and during intimate moments such as direct eye contact (McAssey et al., 2013) and touch (Chatel-Goldman et al., 2014). Taken together, prior literature agrees that physiological synchrony might be a precursor to deeper emotional understanding (Chatel-Goldman et al., 2014; Levenson and Ruef, 1992). Yet, what does physiological synchrony really predict? Is it that couples who feel closer to each other synchronize more? Or does synchrony predict moment-by-moment affective exchanges that are predictive of the quality of that interaction? We elaborate on this theory further and hypothesize that this type of affective alignment might be particularly meaningful for early romantic development.

Taken together, the current literature suggests that attraction emerges from the dynamic exchange of verbal and nonverbal signals (Givens, 1978; Gonzaga et al., 2001; Hall and Xing, 2015), yet the necessary empirical and analytic tools to directly address this hypothesis were not available until recently. Consequently, a direct link between nonverbal behavior, physiology, and attraction has never been directly verified. To define what drives the feeling of attraction, we built a dating lab outside of the regular laboratory setting, at different social events, where meeting a new person is most natural (Fig. 1). Males and females (140 participants), who had never met before, entered the dating cabin and sat at a table. A visual barrier initially occluded their view of each other, but then opened for three seconds, allowing them to form a *first impression* of their partner. The barrier then closed and subjects rated their partner on attraction (0 – 9-point scale). This baseline measure of initial attraction was then followed by one *verbal* and one *nonverbal* interaction of 2 minutes each (the order of which was counterbalanced). After each interaction, the barrier closed and subjects rated their partner on the same scales again. At the end of the experiment, participants could decide whether they wanted to go on another date with their partner.

The benefit of a blind date is that we can observe how attraction between newly introduced partners develops over time and therefore study the relationship between attraction and synchrony in a controlled way. We anticipated *(a)* that dating partners would synchronize on multiple levels of expression including motor movements (facial expressions, nodding, gestures), gaze (face-to-face contact and eye-contact), and physiology (synchrony in heart rate and skin conductance). Although each of these modalities has different characteristics and the literature uses a variety of terms to describe them (“mimicry”, “physiological linkage”, “gaze reciprocity”), for consistency we will refer to the various forms of mirroring as *“synchrony”*. We further hypothesized *(b)* that the strength of heart rate synchrony and skin conductance synchrony would be predictive of attraction over the course of the date. This carefully designed set-up had several other advantages: First, a blind date setting is a stressful context that likely induces strong physiological reactions, which is a desirable state for physiological synchrony measures. Furthermore, introducing verbal and nonverbal conditions allowed us to separate the influence of nonverbal expressions from verbal expressions on attraction. Finally, thanks to the combination of multiple measures and the longitudinal aspect of our study, we could go beyond investigating the putative link between synchrony and attraction (i.e., a between-dyadic effect). Specifically, we were able to investigate whether dyads that increased in synchrony over the course of their date became more attracted to each other (i.e., within-dyad effect predicting attraction over time). To our knowledge this is the the first time that attraction has been studied as a dynamic construct that emerges from behavioral and/or physiological synchrony. For an overview of the collected measures, see Figure S1.

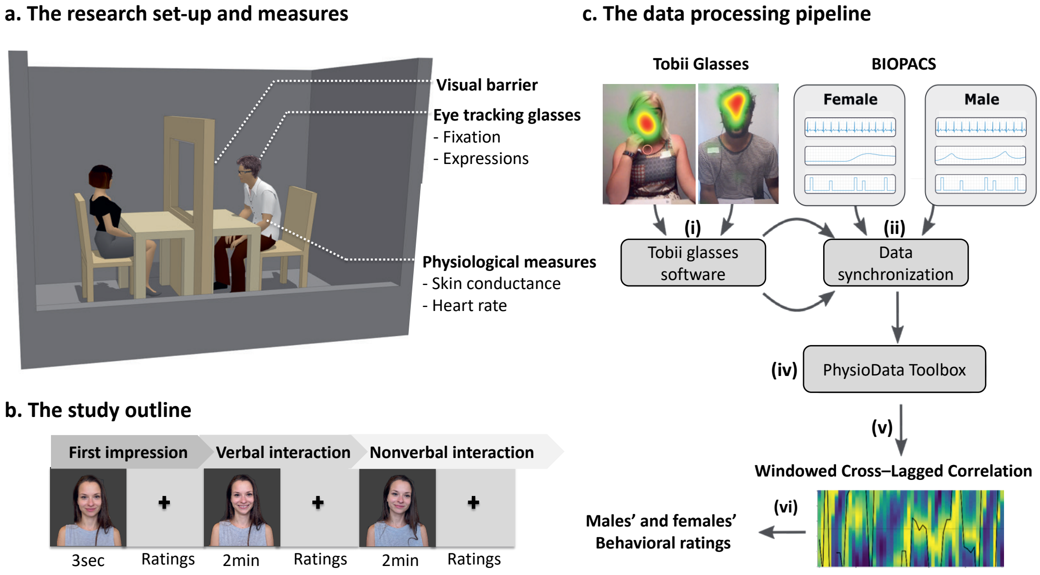
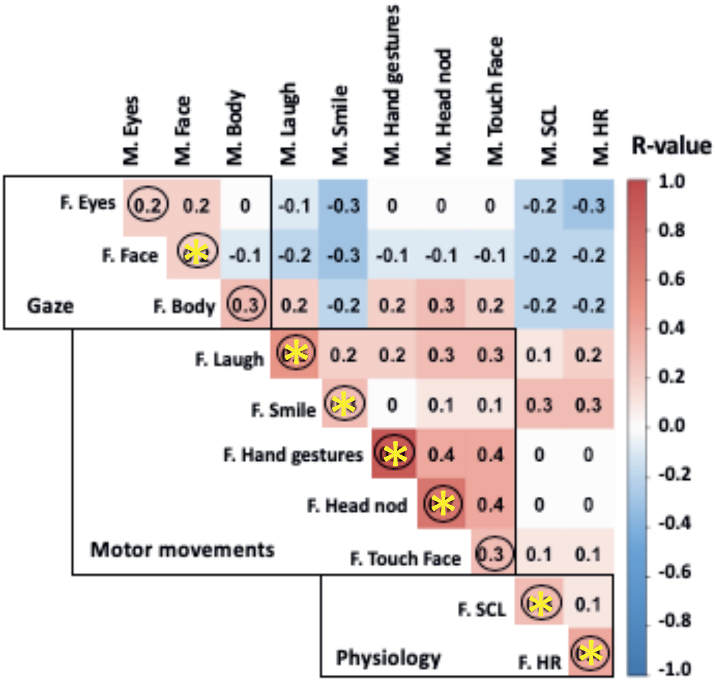


Figure 1. (a) The experimental set-up was situated in a habitable container. Inside the cabin, there was a table with two chairs on opposite sides. A white barrier with a fixation cross was placed in the middle of the table, preventing the dyad from seeing each other and controlling the dating interaction types. Participants were instructed to remain silent until they heard pre-recorded instructions via a speaker. Throughout the experiment, Tobii eye-tracking glasses measured subjects' gaze fixations and expressions while participants' physiology was recorded with two BIOPACs. **(b) Experimental outline.** To collect baseline physiological measures, participants looked at the fixation cross on the closed barrier for 30 seconds. The barrier opened for three seconds and participants saw each other for the first time (first impression). After that, the barrier closed and post-first impression physiological measures were collected during another 30 second fixation period. Subsequently, participants rated their partner on attraction. Two additional interactions followed, each preceded by 30 seconds closed barrier baseline (the barrier closed). During verbal interaction: the visual barrier opened and participants were instructed to talk freely with their partner for 2 minutes. During nonverbal interaction: participants were instructed to look at each other without talking for 2 minutes. After each interaction, the barrier closed and subjects rated their partner on the same scales. The order of verbal and nonverbal interaction was counterbalanced **(c) Pre-processing pipeline.** (i) Two groups of independent coders rated behavioral expressions, and mapped eye gaze fixations on pre-selected areas of interest. (ii) Gaze fixations and expressions were time locked and synchronized with physiological measures (heart rate, skin conductance) using customized scripts. (iii) Video visualizations were created. (iv) The physiological data were further pre-processed with our PhysioData Toolbox (Elío Sjak-Shie, 2018) and down-sampled to 100 ms windows for further (v) Windowed Cross-Lagged Correlation analyses (Boker et al., 2002) before they were (vi) regressed with attraction ratings.

Results

Hypothesis 1: Is there evidence for synchrony?

The first hypothesis predicted that dating partners would synchronize on multiple levels of expression including motor movements, gaze, and physiology. Specifically, we expected that if one of the individuals often shows one type of behavior (e.g., look long into a partner's eyes, smiles, or displays an increase in physiological arousal), his/her partner would also show the same behavioral responses. In the first analysis, we tested for evidence of associations between partners' expressions with a series of Spearman's rank–order correlations in which we included all females' motor movements (frequency of facial expressions, nodding, gestures), duration of eye gaze (i.e., looking at partner's eyes, face or body), and physiological responses (heart rate and skin conductance), and correlated them with expression measures of their male partners. This resulted in a correlation matrix (Figure 2). The circled cells in Figure 2 highlight the synchrony types between male and female partners, which were the main focus of this analysis. The additional cells are other between-partner associations (for the full matrix see Supplementary Figure 1a). Considering that individuals differ in their level of expressiveness, there is a certain baseline chance that partner's expressions are correlated by chance. To test for the significance of associations above random chance, in a subsequent control analysis, we paired each female with a random male whom they had not interacted with but whom had dated another female (see Supplementary Table 1 and Supplementary Figure 1b). We here focus on the results of the different synchrony types (circled cells in Figure 2) and show that for seven out of ten, the correlations between real dyads were significantly higher than the correlations in the randomly shuffled dyads (all Fisher's $z > 2.3$, $p < 0.05$). Specifically, we found evidence for synchrony of (i) smiles, (ii) laughs, (iii) head nods, (iv) hand gestures, (v) face-to-face gaze, (vi) heart rate, and (vii) skin conductance. For eye contact, gaze at partner's body and face touching, the associations were similar across real and randomly shuffled dyads (Fisher's $z < 0.1$, $p > 0.05$). Thus, these three synchrony types were excluded from subsequent analyses. To predict attraction, in the next model we zoom in on the seven significant synchrony types that we observed.



	M. Eyes	M. Face	M. Body	M. Laugh	M. Smile	M. Hand gestures	M. Head nod	M. Touch Face	M. SCL	M. HR
F. Eyes	0.2	0.2	0	-0.1	-0.3	0	0	0	-0.2	-0.3
F. Face		*	-0.1	-0.2	-0.3	-0.1	-0.1	-0.1	-0.2	-0.2
F. Body			0.3	0.2	-0.2	0.2	0.3	0.2	-0.2	-0.2
F. Laugh				*	0.2	0.2	0.3	0.3	0.1	0.2
F. Smile					*	0	0.1	0.1	0.3	0.3
F. Hand gestures						*	0.4	0.4	0	0
F. Head nod							*	0.4	0	0
F. Touch Face								0.3	0.1	0.1
F. SCL									*	0.1
F. HR										*

Figure 2. Correlation table summarizes the associations between real dyad's expressions, eye gaze, and physiology across three interaction time periods (based on Spearman's rank–order correlations, N = 162). The circled cells depict synchrony types between two interacting partners and other cells are other between-partner associations. The asterixis show 7 synchrony types that were significantly higher for real couples versus randomly shuffled dyads. The redder the color, the more positively correlated these variables were. The black boxes framed around naturally occurring clusters demonstrate that associations occurred on all three levels of expression including males' and females' gaze, motor movements, and physiology. F = females, M = males. HR = heart rate, SCL = skin conductance level.

Hypothesis 2: Does synchrony strength predict attraction?

As expected, attraction was not a stable construct as participants' feelings of attraction changed substantially over the course of the date. While some individuals became more attracted to their partners, others became less attracted (Supplementary Fig. 2). At the end of the date, almost half of the participants (44%) wanted to go on another date with their partner (34% females, 53% males), which is a substantial rate considering that couples were paired randomly. However, only 17% of the couples matched and had a mutual wish to date each other again.

Having confirmed our first hypothesis that people synchronized their expressions with each other across multiple levels including motor movements, gaze and physiology, our next analysis investigated whether the strength of different interpersonal synchrony types predicts attraction. To transform synchrony into binary variables (e.g., smiling or not), we calculated the proportion of time both participants' reciprocated expressions for motor movements (smiling, laughing, head nods, hand gestures) and gaze fixations (looking at partners' face). To calculate the strength of synchrony between continuous physiological signals (heart rate and skin conductance level), we used windowed cross-correlation analyses (Boker et al., 2002) (for details see Methods). This resulted in seven synchrony values (synchrony in smiles, laughs, head nods, hand gestures, face-to-face gaze, heart rate, and skin conductance level) for each dyad and time-block (first impression, first interaction, second interaction). These seven synchrony types were used as predictors of attraction in a Multilevel linear mixed model. The multilevel model had the following structure: three time points (Level 1), nested in participants (Level 2). As both the attraction ratings and the synchrony measures were Level 1 (repeated-measures) predictors, the longitudinal design of the study implies that we predict the evolution of attraction by the evolution in synchrony over the course of the three-time intervals. To account for the dependency of measures within subjects, we included a random intercept effect (across participants) and a random slope for time to account for the different trajectories in attraction scores (as outlined above). Apart from different synchrony measures, to account for other variables that may influence attraction, the full model included factors of gender, a dummy variable for interaction type (verbal = 1, nonverbal = 0), a dummy variable for interaction order (verbal first: yes = 1, no = 0), and two-way interactions between interaction type * and each type of synchrony. The final model was selected with a backward stepwise selection of fixed effects. The VIF values of the full and final models were all smaller than 4, suggesting that multicollinearity did not influence our results (Gould, 2010) (for the final and full models see Supplementary Table 2 – 3).

The final model showed a main effect of gender (*F* (1, 298) = 8.38 *p* = 0.004), revealing that males were more attracted to females than females were to males. Importantly, we further found that attraction was predicted by physiological synchrony between partners. Specifically, the more couples' skin conductance and heart rates synchronized, the more attracted participants were to their partner (skin conductance level: *F* (1, 298) = 7.33, *p* = 0.007; heart rate: *F* (1, 298) = 5.49, *p* = 0.020) (Fig. 3b-c). Interestingly, we did not find this association with synchrony in smiles, laughs, head nods, hand gestures, or face-to-face gaze (all *F*s < 1.50, *p*s > 0.05; Fig. 3b-c). Moreover, the lack of an interaction between physiological synchrony and interaction type (*p* > 0.05) implied that physiological synchrony had a positive effect on attraction during both verbal and nonverbal interactions. In sum, these data suggest that physiological synchrony explains more variance in attraction than the synchrony of explicit expressions such as smiles, laughs, head nods, hand gestures, or face-to-face gaze.

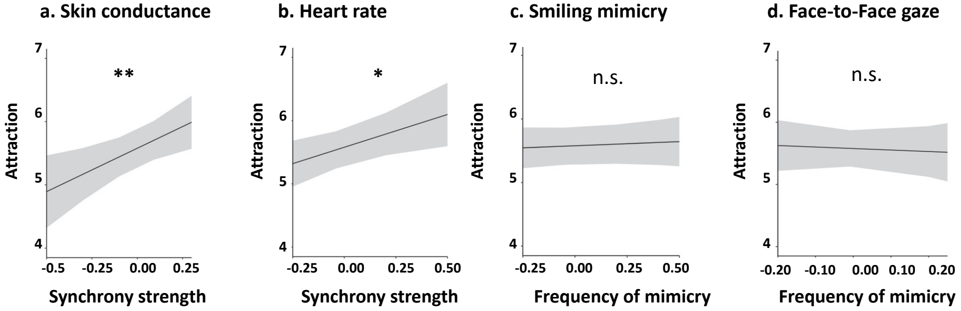
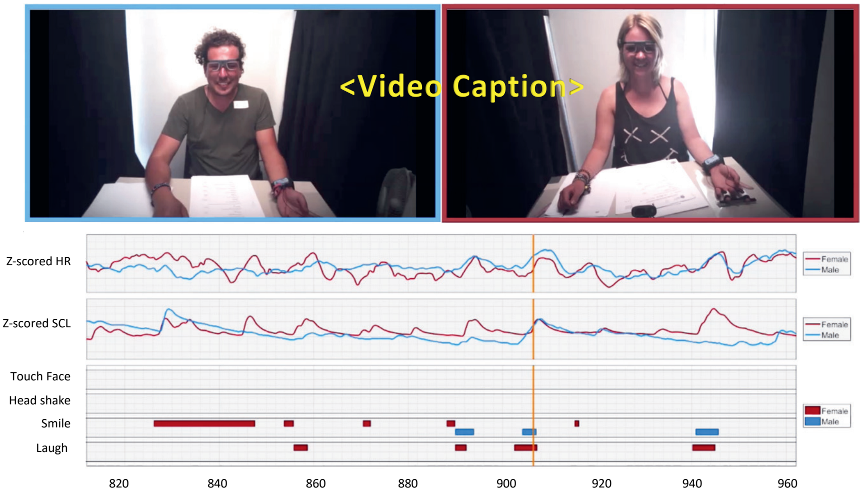


Figure 3. The line graphs represent slopes extracted from our Multilevel linear mixed model **(a)** Attraction based on the synchrony of skin conductance level [β = 1.44, SE = 0.53, CI (0.39, 2.49), *p* = 0.007] and **(b)** heart rate synchrony [β = 0.99, SE = 0.42, CI (0.16, 1.83), *p* = 0.020] **(c - d)** The frequency of smile synchrony and face-to-face gaze did not significantly affect attraction (both *p* > 0.05). The shaded areas represent 95% confidence intervals.

To show an example of what physiological synchrony looks like, we included a video of one couple (see Video 1). We selected this video because these two people first met without exchanging any words and, during this non-verbal interaction, their mean attraction score increased.



Video 1. An example of measures. The video shows a nonverbal interaction where participants were instructed not to talk (825 – 945 seconds). Female's and males' z-scored skin conductance and heart rate (top two rows). In four rows below selection of measured expressions is depicted (Touch face, Head shake, Smile, Laugh). In addition, gaze fixations were collected (not depicted). Notice the contagious spread of emotional information; at 886 second, the female will smile and the male partner reciprocates with a smile back. During this moment, we observe an increase in female's and males' skin conductance and heart rate. Again, at 903 second, the female laughs; in response the male smiles and we again observe synchrony in heart rate and skin conductance (highlighted by orange cursor). Although nonverbal, during this 2-minute interaction couples' physiological synchrony and attraction increased.

Additional Control Analyses

Does within or between dyad physiological synchrony predict attraction?

For a more precise examination of the effect of physiological synchrony on attraction, we conducted three control analyses. First, in the previously described model, the variables for heart rate and skin conductance level synchrony included within and between-dyad level variation in synchrony. It is therefore unclear whether couples that were highly attracted to each other synchronized more than those that were not (i.e., between-dyad effect), or whether changes in physiological synchrony over time predicts attraction changes (i.e., within-dyad effect). To disentangle the two types of variations, we computed two variables: (1) Between-dyad SCL synchrony: the averaged synchrony level across time points per dyad, and (2) Within-dyad SCL synchrony: the deviation in synchrony level (per time point) from the dyad's averaged synchrony level (within-dyad centering). Both variables were included in a Multilevel linear mixed model with a two-level structure (three-time points (Level 1), nested in participants (Level 2). We also included a random intercept effect (across participants) and a random slope for time.

Results clearly showed that the change in synchrony influenced the change in attraction at the within-dyad level (for both synchrony variables; heart rate: (F (1, 296) = 4.67 p = 0.031); skin conductance: (F (1, 296) = 6.23 p = 0.013), but there was no effect at between-dyad levels (Supplementary Table 4). Thus, dyads with more overall synchrony were not significantly more attracted to each other. However, it is worth noting that the effect, although non-significant, was in the predicted direction. A possible confound in this analysis is an asymmetry in variance between and within dyads, with between-dyad synchrony exhibiting greater variance than within-dyad synchrony (Supplementary Figure 4). Nevertheless, the two main effects for within-dyad SCL and HR synchrony demonstrate that the more couples became synchronized over the course of the date, the more their attraction increased. This finding is consistent with the hypothesis that moment-to-moment physiological synchrony correlates with moment-to-moment affective dynamics that are predictive of the quality of that interaction.

Does arousal predict attraction?

The fact that arousal has been linked to attraction invites the possibility that an increase in synchrony of physiological signals is required for attraction to occur. For example, increases in the level of skin conductance and heart rate may yield similar attraction changes without the need for synchrony. If true, this would mean that participants' arousal level alone may promote attraction irrespective of interindividual synchrony. To test this, in an additional control analysis we used the same Multilevel linear mixed model with the same structures as in the second analyses, but instead of heart rate and skin conductance synchrony measures, we used participants' average (baseline corrected) heart rate and skin conductance for each interaction as predictors of attraction (see Supplementary Table 5 for the model summary and more details). The results showed that attraction was not significantly explained by individuals' independent heart rates (*F* (1, 298) = 0.01, *p* = 0.955) or skin conductance levels (*F* (1, 298) = 0.04, *p* = 0.850). This result further confirms that attraction could not be solely predicted by the arousal responses of the two individuals, but by the synchrony of arousal between individuals.

Is attraction a valid outcome variable?

One may wonder whether we really measured attraction in this study or some other phenomenon. To control for this possibility, throughout the experiment we also collected other ratings including trust, liking, feeling of connection, and "click". We also asked whether subjects felt awkward or anxious. These scores were then compared with attraction ratings and participants choice to go on another date (yes/no) with the partner. The results of a principal components analysis (PCA) showed that attraction was closely correlated with positive factors (e.g. liking and connection) and negatively linked with feelings of being shy, awkwardness and low self-esteem (Supplementary Table 6-7). Importantly, among all collected ratings, the feeling of attraction was the strongest predictor of the decision made at the end of the date to date the partner again (F (1, 317) = 6.33, *p* = 0.012, see Supplementary Table 5 for details).

Discussion

Multiple studies have suggested that synchrony on the emotional level promotes connection and affiliation (Mogan et al., 2017), yet the mechanisms mediating the link between attraction and nonverbal communication remain unknown. In this blind date experiment, we measured a whole choreography of movements, gestures, and physiological reactions in order to understand how romantic attraction between people develops. In line with the existing literature (Chartrand and van Baaren, 2009; Palumbo et al., 2017; Procházková and Kret, 2017), we observed that people spontaneously synchronized on multiple levels of expression including: motor movements, eye gaze, and physiological responses. We further demonstrated that attraction was predicted by physiological synchrony between partners; an effect which persists regardless of whether couples were allowed to speak or were forced to remain silent. Since attraction was *not* predicted by visible expressions such as smiling, laughing, or direct eye contact, these results highlight the importance of subconscious physiological coupling in the development of romantic attraction. The current findings are particularly relevant from the perspective of our modern romantic landscape where affective exchange is reduced to quick encounters between strangers.

The finding that physiological synchrony promotes attraction between strangers supports existing theory implicating unconscious synchrony in the development of human connection (Tahhan, 2013; Wheatley et al., 2012). There are several theoretical and methodological reasons for why physiological synchrony is more strongly coupled to levels of attraction than visible mimicry or arousal level. Mimicry in a form of pure motor imitation has been found to increase liking and rapport between individuals (Chartrand and Bargh, 1999). However, especially at the early stages of dating, humans do not disclose their interest in the opposite sex too overtly (Goffman, 1977). Whereas straightforward information exchange would be more evident, research suggests that humans make handy use of a ‘backdoor’, which offers an option of escape when things do not progress as hoped (Grammer, 1990). For instance, while smiling and prolonged gazing has been proposed to be a sign of affection (Givens, 1978; Hall and Xing, 2015; Montoya et al., 2018), ignoring partner’s gaze and looking away is often also a sign of affection (Goffman, 1977). These behavioral inconsistencies likely relate to the lack of visible synchrony effects on attraction found in this and others’ experiments (for review see Montoya et al., 2018). In contrast to visible synchrony (e.g., direct copying of overtly perceived behaviors), physiological synchrony requires both partners’ autonomic nervous systems to become simultaneously activated. Considering that such a response is difficult to regulate, we propose that physiological synchrony potentially captures more ‘genuine emotional exchange’. In support of this theory, our data demonstrate that couples were often smiling and mimicking each other on a superficial level, yet these types of visible signals did not predict attraction (for the analysis of individual expressions see Supplementary Table 8). However, when participants’ physiological signals aligned during these interactions, attraction increased (Fig. 3).

Our data revealed that attraction is not predicted by partners' frequency of expression or eye fixation duration, nor is it linearly related to participant's autonomic nervous system activity. This result suggests that synchrony shapes attraction beyond individuals' nonverbal expressions and autonomic arousal. The fact that arousal plays a role in sexual attraction has been well established (Berscheid and Wastler, 1974; Bryant and Miron, 2003). For instance, it has been found that couples who had been watching a high arousal movie engaged in more affiliative behaviors than did couples who had watched a low-arousal movie (Cohen et al., 1989). Similarly, people who just got off a roller-coaster ride perceived a photograph of an opposite-sex individual as more attractive than people who had been waiting for the roller-coaster ride (Meston and Frohlich, 2003). However, while most contemporary theories suggest that attraction is heightened by the level arousal (e.g., excitation-transfer theory (Zillmann, 1971)), the current study shows that skin conductance and heart rate baseline during dating interactions were no sufficient predictors of interpersonal attraction while the increased synchrony of these signals was. These results imply that attraction is not as much of an arousal response as the ability of two people to put each other in a similar physiological state (ease/or excitement). Indeed, while many social interactions require effort to reach mutual understanding, when we experience the feeling of a "click" or "mental connection" with someone, it often feels effortless.

One thing that merits discussion is the role of synchrony in romantic relationships. Although at this stage, the direction between physiological synchrony and attraction is unclear (synchrony may cause attraction or vice versa), we propose that the ability to synchronize with others allows humans to embody the affective experiences of others. This proposal is in line with the emotional contagion theory (Hatfield et al., 1993) and the Somatic Marker Hypothesis (Damasio, 1996). The underlying mechanism of physiological synchrony is not fully understood but it has been suggested that large spindle shaped neurons located in the fronto-insular region of the brain (present in humans and great apes) may be involved in processes that are underlying complex social interactions (Allman et al., 2010). Through sympathetic and parasympathetic innervations, the insular (INS) and anterior cingulate cortex (ACC) mediate emotion-related motivation, which is often perceived as a bodily sensation (Mayer, 2011). The concept of embodied emotions is closely related to the 'somatic marker' hypothesis (Damasio, 1996) or to the concept of interoceptive memories (Critchley, & Garfinkel, 2018). As people perceive another person's smile, blush, or pupil dilation, their homeostatic reflexes at the level of INS and ACC can be triggered while viewing affects expressed by another individual. This way, people can emotionally and physiologically align. Therefore, ones' 'gut feeling' about others can be defined as the rapid assessment of the probability of a favorable or unfavorable outcome based on somatic experiences (Damasio, 1996). However, since the assessment of others' behavior is dependent on previous experiences rather than on serial processes of inductive/deductive reasoning (Mayer, 2011), a social signal that is perceived as pleasant by one person may trigger unpleasant feelings in another person.

In support of this theory, seminal studies with married couples measured physiological synchrony while couples argued (negative affect). In these experiments, physiological linkage was associated with lower marital satisfaction and higher chance of a divorce (Levenson and Gottman, 1985, 1983). In contrast, in the current study, couples were voluntary on a date, which is generally a positive experience. Consequently, physiological synchrony was predictive of positive affect – attraction. This result aligns with prior research suggesting that physiological linkage can be either good or bad, depending on the environmental context (Helm et al., 2014). Moreover, from a methodological perspective, the reason why physiological synchrony might be a better predictor of interpersonal attraction than physiological arousal is that interindividual metrics might be better suited to capture/normalize physiological patterns. Recently, research has begun to demonstrate that the unified nature of conscious experience consists of temporally interleaved and highly selective activations in the central nervous system (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004). While skin conductance level and heart rate responses lack specificity (high arousal can be both pleasant or unpleasant), by tracking the stream of physiological signals between two interacting partners, physiological synchrony incorporates information regarding affective reciprocity. In this way, physiological synchrony provides deeper insights into human interactions than the level of arousal alone. These findings are particularly relevant if we consider the rapid change in our modern dating culture. With the rise of online dating, the pool of potential partners has substantially grown (50 million people date online today, (Iqbal, 2019)), and dating has become a fast and controllable process. We propose that future studies could use modern divides (wireless watches collecting physiology, mobile apps) to assess this nonverbal form of communication. Further understanding of these processes may shed light on the mechanisms by which humans relate to each other during real life interaction in their everyday natural environments.

In sum, thanks to the unique combination of measures (videos, eye-tracking, and physiological measures), we were able to visualize the contagious spread of emotional information that already emerges during first encounters. Our findings suggest that when interacting partners' subconscious arousal levels rise and fall in synchrony, mutual attraction emerges. Crucially, our findings imply that, on the dyad's levels, the interacting partners' physiological states sync into mutual alignment on a moment-by-moment basis. During these moments, a joint mental state potentially facilitates the feeling of a "click" and attraction. By knowing that physiological synchrony is involved in early romantic development, these data reveal a fundamental mechanism by which an individual's emotional displays trigger neurophysiological responses in others.

Methods

Participants

Our sample size was motivated by those used in previous studies (Levenson and Gottman, 1983; Reed et al., 2013; Thomsen and Gilbert, 1998). In total, 140 participants were recruited (70 opposite-sex dyads). Participants' age ranged from 18 to 37 years old (Male: M = 25.71, SD = 4.639; Female: M = 23.45, SD = 4.265). Participants were recruited at three different yearly events in the Netherlands: during Lowlands (a music festival that takes place in the city of Biddinghuizen), The Night of Arts and Science (a festival that brings art and science together in Leiden), and during InScience (a science film festival in Nijmegen). To participate in the experiment, participants had to be single, between 18 and 38 years old, had to have normal vision or vision corrected by contact lenses (normal glasses could not be worn underneath the eye tracking glasses). Furthermore, participants could not have or have had any psychological illness, use medication, or be undergoing psychological treatment.

Using a digital 1PC alcohol tester we made sure to only include participants who did not exceed a blood alcohol content of 220 micrograms of alcohol per liter of exhaled breath (Dutch driving limit). For the behavioral analysis, one dyad was excluded because they were part of camera crew and their interaction was recorded, in another dyad the male left the experiment prematurely; leaving 69 dyads included in the behavioral analysis. For the physiological analysis an additional 15 dyads were excluded due to artifacts or missing physiological data, meaning that 54 dyads were included in the physiological analysis. Participants were mostly Dutch (92%), highly educated, seventy-three percent of the subjects used dating applications (e.g., Tinder, Bumble, Happn) both males and females were looking for a committed relationship (see Supplementary Table 9). At the end of the study, out of 138 people, in total 58 people (44%) wanted to date their partner at the end of the date (34% females, 53% males) from which eleven couples matched (17%), five people did not report. Furthermore, twenty couples (31%) mutually agreed on not being a good match for each other and in half of the couples (52%) one partner wanted to date their partner but the other did not reciprocate. There were no significant differences between males and females in their level of social anxiety, positive/negative affect, or score on the social desire scale (Supplementary Table 10). The experimental procedures were in accordance with the Declaration of Helsinki and approved by the Ethical Committee of the Faculty of Behavioral and Social Sciences of Leiden University (Number: CEP16 - 0726/258). All participants provided informed consent.

Procedure

Baseline measures. Participants were screened for exclusion criteria, received information about the study and gave informed written consent. Subjects were then asked to fill out some questionnaires to control for psychological factors that could influence a person's ratings of their partner or the general behavior during social interactions (see Materials). In addition, participants filled out baseline ratings reporting on participants' expectations and standards (e.g. how attractive, intelligent, trustworthy and funny their potential romantic partner should be). Subjects also rated themselves on the same items on the 10-point scales. Two researchers (one for male, one for female participants) attached electrodes measuring heart rate (HR) and skin conductance (SC) to participants' skin. They also helped participants to put on the eye-tracking glasses, which were calibrated afterward. Without seeing their partner, participants were led to the dating cabin, females first and after calibration of her equipment, the male partner followed. Upon eye-tracking and skin conductance calibration, participants were instructed to look at the fixation cross (at the closed barrier), while their baseline (30 seconds) physiological measures were collected. Cameras in the glasses recorded video and sound over the whole period of the dating experiment. Participants were instructed to remain silent until they heard instructions via a speaker.

First impression. The screen then opened shortly (3 seconds), giving participants a first impression of their partner. After the first impression, participants looked at the fixation cross for 30 seconds to collect post-first impression physiological measures after which they rated their partner on the same (0 – 9) scales as they rated their imaginary or potential romantic partner during baseline. In addition, participants were asked to rate how much they liked their partner and how much they thought their partner liked them. Other questions included how similar they thought their partner was in terms of personality and how much connection, 'click', and sexual attraction they felt between them. After the first impression, two additional interactions would take place (the order of which was counterbalanced).

Verbal interaction. The visual barrier opened and participants were instructed to talk freely with their partner for 2 minutes. After this interaction, the participant was asked to fill in the same scales as during the first impression, plus rate their impression of the verbal interaction.

Nonverbal Interaction. The visual barrier opened and participants were instructed to look at their partner and not speak for 2 minutes. Afterward, the barrier closed and subjects rated their partner on the same 0 – 9 point scales. Whether participants began with verbal or nonverbal interactions was counterbalanced (Fig. 1b). During the final ratings, participants indicated how much they thought the other person liked them and whether they wanted the experimenters to exchange their email addresses. The pairs were also asked to predict whether they thought their partner wanted to exchange their email addresses and go on another date. Finally, subjects were asked to indicate whether their video recordings could be used for follow-up experiments.

Follow-up. For ethical reasons, participants' decisions to date their partner again or not were not revealed until the festival was over. Only if both of them agreed to exchange contact information, one week after the study they received an email with their partner's email address. They were asked if we could contact them again later to ask if they were still in contact with their partner.

Measures

Ratings. Participants filled in ratings before the experiment, after the first impression and after both the verbal and nonverbal interactions. All questionnaires included the same questions about the partner (or during baseline about a potential partner) in which the participant rated: attraction, funniness, intelligence, trustworthiness, the similarity in personality, connection, sexual attraction, and click, on scales ranging from 1 (not at all) to 9 (very). Additionally, during baseline, participants had to indicate how attractive, funny, intelligent and trustworthy they thought they themselves were (0 – 9 scales). Every questionnaire also contained a mood grid, in which participants had to indicate their level of arousal and valence of their affect. Subjects also rated how shy, awkward, and self-confident they were feeling. Furthermore, every questionnaire (except during baseline), included a question asking how much they liked the partner, and how much they thought their partner liked them. Finally, during the first impression and during their last interaction, participants indicated whether they wanted to see their partner again and whether they thought their partner wanted to see them again. As additional control measures for mood and sexual desire, we included the Liebowitz Social Anxiety Scale (Liebowitz, 1987), Positive and Negative Affect Schedule (Watson et al., 1988) and Sexual Desire Inventory (Spector et al., 1996) (see Supplementary Table 10).

Pre-processing

Behavioral expressions coding. The eye-tracking glasses automatically detected eye-fixations and videotaped participants' behavior. Four independent raters (two raters for males and two for females) rated participants' expressions (smiling, laughing, head nod, hand gestures, face touching) using the Tobii Pro Lab (Version 1.5, 5884). The tapes were coded without sound and coders were blind to participants' ratings. The facial expressions were coded per tenths of seconds and the frequency of each expression was then averaged per interaction (lasting between 3 seconds – 120 seconds). The reliability then was calculated as percentage of agreement between recoded observations. All coders had successfully completed training and reached an agreement ratio of at least .70 for all behaviors, except for the open versus closed body position (agreement was less than 0.7); thus, this particular behavior was dropped from all analyses.

Eye gaze fixations classification. Eye fixations were recorded using Tobii Pro Glasses 2. We defined areas of interest (AOI) including the head, face, eyes, nose, mouth, body, right arm, left arm and background. AOIs were drawn on snapshot images of participants taken at the start of each interaction (size in pixels: 1079 x 605). Eye gaze fixations were then automatically mapped onto the areas of interest (partner's face and body) using the Fixation Classification Method implemented in Tobii Pro Lab (Version 1.5, 5884). The I-VT (Attention) filter (Velocity-Threshold Identification Gaze Filter) was selected to handle eye-tracking data from the glasses recordings conducted under dynamic situations. Same as with facial expressions, the fixations were collected per tenths of seconds for each AOI. This resulted in AOI visit duration (0 excluded). Prior to each interaction, we checked whether the eye-tracker needed recalibration or not. To do so, we asked participants to focus on the fixation point at the barrier. In case the eye fixation did not overlay the fixation cross, we re-calibrated. In the post-experiment pre-processing stage, we calculated the remaining small differences in the x and y coordinates between the glasses' fixation and the fixation cross. The AOI masks were moved with the small differences on the respective x and y coordinates.

Physiological measures. For each participant, ECG and EDA data were collected using BIOPAC's ECG2-R and PPGED-R modules, respectively, and an MP-150 system operated using AcqKnowledge software version 3.2 (BIOPAC, Goleta, CA). All raw signals were recorded at 1000 Hz.

Skin conductance level pre-processing. Two electrodes were attached on the intermediate phalanges of the index and ring finger of the non-dominant hand. Using the PhysioData Toolbox, the raw skin conductance signal was visually inspected and short-duration artifacts were removed and replaced using linear interpolation (maximum interpolation duration was 2 seconds). Longer invalid sections of data were excluded. The skin conductance signal (SC) was then low-pass filtered at 2 Hz to remove high-frequency noise, and for each section of interest, down-sampled to 10 Hz for further analysis.

Heart rate pre-processing. Similarly, the PhysioData Toolbox was used to extract 10 Hz continuous instantaneous heartrate (IHR) signals from the raw ECG signal. This involved bandpass-filtering the raw signal at 1 to 50 Hz, performing peak detection to find the R-peaks, and calculating the interbeat intervals (IBIs). Both the R-peaks and resulting IBIs were visually reviewed, and erroneously derived instances of any of the two were removed. The IHR signal, in BPM, was then generated from the remaining IBIs using piece-wise cubic interpolation (maximum interpolation duration was 2 seconds). Trials (participants' interaction segments) with less than 30% coverage of the sum of the IBIs relative to the duration of the time signal were excluded**.** Participants missing more 50% percent of the IBIs were excluded.

Analysis

Analysis 1. We ran a correlation between all measures. This resulted in a large correlation table showing associations between male's and female's expressions eye fixations and physiological measures as well as associations between female's-female's, male's-male's showing how nonverbal behaviors and physiological responses relate to each other within participants. Then in a control analysis, each female was paired with a random male. To test for significance, we compared correlations coefficients between true couples and randomly matched couples with the cocor package in R studio (Diedenhofen and Musch, 2015) using gender as an independent group, two-sided test with alpha set to 0.05.

Quantifying expressive mimicry and eye fixation synchrony. Mimicry is defined broadly as 'doing what others are doing'. While some studies are very loose on their definition of mimicry (for instance, mimicry might be defined as any movement following the other person's movement (Fujiwara and Daibo, 2016; Tschacher et al., 2014)), we adopt a stricter definition of mimicry where mimicry occurs when person A (directly or within a short time window) shows the same expression as person B. We quantified mimicry for each dyad and interaction by calculating the proportion of time both participants' directly reciprocated expressions (smiling, laughing, head nods, hand gestures, face touching) and gaze fixations (looking at partners' head, eyes, face, body). The proportion of mimicry was calculated for each condition (the first impression, verbal and nonverbal interaction) resulting in N dyads * 3 results * for mimicry in smiles, laughs, head nods, hand gestures, eye-to-eye fixations.

Quantifying physiological synchrony. We conducted a lagged windowed cross correlation analysis to quantify physiological synchrony for the heart rate and skin conductance level measures separately (Boker et al., 2002). The objective of this analysis was to calculate the strength of association between two time series while taking into account the non-stationarity of the signals and the lag between responses, that is, to consider the dynamics of a dyadic interaction. Non-stationarity is accounted for by breaking down the time series into smaller segments and calculating the cross-correlation of these segments, allowing the correlation to change throughout the time series. A more detailed description of the analysis can be found in the Supplementary Material ("Quantification of physiological synchrony"). Based on this analysis, we obtained a measure of the strength of synchrony for each interaction per dyad.

*Analysis 2***.** We here investigate whether attraction can be predicted by synchrony. In this analysis, we used Multilevel linear mixed model to investigate how different types of interpersonal synchronies impact on participant's attraction ratings (0-9). The multilevel model had the following structure: three time points (Level 1) nested in participants (Level 2). Note that we did not consider dyad as a separate third level, as we found little variation in attraction at the dyad level. We also included a random intercept effect (across participants) and a random slope for time, but not allowing a correlation between both random effects. The time variable was specified on continuous scale (as participants displayed (more or less) linear trajectories over time in attraction. The slope for time indicated the evolution of attraction over time. In the model, we included all 7 synchrony predictors including synchrony in (i) smiles, (ii) laughs, (iii) head nods, (iv) hand gestures, (v) face-to-face gaze, (vi) heart rate, and (vii) skin conductance. The full model further included factors of gender, the type of interaction (verbal, nonverbal), the order of interaction (verbal/nonverbal first), and two-way interactions between type of interaction * all synchrony types (smiles, laughs, head nods, hand gestures, face-to-face gaze, heart rate, and skin conductance). The final model was selected with a backward stepwise selection of fixed effects. This method first tests interaction terms, and then drops interactions one by one to test for main effects. All predictors were centered. To check that multicollinearity would not confound our results, we calculated the variance inflation factor (Kohavi, 1995).

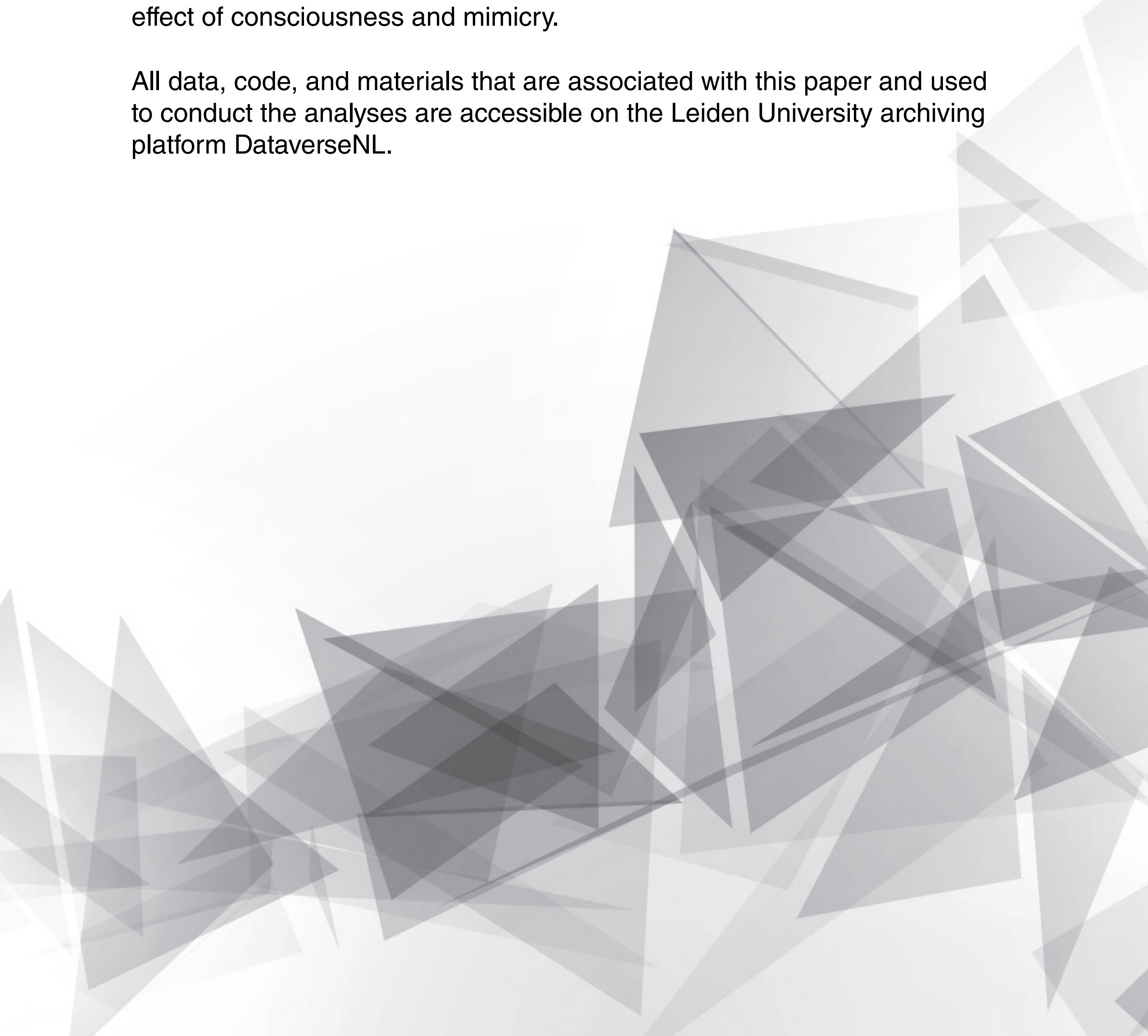
For details regarding control analyses see Supplementary Materials.

Chapter 6

Emotional expressions influence trust: modulatory effect of consciousness and mimicry

Based on: Procházková, E., Venneker, D., de Zwart, R., Tamietto, M., & Kret, M. E. (In preparation). Emotional expressions influence trust: modulatory effect of consciousness and mimicry.

All data, code, and materials that are associated with this paper and used to conduct the analyses are accessible on the Leiden University archiving platform DataverseNL.



Abstract

By observing subtle emotional expressions, humans make rapid inferences about others' thoughts and intentions. For instance, when deciding whether to trust someone or not, individuals observe and mimic facial movements and pupil sizes of others, which aids their trust evaluation. Yet, whether spontaneous mimicry depends on visual awareness of the stimulus and which processes underlie the unfolding development of trust in the observer remains unknown. To investigate how visual awareness modulates the relationship between emotional expressions, mimicry, and trust, participants played a series of trust games with different virtual partners whose faces and eyes were in half of the trials rendered invisible using continuous flash suppression (CFS). Participants would either see their partners' face with a neutral, happy, or fearful expression, or partner's eye region in which the pupils were large, medium, or small in size. Subjects' trust investments, facial movements and pupil responses were measured. Results showed that participants' trust declined as visual awareness of the stimuli decayed, which demonstrates that the ability to perceive partners' facial and pupillary expressions of emotion is vital for the establishment of trust. Moreover, we found that facial expressions were mimicked and influenced trust decisions during the control (conscious) but not during the unconscious (suppressed) condition. On the other hand, partners' pupil size influenced trust only when presented unconsciously. These findings imply that while the neurological path linking facial expressions to facial mimicry and trust is predominantly conscious, pupillary expressions of arousal influence trust mainly non-consciously, potentially via subcortical neurophysiological pathways.

Keywords: **consciousness; affect; pupil mimicry; facial mimicry; continuous flash suppression**

Introduction

Humans are able to decide whether to trust a complete stranger in a split of a second (38-ms) (Bar et al., 2006). They do so seamlessly, effortlessly, and often without explicit awareness of how they arrived at such a trivial decision. This implicitly formed intuition resembles a 'gut feeling', which plays an important role in novel situations. Intriguingly, research has shown that people can recognize emotional facial expressions and mimic others even when these signals are not consciously perceived (Skuse, 2003; Tamietto et al., 2009; Tamietto & De Gelder, 2010). This rapid mimicry is thought to reflect the transmission of affect across individuals and potentially serves as a precursor of more complex social abilities such as trust (Carr et al., 2003; Procházková and Kret, 2017). Apart from facial expressions, the mimicry of subtle cues such as pupil size may signal emotional contagion of arousal (Aktar, Raijmakers, & Kret, 2020; Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Kret, Tomonaga, & Matsuzawa, 2014). Given the speed with which emotional expressions affect our daily social interactions, the current study investigates whether emotional expressions influence trust decisions without perceivers' conscious awareness. We further test if mimicry is part of the emotional process that contributes to the development of trust on the unconscious level ('gut intuition').

According to the Somatic marker hypothesis, before a decision is made, a parallel somatic/visceral response generates a gut feeling that helps people to tip the decision in one direction or another (Damasio, 1996). One physiologically plausible supposition asserts that during social interactions, emotional information is processed unconsciously, possibly via the retino-collicular-pulvinar-amygdala pathway. This subcortical "low road" is assumed to enable rapid processing of emotional information bypassing the visual cortex, and by doing so, facilitates physiological responses such as pupil dilation and facial mimicry, outside of perceivers' awareness of the visual input (Hassin, 2013; Ledoux, 1996; Morris, Öhman, & Dolan, 1999; Öhman, Flykt, & Esteves, 2001; Skuse, 2003; Tamietto et al., 2009). The clearest evidence for the unconscious processing of emotional facial expressions comes from studies with blindsight patients. Although blindsight patients have a lesion in their primary visual cortex, they are still able to distinguish facial and bodily expressions of emotion without conscious awareness of perceiving them (Anders et al., 2004; Tamietto et al., 2009).

In addition, these patients still show emotion recognition capacity accompanied by facial mimicry and pupillary reactions (indicative of autonomic arousal) to unconsciously perceived expressions of fear and happiness (Tamietto et al., 2009). Consistently, numerous studies using blinding methods in healthy subjects imply that salient visual stimuli such as emotional expressions or eye contact evoke physiological and neural responses even when they are not consciously perceived (Carlson and Reinke, 2008; Jiang and He, 2006; Pasley et al., 2004; Stein et al., 2011b; Williams et al., 2004). These studies fostered the view that the unconscious processing of emotional expressions is a general mechanism that helps people to rapidly, effortlessly, and adequately respond. During this process, mimicry potentially provides a feedback mechanism where ones' own visceral changes (e.g. own facial movements in response to facial expressions) contribute to the development of an affective response and social decisions (Preston and Waal, 2002). It is unclear, however, whether mimicry depends on visual awareness and if unconscious processing is shared by healthy individuals and different emotion modalities (for contradicting evidnce see, Hedger, Adams, & Garner, 2015; Stein & Sterzer, 2012; Zhan, Hortensius, & De Gelder, 2015).

Although the majority of studies focus on explicit, prototypical expressions of emotion (e.g. a wide smile signaling happiness; a dropped jaw signaling fear), in real life, people exchange emotional expressions in more subtle ways (Ambadar et al., 2005). For example, several studies have shown that people mimic each other's pupil sizes (Aktar, Raijmakers, & Kret, 2020; Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Kret, Tomonaga, & Matsuzawa, 2014), and if partners' pupils synchronously dilate, pupil mimicry promotes trust (Kret, Fischer, & De Dreu, 2015; Procházková et al., 2018; van Breen, De Dreu, & Kret, 2018). These studies reinforce the view that pupil mimicry is an implicit mechanism that contributes to trust decisions. In support of this hypothesis, observed pupil size is often processed unconsciously (Harrison et al., 2006) and increases amygdala activity (K. E. Demos et al., 2008). In contrast to facial expressions that are coordinated by somatic muscles, changes in pupil size are controlled by autonomic nerves that are fully unconscious and uncontrollable (Bradley et al., 2008; Partala and Surakka, 2003). Despite differences in the involvement of the peripheral nervous system, the mimicry of facial expressions and pupil size share common neural mechanisms in social and emotional brain areas (Harrison et al., 2006; Procházková et al., 2018). It is therefore possible that while different types of emotional modalities (e.g. explicit facial expressions or subtle changes in pupil size reflecting arousal) have a similar impact on trust, they may do so via different neurological pathways (Procházková and Kret, 2017). Thus, presenting participants with facial expressions as well as pupil size in the absence of conscious perception would help to disentangle the underlying mechanisms of emotional contagion.

In the present study, we investigated the link between conscious perception, mimicry, and trust in a series of one-person trust games. During these games (Figure 1), subjects were presented with images of faces or eyes of different partners who varied in facial expressions (happy, neutral, fearful) or pupil sizes (large, medium size, small). To manipulate conscious perception, in half of the trials continuous flash suppression was applied (CFS; Tsuchiya & Koch, 2005). CFS is one of the most powerful blinding techniques during which a stimulus is presented to one eye, while a sequence of rapidly changing 'Mondrian' masks is shown to the other. This method allows the presentation of the stimuli to be masked for up to several minutes. After the image was presented, participants were asked to indicate the location of the stimulus, rate their confidence in having seen it, and decide how much money they wanted to invest in their partner, which reflected trust in that partner. Apart from behavioral responses, we tracked participants' muscle activity via electromyography (EMG) and pupil size via a novel method developed by Brascamp and Naber, 2017 (see Figure 1).

We hypothesized that if intuitive trust decisions rely on unconscious affective processing (H1), emotional information conveyed by faces and pupils should modulate trust-related investments during both conscious (control) and unconscious (suppressed) conditions. Specifically, partners with happy facial expressions and large pupils will be trusted more than partners with fearful faces and small pupils. Moreover, if mimicry informs a 'gut feeling' which through somatic markers (Damasio, 1996) implicitly contributes to trust, mimicry should be particularly useful when visual information fades. Thus, (H2) facial/pupil mimicry will occur during both conscious (control) and unconscious (suppressed) conditions. Finally, (H3) mimicry will further modulate trust (mimicry of partners' happy facial expressions/large pupils will increase trust, whilst mimicry of frowning faces/small pupils will decrease trust).

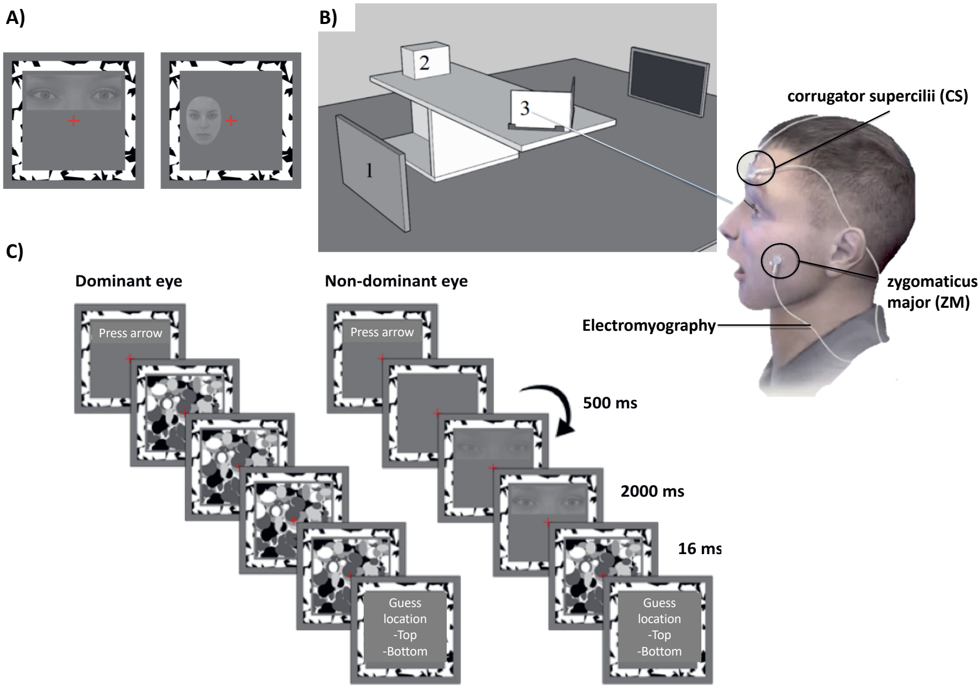


Figure 1. (**A)** Example of neutral facial stimuli on the right, and medium size pupils on the left. All displays were surrounded by a black and white square border to facilitate stable convergence of the images in both eyes. The position was either above or below the fixation cross for the eyes stimuli and left or right of the fixation cross for the faces' stimuli. (**B)** Experimental setup. Screens are numbered 1 the eye tracker is numbered 2 and the mirrors are numbered 3. (**C)** Trial outline for CFS trust game with pupil stimuli as an example. Each trial started with a message indicating the start of a new trial. A red fixation cross was presented during the whole trial. In the dominant eye, the stimulus faded in over a period of 500 ms after which it remained medium size on the screen for 2000 ms, and the trial ended with one Mondrian image presented for 16 ms to mask visual aftereffects. In the non-dominant eye, different Mondrian images were constantly flashed with a frequency of 10 Hz. If no response was given after 2.5 seconds, participants were asked to make a guess for location. After this, they had to indicate confidence in their decision on a 4-point scale (guessing, not confident, quite

confident, very confident). Finally, they were asked to make an investment decision of €0, €2, €4, or €6 in their virtual partner for each trial. After the questions a 5-second inter-trial interval followed. Pictures adapted from (Tamietto & De Gelder, 2010, Figure 3)

Results

Suppression

In our data-set, on average, the suppression broke in 24.3% of the CFS trials (25.9% face trials and in 22.7% eye condition trials). This is in line with earlier work (e.g., Stein, Hebart, & Sterzer, 2011). While many studies use the time until suppression (b-CFS) as the dependent variable (e.g., Stein & Sterzer, 2012; Yang, Zald, & Blake, 2007), for b-CFS results (see Supplementary Table 6-8), the main goal of the current study was to test how conscious awareness of a partner's expression (facial and pupil size) shape (a) trust decisions, (b) mimicry, and (c) the effect of mimicry on trust decisions. This required using awareness as independent variable while keeping a clear-cut separation between conscious and unconscious conditions.

To check for the level of awareness, we used subjective and objective measures (as in Yang, Brascamp, Kang, & Blake, 2014). During CFS, as an objective measure, participants were asked to indicate the location of the stimuli (up/down for eyes, left/right for faces). As a subjective measure, subjects were asked to rate their confidence in seeing the stimuli from 1 (guess) to 4 (very confident) (Oliver et al., 2015; Raio et al., 2012). As expected, the CFS objective measure (the location detection performance) significantly correlated with participant's confidence ratings ($r = 0.825$, $p < 0.0001$, $N = 50$), which confirmed the validity of subjective awareness measures. Moreover, subjective measures showed that during CFS, participants were "guessing" the stimulus location in 43.0% of CFS trials (confidence level = 1) and during these trials, the average detection performance was 54%, which was significantly above chance level: (binomial test: $p < 0.001$). In the rest of the CFS trials (57% of the total number of CFS trials), participant's mean confidence level ranged between 2 and 4 ($M = 2.1$) on a 4-point scale (2 = not confident (15.5% trials), 3 = quite confident (19.6% trials) and 3 = very confident (22.1% trials), after excluding trials where the suppression broke (b-CFS), participants' detection performance reached 84% (above chance level: $p < 0.001$ by binomial test). Finally, in the control condition, participants were correct about the stimulus location in 97.3% of the trials.

The level of awareness varied during CFS, in half of the CFS trials participants were not consciously aware of the stimuli at all, while in the other half of the trials subjects sustained some residual vision. To evaluate the evidence for unconscious affective processing, we split the data into different awareness categories: (*1) The conscious condition* represents the control trials where participants perceived the stimuli without suppression and were confident in seeing it (confidence level = 4). *(2) The semi-conscious condition* represents CFS trials where participants reported to be 'somewhat confident' in spotting the location of the stimuli (confidence level = 2 - 4). Finally, *(3) The unconscious condition* represents the trials where stimuli were shown under suppression and subjects reported that they were guessing the stimulus location (confidence level = 1).

(H1) Does emotional information influence trust during control and suppressed (CFS) conditions?

To test the first hypothesis evaluating the effect of experimental condition on trust, we used a Generalized linear model with a two-level structure defined by trials (level 1) nested in subjects (level 2). In this model, participants' trust (investment level) was subjected to a 2 x 3 x 3 factorial design with expression modality (pupils, face), emotion (Faces: happy, neutral, fearful; Pupils: large, medium, small), and awareness level (conscious, semi-conscious, unconscious) as within-subject factors. As a stimulus, for the pupil and face conditions we used different pictures of four males and four females. We further included the interaction terms between all the above variables (no random effects were included in the final model).

Facial expressions of emotion

The results of a Generalized linear model with the conditions: expression modality (pupils, face), emotion (Faces: happy, neutral, fearful; Pupils: large, medium, small), and awareness levels (conscious, semi-conscious, unconscious) showed a main effect of partner's expression on trust [F (1, 17808,00) = 80619,00, $p < 0.0001$] whereas partners with happy facial expressions were trusted more than partners with neutral ($p < .0001$) or fearful expressions ($p < .0001$, Figure 2). Importantly, in support of the first hypothesis, we show that facial expression can influence participants' trust even under suppressed (CFS) condition. Nevertheless, a significant three-way interaction between suppression, expression modality and emotion [F (2, 17808) = 24.019, $p < 0.0001$] demonstrated that facial expressions modulated trust only when participants had some confidence in having seen the stimuli. Specifically, facial expression modulated trust during both conscious and semi-conscious conditions (happy > neutral > fearful: all *p*s < 0.05), but not when participants were fully unaware of the stimuli (all *ps* > 0.05).

Pupillary expressions of arousal

Partners' pupil size also modulated trust. Post-hoc pairwise comparisons of the significant three-way interaction between suppression, expression modality, and emotion revealed that although during conscious control trials, participants' investments did not differ between partners' pupil sizes (all *p*s > 0.05, Figure 2), partners' pupil size moderated trust decisions during suppressed (CFS) trials. Specifically, in the semi-conscious condition partners with large pupils were trusted more than partners with medium ($p < .0001$) and small pupils ($p < .0001$). Further, a similar pattern emerged during the unconscious (fully suppressed) condition where partners with large pupils were trusted more than partners with small pupils ($p < 0.05$). We additionally found a significant effect of emotional modality, whereas subjects trusted partners more when they saw their eye-regions as compared to partners' whole faces [F (1, 17808) = 19.87, $p < 0.0001$], (Supplementary Table 1). A main effect of awareness levels [F (1, 17808) = 770.61, $p < 0.0001$] indicated that participants trusted their partner more during control trials compared to suppressed (CFS) semi-conscious trials and unconscious trials.

Together, these data imply that people tend to withhold trust when they cannot see their partners' eyes or face properly. Crucially, in line with the first hypothesis, we show that emotional cues can influence participants' trust even under visual suppression. Nevertheless, after controlling for subjective awareness scores, our data demonstrate that some level of visual percept is necessary for emotional facial expressions to influence trust evaluation. On the other hand, partner's pupil size seems to impact trust unconsciously.

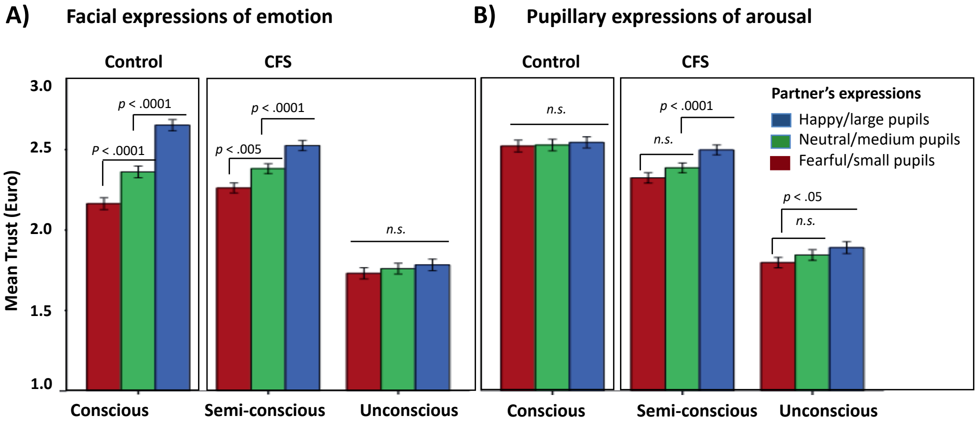


Figure 2: (A) Bar plots display investment level (mean +/- standard error) split by subjects' level of awareness. On average, participants trusted their partner more during un-suppressed control trials compared to suppressed semi-conscious trials [β = - 0.069, SE = 0.013, CI (0.044, 0.095), $p < .0001$] and unconscious trials [β = 0.588, SE = 0.014, CI (0.560, 0.616), $p < .0001$]. In the facial expression condition, expression affected trust in both the control and CFS conditions: Partners with happy facial expressions were trusted more than partners with neutral [β = 0.113, SE = 0.014, CI (0.086, 0.140), $p < .0001$] or fearful expressions [β = 0.182, SE = 0.014, CI (0.155, 0.209, $p < .0001$]. However, this effect was modulated by the level of awareness. When subjects reported some level of awareness, in the semi-conscious condition partners with large pupils were trusted more than partners with medium [β = 0.113, SE = 0.033, CI (0.062, 0.192), $p < .0001$] and small pupils [β = 0.181, SE = 0.035, CI (0.112, 0.249), $p < .0001$]. (B) In the pupillary expression condition, partners' pupil size affected trust only in the two CFS conditions but not in the conscious condition. A similar pattern emerged during the unconscious (fully suppressed) condition where partners with large pupils were trusted more than partners with small pupils [β = 0.082, SE = 0.041, CI (0.003, 0.162), $p < 0.05$].

(H2) Will facial/pupil mimicry occur during the control and suppressed (CFS) conditions?

Facial Mimicry

To test for facial muscle mimicry, we selected trials where participants observed their partners' faces. We then used two separate Generalized linear models to predict changes in the two EMG amplitudes of the corrugator supercilii (CS) and the zygomaticus major (ZM) muscles. As predictors, we used partner expression in the 3 conditions (happy, neutral, fearful) and awareness levels (conscious, semi-conscious, unconscious). The interactions between the two predictors were included as well. Furthermore, we added three orthogonal polynomials to account for linear, quadratic, and cubic trends in the growth curves. These models had a 3 level structure defined by time segments (level 1), nested in trials (level 2), nested in subjects (level 3), whereas time segments (100-ms time slots) were used as a repeated factor with a First-Order Autoregressive covariance structure (AR1) to control for autocorrelation while including a random intercept for individuals (no random effects were included in the final model, for full models see Supplementary Table 2-3).

Mimicry of frowns

Figure 3A displays the mean corrugator supercilii (CS) responses from pre-stimulus baseline. The main effect of partner's emotion [F (2, 163802) = 9.935, $p < 0.0001$] showed that on average participants frown more in response to fearful facial expressions compared to neutral ($p < 0.05$) and happy expressions ($p < 0.0001$). Intriguingly, in line with the second hypothesis, facial mimicry occurred during both control and suppressed (CFS) conditions. However, a significant interaction between emotion and awareness level [F (4, 163802) = 2.540, $p < 0.0001$] revealed that facial mimicry was influenced by the level of subjective awareness. Post-hoc pairwise comparisons (LSD tests) showed that in the control condition, participants displayed complete mimicry: they frowned more in response to fearful facial expressions compared to neutral and happy expressions (all *p*s < 0.05). In the semi-conscious condition, participants frowned more in response to fearful facial expressions compared to neutral and happy expressions (all *p*s < 0.005), but no difference was found between neutral and fearful expressions ($p > 0.05$). Finally, in the CFS fully unconscious condition, no difference was observed between happy and neutral faces or fearful and neutral faces (all *p*s > 0.05). This result implies that as the level of visual awareness declines, the influence of the partner's emotional expression on facial mimicry also decreases. Apart from the above effect with emotion, these results showed a main effect of awareness on CS muscle [F (1, 3094) = 6.355, *p* < 0.05], where participants' average CS activity increased with increasing awareness of the stimuli.

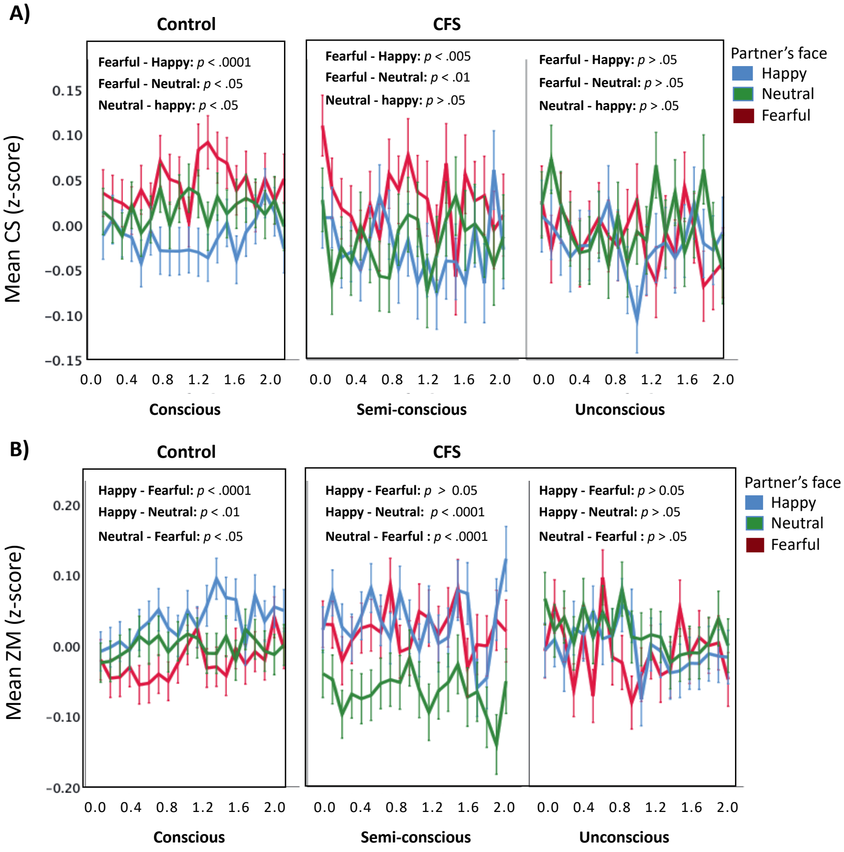
Mimicry of smiles

Figure 3B displays the mean z-scored zygomaticus major (ZM) responses from pre-stimulus baseline. We found a main effect of partner emotion [F (2, 163803) = 7.603, *p* < 0.0001] implying that participants smiled more in response to happy facial expressions compared to neutral expressions (*p* < 0.0001) and fearful expressions (*p* < 0.01). We found no difference between fearful and neutral expressions (*p* > 0.05). Importantly, a significant interaction between expression and awareness level [F (4, 163803) = 8.246, *p* < 0.0001] revealed that, while in the control (visible) condition, participants exhibited mimicry too all facial expressions, smiling more in response to happy facial expressions compared to neutral and fearful expressions (all *p* < 0.01). No difference in ZM activity was found between neutral and frowning (*p* > 0.05). In the semi-conscious condition, participants showed partial mimicry: they smiled more in response to happy facial expressions compared to neutral (all *p*s < 0.0001) but not fearful expression (*p* > 0.05). They also smiled more in response to fearful expressions than neutral expressions (*p* > 0.0001). Finally, in the CFS fully unconscious condition, there was no difference found between happy and neutral faces or fearful and neutral faces (*p* > 0.05).

Although the current results partially support the second hypothesis suggesting that facial mimicry emerges also during suppressed (CFS) conditions, after controlling for subjective awareness scores, our data imply that some level of visual perception is necessary for emotional facial expressions to influence muscle movements.

Pupil Mimicry

As in the previous facial mimicry analysis we used a Generalized linear model to predict participants' z-scored baseline-corrected pupil response (for full model see Supplementary Table 4). The main effect of awareness [F (1, 140,399) = 9.343, *p* < 0.0001] demonstrated that pupil dilation was stronger during the CFS unconscious condition and the semiconscious than during the conscious control condition (both *p* < 0.001, Figure 3), no difference was found in the CFS conscious between semiconscious and unconscious conditions (*p* = 0.982). However, contrary to our expectations and previous research, we did not find evidence for pupil mimicry (Kret et al., 2015; Procházková et al., 2018; van Breen et al., 2018). Although Figure 3C shows that in the control condition, the mean pupil responses showed the expected pattern (participants' pupils were larger in response to partners' large pupils compared to medium sized and small pupils), this effect did not reach significance.



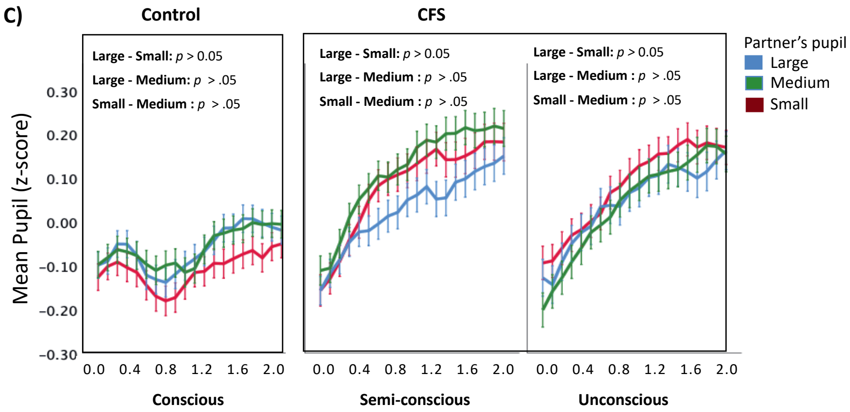


Figure 3. Line plots depict baseline corrected z-scored physiological signals per 2 seconds split by subjects' level of awareness. (**A)** The mean corrugator supercilii (CS) responses from pre-stimulus baseline shows that on average participants frown more in response to fearful facial expressions compared to neutral [β = 0.021, SE = 0.009, CI (0.003, 0.038), $p < 0.05$] and happy expressions [β = 0.040, SE = 0.009, CI (0.023, 0.058), $p < 0.0001$] during conscious and semi-conscious conditions but not during unconscious conditions. (**B)** The mean z-scored zygomaticus major (ZM) responses from pre-stimulus baseline shows that on average participants smile more in response to happy facial expressions compared to neutral expressions [β = 0.038, SE = 0.010, CI (0.018, 0.058), $p < 0.0001$] and fearful expressions [β = 0.028, SE = 0.010, CI (0.008, 0.048), $p < 0.01$] but not during semiconscious or unconscious conditions. **(C)** The mean z-scored pupil response from pre-stimulus baseline to partners' pupils split by subjects' level of awareness.

(H3) Does mimicry modulate trust-related investments?

In the final models, we examined whether facial mimicry modulates trust. Since we found no evidence for pupil mimicry, we focused on facial mimicry only (for detailed mimicry classification see Methods); (for a similar approach, see Procházková et al., 2018).

In this Generalized linear model, we used a two-level structure defined by trials (level 1) nested in subjects (level 2). Participants' trust (investment level) was predicted by partners' emotion (happy, fearful/ large, small), awareness levels (conscious, semi-conscious, unconscious), and occurrence of mimicry (mimicry, no-mimicry) as well as two and three-way interactions between these factors. Contrary to our third hypothesis, our results showed that there was no main effect of mimicry ($p > 0.05$), and no interaction effects predicting trust (all *p*s > 0.05, Supplementary Table 5). Results were descriptively consisted with our prediction; when participants mimicked their partners' happy facial expressions, they trusted their partner slightly more than when they did not mimic, this effect, however, was not significant (Figure S1).

Discussion

The present study investigated whether consciousness modulates the relationship between the processing of emotional expressions and the development of trust. Participants played a series of trust games with different virtual partners whose faces and eyes were rendered invisible with continuous flash suppression (CFS). We hypothesized that if trust relies on-unconscious processes, (H1) emotional information should modulate trust decisions during both conscious and non-conscious presentation. Moreover, we hypothesized that if mimicry is part of the unconscious emotional process which contributes to trust, (H2) facial/pupil mimicry will occur during both conscious (control) and unconscious (suppressed) conditions, and (H3) facial/pupil mimicry will modulate trust. The current study provided mixed findings. We found that facial expressions were mimicked and did influence trust decisions (regardless of mimicry) during the conscious condition, whereas partners' pupil size influenced trust non-consciously. This suggests that pupil mimicry and facial mimicry potentially influence trust via separate neurophysiological pathways.

These results are important from the perspective of emotion theories postulating that emotional expressions can influence social behavior without the observer's visual awareness (LeDoux, 2012; Tamietto and De Gelder, 2010). Prior research implies that blindsight patients potentially receive emotional information via interceptive feedback from their own body (Tamietto & De Gelder, 2010). Nevertheless, whether non-conscious processing is shared by healthy subjects is a debated topic (Hedger et al., 2016, 2015b, 2015a; Pessoa and Adolphs, 2010; Straube et al., 2010), and whether it extends to the more subtle expression of pupil size was still unknown. Several methodological variations may give rise to these inconsistencies in the literature. For instance, while in many studies researchers assume that participants did not perceive the stimuli under CFS, we show that even though in many trials participants did not break the suppression (b-CFS), they still reported to have some residual vision. This was confirmed by high stimuli detection accuracy (84%) during these trials. Thus, in order to prevent false positives and account for subjective awareness measures, we split the data into conscious, semiconscious and unconscious conditions.

With regards to trust, in line with the first hypothesis (H1), we found that during both visible (control) and CFS conditions, partners displaying happy facial expressions were trusted more than partners with neutral or fearful expressions. At first sight, this finding seems to support the view suggesting that emotional stimuli are recognized even when suppressed from visual awareness (e.g., Pasley et al., 2004; Williams et al., 2004). However, the comparison between semiconscious and unconscious conditions revealed that emotional expressions modulated trust only when participants had some level of awareness of the facial stimuli. When subjects had no awareness of their partners' facial expressions of emotion, they were not influenced by their expressions. Moreover, we found that participants trusted their partners more during control trials compared to CFS trials, where their vision was either partially or fully suppressed. This demonstrates that the ability to perceive partners' emotional expressions is vital for the establishment of trust.

Participant trust also increased when they could see their partner's eye-region as compared to seeing their partner's whole face. These results aligns with previous studies showing that when it comes to emotion processing, eyes are the most important part of the face (Adolphs et al., 2005; Farroni et al., 2002). This evidence suggests that in healthy subjects: (a) the ability to perceive partners' face and eyes is vital for the establishment of trust, and (b) the neurological path linking emotional expressions and trust requires visual awareness.

Apart from facial expressions, partner pupil size also modulated trust, yet not entirely according to our expectations. In contrast to prior research, participants did not trust partners with large pupils more than partners with smaller pupils – at least not during the visible (control) condition (Kret et al., 2015; Procházková et al., 2018;

Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018). Instead, partner pupil size influenced participants' trust decisions during the suppressed condition only. Why pupil influenced trust during suppression but not during fully visible control condition is open to interpretation. One possible explanation ties to prior research suggesting that observed pupil size influences emotion perception primarily unconsciously (Harrison et al., 2007, 2006). Another possibility is that autonomic cues (e.g. pupil dilation, blushing, sweating) are processed via distinct neurological pathway (e.g., retino-collicular-pulvinar-amygdala pathway) from facial mimicry, however future research is needed to establish to veracity of this interpretation. Finally, it is important to note methodological differences between our design and previous studies. The stimuli in the current study were presented for a shorter duration than in earlier studies, and it is possible that participants' pupils were not given enough time to mimic the stimulus pupils, an effect we know influences trust.

Facial mimicry was also affected by the level of subjective awareness. Our results showed that participants displayed facial mimicry during both conscious (control) and suppressed conditions. However, after we controlled for subjective measures of awareness, we did not find strong evidence for facial mimicry during the fully suppressed unconscious condition. Again, while the current results support our second hypothesis (H2) suggesting that facial mimicry emerges also during the suppressed (CFS) condition, our findings imply that facial mimicry deteriorates with a decline in visual awareness. Finally, we did not find significant evidence for mimicry-trust-linkage in the current study (H3). Together these finding suggest that while facial muscles might unconsciously move in response to partners' facial expressions (Fig. 2a), trust decisions are not significantly influenced by participants' own facial muscle responses.

Moreover, in contrast to prior literature (Kret et al., 2015; Procházková et al., 2018; Wehebrink et al., 2018), we did not observe pupil mimicry in our participants. There were several methodological distinctions that may provide a possible explanation for the lack of mimicry in current study. First of all, to keep the stimuli comparable to static facial expressions that were used in a prior blindsight study (Tamietto et al., 2009), in the current study we adapted static pupil sizes. Compared to dynamic expressions used in prior research (Kret et al., 2015; Procházková et al., 2018; Wehebrink et al., 2018), the drawback of static stimuli is that the accuracy of emotion expressions identification decreases – especially if the expression is subtle (Ambadar et al., 2005). Therefore, the lack of dynamic movement could be one of the reasons why pupil mimicry did not reach significance in the current experiment. Furthermore, to make the experimental procedure directly comparable with the blindsight study, this study also adapted a two-second window to measure pupillary signals (Tamietto et al., 2009). Yet, this time window may not be sufficient to capture the full pupil mimicry response (prior experiments measured pupil mimicry during longer windows; Kret et al., 2015; Procházková et al., 2018). Finally, we used a novel technology developed by Brascamp and Naber (2017) that has been designed to track pupil changes under CFS. To our knowledge, this method has only been used once in the literature. Thus, more research is required to validate this method. For instance, Figure 2 shows that the initial light dip that commonly occurs when a new stimulus is presented disappeared during CFS. The concern is that the continually flashing effect of CFS could potentially disrupt pupillary responses. We recommend that future studies adapt dynamic pupil stimuli, use a longer time window than two seconds and try an alternative 'blinding' method (e.g. Masking) to verify results.

In sum, the unique combination of a trust game, physiological measures, and CFS allowed us to test how emotional expressions dynamically shape participants' trust and physiology. Our data imply that by diminishing people's ability to read other's facial expressions, trust breaks down – thus supporting the view that trust depends on visual input. We further found that facial expressions were mimicked and influenced trust decisions during the control condition but not during the unconscious (suppressed) condition. On the one hand, this result contradicts the proposed hypotheses suggesting that emotional cues influence trust and facilitate mimicry unconsciously via subcortical pathway. On the other hand, the current results are some of the first to show that pupil size influences trust primarily through unconscious processes. Our findings support the empirical view (Procházková and Kret, 2017) that autonomic cues and facial expressions influence social behavior via two separate neurophysiological pathways. In line with this theory, we conclude that in healthy subjects, the path from facial expressions to mimicry and trust is predominantly conscious, while pupil size influences trust unconsciously.

Method

The CFC experiment aimed to replicate and extend the results of a blind sight study by (Tamietto et al., 2009) while measuring facial mimicry and pupil mimicry during trust games (Kret et al., 2015; Procházková et al., 2018).

Participants

We planned to include *N* = 50 participants in our main analyses. This sample sizes was determined by sample sizes in previous studies using CFS (Vieira et al., 2017) and measuring physiology (Kret et al., 2015; Schlossmacher, Junghöfer, Straube, & Bruchmann, 2017). Data collection was terminated when this sample size was achieved, after exclusion of participants fulfilling the exclusion criteria related to above-chance prime discrimination (see below).

We recruited 65 Leiden University students to participate in our experiment (77% female, mean age 23.6 years, range 18-60 years old). They had normal vision or corrected-to-normal vision (contact lenses only), no history of neurological or psychopathological conditions, and no history of substance use or abuse. Four participants were excluded from all analyses because they did not return for their second session, and for eleven other participants the eye-tracking and physiological data had to be excluded because of physiological artefacts resulting in more than 50% of their data missing (for similar outlier-criteria, see Kret et al., 2015). This left us with 50 full datasets for behavioral and facial mimicry analyses. Five additional subjects were excluded from the pupil analysis as they were missing more than half of their pupil data. Thus, we had valid pupil data for 45 people. The ethics committee of Leiden University approved the experimental procedures (ethics number: CEP18-0403/201).

Design

This study consisted of 2 (face versus eyes) × 2 (suppressed versus conscious) × 3 (positive versus neutral versus negative) within-subject design (32 trials per condition). Participants completed two independent sessions on two different days, each session consisted of two blocks where they either saw faces (CFS/control) or eyes (CFS/control). Each block had 96 trials (96 x 4 = 384 trials per subject). In both tasks, participants had to make an investment in a virtual partner during each trial.

Participants were told that they would sometimes see an image of this partner right before the investment decision. For the first task, they were presented with images of an eye region with different pupil sizes (small, medium, large size). For the second task, they were presented with whole faces that showed different emotional expressions (fearful, neutral, happy). Each expression appeared 32 times per block. The order of the tasks (eye or face) was random for each participant. In both investment tasks, stimuli in half of the trials were suppressed with CFS (implicit test condition), while stimuli in the other half of the trials were not suppressed and therefore consciously perceivable (explicit control condition). In each session, participants first completed the implicit CFS test block followed by the explicit control block. This was done to prevent a recognition effect from interfering with the suppression time: If participants were repeatedly exposed to the stimuli in the conscious condition before they completed the suppressed condition, this might cause the stimuli to break through suppression more easily because of familiarization. The session order of eyes and face conditions was randomly varied between participants. As outcome variables, we measured investment decisions as a reflection of perceived trust and response accuracy. In addition, we assessed the participant's pupil size, facial muscle activity (frowning and smiling), and skin conductance as physiological measures over 2 seconds of stimulus presentation. Skin conductance measures were collected for control purposes to assess whether the observed mimicry effects (e.g., increased EMG activity) were a mere by-product of arousal responses. If true, such a response would not necessary reflect mimicry but rather a general arousal response reflected in increased phasic skin conductance. The control analysis confirmed that phasic skin conductance did not significantly differ between any of the tested conditions (see Supplementary Figure 2).

Stimuli

Stimuli consisted of 8 pictures of faces and 8 pictures of eyes (each appeared 12 times per block). The stimuli were similar to those used in a previous study by Kret, Fischer, and De Dreu (2015). Pictures of the eye region of four men and four women with Caucasian nationality were used. Everything between the eyelashes was removed from the images and replaced with artificial eye white, an artificial iris, and an artificial pupil to allow for precise control over pupil size. Three sizes of pupil were used: small, medium, and large. The medium size pupil was considered to be the reference pupil size and was set at 100%; the large pupil had a size of 160% relative to the reference; the small pupil had a size of 60% relative to the reference. The same sizes were used across all eyes so no other differences were present. All pictures were converted to grayscale to remove any impact potential impact of eye or skin color. The contrast of the pictures was brought down to 30% to allow for better masking (Carmel, Arcaro, Kastner, & Hasson, 2010) and prevent luminance differences within the eye region for the different pupil sizes. The pictures of the whole faces were taken from the Amsterdam Dynamic Facial Expression Set (ADFES; van der Schalk, Hawk, Fischer, & Doosje, 2011). Four men and four women with fearful, neutral and happy expressions were selected. The images were standardized, converted to grayscale and cropped to only reveal the facial area without hair or ears (see Figure 1). All facial images were scaled to have the same dimensions in order to prevent differences in detectability. After cropping, the contrast was decreased to 30% to allow for better masking. In order to make sure that both the eye and face images had the same luminance level, the average luminance of all images was checked with a MATLAB script and then adjusted in Adobe Photoshop to a brightness of 113 out of 255.

Apparatus

In order to combine CFS with eye-tracking, a custom-built stereoscope designed by Brascamp and Naber (2016) was used (see Figure 1b). Pupil and gaze data were collected with an Eyelink 1000 Plus (SR Research Ltd., Mississauga, Ontario, Canada) at a rate of 2000 Hz. It was placed in between two monitors of 23.8 inches, displaying at a 60 Hz refresh rate with a 1920x1080 resolution. The brightness of the screen was set to 70%. Two cold mirrors were placed in such a way that they directed the participant’s sight towards the monitors while allowing the infrared light of the eye tracker to pass through. The distance between participants' eyes and the monitors was 63 cm, the visual angle of the displayed images was 16.6° horizontal and vertical. Testing was done in a dark room without artificial illumination. The experiment was programmed in MATLAB® 2012b and Psychtoolbox-3. The timing of behavioral and physiological responses was synchronized by means of pulses sent through a parallel port.

Procedure

Task outline

Each trial started with a message telling the participant that they could start the new trial by pressing the corresponding key. A gray background and a red fixation cross were present during the whole trial (see Figure 1c for an overview of a trial). After the participant's keypress, random Mondrians were presented to the dominant eye with a frequency of 10 Hz. At the same time, the image of the eyes or faces was presented to the non-dominant eye over a period of 2.5 seconds on a gray background. The opacity of the stimulus was increased from 0 to 100% in the first 0.5 seconds. After this, the fully opaque image remained on the screen for another 2 seconds. The position was either above or below the fixation cross for the eyes stimuli and left or right of the fixation cross for the faces stimuli. The fixation cross remained visible throughout the whole trial. Participants had to respond as soon as they could determine the location of the upcoming stimulus. If the participant did not press during the 2.5-second period, a screen appeared that asked participants to make their best guess regarding the location of the stimulus. After this, they had to indicate confidence in their decision on a 4-point scale (guessing, not confident, quite confident, very confident). Finally, they were asked to make an investment decision of €0 - €6 in their virtual partner for each trial. There was no time limit for answering the confidence question and the investment decision. If participants responded within the first 2500 ms of a trial, the screen that asked participants to make their best guess was skipped. After the questions, a 5-second break was implemented to allow physiological response to come down and establish the next trial's physiological baseline. A full trial lasted for around 10 seconds depending on the participant's response times.

Experiment procedure

Upon arrival at the laboratory, participants read the information letter, signed an informed consent form, and filled in a short questionnaire assessing demographic information. They were then seated in front of the set-up and rested their heads in a chinrest. Participants performed a short test to determine if their left or right eye was dominant. This test is an adjusted version of the test described in Yang, Blake & McDonald (2010) and consisted of 32 trials total. Instead of using a square Mondrian image to suppress the arrow, we decided to use the same circle, Mondrian, we use during the experiment to ensure no differences were present. This dominance test indicated right eye dominance for 56% of the participants. After this, participants were familiarized with the different parts of a trial and the keys they had used to respond. They were also introduced to the rules of the trust game and were familiarized with some example scenarios. The trust game was always referred to as an "investment game" to prevent priming participants that trust was a key element in the study. Participants were asked to make an investment of €0, €2, €4, or €6 in their virtual partner for each trial. Their investments were tripled and the partner would then decide how much money they wished to return. Participants were informed that we had recordings of their partners and that these would be shown prior to making an investment decision. They were told that no feedback would be given between trials but that their investments and partner choices would determine the bonus received at the end of the experiment. Four practice questions were given to ensure participants understood the investment game and were aware of the consequences of their answers. Partner payments were based on decisions made by 15 students in the role of trustee, who was given a form with four investment decisions of others and asked how much they would give back if they received a certain amount of money. After the experiment, participants chose a random number and were matched with the corresponding partner. That partner's investment decision was used to determine the amount of bonus money received. When everything was clear, the physiological equipment was applied to the participants' face and hand, after which the real experiment began.

Participants were asked to ensure that they could put their head on the chin rest comfortably. Stable binocular fusion was achieved by letting participants adjust the coordinates of the screen where stimuli were presented so that they merged into one clear picture. After a nine-point calibration of the eye tracker, participants performed two practice trials after which they could ask their final questions. The test block followed the practice trials. Participants were provided with the option to take a break after they had completed half of the trials. If they chose to take the break, the screen and eye tracker were calibrated again. After the test block, all participants took a break and they were allowed to rest as long as they wanted. Next, the control block began, in which they again were provided with the option to take a break. At the end of the second session, participants were debriefed and compensated with either money or participant credits. Each participant also received a monetary bonus ranging between € 0 and € 3 based on their performance in the investment game.

Data acquisition and preparation

Pupil size

Pupil diameter was sampled with a rate of 1000 Hz per eye and was later down-sampled to 100-ms slots. Gaps smaller than 250 ms were interpolated, and a 10th-order low-pass Butterworth filter was used to smooth the data in PhysioData Toolbox v0.3.5. If the pupil sizes across two-time samples exceeded two standard deviations, the data were identified as outliers and excluded from the analysis. For each trial, we averaged 500 ms prior to stim onset, which served as a baseline measure. Pupil responses were then expressed as differences from baseline by subtracting the mean baseline pupillary diameter from all subsequent samples. Participants that missed more than 50% of their pupil data had been excluded (for similar outlier-criteria, see Kret et al., 2015). Control analysis confirmed that participants blinked or missed pupil data equally across all conditions. Moreover, the distribution of pupil was comparable across CFS and control conditions (see Supplementary Materials for details).

Electromyography

The parameters for facial EMG acquisition and analysis were selected according to the guidelines by van Boxtel (2010). Flat-type active electrodes were used and activity was measured bipolarly over the zygomaticus major (smiling muscles) and the corrugator supercilii (frowning muscles) on the left side of the face at a sample rate of 1,024 Hz. The grounding electrode was positioned behind the left ear. Before attachment, the skin was cleaned with alcohol and the electrodes were filled with electrode paste. Raw data were first filtered offline in the PhysioData Toolbox v0.3.5 with a 28 Hz high-pass and 500 Hz low-pass FIR filter. Data were smoothed with a

Boxcar filter of 100ms and visually inspected for artefacts. Parts of the data considered problematic were discarded. Subsequently, data were segmented into 2,500 ms epochs, including 500 ms of prestimulus baseline and 2,000 ms of stimulus exposure for each muscular region separately, full-wave rectified and smooth signal. Per trial, a baseline of EMG signals was calculated by averaging the activity recorded during the 500 ms preceding stimulus onset (the last 500 ms of the 5000 ms inter-trial interval period). Phasic EMG responses were averaged over 100 ms intervals starting from stimulus onset (overall corresponding to 20 time-bins) and expressed as µV of difference from baseline activity by subtracting the mean baseline EMG signal from all subsequent samples.

Skin conductance

Disposable electrodes filled with isotonic gel were used. They were placed on the inside distal phalanx of the ring finger and middle finger of the left hand. Raw data were first filtered offline with a 2 Hz low-pass filter and a 0.05 Hz phasic high-pass filter in PhysioData Toolbox v0.3.5. Data were visually inspected for artefacts and parts considered problematic were discarded. The average skin conductance response (SCR) was expressed by the skin conductance level difference from the baseline (the last 500 ms of the inter-stimuli interval, preceding stimulus onset). Upon baseline correction, all physiological measurements (EMG, Pupil, SCR) were normalized using the two-step transformation by Templeton (2011).

Statistical analysis

Multilevel models

Because the data had a hierarchical structure, results were analyzed by using multilevel modelling. This method allowed us to not only account for between-person variation but also for within-person variation. Analyses were performed in IBM SPSS Statistics (v25) by means of generalized linear mixed models. We took a backward selection approach, starting with a full model. One by one, insignificant interaction effects were removed from the model, followed by insignificant main effects. If the model fit improved, the factor was deleted from the model. If the model fit became worse, we used the log-likelihood test (LRT) to check if the change in fit statistic was significant. In favor of parsimony, the non-significant effect was left out when the model fit did not decline significantly.

Defining Facial Mimicry

Facial mimicry was conceptualized as increased smiling Zygomaticus major (ZM) muscle activity in response to happy expressions, and an increase in frowning Corrugator Supercilii (CS) muscle in response to fearful expressions. First, we z-scored the ZM and CS signals for each participant across four conditions (Face/eyes), (CFS/Control). We then subtracted the z-scored ZM signal from the CS signal combining the data into a continuous EMG (smile-frown) signal. As a result, the positive values represented increase smiling and negative values represented an increase in frowning. We then excluded all neutral trials (neutral faces/middle pupil size) and averaged the continuous z-scored EMG (smile-frown) signal over each trial. This mean value represented a mean increase/decrease in smiling/pupil size per trial. If participants saw happy expression (coded as 1) and they displayed baseline increase in smiling (mean EMG > 0), this trial would result in positive values, which would be classified as mimicry (coded as 1). On the other hand, if smiling activation decreased during the smiling trial resulting in negative values (mean EMG < 0), we classified this as no-mimicry (coded as -1). If participants saw fearful expression (coded as -1) and they displayed higher EMG activation (mean EMG > 0) this would be a non-mimicry trial. On the other hand, if they displayed lower EMG activation (mean EMG < 0) this would be mimicry trial.

Defining Pupil Mimicry

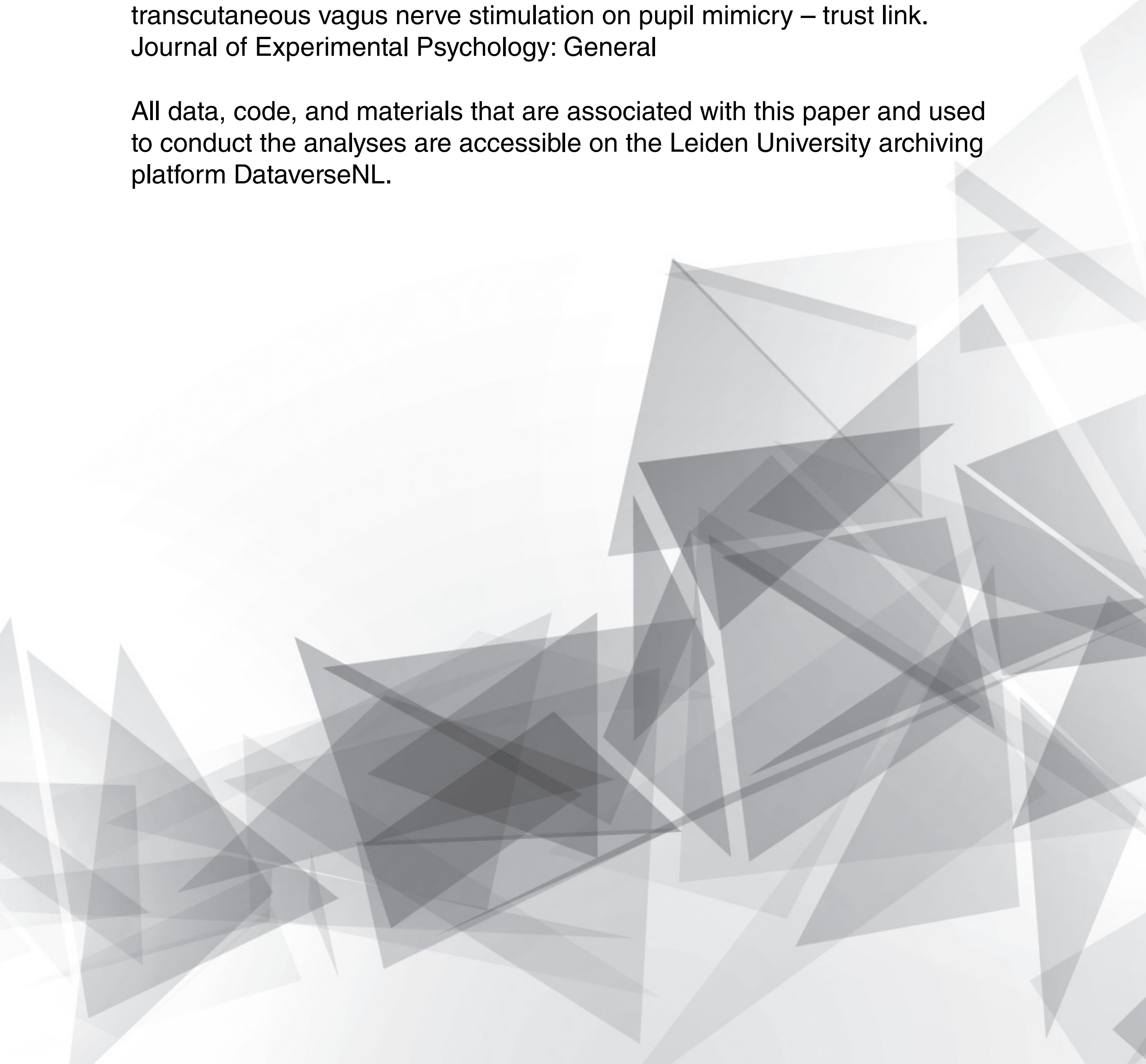
Pupil mimicry is described as synchrony in pupil sizes between a participant and a (virtual) partner (Kret et al., 2015). To define pupil mimicry, first, we z-scored participants' pupil size over trials and conditions. This resulted in a mean-centered continuous pupil variable (20 bins of 100 ms in each trial) with positive values corresponding to participant's pupil dilation and negative values to constriction. We classified each trial as mimicry/non-mimicry trial: if participants displayed a mean increase in pupil size during large trial and decrease during small trial, we would classify this as pupil mimicry trial. On the other hand, if participants' pupil decreased during partners’ large trials and increased during the partner’s small trials, this would be classified as a non-mimicry trial. We would like to note that our stimulus presentation duration was on the short side compared to previous literature (Kret et al., 2015; Procházková et al., 2018). In these previous studies, the eye regions were presented for 4 seconds. The pupils were static for the first 1.5 second and then dilated, remained static, or constricted. In those studies, the pupil mimicry response was analyzed over 2.5 seconds (from 1.5 – 4 seconds), whereas in the current, it was analyzed over 2 seconds. In addition, in order to be in line with research conducted by Tamietto & Castelli (2009), we decided to analyze pupil size directly after 500 ms of prestimulus baseline, while this is not common in the pupil mimicry (Harrison et al., 2006; Kret et al., 2015; Procházková et al., 2018) or pupillometry literature in general (e.g. Bradley et al., 2008).

Chapter 7

The effect of transcutaneous vagus nerve stimulation on pupil mimicry – trust link

Based on: Procházková & Kret, M. E. (under review). The effect of transcutaneous vagus nerve stimulation on pupil mimicry – trust link. Journal of Experimental Psychology: General

All data, code, and materials that are associated with this paper and used to conduct the analyses are accessible on the Leiden University archiving platform DataverseNL.



Abstract

During social encounters, people make eye contact to invite approach and foster bonding. In these moments, if both partners' pupils align and simultaneously dilate, pupil mimicry boosts trust. So far, little is known about the neuromodulation of this pupil mimicry-trust link, but it has been proposed that the locus coeruleus–norepinephrine (LC-NA) system might be at play. In this experiment, we investigate the role of the LC-NA system in the pupil contingent trust formation by using transcutaneous vagus nerve stimulation (tVNS); a method that has been proposed to increase norepinephrine concentrations in the brain and which we expected would induce pupil dilation. Participants' pupil sizes and investments were measured as they played trust games with partners whose pupils changed in size. Using a single-blind, sham-controlled, within-subject design, we also manipulated the background luminance of stimuli to induce pupil dilation without targeting the LC-NA system. The results revealed that neither tVNS nor a dark stimulus modulated pupil mimicry, which demonstrates that pupil mimicry is a robust phenomenon resistant to mechanistic manipulation. Moreover, in support of our hypothesis, active as compared to sham stimulation decreased trust in partners with static pupils compared to dilating pupils. These results support the theory that the vagal nerve plays a causal role in the recognition of eye signals. However, since tVNS did not modulate participants' overall (non-baseline-corrected) pupil size, we conclude that behavioral influences induced by tVNS cannot be fully attributed to the LC-NA system. We discuss a potential alternative neurological pathway through which tVNS influences trust along with implications for future investigation using this method.

Keywords: Norepinephrine, Locus coeruleus, Pupil diameter, Pupil mimicry, Trust

Introduction

Over the past decade in the field of cognitive neuroscience, there has been an increased interest in pupillary responses as reflections of cognitive states. Apart from responding to changes in ambient light, pupils dilate with activation of the locus coeruleus–norepinephrine (LC-NE) system (Aston-Jones, Chiang, & Alexinsky, 1991; Eldar, Cohen, & Niv, 2013; Jepma & Nieuwenhuis, 2011). What makes pupil size particularly interesting is that, in contrast to other autonomic responses (e.g. skin conductance, heart rate), pupils are visible to the human eye if one's eyes are light enough, which is why they have the potential to modulate social interactions (Kret, 2015; Procházková & Kret, 2017). For example, previous research has shown that people with large pupils are perceived more positively than people with small pupils (Hess, 1975; Hess & Fischer, 2013; Kret, Fischer & De Dreu, 2015; Kret, 2017; Kret & De Dreu, 2017). Moreover, existing evidence has shown that people mimic the pupil size of others (Harrison, Wilson & Critchley, 2007; Kret et al., 2015; Kret & De Dreu, 2017). Apart from human adults, this phenomenon has been found in infants (Aktar, Raijmakers & Kret, 2020; Fawcett, Wesevich & Gredebäck, 2016) and chimpanzees (Kret, Tomonaga & Matsuzawa, 2014), which implies that pupil mimicry might be an innate and evolutionarily old phenomenon. Intriguingly, prior research has shown that pupil dilation mimicry is positively related to measures of trust (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018). In this previous work, participants played trust games with partners whose pupils were manipulated to dilate, remain static, or constrict (Kret et al., 2015). Results revealed that when participants mimicked their partner's dilating pupils, they trusted their partner more than when they did not mimic. In order to better understand the functional significance of the relationship between pupil dilation mimicry and trust (and the order of their effects), it is essential zoom in on the underplaying mechanisms.

Previous neuroimaging research has shown that observed pupil size in another person is processed by the amygdala (Amemiya and Ohtomo, 2012; K. E. Demos et al., 2008). An individual's own pupil size positively correlates with norepinephrine, which the locus coeruleus (a nucleus situated in the brainstem) elicits during arousal (Lavín et al., 2014; Sara and Bouret, 2012). We propose that when a partner's pupils dilate, the observer's amygdala sends excitatory projections to the LC that make the observer's pupils dilate as well (pupil-mimicry occurs, Figure 1). The LC-NE system in the brain further influences cortical areas engaged in decision-making (Donner and Nieuwenhuis, 2013; Eldar et al., 2013; Lavín et al., 2014; Sara and Bouret, 2012). When NE concentration in the brain is high, communication between distinct areas of the brain increases, which consequently biases individuals towards their dominant modes of thought and behavior, potentially facilitating appropriate behavioral and physiological responses to perceived stimuli. Considering that humans have a natural tendency to perceive large pupils as more positive (Hess, 1975; Hess & Fischer, 2013; Kret et al., 2015; Kret, 2017; Kret & De Dreu, 2017), the positive association between large pupils and trust is likely to increase with NE release - which can be noninvasively tracked by measuring pupil size. From this perspective, it makes sense that when participants mimic partners' dilating pupils, trust increases. In support of this theoretical model, in our recent fMRI study we showed that when participants perceived partners' dilating or constricting pupils, their visual brain areas (V5) related to luminance changes became active (Procházková et al., 2018). However, when subjects mimicked partners' dilating pupils compared to when they did not mimic, the neural activity in social brain regions (Theory of Mind network; Temporo-Parietal Junction and anterior cingulate cortex) increased. This evidence further supports the view that pupil mimicry stimulates higher cognitive functions involved in social cognition, and that the association between large pupils and trust may become pronounced with higher concentrations of NE (reflected in pupil diameter). Nevertheless, since the neurological underpinnings of pupil mimicry have been thus far tested only with correlational measures (e.g. fMRI), the causal role of the noradrenergic system and pupil mimicry in pupil-contingent trust has not been established.

The present study investigates the causal role of LC-NA in the pupil mimicry-trust linkage by manipulating participants' pupil size with two methods: transcutaneous vagus nerve stimulation (tVNS) and by global luminance manipulation (Figure 1). tVNS is a non-invasive method that has been proposed to increase NE concentrations in the brain (Follesa et al., 2007; Hassert et al., 2004; Roosevelt et al., 2006). The NE increase is believed to be a result of the anatomical connections between the vagus nerve and the LC - the noradrenergic supply center of the brain (Assenza et al., 2017;

Frangos et al., 2015; Hulsey et al., 2017; Samuels and Szabadi, 2008), which further modulates emotional and social areas in the cortex (Capone et al., 2015; Dietrich et al., 2008; Frangos and Komisaruk, 2017; Kraus et al., 2013; Yakunina et al., 2017). Apart from invasive LC recordings, pupil size is proposed to be the most reliable marker of LC-NE activity under constant luminance (Joshi, Li, Kalwani, & Gold, 2016). Due to close correlations between the activity of LC neurons and fluctuations in pupil size (Aston-Jones, et al. 2005), a consequence of stimulating this system could be an increase in pupil dilation (but see; Burger, Van der Does, Brosschot, & Verkuil, 2020; Warren et al., 2019). Moreover, the prepotent pathways between the brainstem and theory of mind (ToM) network in the cortex may become more enhanced during tVNS and boost trust when individual's and partner's pupils dilate. In contrast to pupillary responses related to NE release, a global luminance manipulation should only influence pupil size and therefore have no impact on pupil dilation mimicry.

In sum, while both luminance and tVNS manipulations are expected to **(a)** increase participants' pupil size. Due to their distinct underlying mechanisms, they should have different effects on pupil mimicry and pupil contingent trust. Specifically, in line with prior literature (Harrison, Wilson & Critchley, 2007; Kret et al., 2015; Kret & De Dreu, 2017), we expected participants to mimic their partners pupil sizes. Since pupil dilation (as a proxy of NE release) biases individuals towards their dominant predispositions (Donner and Nieuwenhuis, 2013; Eldar et al., 2013), and large pupils are perceived as more positive (Hess, 1975; Hess & Fischer, 2013; Kret et al., 2015; Kret, 2017; Kret & De Dreu, 2017), we hypothesized that if tVNS it should enhance the positive association between dilated pupils and trust. In other words, we expect that tVNS will **(b)** enhance pupil mimicry and (**c)** make subjects' pupil sizes and investments more dependent on partners' pupil size changes (compared to sham and luminance conditions). Finally, since tVNS is believed to increase NE in the brain, **(d)** tVNS should boost the pupil dilation mimicry-trust linkage by enhancing the neural connectivity between the brainstem and ToM regions. The objectives are summarized in Figure 1.

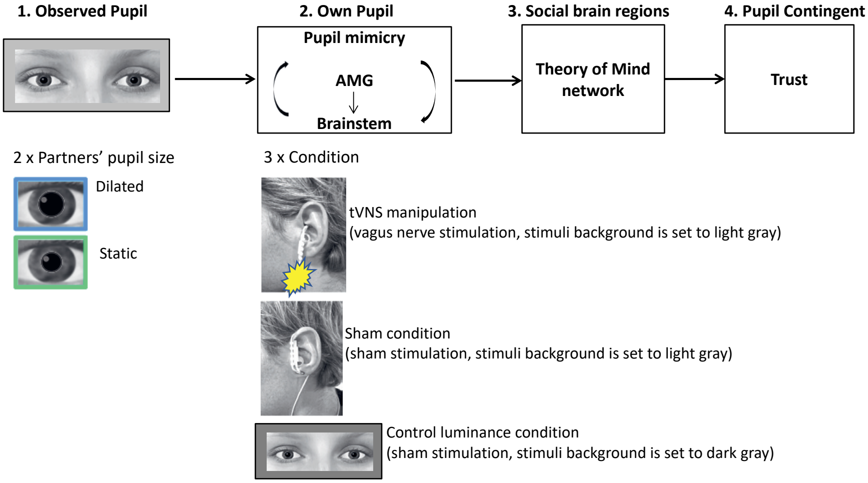


Figure 1: Theoretical model of neurological mechanisms underlying pupil mimicry-trust linkage: (1) observed pupil change (dilating vs. static partners' pupils) activate the amygdala (Amemiya and Ohtomo, 2012; K. E. Demos et al., 2008). (2) which projects to the locus coeruleus–norepinephrine (LC-NE) system that (3) modulates widespread cortical activation including neural regions involved in trust decisions. Pupil contingent trust is a result of prepotent pathways between the brainstem - theory of mind (ToM) network in the cortex, which becomes enhanced when individual's own pupil dilates. **Conditions:** Transcutaneous vagus nerve stimulation (tVNS) is a novel non-invasive brain stimulation technique. By applying an electrode to the outer ear to deliver electrical impulses to the auricular branch of the vagus nerve, the afferent fibers of Arnold's nerve are excited and the signal penetrates from peripheral nerves to the brainstem and, ultimately, to LC (Colzato et al., 2017; Frangos et al., 2015). To provide a control situation, we further included a luminance condition in which participants' pupils were manipulated to dilate as a consequence of a darker stimuli background.

Results

(a) The effect of tVNS and luminance manipulations on pupil size

Before we evaluated the effect of the tVNS and luminance (a darker stimulus background) manipulations on mimicry, we checked whether participants' non-baseline corrected pupil size increased in response to the luminance and tVNS manipulation. In the first multilevel model (see Methods) we tested the effect of condition coded as –1 (luminance), 0 (sham), 1 (tVNS) on participants' pupil size (without baseline correction). A main effect of condition was observed $F(2, 114607) = 11.070$, $p < .0001$, Table S1). Post-hoc pairwise comparisons show that participants' mean pupil size was significantly larger in the luminance condition compared to the control condition ($p < 0.0001$). However, there was no difference in participants' pupil size between the tVNS and control condition ($p > 0.05$) (Supplementary Fig. 1).

These results show that our luminance manipulation worked in that it increased participants' pupil size as we anticipated. We also expected that the tVNS manipulation would boost norepinephrine levels, and therefore, would also increase participants' pupil sizes. This did not occur, so from this analysis, we cannot infer whether tVNS had any effect on participants, a point we return to below.

(b) The effect of tVNS and luminance manipulations on pupil mimicry

In our previous work we have shown that participants' pupil sizes enlarge when looking into the eyes of another person with dilating compared to static or constricting pupils. In a second multilevel model, we investigated whether pupil mimicry (comparing partners' static and dilating pupils) is modulated by our *tVNS and* luminance manipulation. In addition to the fixed factor condition, we added partners' pupil size coded as 0 (static), and 1 (dilating) and partner pupil size × condition as predictors of participants' baseline-corrected pupil size. Results revealed evidence of pupil mimicry with an effect of partner pupil size, $F(1, 106385) = 13.483$, $p < .0001$, (Fig 3. and Table S2) and a Partner Pupil Size × Linear Trend interaction, $F(1, 106385) = 5.840$, $p < .016$), which shows that participants' pupils were largest and increased fastest over stimulus-presentation time when partners' pupils dilated as compared to remained static. We did not find significant effects of condition, or the interaction between condition and partner pupil size, which implies that pupil mimicry was not influenced by our tVNS or luminance manipulation.

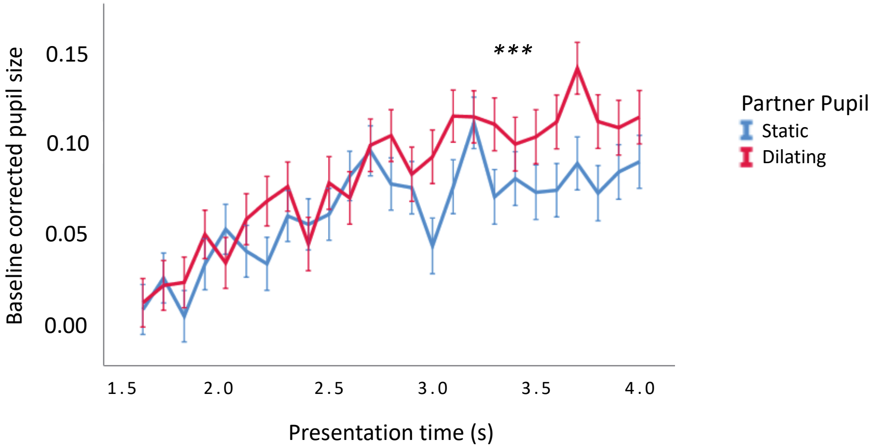


Figure 3: The effect of tVNS and background luminance manipulations on pupil mimicry. Error bar = ± 1 standard error. *** $p < 0.001$. Time (in seconds) is from 1.5 sec after stimulus onset, that is, the moment at which partners' pupils started to dilate or not, to 4 seconds, which was stimulus offset.

(c) The effect of partners' pupil size, tVNS and luminance manipulations on trust-related investments

Next, we investigated whether our two manipulations influenced participants' trust. A third multilevel model including condition, partner pupil size, and their interaction as fixed factors predicted participants' trial-by-trial investments. We found no main effects of partners' pupils on condition. However, we did find a significant interaction between partner pupil size and condition $F(1, 5280) = 3.268$, $p = .038$, (Figure 4, Table S3) revealed that participants' trust was lower when looking into partners' eyes with static pupil size, but this effect was only observed under tVNS ($p = 0.003$) and not significant in the other two conditions.

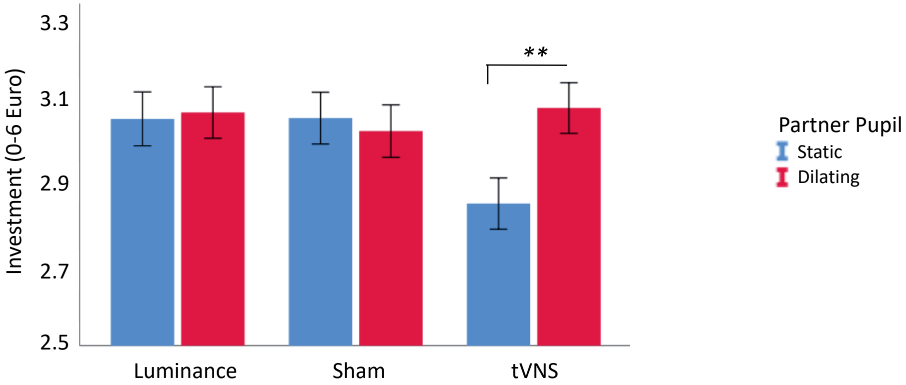


Figure 4: The effect of tVNS and luminance manipulations and partners' pupil size on trust-related investments. Error bar = ± 1 standard error. ** *p* < 0.005.

(d) Does pupil dilation mimicry modulate changes in trust

In a final analysis, we tested whether pupil dilation mimicry modulates pupil-contingent trust (see Methods for details). Contrary to our expectations and prior literature (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018), we did not find a main effect of pupil dilation mimicry ($p > 0.05$), or an interaction effect of condition and participant's dilation mimicry on trust ($p > 0.05$, Table S4).

Discussion

Previous research has shown that looking into the eyes of someone with large or dilating pupil sizes boosts trust, especially when observers' pupils mimic those of the observer (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018). In the current study, the left vagus nerve was stimulated to gain insight into the role of the LC-NA system in this pupil dilation mimicry-trust linkage. Our results are threefold. First, we observe that participants mimic partners' pupil size independent of our manipulations (luminance, sham, tVNS). Second, active as compared to sham stimulation lowered trust in partners with static compared to dilating pupils. Third, we found no evidence for a relationship between pupil dilation mimicry and pupil-contingent trust. In the following section, we discuss each result in detail in the context of the existing literature.

First, we observe that participants mimicked their partners' pupil size independent of our manipulations (luminance, sham, tVNS). Previous studies have shown that tVNS increases activity in the LC-NA system (Chen and Williams, 2012; Dorr and Debonnel, 2006; Follesa et al., 2007; Frangos et al., 2015; Groves et al., 2005; Hassert et al., 2004; Hulsey et al., 2017; Manta et al., 2013; Roosevelt et al., 2006; Vonck et al., 2014). Concerning these findings, we anticipated that tVNS would increase participants' level of arousal and as a consequence, that this would be reflected by enlarged pupil sizes. In the current study we aimed to pull apart the putative effects of *arousal* from potential effects of *luminance* on pupil contingent trust. Specifically, we anticipated that a low luminance stimulus background would increase baseline pupil size but have no influence on pupil mimicry. Pupil dilation mimicry, on the other hand, has been predicted to increase with levels of neural arousal (gain) induced by tVNS activity. In contrast to this hypothesis, participants' pupil sizes did not differ between the tVNS and the sham condition. In the luminance condition where pupil size was successfully manipulated and increased as a result of a darker stimulus background, pupil mimicry was unaffected, contrary to our predictions. This shows that manipulating participants' pupil size, at least to the extent we did (an increase of 19%), does not modulate pupil mimicry. The null effect of tVNS on pupil size/pupil mimicry contradicts prior studies that imply that vagus nerve stimulation (iVNS) increases norepinephrine (NE) via the locus coeruleus (LC) activation (Chen and Williams, 2012; Dorr and Debonnel, 2006; Follesa et al., 2007; Groves et al., 2005; Hassert et al., 2004; Hulsey et al., 2017; Manta et al., 2013; Roosevelt et al., 2006; Vonck et al., 2014). Instead, this result aligns with previous research that also found no impact of tVNS on pupil size (Burger et al., 2020; Keute et al., 2019; Warren et al., 2019). In addition, here we demonstrate that pupil mimicry is a resilient effect that is not easily disrupted by mechanistic manipulation.

Our second key finding shows that tVNS lowered participants' trust in partners with static pupil sizes**.** This result confirms the third hypothesis suggesting that tVNS will make subjects' investments more dependent on partners' pupil size changes. Previous neuroimaging work has shown that activity in the LC-NA system modulates activity in social and emotional areas in the cortex (Dietrich et al., 2008; Kraus et al., 2013; Yakunina et al., 2017). Accordingly, our recent fMRI research revealed an association between these areas and pupil dilation mimicry (Procházková et al., 2018), which fosters the view that phasic pupillary responses (reflective of NE increase) upregulate neocortical networks involved in trust. Based on these findings, we predicted that tVNS would enhance communication between the brainstem and the ToM network and modulate the positive association between large pupils and trust. In support of this theory, we find that tVNS reduced trust in partners with static pupils compared to dilating pupils and therefore strengthen the association between average-sized pupils and lower levels of trust. Yet, tVNS did not boost trust in partners with dilating pupils. An explanation for why tVNS lowered participants' trust to partners' static pupils instead of increasing trust to dilating pupils is highly speculative. A plausible explanation is that tVNS influences human behavior via an alternative neurochemical pathway. Converging evidence from animal and clinical studies imply that apart from NE, tVNS increases levels of GABA (Ben-Menachem et al., 1995) and acetylcholine (ACh) involved in inhibitory and parasympathetic processes (Borovikova et al., 2000). GABA (γ-aminobutyric acid) is the main inhibitory neurotransmitter in the adult vertebrate brain that plays a key role in the neuromodulation of response selection (Bar-Gad et al., 2003) and cortical inhibition in healthy adults (Capone et al., 2015). Moreover, tVNS has been shown to reduce sympathetic activity and produce a shift toward parasympathetic functions (e.g., slowing heart rate; Clancy et al., 2014). It is, therefore, possible that tVNS modulates social cognition via activation of parasympathetic processes instead of noradrenergic/sympathetic responses. In support of this interpretation, it has been shown that parasympathetic activity measured by heart rate variability predicts individuals' ability to read others' emotions from their eyes (Quintana et al., 2012). Thus, a possible explanation is that tVNS may inhibit trust in partners with static and average-sized pupils (slightly aversive stimuli, especially in the context of other partners with dilating pupils) compared to dilating pupils (positive stimuli) via activation of the GABAergic system. Such an interpretation would also account for the lack of tVNS effects on pupil size.

Another finding that merits interpretation is why partners' pupils did not influence trust during sham and luminance conditions. Previous research has shown that looking into the eyes of someone with large or dilating pupil sizes boosts trust (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; van Breen et al., 2018; Wehebrink et al., 2018). Yet here we only found such pupil contingent trust effects when the participant's vagus nerve was stimulated. The lack of a main effect is not in complete contradiction to previous research. In some of our earlier studies, partners' dilating pupils only yielded a small increase in trust and had smaller effects than constricting pupils (the latter of which were not included in the current study, which could have dampened the effect of dilating pupils as the contrast with static pupils is smaller; e.g. Kret et al., 2015; Kret & De Dreu, 2017). An alternative explanation is tied to our most recent study (Procházková et al, in prep), which shows that perceived pupil size impacts trust mainly subconsciously, possibly through a direct subcortical pathway (Tamietto and De Gelder, 2010). Since tVNS targets subcortical structures (Frangos et al., 2015; Frangos and Komisaruk, 2017; Roosevelt et al., 2006), this result may also offer a potential insight into why tVNS induced pupil contingent trust and control conditions did not. Nevertheless, more research is needed to validate these interpretations.

Finally, we did not find the pupil mimicry-trust linkage in any of our conditions (tVNS, sham, or luminance). Multiple previous studies have consistently shown that pupil mimicry modulated trust decisions (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018). Several methodological differences may provide an explanation as to why we do not find this effect in the current study. The most obvious difference between the current study and prior research is that we used an invasive intervention. Even though tVNS is not painful, it can cause considerable discomfort, also in the sham condition. Considering that the effects of pupil mimicry on trust are very subtle (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018), it is therefore possible that our manipulations influenced participants mood. Such an intrusion might be particularly detrimental to the pupil mimicry-trust link, which relies on participants' ability to attune to subtle internal signals. This effect could spill over to the luminance condition, which followed one of the two types of stimulations (active/sham). We therefore recommend that future studies interested in the effects of pupil mimicry in human behavior refrain from invasive manipulations. Another difference between the current and prior research is that the main focus here was on sympathetic influences of partners' pupils on trust. We therefore omitted pupil constriction from the research design entirely. In consequence, we were not able to assess the effect of partners' constricting pupil mimicry on trust. Thus, we propose that future studies include three levels of pupillary changes (dilating, static and constricting) as these methodological differences may explain the lack of the pupil mimicry influence on trust found in the current study.

In sum, this experiment yielded three main outcomes. First, we demonstrate that pupil mimicry is a robust phenomenon resilient to manipulation. Second, active as compared to sham stimulation lowered trust in partners with static compared to dilating pupils. Third, tVNS did not affect participants' pupil size, nor the expected pupil mimicry contingent trust relationship. Together these results support the theory that the vagal nerve plays a causal role in the recognition of social signals. However, as we did not observe any effect of tVNS on pupil mimicry or other pupillary responses, we conclude that the behavioral effect induced by tVNS cannot be simply ascribed to activation of the LC-NA system. Instead, we propose that tVNS affects pupil contingent trust via alternative neurological pathway.

Methods

To evaluate the effect of partners' pupils on participants' pupils and trust, we used the same stimuli and trust games as in the Kret's, Fischer's and De Dreu (2015) previous research. Participants' task performance (trusting behavior) and eye-tracking data were measured in two sessions during which subjects played trust games with virtual partners whose pupils changed in size. Each participant played three rounds of the game under three different experimental conditions. Once during active tVNS stimulation where a constant current of 0.5mA was delivered to the vagus nerve, once with the same current intensity and duration, but during earlobe sham stimulation (Figure 1; Control condition). Once without simulation but under global luminance manipulation (Figure 1; Global luminance manipulation). The tVNS and sham conditions were counterbalanced across sessions. Unlike in previous studies (Kret et al., 2015; Kret & De Dreu, 2017; van Breen, De Dreu, & Kret, 2018; Wehebrink et al., 2018), the main focus of this research was on the perception of partners' pupil dilation and not constriction. This is because pupil dilation has been linked to LC activity and sympathetic nervous system activity, but not pupil constriction.

Participants

Fifty-one participants were recruited at Leiden University (age: 18 – 25 (M = 21.16, SD = 1.67) who had no history of neurological or psychiatric disorders. The study consisted of 2 experimental sessions approximately four weeks apart. For the majority of participants (85.7 percent) both sessions were scheduled at the same time of the day or within two hours, reducing potential effects of diurnal cycle fluctuations of norepinephrine (Bleske et al., 1999). One participant failed to show up for the second session for undisclosed reasons and was subsequently excluded from all analyses. To ensure enough observations of sufficient quality, the data of the remaining 50 subjects (25 females) were analyzed. This sample size was based on earlier work investigating pupil mimicry (which included between 40 - 69 participants; e.g., Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Kret et al., 2015). In eight runs (of seven participants) data were missing for more than 50% of valid pupil trials, following standard procedures we excluded those subjects' runs from models assessing subjects' pupil analyses (*n* = 42) (e.g. Kret et al., 2015). The participants filled out the Informed Consent form prior to the start of the first session and were debriefed following the second session. Participants were informed that they were free to stop their participation at any moment. No participant quit the study during an experimental session. The experimental procedures were in accordance with the Declaration of Helsinki and approved by the Psychology Research Ethical Committee (PREC15-1113/64) of Leiden University.

Stimuli

To create virtual partners in the trust game, we used the same stimuli as in previous research by Kret, Fischer and De Dreu (2015). In total, 18 pictures of eyes (9 females, 9 males) of Western European descent were selected. Pupil dilation was created by increasing the pupil diameter of a static image using Adobe After Effects. In the pupil dilation condition, pupil size was 5 mm for 1.5 seconds and then gradually started to increase to 7 mm over the course of 1.5 seconds after which it remained at its maximum size (7mm) for another second. In the static pupil size condition, pupil size remained 5 mm over the course of 4 seconds of stimulus presentation time (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; van Breen et al., 2018; Wehebrink et al., 2018). The current study deviates from our previous work in that we did not include a pupil constriction condition.

Trust game

In the current study, participants played a series of Trust Games with virtual partners where they had the role of the trustor (see Figure 2). The trustor is endowed with a certain amount of money which can be shared with the virtual trustee. Participants were instructed to decide what share of their six euros they wished to invest after seeing the other player's eyes. The investment was then multiplied by a factor three and the trustee could return a portion of the money. The participants were told that they would be partnered with different student players whose decisions on reciprocation were recorded in previous sessions (which was the truth). The choices were made using a button box with four buttons (€0, €2, €4, €6). Participants were told that they would not receive any immediate feedback regarding partners' decisions. In total, the game consisted of 18 trials per condition and partner pupil size (3 x Condition, 2 x Pupil size, Total = 118 trials).

Procedure

Before the experiment, participants were instructed not to drink coffee or other caffeinated beverages and be well-rested. On arrival to the laboratory, the tVNS stimulator, heart rate electrodes, and Electromyography (EMG) sensors to measure facial muscle activity were attached to collect physiological data. These physiological measures were collected for purposes of a different question, which is outside the scope of the current paper. At this point, luminance in the room was reduced to a constant minimal level for the remainder of the procedure. Participants were then given questionnaires regarding their demographics, after which they played the Trust Game (Figure 1, for details). Finally, participants were given the Reading the Mind in the Eyes task (Baron-Cohen et al., 2001), lasting around four minutes. This task was not related to the current research question and thus was not analyzed for the purposes of this study. The second session followed the same sequence only with another Trust game played at the end of the session, this time with changing background luminance to manipulate pupil dilation. In total, experimental sessions lasted 40 – 50 minutes. Throughout the game, participants chin was placed on a chinrest. The screen was at 50 cm distance from the face.

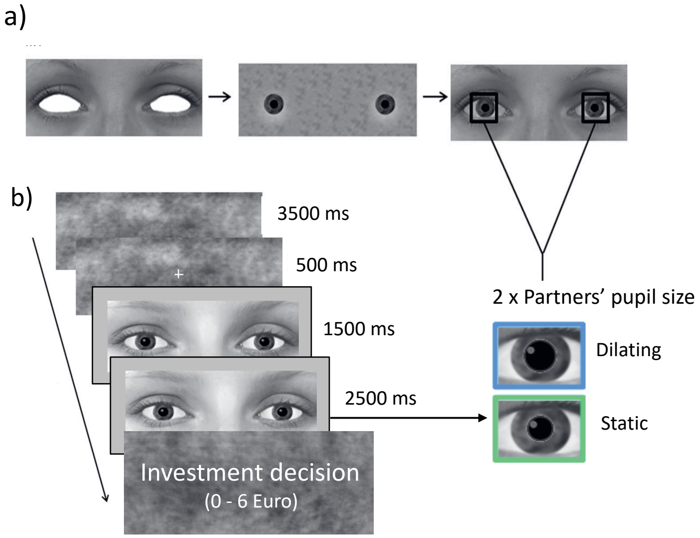


Figure 2: (*a*) To create partner stimuli, we removed the eyes from pictures of the eye regions of faces and then added the same eye white, iris, and pupil to each stimulus. (b) Each trial consisted of the following sequence: (1) a grey screen with scrambled image appears for 3500 milliseconds, (2) a fixation cross appears in the middle of the grey screen for 500 milliseconds, (3) a person's eye area appears on the screen for 4000 milliseconds with a static image for 1500 milliseconds, (4) static or dilating pupils presented for 2500 milliseconds, (5) a screen with four options of the amount to be shared appears.

tVNS

In the experimental condition, the neurostimulation device (CM02, Cerbomed, Erlangen, Germany) was attached to the Cymba conchae part of the left outer ear, under the Inferior crus of antihelix (see Figure 1), an area that has been found to be consistently innervated by the auricle branch of the vagus nerve (ABVN); (Frangos et al., 2015). In the sham condition the tVNS stimulator was attached to the lobule of the auricle of the left ear, which is not innervated by the ABVN (Peuker and Filler, 2002) and has been used in previous research on the effects of tVNS as sham condition (Colzato et al., 2017; Frangos et al., 2015). tVNS has previously been found to be a safe procedure with no known side effects (Kreuzer et al., 2012). tVNS stimulation was intermittent, with 30 seconds of active stimulation followed by 30 seconds break.

Pupil pre-processing

Participants' pupil size was continuously collected with Tobii T120 eye tracker. We interpolated gaps smaller than 250 ms. Trials were excluded if more than 50% of the data within that trial were missing (e.g., because the eye tracker lost the pupil). We also excluded participants that had more than 50% of their pupil data missing per session. We smoothed the data with a 10th-order low-pass Butterworth filter. Preprocessing of pupil size data was conducted using a customized open-source MATLAB script (Kret & Sjak-Shie, 2019). The average pupil size 500 ms before the start of the changes in a partner's pupils (computed per participant and trial) served as a baseline (i.e., 1,000–1,500 ms after stimulus onset) and was subtracted from each sample during the remaining stimulus presentation (1,500–4,000 ms).

Statistical analysis

To investigate whether tVNS and luminance manipulations influenced participants' pupil size, data were analyzed with multilevel models. In the first model, we tested the effect of condition coded as –1 (luminance), 0 (sham), 1 (tVNS) on participants' pupil size (without baseline correction). The multilevel structure was defined by the repeated measures, that is, time (Level 1) nested in trials (Level 2) nested in participants (Level 3). Time (twenty-five 100-ms slots) was included as a repeated factor with a first-order autoregressive covariance structure to control for autocorrelation. Also, we included linear, quadratic, and cubic terms and their interactions with the previously mentioned factors to model the curvilinear relationship between participants' pupil size and time.

According to Aston-Jones and Cohen (2005) and others (Keute et al., 2019) there are two functionally distinct modes of LC activity: tonic activity, leading to a global increase in NE transmission, and phasic activity, leading to an upregulation of NE transmission in response to environmental requirements. While pupil size without baseline correction between individuals can be used to monitor tonic changes of neural gain in individuals, phasic pupil size normalized to baseline are better suited for between-subject comparisons (Eldar et al., 2013). In the second model, we used the same multilevel structure as in the previous model. Condition coded as −1 (luminance), 0 (sham), 1 (tVNS), partner pupil size coded as 0 (static), and 1 (dilating) and partner pupil size × condition were added as predictors of participants' baseline-corrected pupil size. In addition, we included linear, quadratic, and cubic terms and their interactions with the previously mentioned factors to model the curvilinear relationship between participants' pupil size and time.

In the third multilevel model, we predicted participants' trust-related investments. In this model, we included a 2 level structure where different trials (Level 1) were nested within participants (Level 2). Participants' investment decisions (per trial) were used as the target variable and condition, partner pupil size and partner pupil size × condition were used as predictors. Furthermore, since some faces may be perceived as more/less trustworthy, we also included a random effect of stimulus face (9 pictures for males, 9 pictures for females) in the model.

In the final analysis, we tested whether pupil dilation mimicry modulates pupil-contingent trust. We included a 2-level structure where different face stimuli (Level 1) were nested in participants (Level 2). We computed a dilation-mimicry score (per stimulus face: participant's pupil size when partner's pupils dilated minus when partner's pupils were static) and partner-pupil contingent trust (investments in partners with dilating pupils minus investments in partners with static pupils). The multilevel model included the factors condition, dilation mimicry, and condition × dilation mimicry. The dependent variable was partner-pupil contingent trust. Models were implemented in SPSS Version 20. In the Supplemental Material available online, the full model of pupil mimicry in Tables S1, investments are shown in Table S2, and of the link between these two in Table S3.

Chapter 8

General discussion

General Discussion

The research that comprises this dissertation investigated the function and mechanism of mimicry in human interactions. In this final chapter, I will highlight and integrate the key findings from the different chapters and discuss them in a broader context. At the end, I will further propose important questions that can be gathered by these chapters' findings.

Theoretical framework

The first section **(Chapter 2 - 3)** of this dissertation introduced the idea that mimicry is a mechanism that helps humans to recognize and share emotions. Building upon the perception-action model (PAM) of empathy (Preston and de Waal, 2002), we described how automatic mimicry may give rise to basic emotional contagion, which then matures into a more complex form of empathy (perspective-taking). This theory has been supported by a large number of studies showing that mimicry is one of the earliest forms of emotional communication between a child and a caregiver (Baron-Cohen et al., 1995, Feldman et al., 2011, Field et al., 1982; Jones, 2006, Martin and Clark, 1982). A distinction was made between 'motor mimicry' (e.g. facial expression mimicry) controlled by the motor muscles and 'autonomic mimicry' controlled by the autonomic nervous system (e.g. heart-rate synchrony). In **Chapter 3**, we zoomed in on the underlying mechanisms of mimicry. The Neurocognitive Model of Emotional Contagion (NMEC) was introduced (Procházková & Kret, 2017), proposing two neurological pathways; one for autonomic mimicry and a separate one for motor mimicry. We proposed that autonomic mimicry is facilitated by the superior colliculus (CS) - pulvinar (Pulv) pathway, which projects to the amygdala and HPA axis (Tamietto & de Gelder, 2010). This subcortical pathway is believed to allow for nonconscious affective processing that regulates human physiology and behavior outside of perceiver's conscious awareness. On the other hand, motor mimicry was linked to the mirror neuron system (MNS) including cortical regions such as the inferior frontal gyrus (IFG), inferior parietal lobe (IPL) and superior temporal sulcus (STS), which gives rise to goal directed behavior and the imitation of motor movement (Gallese & Goldman, 1998; Gazzola et al., 2006). In sum, the first section **(Chapter 2 - 3)** of this dissertation provided foundations for the view that mimicry might be a primitive, automatic, and implicit form of empathy and introduced two possible neurological mechanisms through which mimicry shapes social perception and behavior.

Summary of empirical studies

To test this theoretical model, in the next sections (**Chapter 4 - 5**) we conducted two empirical studies that examined the relationship between autonomic mimicry and pro-social behavior.

During social interactions people are extremely aware of signs that show whether or not interaction partners are paying attention. One method for accomplishing this is registering eye gaze, which is such a fundamental skill that it is present at birth (Farroni et al., 2002). When we notice that someone is paying attention and looking at us, a signal that is unconsciously perceived is the pupil size of that person, which dilates with social interest (Harrison et al., 2009). Precisely because pupillary changes are unconscious, they provide a veridical reflection of a person's inner state, rendering them particularly relevant for observers (Kret, 2015). In the first fMRI study **(Chapter 4)**, we looked into the neural correlates of the pupil mimicry-trust linkage while participants played a one-person trust game in an MRI scanner (Procházková, et al. 2018). This study replicated previous findings and showed that when the pupils of interacting partners synchronously dilate, trust was promoted (Kret et al., 2015; Kret & De Dreu, 2017; Procházková et al., 2018; Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018). Moreover, we found that pupil mimicry modulated trust decisions along with the activation of the precuneus, temporoparietal junction, superior temporal sulcus, and medial prefrontal cortex – neural areas that are part of the theory-of-mind network (Saxe and Wexler, 2005b; Schaafsma et al., 2015). This study provided support to the NMEC (Procházková, et al. 2018) by showing that autonomic mimicry modulates neural areas involved in pro-social behavior.

A similar effect was found in a real-life interaction study **(Chapter 5).** In the experiment described in that chapter, physiological and nonverbal signals of participants were measured during a blind date. Intriguingly, the results showed that synchrony in heart rate (HR) and skin conductance levels (SCL) between partners predicted couples' attraction, while the synchrony of more explicit facial expressions such as smiles, laughter and eye contact did not. These findings demonstrate that when interacting partners' subconscious arousal levels rise and fall in synchrony, mutual attraction increases. These results aligns with the emotional contagion theory (Cacioppo et al., 2000) arguing that spontaneous mimicry allows humans to come to feel reflections of the inner states of others. Theoretically, through subtle changes in the face and body, changes in physiological arousal can become visible to others, allowing physiological synchrony to emerge. In return, bodily information provides feedback perceived as a "gut feeling" that shapes perceivers' cognition and behavior. In this way, autonomic mimicry potentially promotes pro-social behavior. Based on **Chapter 4** and **5**, we conclude that measures of autonomic synchrony may serve as a proxy of the emotional transfer.

In the final section of this dissertation (**Chapter 6 - 7**), to probe the underlying mechanisms of the pupil mimicry-trust lineage further, we shifted from correlational measures to manipulations. The aim of **Chapter 6** was to test whether partners' facial expressions and pupils would be mimicked and influence trust decisions even during an experimental condition where stimuli were processed unconsciously (suppressed). In this experiment, participants played trust games and would either see their partners' facial expressions (neutral, happy or fearful), or partner's eye region with varying pupil sizes (large, medium, or small). In half of the trials, we used continuous flash suppression (CFS) to render the stimuli subjects were being presented with subjectively invisible. Results showed that facial expressions were mimicked and influenced trust during the control (conscious) but not during the unconscious (suppressed) condition. Based on these findings, we conclude that the path from facial expressions to mimicry and trust is predominantly conscious. On the other hand, partners' pupil size influenced trust only when this information was presented under suppression. These findings imply that the ability to perceive partners' facial expressions is required to influence facial mimicry and investments, while pupil size can be processed non-consciously. Yet, this study yielded no significant modulation of a pupil mimicry effect on trust in either condition. This result potentially relates to the study reported in **Chapter 5** where we observed that synchrony in not directly visible physiological signals (HR and SCL – autonomic mimicry) implicitly promotes attraction while more explicit facial signals and their mimicry (e.g., the mimicry of smiles – motor mimicry) did not. This finding fits with the view of NMEC that autonomic cues compared to facial expressions influence social behavior via distinct neurophysiological pathways.

To explore the underlying mechanisms of the pupil mimicry-trust link deeper, in **Chapter 7** we tested the causal influence of the subcortical noradrenaline system in the pupil mimicry-trust relationship. In this study, subjects again played several rounds of the trust game while we used transcutaneous (through the skin) vagus nerve stimulation (tVNS) and a luminance manipulation. The tVNS technique is often used to treat epilepsy patients, as it can enhance the release of the inhibitory neurotransmitters GABA and noradrenaline levels in the brain (Chen and Williams, 2012; Dorr and Debonnel, 2006; Follesa et al., 2007; Groves et al., 2005). Because of the increase in these neurotransmitters, intracortical noradrenaline levels should increase, presumably making it easier for the brain to select the appropriate behavioral and physiological response to partners' dilating pupils. Consistent with this idea, results showed that active as compared to sham stimulation decreased trust in partners with static pupil sizes compared to partners with dilating pupils. This finding fostered the theory that tVNS stimulates subcortical circuits and aids the recognition of eye signals (Colzato et al., 2017; Sellaro et al., 2018). However, since we did not observe any effect of tVNS on participants' pupillary responses, the effect of partners' pupils on trust decisions could also be achieved via an alternative system. For instance, the GABAergic system (Boy et al., 2011; Dharmadhikari et al., 2015; Sumner et al., 2010). Taken together, our results supported the theory that the vagal nerve plays a causal role in the recognition of eye signals, although the causal role of the noradrenaline system in pupil mimicry-trust relationship remains inconclusive.

Integration of main findings

In sum, the first section of this dissertation proposed that empathic abilities emerge from a dynamic synchronous activity between two interacting brains. In the NMEC we further proposed two separate neurological pathways explaining how the transition of perceptual inputs builds emotional understanding through synchrony. The following four empirical studies reported in this thesis provided support for the NMEC in the following ways:

(i) We show that spontaneous mimicry occurs on many levels of expression including motor movements, gaze, and physiology.

(ii) We found that mimicry affected pro-social behavior fostering approach (trust and attraction).

(iii) Autonomic mimicry (pupil mimicry) correlates with enhanced activation of social brain regions (ToM) involved in cognitive empathy and perspective taking.

(iv) During real life interactions, although autonomic signals cannot be consciously perceived, autonomic mimicry (e.g. heart-rate synchrony) can explain more in terms of interpersonal attraction than motor mimicry (e.g. facial expression mimicry) that is more under voluntary control.

(v) In line with NMEC, we further demonstrate that autonomic signals (pupil size) can influence trust outside of participants' visual awareness, while facial expressions require conscious perception.

(vi) Finally, we observed that the influence of pupil size on trust decisions becomes enhanced when subcortical structures were transcutaneously stimulated with tVNS.

Overall, the current thesis supported the NMEC theory that the mimicry of autonomic signals subconsciously promotes pro-social behavior. This dissertation, however, also reports some conflicting findings that require discussion. In particular, in **Chapters 5 – 6**, a significant relationship between the autonomic mimicry and pro-social behavior (trust and attraction) was found. These results converge with previous pupil mimicry studies (Kret et al., 2015; Kret & De Dreu, 2017; van Breen et al., 2018; Wehebrink et al., 2018) as well as the view that autonomic mimicry might be a precursor of emotional understanding (Preston & de Waal, 2002). Yet, in subsequent studies **(Chapter 7 and Chapter 8)**, no significant relationship between pupil mimicry and trust was found. The main difference between **Chapter 5 - 6** and **Chapter 7 - 8** is that in the latter studies we used manipulations. An external intrusion of synchrony can be useful as it can help us to disentangle the directionality between synchrony and pro-social behavior. At the same time, physiological signals are outside of voluntary control and that makes it difficult to precisely manipulate them. For instance, in a recent study, Derksen and colleagues (2018) manipulated mimicry with local luminance changes. The stimuli used in this study were unnatural (i.e., gray pupils) and thus different from the black pupil stimuli used in our studies. With these luminance-controlled stimuli, the authors did not observe any pupil mimicry. Interestingly, these authors found that pupil mimicry occurred between members of the same group but not between outgroup – an effect that is difficult to explain by luminance changes. In parallel to this result, multiple prior studies have shown that social context reliably modulates pupil mimicry, including own-versus-partner ethnicity (Kret et al., 2015; Kret & De Dreu, 2017), own-versus-other species (Tomonaga, & Matsuzawa, 2014), or a cooperative-versus-competitive context (van Breen et al., 2018). Together these findings imply that pupil-mimicry can be manipulated also psychologically. It is therefore important to contrast different experimental paradigms to clearly compare under which circumstances the phenomenon in question occurs. While manipulation is common practice in cognitive neuroscience research, a reliable method to manipulate autonomic mimicry has not been definitively established. Until then, the causal link between autonomic mimicry and pro-social behavior will remain largely speculative. Therefore, researchers should be cautious when generalizing results from manipulation of a neurotransmitter system to naturally-occurring differences in the activity of that system.

Further questions and directions

The current dissertation focused on the relationship between mimicry and pro-social behavior. Specifically, we looked at the linkage between pupil mimicry and trust, and between physiological synchrony and attraction. However, since these measures are dependent on correlations, it is not clear whether the link between synchrony and these different pro-social behaviors is caused by similar underlying processes. So, what, if anything, does mimicry really predict? According to the Perception-Action Model (Preston & de Waal, 2002), what different types of pro-social behaviors have in common is empathy (the capacity to relate to others' emotions, thoughts and intentions). From this theoretical perspective, although trust and attraction are different social concepts, both trust and attraction require empathy for people to be able to relate to each other. Thus, in line with previous findings, we argue that if autonomic synchrony is an indirect measure of emotional contagion (as suggested in **Chapter 4 - 5**), which is the building block of empathy. It makes sense that the strength of this synchrony predicts different types of pro-social behaviors (trust, liking and attraction).

Moreover, we proposed that physiological synchrony might be a product of brain-to-brain coupling (Procházková & Kret, 2017). In recent years, researchers have begun to acknowledge that during social interactions peoples' brain responses get coupled (Hasson et al., 2012; Hennenlotter et al., 2009; Stephens et al., 2010). Regardless of the medium (verbal/nonverbal), neurophysiological synchrony has been suggested to improve interpersonal communication. For instance, it has been shown that during verbal communication, the more listeners understand what a speaker is saying, the more closely their brain responses mirror the speaker's brain responses (Stephens et al., 2010). Intriguingly, while normally there is a slight delay in listener's brain response matching up with the speaker's, during extremely high comprehension, the delay in listers' neural response nearly diapered or even preceded the speakers (Stephens et al., 2010). These results demonstrate that when two people' brain responses synchronize well; they start to predict each other's intentions and thereby communicate better. **In other words, for person A to understand person B, person B needs to be able to adapt a similar neurophysiological state. From this perspective, neural/physiological synchrony is not *a result or cause of understanding*. Instead, understanding is a single act performed by two brains.** Similarly, just like a phone that receives a radio signal, converts it into an electrical signal, and sends that signal to a speaker which converts it into sound, neurophysiological synchrony represents the basis on which we understand one another (Hasson et al., 2012). This analogy is important as it implies that interpersonal synchrony could potentially provide insight into why some people are better at communicating than others. Could it be that some people are better at expressing themselves and therefore others synchronize with them more easily? Or, is it that people synchronize with some people but not others? What are the mechanisms that allow a sender's and receiver's physiology to couple and can we interfere that signal? Future studies of synchrony may provide an answer to these questions.

Conclusion

In conclusion, social interactions are highly complex, involving many different affective signals as well as the interaction between different brain regions that contribute to social behavior. This thesis has shown that it is possible to measure different types of mimicry in relation to pro-social behavior. With the use of eye-tracking, physiological measures, brain stimulation, optical illusions, and neuroimaging, we showed that the mimicry of nonverbal signals, even those which are subconscious and outside of voluntary control, can affect trust and attraction. A better understanding of how and why autonomic mimicry modulates pro-social behavior is an endeavor that is sure to stimulate research for many years to come. Considering that there is a whole spectrum of communication channels (verbal, motor, autonomic), I propose that embracing measures of interpersonal synchrony on multiple levels of expression simultaneously during real-life interactions is a promising direction to take to improve our understanding of social capacities among individuals.

Appendices

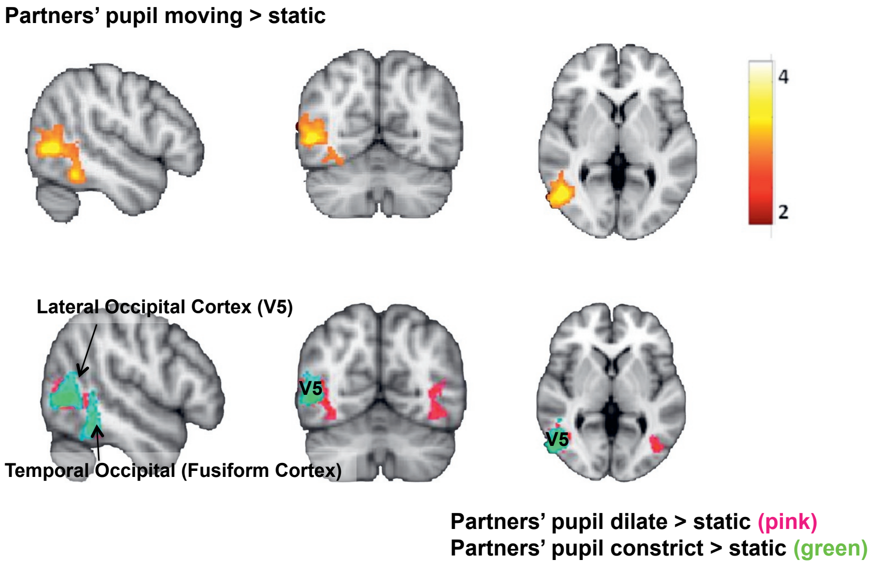
Appendix A

Supplementary Material for Chapter 4

This file includes:

Figure S1

Tables S1 to S12


Partners' pupil moving > static

Partners' pupil dilate > static (pink)
Partners' pupil constrict > static (green)

Supplementary Figure 1I Neural correlates of partners' pupil change. Top figure: The whole-brain analysis contrast compares partner's moving (dilating & constricting) versus static pupils (thresholded at $P < 0.05$ (cluster-level FWE correction with multiple comparisons at 2.3. (n=34)). For the visualization threshold was set at $z = 2 – 4$. Bottom figure: shows the overlap between partner's dilating and partner's constricting pupils.

Neural correlates of partners' pupil change. To determine the effect of pupillary signals on the brain, irrespective of whether subjects mimicked or not, we evaluated the fMRI data acquired during the encoding of partner pupils: constricting, static and dilating conditions. We created the following contrasts: constrict versus static, dilate versus static, and changing versus static (combination of partner dilating and constricting conditions). This analysis revealed that compared to static pupils both partner pupil dilation and constriction were associated with enhanced activity in spatially overlapping right lateral occipital gyrus [50, -62, 2] and temporal occipital fusiform gyrus [52, -44, -6]. The contrast between dilating versus constricting pupils did not result in significant differences. This analysis depicts that processing of partner's dilating and constricting pupil movements share common neural underpinnings in lateral occipital and temporal areas.

Table S1. The effect of partner's pupil on participants' trust

Fixed Factors*	F	Df1	Df2	*p*-value
Corrected Model	38	2	5,933	0.000
Pupil Partner	38	2	5.213	0.000

Random Factors	Estimate	SE	Z	*p*-value
Variance	2.955	0.055	53.93	0.000
Var(intercept)	1.048	0.244	4.288	0.000

Table S2: The effect of partner's pupil on participants' pupil size

Fixed Factors	F	Df1	Df2	*p*-value
Intercept	14.201	11	153,986	0.000
Pupil Partner	1,274	2	153,986	0.280
lin	19,504	1	153,986	0.000
quadr	82,079	1	153,986	0.000
cub	15,234	1	153,986	0.000
Pupil Partner * lin	8,276	2	153,986	0.000
Pupil Partner * quadr	1,923	2	153,986	0.146
Pupil Partner * cub	15,783	2	153,986	0.000

Random Factors	Res. Eff.	Est.	SE	Z	p-value	95% Confidence Interval	
						Lower	Upper
Repeated Measures	AR1	0.255	0.004	64.219	0.000	0.247	0.263
Intercept	Variance	0.015	0.004	3.906	0.000	0.009	0.0026

Table S3: The effect of partner's pupil on participants' trust

Fixed Factors	F	Df1	Df2	*p*-value
Intercept	15.229	5	5,750	0.000
Pupil Partner	32	2	5,750	0.000
Mimicry (yes/no)	19,504	1	5,750	0.312
Pupil Partner*Mimicry	6	2	5,750	0.003

						95% Confidence Interval	
Random Factors	**Res. Eff.**	**Estimat**	**SE**	**Z**	**p-value**	**Lower**	**Upper**
Intercept	Variance	2.954	0.056	53.099	0.000	2.847	3.066
Int. [subject=ID*Run]	Variance	0.0054	0.001	3.297	0.001	0.0029	0.0098

Table S4. Mimicry > no mimicry

Region	BA	Side	Cluster size	x	y	z	Z-Max
1. Occipital pole	18	L	39834	-6	-92	14	5.32
1. Middle Temporal Cortex	37	L		-58	-54	0	5.14
1. Supramarginal Gyrus (TPJp)	39	L		-54	-44	36	5.13
1. Lateral Occipital Cortex	19	L		-38	-74	26	5.13
1. Occipital pole	18	L		-10	-90	16	5.09
1. Lingual Gyrus	18	L		-8	-76	-6	5.08
2. Angular Gyrus (TPJp)	39	R	1184	54	-48	32	5.07
2. Middle Temporal Gyrus	22	R		64	-26	-4	4.86
2. Angular Gyrus (TPJp)	39	R		50	-48	28	4.81
2. Angular Gyrus (TPJp)	39	R		56	-48	26	4.75
2. Parietal Operculum (TPJa)	22	R		52	-34	20	4.74
2. Superior Temporal Gyrus (STS)	22	R		48	-30	-2	4.67

The activation survives whole-brain correction ($p < 0.05$) for multiple comparisons at the cluster level 2.3. (N=34). Locations coordinates are in stereotactic MNI space with 2x2x2 voxel size. The source of anatomical labels: FSL Atlas tools. Subpeaks of the clusters= Z-score; R= right; L = left; BA = Brodmann area.

Table S5. Regions that show heightened activation for mimicry with constricting pupils

Region	BA	Side	Cluster Size	x	y	z	Z-Max
1. Lateral Occipital Gyrus – V5	19	L	13971	-36	-82	-10	6.46
1. Precentral Gyrus	4	L		-34	-18	56	5.74
1. Lateral Occipital Sulcus–V5	19	L		-38	-78	-10	5.62
1. Lateral Occipital Gyrus-V5	19	L		-42	-80	-4	5.59
2. Lateral Occipital Gyrus-V5	19	R	7948	36	-84	-2	6.4
2. Lateral Occipital gyrus	19	R		36	-66	62	6.4
2. Fusiform Gyrus	20	R		40	-38	-22	5.69
3. Precentral Gyrus	44	R	3020	44	8	30	5.76
3. a. Insula	47	R		32	28	0	5.76
3. Precentral Gyrus	44	R		44	10	30	5.57
3. Middle Frontal Sulcus	6	R		32	-2	50	4.62
4. Insula	48	L	768	-36	18	2	5.71
4. a. Insula	47	L		-32	26	-2	5.12

The activation survives whole-brain correction (p 0.05) for multiple comparisons at the cluster level 2.3. (n=34). Locations coordinates are in stereotactic MNI space with 2x2x2 voxel size. The source of anatomical labels: FSL Atlas tools. Subpeaks of the clusters= Z-score; R= right; L = left; BA = Brodmann area.

Table S6. Regions that show heightened activation for mimicry with dilating pupils

Region	BA	Side	Cluster Size	x	y	z	Z-Max
1. Occipital temporal Gyrus	37	R	763	50	-62	-14	6.46
1. Lateral Occipital Gyrus–V5	19	R		46	-76	-2	5.74
1. Lateral Occipital Gyrus–V5	19	R		44	-82	-14	5.62
1. Precentral Gyrus	3	L		-36	-18	62	5.59
1. Paracingulate Gyrus	32	R		8	26	36	6.4

The activation survives whole-brain correction (p 0.05) for multiple comparisons at the cluster level 2.3. (n=34). Locations coordinates are in stereotactic MNI space with 2x2x2 voxel size. The source of anatomical labels : FSL Atlas tools. Subpeaks of the clusters= Z-score; R= right; L = left; BA = Brodmann area.

Table S7: TOM and Threat Masks' links for download

Network	Studies	Date of Download	Link to download
TOM	140	10/03/2015	http://neurosynth.org/analyses/terms/theory%20mind
Threat	170	15/03/2015	http://neurosynth.org/analyses/terms/threat/

Table S8. Partners' Pupils Constricting > Static

Region	BA	Side	Cluster Size	x	y	z	Z-Max
1. Lateral Occipital Gyrus –V5	37	R	868	50	-62	2	4.56
1. Lateral Occipital Gyrus –V5	37	R		52	-70	0	4.12
1. Lateral Occipital Gyrus –V5	37	R		58	-70	0	4.1
1. Inferior Temoral Gyrus (ITG)	37	R		48	-46	-18	3.65
1. Middle Temoral Gyrus	37	R		52	-44	-6	3.26
1. Middle Temoral Gyrus	37	R		46	-60	14	3.17

The activation survives whole-brain correction ($p < 0.05$) for multiple comparisons at the cluster level 2.3. (n=34). Locations coordinates are in stereotactic MNI space with 2x2x2 voxel size. The source of anatomical labels: FSL Atlas tools. Subpeaks of the clusters= Z-score; R= right; L = left; BA = Brodmann area.

Table S9. Partners' Pupils Dilating > Static

Region	BA	Side	Cluster Size	x	y	z	Z-Max
1. Lateral Occipital Gyrus –V5	37	R	1152	50	-62	2	2
1. Lateral Occipital Gyrus –V5	37	R		52	-70	0	-16
1. Lateral Occipital Gyrus –V5	37	R		58	-70	0	8
1. Lateral Occipital Gyrus –V5	37	R		48	-46	-18	12
1. Lateral Occipital Gyrus –V5	37	R		52	-44	-6	2
2. Temporal occipital (Fusiform Gyrus)	37	L	556	42	-50	-14	-14
2. Lateral occipital sulcus	19	L		-40	-68	8	3.68
2. Lateral Occipital Gyrus –V5	19	L		-40	-70	-6	3.16
2. Lateral Occipital Gyrus –V5	19	L		-42	-58	8	3.15
2. Lateral Occipital Gyrus –V5	19	L		-52	-66	12	2.89
2. Lateral Occipital Gyrus –V5	37	L		-44	-62	-10	2.88

The activation survives whole-brain correction ($p < 0.05$) for multiple comparisons at the cluster level 2.3. (n=34). Locations coordinates are in stereotactic MNI space with 2x2x2 voxel size. The source of anatomical labels: FSL Atlas tools. Subpeaks of the clusters= Z-score; R= right; L = left; BA = Brodmann area.

Table S10. Partners' Pupil Changing > Static

Region	BA	Side	Cluster Size	x	y	z	Z-Max
1. Lateral Occipital Gyrus –V5	37	R	1419	50	-62	2	4.75
1. Inferior Temoral Gyrus (ITG)	37	R		48	-46	-18	4.22
1. Lateral Occipital Cortex	37	R		60	-70	0	3.99
1. Lateral Occipital Gyrus –V5	39	R		46	-60	14	3.63
1. Temporal Occipital (Fusiform Gyrus)	37	R		42	-50	-14	3.54
1. Middle Temoral Gyrus	37	R		52	-44	-6	3.36

*The activation survives whole-brain correction ($p < 0.05$) for multiple comparisons at the cluster level 2.3. (n=34). Locations coordinates are in stereotactic MNI space with 2x2x2 voxel size. The source of anatomical labels: FSL Atlas tools. Subpeaks of the clusters= Z-score; R= right; L = left; BA = Brodmann area.

Table S11: The subjects' sex, age and questionnaire scores

Participants'	N	Min	Max	Mean	Std.
BDI	36	0	18	4,08	3,988
State	27	36	57	46,30	4,445
Trait	35	43	56	48,66	3,412
EC	40	0	6,57	4,686	1,275
PT	40	0	6,71	4,814	1,203
LSAS Fear	40	0	1,42	0,519	0,334
LSAS Avoid	40	0	1,25	0,486	0,308

Characteristics of subjects. The average score of the BDI questionnaire was 4, 08 which means that the group has minimal depression (Beck, Guth, Steer, & Ball, 1997). The average STAI score was 46,30 and 48,6 while the cut-off score for anxiety is 54-55 (Kvaal, Ulstein, Nordhus, & Engedal, 2005), therefore, we can conclude that the group is not anxious. For the Interpersonal Reactivity Index (IRI), the average score per question is among 3.5 (the half of the seven subscales). This group has an average of 4.68 per empathic concern (EC) and 4,8 for perspective taking (PT), suggesting that participants were empathetic towards other people. The average score for the LSAS is 0.5, concluding that the group does not have any fear or avoidance. BDI = Beck Depression Inventory, State & Trait = two subscales of State-Trait Anxiety Inventory, LSAS = Liebowitz Social Anxiety Scale.

Table S12. Localizers

TOM-Localizer		Threat-Localizer	
1. TOM story	**1. Photography story**	**1. Threatening story**	**1.Non-threatening story**
Larry chose a debated topic for his class paper due on Friday. The news on Thursday indicated that the debate had been solved but Larry never read it.	A large oak tree stood in front of City Hall from the time the building was built. Last year the tree fell down and was replaced by a stone fountain.	Imagine the following situation: At night on the way home, you decide to take a shortcut through the dark park. From the middle of the park, a man with a knife approaches you. You run for your life.	Imagine the following situation: You are watching an animal documentary on TV. The doorbell rings. Your neighbour is at the door and asks whether you have some sugar for her. You go to kitchen to get it for her.
2. Question	**2. Question**	**2. Question**	**2. Question**
When Larry writes his paper he thinks the debate has been solved.	An antique drawing of City Hall shows a fountain in front.	The situation is threatening	The situation is threatening
3. Answer	**3. Answer**	**3. Answer**	**3. Answer**
True/False	True/False	True/False	True/False

Localizer tasks. Two localizer tasks were performed to map TOM and threat-related networks. The inclusion masks derived from the localizers consisted thus of voxels that showed a significant difference between conditions where participants had to use TOM or had to think about a threatening event as compared to a control condition. Scan settings was the same as for the trust-game task **(Methods, fMRI data acquisition**). The threat and TOM localizers were matched in terms of the number of words they contained. Both localizers lasted 8 minutes and their order was counter-balanced across participants.

Appendix B

Supplementary Material for Chapter 5

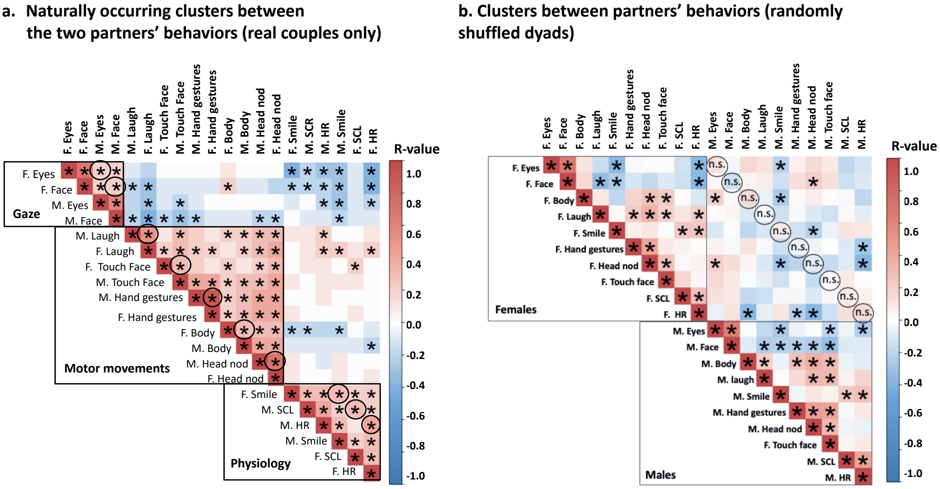
This file includes:

Figure S1 to S3

Tables S1 to S10

Quantification of physiological synchrony

Figure S1 shows that while in real couples we found significant associations in expressions between male and female participants, in randomly paired couples, significant associations were only formed within subjects.



a. Naturally occurring clusters between the two partners' behaviors (real couples only)

b. Clusters between partners' behaviors (randomly shuffled dyads)

Figure S1. Correlation tables summarizing the associations between males and females and within-subject correlations in participants' expressions, fixations and physiology for three interaction time periods (based on Spearman's rank – order correlations, $N = 162$). The columns of the correlation matrix are placed according to the hierarchical clustering with similar values near each other. F = females, M = males. HR = heart rate, SCL = skin conductance level. **(a) Real couples:** The black boxes framed around naturally occurring clusters demonstrate that synchrony occurred on all three levels of expressions including males' and females' gaze reciprocity, expression mimicry and physiological synchrony. The circles represent ten types of synchrony including: smiles, laughs, head nods, hand gestures, face touching, eye contact, face-to-face gaze, body gaze, heart rate, and skin conductance level (all $\rho > 0.28$, $p < 0.05$). **(b) Randomly matched couples:** The heat map shows that in randomly paired couples the significant associations were almost exclusively formed within subjects, while in real couples the behavior clustered also between male and female participants, we used the FDR Benjamini-Hochberg's p-value < 0.05 to define significance (Benjamini and Hochberg, 1995).

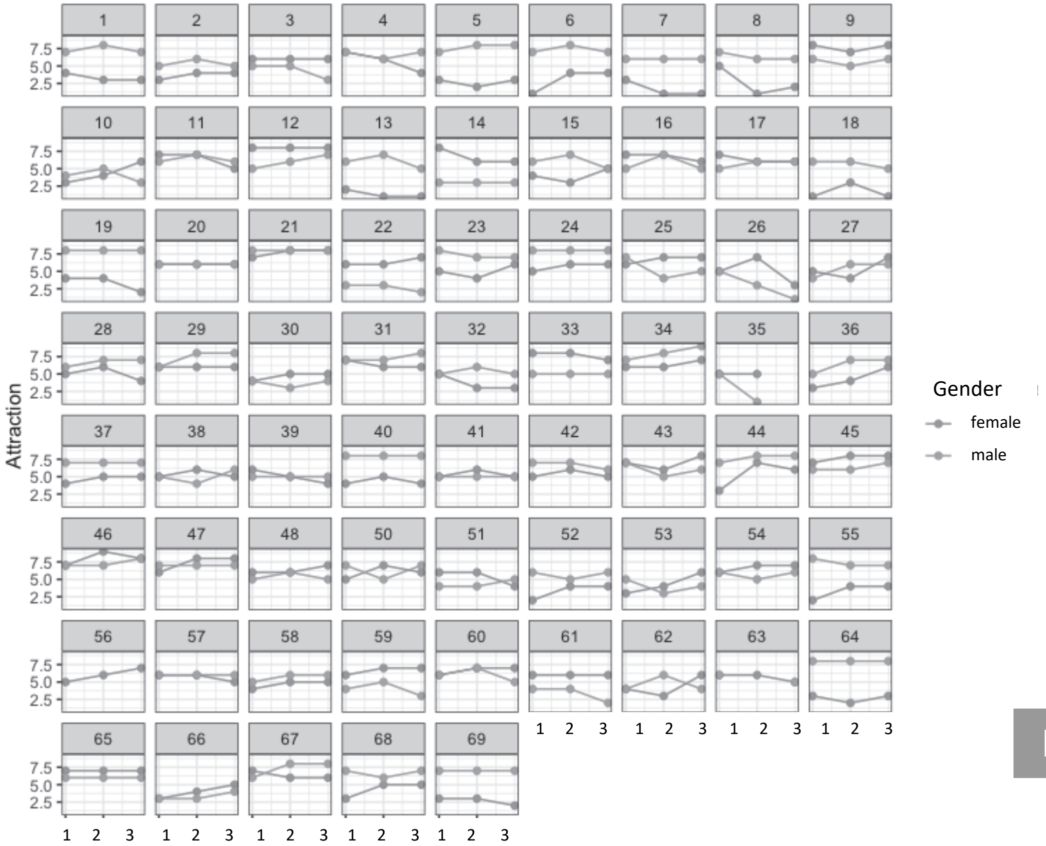


Figure S2. These line graphs provide an example of how attraction changed over time. Time: 1 = first impression, 2 = second interaction, 3 = third interaction. The rating scale was 0 – 9.

Individuals' expressions

During couples' dating interactions, we observed gender differences in naturally occurring expressions. Specifically, the results obtained from a Multivariate Multilevel linear mixed model (F (11, 98) = 4.06, *p* < 0.0001; Pillai's Trace = 0.34, Partial Eta = 0.34) indicated that females were significantly more expressive than males: females smiled, nodded and touched their face more frequently than males did (all *p*s < 0.01, **Figure S2**). Males, on the other hand, stared at their female partner more; they fixated at the female's head and eyes significantly longer than females looked at them (all *p*s < 0.01), while females had a tendency to look around and fixate longer at the background than males did (*p* = 0.025). Additionally, females' heart rate (F (1, 108) = 5.39, *p* = 0.002) and skin conductance level (F (1, 108) = 9.68, *p* < 0.0001) were higher than males' (Fig. 2) and females also reported to feel more "aroused" and less self-confident than men (all *p*s < 0.01). Together these data suggest that during a date, males' and females' behavior and physiology differs.

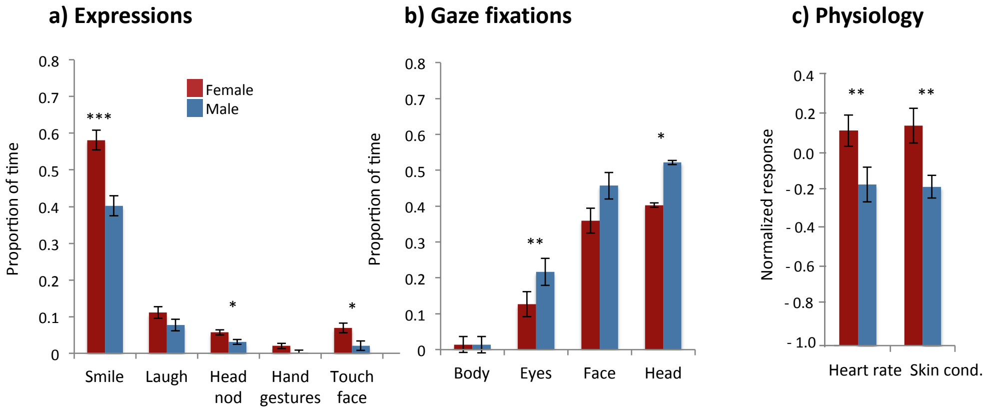


Figure S3. Bar graphs represent gender differences in the proportion of time males and females displayed specific **(a)** expressions, **(b)** gazed at specific areas of interest and **(c)** average heart rate (HR) and skin conductance responses (SCR) across the three interaction types; physiological responses were normalized by baseline correction and z-transformation. Significance was defined using FDR 0.05. All *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, N = 54 couples, error bars: ± SE.

Table S1 shows synchrony associations (focusing on the circles in Figure 1) within real dating partners compared to randomly matched pairs. Significant evidence was found for seven types of synchrony in: smiles, laughs, head nods, hand gestures, face-to-face gaze, heart rate, and skin conductance. There is no significant difference in touching face, body gaze and eye contact fixations between true couples and randomly matched couples.

Table S1. Correlation comparisons between true couple and randomly matched couples

	True Male	Random Male	Fisher's Z	*p*
Female's Eyes	0.23	0.13	0.99	0.31
Female's Face	0.22	-0.14	3.26	**0.00**
Female's Body	0.28	0.15	1.24	0.21
Female's Laugh	0.50	-0.02	5.20	**0.00**
Female's Smile	0.31	0.07	2.23	**0.02**
Female's Hand gestures	0.87	-0.04	12.11	**0.00**
Female's Head nod	0.66	-0.07	7.71	**0.00**
Female's Touch Face	0.27	0.11	1.53	0.12
Female's Skin conductance	0.32	0.09	2.13	**0.03**
Female's Heart rate	0.36	0.16	2.01	**0.04**

Table S2 summarizes results of the Multilevel linear mixed models where we investigated how different types of interpersonal synchronies impact on participant’s attraction ratings (0-9). The multilevel model had following structure: three time points (Level 1) nested in participants (Level 2). We included all 7 synchrony predictors including synchrony in (i) smiles, (ii) laughs, (iii) head nods, (iv) hand gestures, (v) face-to-face, (vi) heart rate, and (vii) skin conductance. The full model further included factors of gender, time **(first impression, first interaction, second interaction),** the type of interaction (first impression, verbal, nonverbal), the order of interaction (verbal/nonverbal first) and two-way interactions between the type of interaction * and the type of synchrony (smiles, laughs, head nods, hand gestures, eye-to-eye, heart rate, and skin conductance). The final model was selected with a backward stepwise selection of fixed effects. The VIF values of the full and final were all smaller than 4 showing that multicollinearity did not influence our results.

Table S2. The Summary of the Full Multilevel linear mixed model Predicting Attraction Based on Synchrony Measures, gender, time, the type of interaction, the order of interaction and interactions between the type of interaction * synchrony

	Attraction			
Predictors	F	df1	df2	*p*
Intercept	1.616	19	285	**.055**
Gender (0 = female, 1 = male)	8.365	1	285	**.004**
Time	2.477	2	285	.086
Interaction type (0 = nonverbal/ 1 = verbal)	.330	1	285	.566
Verbal interaction first (0 = no, 1 = yes)	.563	1	285	.454
SCL synchrony	8.045	1	285	**.005**
HR synchrony	3.889	1	285	**.050**
Face-to-face contact	.411	1	285	.522
Smile mimicry	.322	1	285	.571
Laugh mimicry	.066	1	285	.797
Nodding mimicry	.252	1	285	.616
Gestures mimicry	.001	1	285	.978
Interaction type * SCL synchrony	1.189	1	285	.276
Interaction type * HR synchrony	.320	1	285	.572
Interaction type * Face-to-face contact	.304	1	285	.582
Interaction type * Smile mimicry	.006	1	285	.939
Interaction type * Laugh mimicry	.271	1	285	.603
Interaction type * Nodding mimicry	.078	1	285	.780
Interaction type * Gestures mimicry	.001	1	305	.987
Residual Effect	Estimate	Std. Error	Z	*p*
Variance	.759	.075	10.150	**.000**
Var (Intercept) Participant	2.142	.333	6.427	**.000**

Note: Time had three time points: first impression, first interaction, second interaction.

Table S3. The Summary of the Final Multilevel linear mixed model Predicting Attraction Based on Synchrony Measures

		Attraction		
Predictors	F	df1	df2	*p*
Intercept	4.954	5	298	**.000**
Gender	8.389	1	298	**.004**
Time	4.330	2	298	**.014**
SCL synchrony	7.332	1	298	**.007**
HR synchrony	5.498	1	298	**.020**
Random Effect	Estimate	Std. Error	Z	*p*
Variance	.745	.072	10.304	**.000**
Var (Intercept) Participant	2.154	.331	6.510	**.000**

Note: Time had three time points: first impression, first interaction, second interaction.

Control analysis – Does within or between dyad synchrony predict attraction?

In the previously described model, the variables for heart rate and skin conductance level synchrony included within- and between-dyad level variation in synchrony. It is therefore unclear whether couples that are highly attracted to each other synchronize more than those who are not (i.e., between-dyad effect), or whether changes in physiological synchrony over time predict attraction changes (i.e., within-dyad effect). To disentangle the two types of variations, we computed two variables: (1) Between-dyad SCL synchrony: the averaged synchrony level across time points per dyad, and (2) Within-dyad SCL synchrony: the deviation in synchrony level (per time point) from the dyad's averaged synchrony level (within-dyad centering). Both variables were included in a Multilevel linear mixed model with a two-level structure (three-time points (Level 1), nested in participants (Level 2). We also included a random intercept effect (across participants) and a random slope for Time, but not allowing a correlation between both random effects. Time variable was specified on continuous scale (as participants displayed (more or less) linear trajectories over time in attraction. The slope for time indicated the evolution of attraction over time.

Table S4. The Summary of the Final Multilevel linear mixed model Predicting Attraction Based on Synchrony Measures reflecting between-dyad variations (dyad's overall level of synchrony), and within-dyad variation (changes in synchrony level over time within each dyad)

	Attraction			
Predictors	F	df1	df2	*p*
(Intercept)	3.523	7	296	**.001**
Gender	8.240	1	296	**.004**
Time	4.151	2	296	**.017**
Within-dyad SCL synchrony	6.236	1	296	**.013**
Between-dyad SCL synchrony	1.013	1	296	.315
Within-dyad HR synchrony	4.679	1	296	**.031**
Between-dyad HR synchrony	.824	1	296	.365
Random Effect	Estimate	Std. Error	Z	*p*
Variance	.762	.077	9.957	**.000**
Var (Intercept) Participant	2.178	.349	6.250	**.000**

Note: Time had three time points: first impression, first interaction, second interaction.

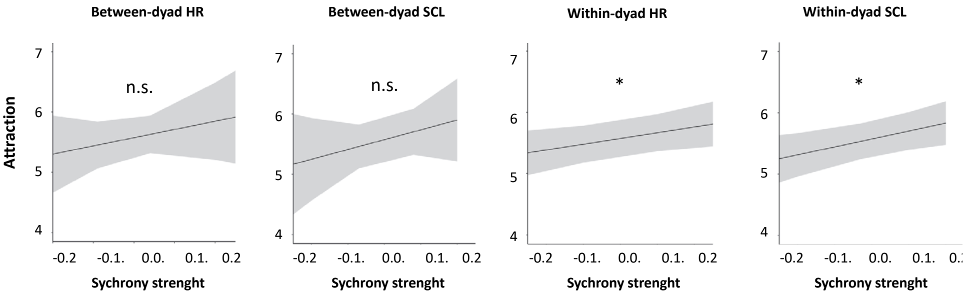


Figure S4: The line graphs represent slopes extracted from our Multilevel linear mixed model predicting attraction based on synchrony measures reflecting between-dyad variations and within-dyad variation (Table S4). The shaded areas represent 95% confidence intervals. Attraction based on Between-dyad HR synchrony [β = 1.34, SE = 1.47, CI (-1.56, 4.25), *p* = 0.365] and Between-dyad SCL synchrony [β = 1.63, SE = 1.62, CI (-0.56, 4.83), *p* = 0.315], Within-dyad HR synchrony [β = 0.96, SE = 0.44, CI (0.08, 1.83), *p* = 0.031] and Within-dyad SCL synchrony [β = 1.41, SE = 0.56, (CI 0.30, 2.53), *p* = 0.013]. The shaded areas represent 95% confidence intervals.

Control analysis – does arousal predict attraction?

In the current study we observed that synchrony in skin conductance level and heart rate could predict attraction. One possible confound is that it is not the synchrony on the dyadic level, but the arousal responses of the two individuals that drive these findings. For example, skin conductance levels might rise if a participant feels attracted to his/her partner. Consequently, the responses of the two participants would highly correlate reflecting the individuals' decisions rather than an interpersonal process. To test this, we conducted a control analysis where attraction was regressed against the participants' skin conductance (baseline corrected) heart rate and skin conductance levels for each interaction. For the skin conductance level, we first standardized the responses per participant and then computed the mean skin conductance and heart rate level per each interaction (first impression, verbal, nonverbal). Consistent with the model of the main analysis, we included gender and time as a control variable including individual as a random intercept effect. The model summary is shown in Table S4 which shows that attraction could not be predicted by the arousal responses of the two individuals.

Table S5. Summary of Multilevel linear mixed model with the Heart Rate (HR) and Skin Conductance Level (SCL) Predicting Participants' Attraction Ratings

	Attraction			
Predictors	F	df1	df2	*p*
Intercept	2.383	5	298	.039
Gender	8.269	1	298	**.004**
Time	1.637	2	298	.196
SCL level	.036	1	298	.850
HR level	.003	1	298	.955
Random Effect	Estimate	Std. Error	Z	*p*
Variance	.802	.081	9.951	**.000**
Var (Intercept) Participant	2.173	.347	6.258	**.000**

Note. SC = Skin Conductance; HR = Heart Rate.

Control analysis – is attraction a valid outcome variable?

One may wonder whether we really measured attraction in this study or possibly something else. To control for this possibility, throughout the experiment we also collected other ratings including trust, liking, feeling of connection and click. We also asked whether subjects felt awkward or anxious **(Table S3)**. Theses scores were then compared with attraction ratings **(Part 1)** and participants choice to go for another date (yes/not) with the partner **(Part 2)**.

Table S6a. Descriptive Statistics of Participants' Ratings

	N	Minimum	Maximum	Mean	Std. Dev.
	Self-ratings				
Valence	362	2	9	6.01	1.632
Arousal	362	1	9	5.94	1.757
Self-confident	397	1	9	5.65	1.467
Awkward	395	1	9	4.80	2.197
Shy	398	1	9	4.34	2.003
	Partner ratings				
Trustworthy	408	1	9	6.87	1.438
Intelligent	409	2	9	6.59	1.318
Funny	409	1	9	5.96	1.611
Attractive	408	1	9	5.57	1.711
	Self - Partner ratings				
Similar personality	408	1	8	4.86	1.712
Connection	411	1	8	4.48	1.838
Click	404	1	9	4.38	1.871
Sex. Attraction	410	1	9	3.83	1.945

The scale for all ratings ranged between 0 – 9, Descriptive statistics are based on 138 subjects (*N* = 69 dyads) rating their partner three times (after first impression, verbal and nonverbal interaction). Valence = higher number represents positive valence. Arousal = higher number represents more arousal levels.

Control analysis – is attraction a valid outcome variable? (Part 1)

To identify the common dimensions of ratings, we took all thirteen ratings and submitted them to a principal component analysis (PCA), using the Oblimin with Kaiser Normalization rotation method **Table S4)**. The first principal component (PC) accounted for 37.7% of the variance and the second PC accounted for 17.2% of the variance of the mean trait judgments. All positive judgments (e.g., attractive, funny, similar in personality, feeling of click, connection) had positive loadings, and all negative feelings (e.g., awkward, shy, low self-confidence) had negative loadings on the first PC (Table S4), suggesting that it can be interpreted as valence evaluation.

Table S6b. Principal Component Analysis: Loadings of Participants' Ratings

	Component 1 (Positive)	Component 2 (Negative)
Click	**.876**	-.035
Connection	**.861**	-.003
Sexual Attraction	**.826**	.070
Attractive	**.775**	.089
Funny	**.720**	.094
Similar personality	**.699**	.011
Intelligent	.562	.002
Trustworthy	.514	-.104
Valence	.483	-.285
Arousal	.235	.169
Awkward	-.049	**.880**
Shy	.183	**.851**
Self-confident	.092	**-.751**

Note. Self-confidence is negatively loaded to feelings of awkwardness and shyness because more confident people were less awkward and shy, they felt. The PCA was based on N = 344 valid cases.

Control analysis – is attraction valid outcome variable? (Part 2)

Multilevel binary logistic regression investigates how different types of ratings predict participants' choice to go for another date (yes/ no, coded 1 and 0 respectively). The multilevel model had the following structure: three time points (Level 1) nested in participants (Level 2). We included all 13 ratings (Table ST4) as predictors. The results showed that the model was highly predictive of participants' choice to date their partner again (Overall percentage reached 99.7% accuracy). Among all the ratings only positive affect and attraction predicted participants decisions significantly **(Table S5)**, whereas attraction ratings explained the most variance in participants' binary decision to date their partner (yes/no).

Table S7. Summary of Multilevel Binary Logistic Regression

			Date partner (yes/no)	
Predictors	F	df1	df2	*p*
Intercept	2.469	13	317	**.003**
Valence	3.936	1	317	**.048**
Arousal	.049	1	317	.825
Shy	.030	1	317	.863
Awkward	.207	1	317	.650
Self-confident	.964	1	317	.327
Attractive	6.331	1	317	**.012**
Funny	.096	1	317	.757
Intelligent	1.088	1	317	.298
Trustworthy	.565	1	317	.453
Similar personality	.025	1	317	.876
Connection	.536	1	317	.464
Sex. Attraction	.591	1	317	.443
Click	1.332	1	317	.249
Random Effect	Estimate	Std. Error	Z	*p*
Var (Intercept)	.117	.156	.749	.454

Control analysis – do partner’s expressions predict attraction?

We conducted a follow-up control analyses to test whether specific behavior enacted by one individual promotes attraction in the other individual. In the Multilevel linear mixed model, we used five predictors. This time, instead of synchrony measures, we used the proportion of time a participant displayed specific expressions (smiling, laughing, head shaking, hand gestures) or gaze fixations (looking at partners’ face) as predictors of partner’s attraction ratings (0 - 9). The full model further included factors of gender, time **(first impression, first interaction, second interaction)** and the interaction between gender * expression as additional predictors. The multilevel model had following structure: three time points (Level 1) nested in participants (Level 2). The VIF values of the full and final were all smaller than 4 showing that multicollinearity did not influence our results. The results of Multilevel mixed effects models revealed that none of the directly visible signals such as participants’ expressions and gaze fixations were significant predictors of male’s or female’s partner attraction scores.

Table 8. Summary of Multilevel linear mixed model with Participants' Visible Expressions Predicting Partners' Attraction Ratings

	Partners' Attraction			
Predictors	*F*	*df1*	*df2*	*p*
Intercept	1.523	13	310	.108
Gender	6.542	1	310	**.011**
Time	1.467	2	310	.232
Face-to-face contact	1.215	1	310	.271
Smile	.001	1	310	.980
Laugh	.337	1	310	.562
Nod	.030	1	310	.863
Gestures	.346	1	310	.557
Gender * Face-to-face contact	.506	1	310	.477
Gender * Smile	.507	1	310	.477
Gender * Laugh	1.365	1	310	.244
Gender * Nod	.014	1	310	.905
Gender * Gestures	.706	1	310	.402
Random Effect	Estimate	Std. Error	Z	*p*
Variance	2.106	.186	11.347	**.000**
Var (Intercept)	.865	.243	3.556	**.000**

Table S9. Participants' Demographics and Other Descriptive Statistics

	Female			Male			
Characteristics	N	M	SD	N	M	SD	*t*
Age	69.00	23.45	4.18	69.00	25.71	4.64	-2.96 **
Weight	68.00	65.84	10.34	67.00	78.06	8.70	-7.42 ***
Height	69.00	171.90	6.98	68.00	182.51	6.44	-9.24 ***
Number of alcohol drinks	68.00	0.01	0.55	68.00	0.58	0.55	-3.13 **
How much commitment (0-9)	64.00	5.92	1.64	65.00	5.72	1.43	0.73
Time single in months	62.00	38.69	65.31	59.00	37.03	65.45	0.14

	Average per cent	
Education	Female (N = 69)	Male (N = 69)
VMBO	0.02	0.00
HAVO	0.04	0.02
VWO	0.02	0.15
MBO	0.13	0.08
HBO	0.30	0.38
WO	0.47	0.38

Note: *** $p < .001$, VMBO: the lowest completed high-school level, WO: the highest level (scientific education, Bachelor or Master degree). How much commitment is on 0-9 scale.

Table S10. Comparisons (t-test) variables by sex: Liebowitz Social Anxiety Scale (LSAS), Positive and Negative Affect Schedule (Watson et al., 1988)(Watson et al., 1988)(Watson et al., 1988)(Watson et al., 1988) (PANAS) and Sexual Desire Inventory (SDI). The SDI is comprised of 11 items about various sexual behaviors, on a 5-point Likert scale. The total score on the SDI is the sum of all 11 items, with higher scores reflecting a higher sexual desire. The LSAS is comprised of two subscales: performance and social interaction. The 24 questions ultimately lead to six subscale scores: total fear, fear of social interaction, fear of performance, total avoidance, avoidance of social interaction and avoidance of performance. The statements had to be answered on a 4-point scale (0 = not at all, 4 = totally). The PANAS: consists of two 10-item mood scales, measuring positive affect (PA) and negative affect (NA). Participants are asked to rate their experience with a certain emotion on a 5-point scale (1 = very slightly or not at all, 5 = very much).

Table S10. Comparisons (t-test) variables by sex

	Female		Male			
Variable	M	SD	M	SD	*t*	*p*
SDI	4.25	1.47	4.68	0.93	-1.692	0.094
LSAS Fear	0.46	0.49	0.45	0.64	0.099	0.921
LSAS avoidance	0.77	0.67	0.81	0.69	-0.271	0.787
PANAS negative	1.69	0.45	1.72	.40	-.280	0.780
PANAS positive	3.20	0.56	3.41	.53	-1.853	0.067
Trust baseline	8.10	0.94	7.75	1.02	2.084	**0.039**
Trust overall	6.85	1.56	6.89	1.29	.186	0.817

Note: Trust baseline measures how trustworthy a potential partner should be, trust overall measures average trust across three interaction periods.

Quantifying expressive mimicry and eye fixation synchrony.

Mimicry is defined broadly as ‘doing what others are doing’. While some studies are very loose on their definition of mimicry; for instance, mimicry might be defined as any movement following the other person's movement (Fujiwara and Daibo, 2016; Tschacher et al., 2014). We adopt a stricter definition of mimicry where mimicry occurs when a person A directly does the same expression as person B (LaFrance, 1979; LaFrance and Broadbent, 1976). The advantage of this stricter definition is that in contrast to movement synchrony, it can be easily operationalized. Indeed, the observation of movement echo proved to be difficult to define and often leads to inconsistent results (Grammer et al., 1998). Motor movements (smiling, laughing, head nod, hand gestures, face touching) were coded by four independent raters (two raters for males and two for females). Eye fixations falling on pre-defined areas of interests were automatically recorded using Tobii Pro Glasses 2. Both emotional expression or eye fixation were classified per tenths of seconds as binary variable (1 for occurrence, 0 for no occurrence). We then quantified mimicry for each dyad and interaction by calculating the proportion of time both participants' directly reciprocated expressions (smiling, laughing, head nod, hand gestures, face touching) and gaze fixations (looking at partners' head, eyes, face, body). The proportion of mimicry was calculated for each condition (the first impression, verbal and nonverbal interaction) resulting in N dyads * 3 results * for mimicry in smiles, laughs, head nods, hand gestures, eye-to-eye fixations.

Quantification of physiological synchrony

Two methods that take non-stationarity into account are lagged windowed cross-correlation (Boker et al., 2002) and recurrence quantification analysis (Gates and Liu, 2016). The latter method is frequently used which has the advantage of having very few assumptions. However, the disadvantage is that it determines synchrony on a binary scale of moments being classified as either synchronized or not. The former method, albeit constraint by more assumptions, has the advantage of differentiating the degree of synchronization by quantifying it on a continuous (correlation) scale. Additionally, we feel that windowed cross-correlation is more intuitive to interpret. Consequently, we decided to apply this method which provides measures of the strength of synchrony. The objective of the lagged windows-cross correlations analysis (Boker et al., 2002) is to calculate the strength of association between two time series while taking into account the non-stationarity of the signals and the lag between responses, that is, to consider the dynamics of a dyadic interaction. Specifically, the time series are segmented into smaller intervals, calculating the cross-correlation for each segment. This allows the means and variances to differ between segments accounting for non-stationarity. This is important as the level of synchrony may change during the experiment, sometimes having moments of strong synchronization while during other times responding less strong to one another. Additionally, as the strength of association between two time points may differ depending on how far apart they are from each other, the segments are moved along the time series by an increment such that two adjacent segments overlap. Hence, segmenting the time series into smaller intervals and partially overlapping these intervals while moving along the time series provides a better estimate of the local strength of association between the physiological signals of two participants.

Besides the dynamics in the strength of synchronization during the course of the experiment, participants differ in how fast one might respond to a certain event or the other person. In other words, participants might not always be perfectly “in sync” whereby one participant might sometimes respond to the other person or vice versa introducing a delay between the responses of two individuals. To account for this, for each segment, the signals of the two participants are lagged in relation to one another. Specifically, the signal of participant 1 is kept constant while the signal of participant 2 is shifted more and more by a specified lag increment until a maximum lag is reached. Next, the same procedure is performed the other way around with participant 2 being kept constant. The maximum lag determines what is still considered synchrony. For example, if the maximum lag is four seconds, responses from two participants that are four seconds apart from each other are still considered synchronized. On the other hand, if one participant reacts to a certain event and the other participant shows a response 5 seconds later, it is not considered a response to the same event anymore and therefore does not count as synchrony. Based on this approach, there are four parameters that need to be determined: (1) the length of each segment, referred to the window size w_{max}; (2) the increment with which the segments are moved along the time series, the window increment w_{inc}; (3) the maximum with which two segments can be lagged from one another, the maximum lag τ_{max}; and (4) the increment with which two segments are lagged from each other, the lag increment τ_{inc}. We determined the parameters following an extensive process by comparing previous studies using similar statistical methods, by looking at what is physiologically plausible given the time course of the physiological signals and by employing a data-driven bottom-up approach where we investigated how changing the parameters affected the outcomes using a different dataset. As expected, the absolute values of the synchrony measures varied depending on the parameters, but as supported by (McAssey et al., 2013), the relative results were not affected (e.g. a dyadic manifesting relatively high synchrony showed such tendency for the different parameters). Based on these three factors, we set the parameters as follows: the window size was 8 seconds (160 samples), the window increment was 2 seconds (40 samples), the maximum lag was 4 seconds (80 samples) and the lag increment was 100ms (2 samples).

Calculating the cross correlations of each lag for each window segment generates a result matrix with each row representing one window segment and each column indicating a lag. The middle column represents the cross-correlation with a lag of zero, while the first and last column contain the cross-correlations for the maximum lag of participant 1 and 2. Hence, the number of columns in the result matrix is $(2^* \tau_{max} / \tau_{inc}) + 1$. The number of rows is given by $(N - w_{max} - \tau_{max})/ w_{inc}$, with N being the number of observations in the whole time series. Based on this result matrix, a so-called peak picking algorithm is applied. For each segment (i.e., each row in the matrix), the maximum cross-correlation across the lags is detected closest to the zero-lag (i.e., across all columns in a given row). If that maximum correlation is preceded and followed by smaller correlations, it is marked as a peak. For example, if participant 2 synchronizes with participant 1 with a lag of one second, the cross-correlations will become higher the closer the segments from the two participants are shifted towards the point where they are one second apart from each other. When the two signals are lagged by exactly one second the cross-correlation is highest (the peak). If the signals are lagged further away from each other, the cross-correlation decreases again. If, however, a peak cannot be detected, the algorithm assigns a missing value for that segment. This might be the case, for example, if people do not respond to an event or to each other (e.g., both participants wait and do nothing). The peak picking algorithm outputs a matrix with two columns, containing the value of the maximum cross-correlation (the peak) and the corresponding lag at which the peak cross-correlation is detected. The output has the same number of rows as the result matrix as it searches for a peak cross-correlation for each window segment. Both the windowed cross-correlations and the peak picking algorithm were conducted 6 times per dyad, once for the heart rate responses and once for the skin conductance responses for each condition (the first impression, verbal and nonverbal interaction) resulting in 54 dyads * 6 result and peak picking matrices. Finally, the mean cross-correlations of all window segments were calculated for both physiological measures for each condition per dyad.

Appendix C

Supplementary Material for Chapter 6

This file includes:

Figure S1 to S2

Tables S1 to S8

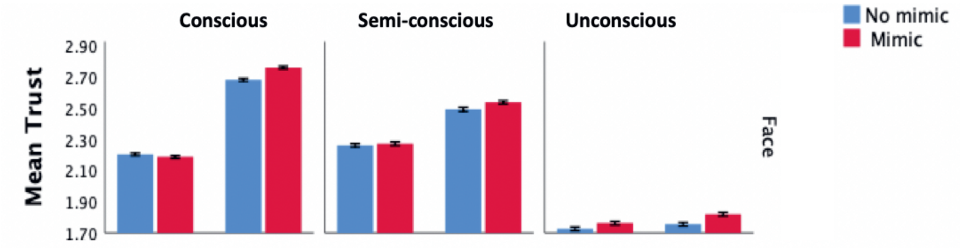


Figure S1: The effect of facial mimicry on trust. On average, the suppression broke in 25% of CFS trials (27% face trials and in 22% eyes condition trials). To test whether suppression breaks quicker for in response to negative emotions, we selected the trials in which suppression broke and checked whether suppression was modulated by the stimuli type (eyes/faces) and emotional expressions (positive, neutral, negative). In line with previous studies, Generalized linear model showed that emotional expressions ([F (1, 2309) = 17.547, P < 0.0001]) and the interaction between the stimuli type * emotional expressions had a main effect on reaction time within which the CFS broke ([F (1, 2309) = 9.416, P < 0.0001]). The pairwise comparison (Table S7) revealed that positive expressions broke the suppression quicker then negative ones. Table S8 demonstrates that this effect was driven mainly by eye stimuli, where dilated pupils broke the suppression quicker than static and constricted pupils. In faces, the happy facial expressions broke suppression quicker then neutral but not quicker than fearful faces.

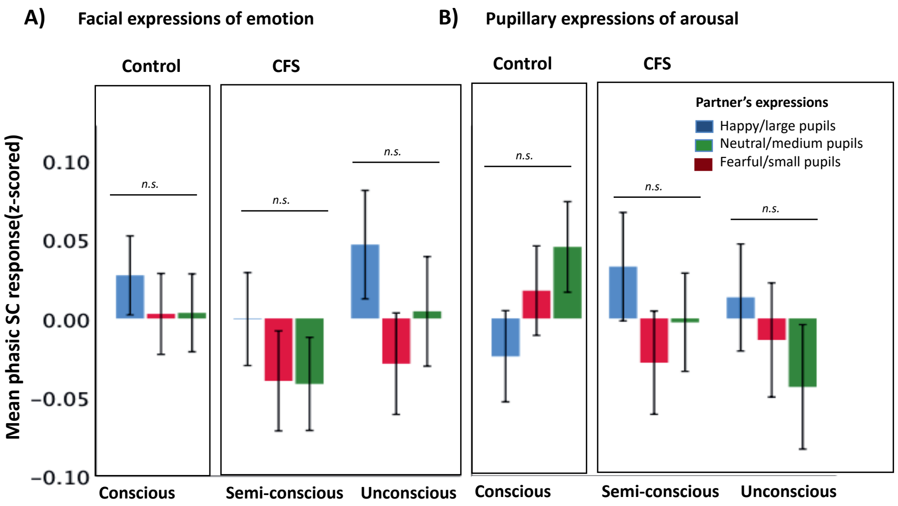


Figure S2: The phasic skin conductance measures did not differ across conditions.

Table S1. Summary of Generalized linear model predicting subjects' trust (investment as DV)

Fixed Effects	F	df1	df2	*p*
Intercept	121.011	17	17808	.000
Expression modality (Eyes/Face)	19.878	1	17808	.000
Emotion	79.913	2	17808	.000
Awareness level	770.611	2	17808	.000
Awareness level * Emotion	10.846	4	17808	.000
Awareness level * Expression modality	.805	2	17808	.447
Emotion * Expression modality	21.441	2	17808	.000
Awareness level * Emotion * Expression modality	24.019	4	17808	.000

Table S2. Frowning mimicry (CS signal as DV)

Fixed Effects	F	df1	df2	*p*
Intercept	3.501	17	163803	.000
Linear trend	.007	1	163803	.933
Cubic trend	.578	1	163803	.447
Quadratic trend	4.860	1	163803	.027
Emotion	9.935	2	163803	.000
Awareness level	6.355	2	163803	.002
Awareness level * Emotion	2.540	4	163803	.038
Emotion * Linear	.128	2	163803	.880
Emotion * Cubic	1.222	2	163803	.295
Emotion * Quadratic	.569	2	163803	.566

Table S3. Smiling mimicry (ZM signal as DV)

Fixed Effects	F	df1	df2	*p*
Intercept	3.312	17	163803	.000
Linear trend	.570	1	163803	.450
Cubic trend	.100	1	163803	.752
Quadratic trend	.081	1	163803	.775
Emotion	7.603	2	163803	.000
Awareness level	.273	2	163803	.761
Awareness level * Emotion	8.246	4	163803	.000
Emotion * Linear	.708	2	163803	.493
Emotion * Cubic	.291	2	163803	.747
Emotion * Quadratic	.895	2	163803	.408

Note: Emotion had 3 levels (Faces: happy, neutral, fearful/Pupils: large, medium, small), Awareness levels had 3 levels (conscious, semi-conscious, unconscious).

Table S4. Pupil mimicry (pupil size as a DV)

Fixed Effects	F	df1	df2	*p*
Intercept	21.185	17	136071	.000
Linear trend	209.712	1	136071	.000
Cubic trend	62.896	1	136071	.000
Quadratic trend	.850	1	136071	.357
Emotion	.276	2	136071	.759
Awareness level	8.961	2	136071	.000
Awareness level * Emotion	1.062	4	136071	.374
Emotion * Linear	.076	2	136071	.927
Emotion * Cubic	.215	2	136071	.806
Emotion * Quadratic	.153	2	136071	.858

Table S5. Facial Mimicry - Trust

Fixed Effects	F	df1	df2	*p*
Intercept	89.686	11	5911	.000
Awareness level	299.688	2	5911	.000
Emotion	167.514	1	5911	.000
Mimicry	.082	1	5911	.775
Emotion * Awareness level	51.489	2	5911	.000
Emotion * Mimicry	.921	1	5911	.337
Awareness level * Mimicry	.496	2	5911	.609
Emotion * Awareness level * Mimicry	.432	2	5911	.649

Table S7. RT b-CFS: Pairwise Contrasts

Expressions: Pairwise Contrasts	Contrast Estimate	Std. Error	t	df	*p*
negative - neutral	.012	.022	.546	2309	.585
negative - positive	.121	.022	5.466	2309	0,00
neutral - negative	-.012	.022	-.546	2309	.585
neutral - positive	.109	.023	4.821	2309	0,00

The least significant difference adjusted significance level is .05.

Table S6. RT b-CFS

Fixed Effects	F	df1	df2	*p*
Corrected Model	10.203	5	2309	.000
Emotion	17.547	2	2309	.000
Expression modality (Eyes/Face)	1.807	1	2309	.179
Expression modality * Emotion	9.416	2	2309	.000

The least significant difference adjusted significance level is .05.

Table S8. RT b-CFS: Pairwise Contrasts

Modality	Expression Pairwise Contrasts	Contrast Estimate	Std. Error	t	df	*p*
Face	negative - neutral	-.043	.031	-1.42	2309	.155
	negative - positive	.025	.030	.82	2309	.411
	neutral - negative	.043	.031	1.42	2309	.155
	neutral - positive	.068	.030	2.29	2309	.022
Eyes	negative - neutral	.067	.033	2.05	2309	.040
	negative - positive	.218	.032	6.72	2309	0,00
	neutral - negative	-.067	.033	-2.05	2309	.040
	neutral - positive	.150	.032	4.73	2309	0,00

The least significant difference adjusted significance level is .05.

Appendix D

Supplementary Material for Chapter 7

This file includes:

Figure S1

Tables S1 to S4

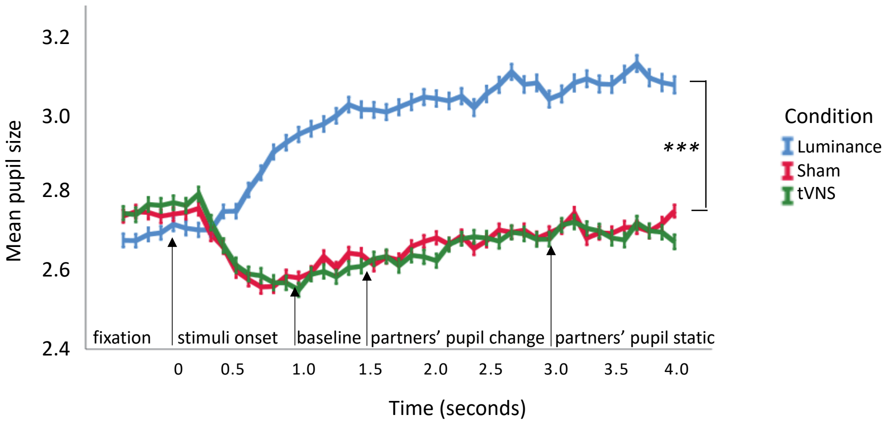


Figure 1. The effect of **condition** on participants' pupil size. The average pupil size of 500 ms of each participant and the trial (thus five values) before the partners' pupils started to change (1.000 ms-1.500 ms after stimulus onset) served as a baseline and was subtracted from all remaining pupil size values.

Table 1. The effect on participants' uncorrected pupil size (all participants)

	F	df1	df2	Sig.
Intercept	21.524	11	115248	.000
Condition	11.813	2	115248	.000
lin	185.531	1	115248	.000
quad	18.767	1	115248	.000
cub	1.158	1	115248	.282
Condition*lin	.206	2	115248	.814
Condition* quad	1.546	2	115248	.213
Condition* cub	2.423	2	115248	.089

Table 2. The effect on participants' corrected pupil size

	F	df1	df2	Sig.
Intercept	14.171	11	108997	.000
Partner Pupil Size	14.535	1	108997	.000
Condition	.368	2	108997	.692
lin	121.288	1	108997	.000
quad	13.501	1	108997	.000
cub	.346	1	108997	.556
Partner Pupil Size * lin	4.573	1	108997	.032
Partner Pupil Size * quad	.022	1	108997	.882
Partner Pupil Size * cub	.312	1	108997	.576
Condition * Partner Pupil Size	.519	2	108997	.595

Table 3. The effect on participants' investments (Trust)

	F	df1	df2	Sig.
Intercept	2.496	5	5280	.029
Partner Pupil Size	2.583	1	5280	.108
Condition	1.632	2	5280	.196
Partner Pupil Size* Condition	3.268	2	5280	.038

Table 4. The effect on participants' pupil contingent trust

	F	df1	df2	Sig.
Intercept	.780	5	138	.566
Condition	.456	2	138	.635
Subject Pupil Size	.178	1	138	.673
Condition * Subject Pupil Size	1.292	2	138	.278

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