Connecting minds and sharing emotions through human mimicry
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Chapter 8

General discussion

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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.