Physiological synchrony in the context of cooperation: Theoretical and methodological considerations

Behrens, F.

Author: Behrens, F.
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Chapter 1

General introduction

Humans donate thousands of dollars to strangers they will never meet, start societal and political movements to fight climate change, share their possessions with people in need, and build enormous constructions from pyramids to skyscrapers. These are all examples of prosocial behavior, an umbrella term referring to actions that are intended to help others (Batson & Powell, 2003). In the current dissertation, I first take a look at what this broad term means in terms of testing it in the lab and then focus on cooperation and its link with how we nonverbally communicate with each other.

What makes cooperation particularly interesting is that humans are unique in the complexity, scale, and frequency of working together with other individuals. One key ingredient for cooperation to flourish is nonverbal communication which allows us to distinguish cooperators from defectors (Boone & Buck, 2003; Frank, 1988). Research has shown that such communication is a back-and-forth process where people tend to automatically and unconsciously synchronize the nonverbal signals they receive from their interaction partner (Chartrand & Bargh, 1999; Kret, 2015; Levenson & Gottman, 1983; Prochazkova et al., 2018). Preliminary evidence suggests that such synchrony affects cooperative behavior. However, theoretical and methodological questions remain to understand such link, which is the focus of my dissertation.

The aim of the current dissertation is to investigate how nonverbal communication between individuals affects cooperative success and how it can be best investigated in the lab. I shed light on these questions in four chapters. In Chapter 2, I zoom out from cooperation and investigate how different measures of prosocial behavior, some of which we use in the following chapters, relate to one another. In the next chapters, we zoom back in on cooperation and investigate the question of what makes cooperation successful. In Chapter 3, I test the effect of face-to-face contact on cooperation. Face contact allows for nonverbal communication and therefore potentially fosters cooperation. Another factor people rely on when making the decision to work together is past experiences with the interaction partner. In Chapter 3, I investigate how these two sources of information are integrated to make a cooperative decision. In Chapter 4, I follow up on the beneficial effect of face contact on cooperation and investigate the link between synchrony and cooperative success as a potential mechanism of such beneficial effect. In Chapter 5, I zoom in on how to optimize the statistical quantification of synchrony. Specifically, I develop guidelines on how to apply a statistical method to different physiological measures. In Chapter 6, I finalize the dissertation with a general discussion. In the following, I will provide a general overview and introduction of the key questions addressed in this dissertation.

The main focus of my dissertation is on how humans cooperate. In Chapter 2, I start by zooming out and investigate how two of the cooperation games used in Chapter 3 and 4 can be placed into the context of the overarching umbrella term of prosocial behavior by making comparisons with four other games. Prosocial behavior refers to "a broad range of actions intended to benefit one or more people other than oneself— behaviors such as helping, comforting, sharing, and cooperating" (Batson & Powell, 2003, p. 463). Previous studies have shown that people behave similarly across a range of tasks. Such studies have focused on anonymous, one-shot economic games. In Chapter 2, I extend these findings by investigating whether the consistent behavior observed in these economic games generalizes to more naturalistic, interactive games. Specifically, I compare six different paradigms: three variants of a social dilemma game, and three naturalistic games (an egg-hunt game, a puzzle game, and a hidden-profile game where people needed to exchange information in order to reach a common goal). This comparison can shed light on questions such as: How robust are the behavioral consistencies across economic games when looking at more ecologically valid games? Can we use the different games interchangeably or does the choice of a paradigm crucially affect the behavior we measure and the conclusions we draw? Can we generalize findings from one task to another?

Besides these general questions of how these six games compare to each other, I was specifically interested in two of the six tasks, which are both measures of cooperative behavior and on which I zoom in during later chapters. In the comparison study, I aimed to verify that they indeed capture comparable behavioral tendencies. The two games were the classical Prisoner's Dilemma game and an extended version of it where the binary choice to cooperate or defect was extended to a six-option scale. The principles stayed the same which were as follows: Participants can choose between maximizing one's own or the collective outcome by deciding to cooperate or defect. To induce such conflict, two premises hold for the payoff structure: (1) a person receives the highest individual outcome for choosing to defect independent of whether the other player chooses to defect or cooperate; (2) if both participants choose to cooperate, they will receive higher joint outcomes than if they both defect (Dawes, 1980). This most common version of the social dilemma game has been used to measure cooperative behavior for decades, a popularity that can be devoted to its simplicity in tapping into complex motives, emotions, and cognition. I used this game to measure cooperative behavior in Chapter 3. In the Chapter 4, I extended the payoff structure from a binary to a six-option scale in order to measure the *degree* of cooperation rather than the binary decision to cooperate or not. A positive moderate correlation between these two versions of the social dilemma game in the first study supported the claim that they measure similar behavioral tendencies. After taking a methodological perspective on *how* to measure cooperation, the next question to be addressed in Chapter 3 is "*what* makes cooperation successful?".

Given the widespread potential of successful cooperation from building an IKEA wardrobe to international collaborations in research, businesses, and politics, it is crucial to understand which factors contribute to its success. When looking at real-life examples, one aspect that stands out is that people fly around the world to cooperate. In other words, despite the great technological advances in phone calling and video chatting, people still prefer to meet face-to-face. Is it worth the effort? Previous studies suggest that people are indeed more willing and more successful in cooperating when they face each other compared to when they write messages, call via the phone, or interact with a human-like avatar (Balliet, 2010; Bohnet & Frey, 1999; Drolet & Morris, 2000; Frohlich & Oppenheimer, 1998; Kiesler, Sproull, & Waters, 1996). The reason for such boost in successful cooperation has been attributed to the possibility to exchange nonverbal signals that give away the intentions of the other person. I will elaborate on this topic below.

Another factor that crucially determines cooperative behavior is the knowledge we have about the interaction partner, a factor I explore in Chapter 3. Outside the lab, cooperation often occurs between people who have some information about that person's previous behavior either from personal experiences or via gossip or other indirect sources. From an evolutionary perspective, exchanging information about other's behavior has been suggested to be the driving factor that allowed humans to live in large-scaled groups and succeed in forming alliances with a large number of individuals (Dunbar, 2004). If you know that a person has been cooperative in the past, that person is more likely to act selflessly in the future. Likewise, in the case of the social dilemma game, the outcome of one individual depends on the decision of the other, so knowing what the other person chose in previous rounds can help predict future decisions. Not surprisingly then, research has shown that people show higher cooperation rates when they receive direct feedback about each other's choices when playing multiple rounds (Bixenstine & Wilson, 1963; Jorgenson & Papciak, 1981; Monterosso, Ainslie, Pamela Toppi Mullen, & Gault, 2002; Tedeschi, Lesnick, & Gahagan, 1968). In Chapter 3, I investigated how humans integrate the two sources of information: nonverbal signals and explicit information. Do people rely more on nonverbal information when no explicit information is available? To answer this question, two individuals played the Prisoner's Dilemma game in a dyadic interaction setting where they sometimes played face-to-face and sometimes with a visual cover between them preventing nonverbal communication. Additionally, dyads received either no, correct, or random feedback about each other's decisions. This mixed design allowed us to deepen our understanding of the beneficial effect of face contact on cooperation and how it operates in the face of the less uncertain, but sometimes false information from the explicit feedback. From establishing the beneficial effect of face contact on cooperation in Chapter 3, I aimed to investigate its underlying mechanisms in Chapter 4.

What is it about face contact that makes people more cooperative? In a classic study conducted by Axelrod and Hamilton (1981), they showed that cooperation can evolve under three conditions: (1) individuals are likely to meet again, (2) cooperators can be distinguished from defectors, and (3) the fruits of cooperation can be harvested by other cooperators. Focusing on the second condition, how can we distinguish cooperators from defectors? Humans use nonverbal dynamic signals that help us identify the intentions and emotions of others[1]. Over thousands of years humans have developed a unique signaling system that started as simple ritualized acts and that has developed into a multilevel, fine-grained system of nonverbal signals and cues (Boone & Buck, 2003). Such system is the foundation of (nonverbal) communication which "involves a pair of behaviors–a signal and a response–that are functionally interdependent" (Scott-Phillips, Blythe, Gardner, & West, 2012, p. 1943). There is a debate about whether such behavior is restricted to socially shared, intentional signals or whether they also include spontaneous, nonvoluntary and non-intentional expressions (Buck & VanLear, 2002; Ekman, 1997; Gibbs & Van Orden, 2003). In this dissertation, I focus on physiological responses within social interactions which cannot be controlled and therefore not expressed intentionally, favoring the proposition to include both spontaneous and symbolic signals in nonverbal communication.

[1] The signaling system communicates both intentions and emotions. Albeit different concepts, here they are strongly linked as making cooperative decisions *is* emotional. If a person decides to cooperate, she might feel fear that the other person will exploit her. If the other person indeed exploits her selfless act, she might feel anger or disappointment. Such emotional responses can in turn influence the other person's decision. It is therefore difficult to disentangle intentions from emotions which is why we treat them similarly in the present context (Van Kleef, 2010).

One body part that is particularly salient in the signaling system is the face. The substantial amount of fine muscles, the hairless skin, and the high contrast between the sclera and the iris in the eyes offer a unique landscape that allows for an enormous variety of fine-tuned expressions (Kret, 2015). Such variation and nuances in expressions facilitate and enrich the communication of our intentions and emotions, and thereby help us distinguish cooperators from defectors. Tweaking the facial expressions and other cues in computer tasks and observing individuals' expressions while making prosocial decisions have identified a range of signals that are considered communicating selfless intentions such as smiling (Krumhuber et al., 2007; Reed, Zeglen, & Schmidt, 2012), pupil dilation (Kret et al., 2015), blushing (Dijk, Koenig, Ketelaar, & de Jong, 2011), and eye contact (Kleinke, 1986). However, there is not a single expression or a fixed combination of expressions that reliably reflect prosocial intentions as the interpretation of nonverbal signals is highly context-dependent (Barrett, Mesquita, & Gendron, 2011; De Melo, Carnevale, Read, & Gratch, 2014). Although we cannot pinpoint to a specific set of expressions used to communicate our intentions, it is well-established that face contact boosts cooperative behavior by being able to exchange prosocial intentions through nonverbal signals.

The emotional expressions and other nonverbal indices of cooperative intent which we perceive from our interaction partners influence the social decisions that are being made during cooperative endeavors, partly because they impact our own emotions and cognition (Prochazkova & Kret, 2017). As illustrated by Loewenstein and Lerner (2003), our decisions are influenced by the expected outcome of our decision and its associated emotions. Such anticipatory changes in affect influence our immediate inner state which guides our decisions. Damasio, Everitt, and Bishop (1996) referred to such an internal signaling system as "somatic markers" that unconsciously and automatically influence our decisions. The focus from a communicative (explicit) to an internal (implicit) signaling system has great implications for studying social decision-making as it opens a new layer of cues that are evident *within* a person such as changes in arousal levels as measured by skin conductance responses and heartrate changes. The integration of the two sources of information from signals of oneself and the other person is particularly important for the topic I will introduce next.

The majority of research on how we perceive and express our intentions has been focused on intrapersonal processes in computerized paradigms (Kret et al., 2015; Krumhuber et al., 2007; Scharlemann, Eckel, Kacelnik, & Wilson, 2001). Although such an approach provides a controlled setting that allows researchers to disentangle the many factors at play in social decision-making, it neglects the two-directional back-and-forth interplay between two individuals engaging in an actual interaction. Acknowledging such interplay has unraveled a new layer of interpersonal processes where people have been shown to mimic or synchronize each other's explicit and implicit emotional expressions[2]. Such synchronization has been shown to be a multifaceted phenomenon occurring on the behavioral, physiological, and neural level impacting a broad range of interper-

[2] The words mimicry and synchrony are often used interchangeably in the broader context. In the case of physiological responses, we use the term physiological synchrony rather than mimicry as this term has been prominently used in this context (e.g., Prochazkova & Kret, 2017). Researchers have distinguished the two terms based on time lags between responses (Rennung & Göritz, 2016). In our analyses, we took a data-driven approach and included aligned responses with and without time lags.

sonal processes such as cooperative success between strangers, marital satisfaction in couples, mother-child relationships, and therapeutic outcomes (Chartrand & Bargh, 1999; Hasson, Nir, Levy, Fuhrmann, & Malach, 2004; Levenson & Gottman, 1983; Prochazkova et al., 2018; Ramseyer & Tschacher, 2011). In their perception-action model, Preston and de Waal (2002) proposed that synchrony forms the basis of emotional contagion which is proposed to be the most basic manifestation of empathy and provides the fundament for higher-order cognitive empathy and prosocial behavior. Hatfield, Cacioppo, and Rapson (1993) described emotional contagion as follows: "by attending to this stream of tiny moment-to-moment reactions, people can and do 'feel themselves into' the emotional landscapes inhabited by their partners." (p.96). Such landscape includes the sensory, motor, physiological, and emotional state of the partner which is in line with the notion that emotional responses constitute behavioral, physiological, and cognitive components that activate each other (Wood, Rychlowska, Korb, & Niedenthal, 2016). This implies that people will only feel the same emotional experience if synchrony emerges on most of these levels. Successfully aligning emotionally with another person then helps to recognize and understand the other person's emotional state and subsequently respond appropriately (e.g., show empathy and/or helping behavior towards a distressed person; Preston & de Waal, 2002). From a developmental perspective, when language is yet to develop in infants and communication with the caregiver is mostly nonverbal, imitation constitutes an innate and automatic learning process to develop emotion regulation abilities, learn about the dangers in the environment, and acquire increasingly more complex social abilities (Preston & de Waal, 2002). As such abilities become more and more automatic, synchrony has been suggested to mostly serve affiliative purposes (Lakin & Chartrand, 2003). Thus, the link between aligning nonverbal signals and social decision-making provides a potential mechanism for explaining the beneficial effects of face contact on cooperation observed in Chapter 3.

In Chapter 4 of this dissertation, I examine this potential link by investigating whether physiological synchrony is positively related to cooperative success in a dyadic interaction study. The setting was similar to the study presented in Chapter 3 with the addition of measuring skin conductance level and heartrate responses throughout the experiment. In the literature, two lines of research have emerged by either manipulating synchrony or the prosocial setting. The former has concentrated on motor and vocalization synchrony asking people to dance, tap, or sing together and investigate how prosocial behavior changes between synchronized and non-synchronized conditions. Two recent meta-analyses showed that being in sync has a medium-sized positive effect on prosocial behavior (Mogan, Fischer, & Bulbulia, 2017; Rennung & Göritz, 2016). In the context of physiological synchrony, manipulating the level of synchrony in, for example, heartrate or skin conductance responses is less straightforward, which is why research has focused on manipulating the cooperative setting and investigating its effect on synchrony. For example, people were asked to play a computer game with or against another player (Chanel, Kivikangas, & Ravaja, 2012; Järvelä, Kivikangas, Kätsyri, & Ravaja, 2014) or to build something together (Mitkidis, McGraw, Roepstorff, & Wallot, 2015; Mønster, Håkonsson, Eskildsen, & Wallot, 2016). Although there were some inconsistencies with regard to which measures exactly played a role, these studies generally support a link between physiological synchrony and cooperation.

Synchronization between individuals and its effect on social processes has been observed at different levels. In our study, we focused on *physiological* synchrony for three reasons: first, this type of synchrony and its effect on prosocial behavior is less understood than other forms of synchrony. Although there is preliminary evidence that physiological synchrony plays a role in cooperative decision-making, the findings are equivocal (Järvelä et al., 2014; Mitkidis et al., 2015; Mønster et al., 2016; Vanutelli, Gatti, Angioletti, & Balconi, 2017). Second, as mentioned above, emotional experiences constitute a multifaceted combination of behavioral, physiological, and cognitive components, making physiological changes a crucial part of the experience. Likewise, "feeling into" the emotional state of another person eases the synchronization of these responses (Prochazkova & Kret, 2017). In other words, to most optimally experience the emotional state of another person, synchronizing on an arousal level is essential. And as described above, such changes have been shown to influence our decision-making (Bechara, Damasio, Tranel, & Damasio, 1997; Crone, Somsen, Van Beek, & Van Der Molen, 2004). Third, while motor movements such as gestures and facial expressions can be consciously controlled, physiological responses are difficult to control. Therefore, physiological responses and their synchronization between interaction partners might provide more genuine information about their relationship. In line with this, Prochazkova and her colleagues demonstrated that attraction between individuals on a blind-date was positively associated with the level of physiological synchrony, but not with the mimicry of explicit signals such as gestures and facial expressions (Prochazkova, Sjak-Shie, Behrens, Lindh, & Kret, 2019). In sum, given the lack of conclusive results regarding the role of specific physiological measures affecting cooperation, their importance in emotional states, and its elusive nature, we focused on physiological synchrony.

There is a range of physiological measures that has been shown to synchronize between two individuals and in the current thesis I concentrated on two measures most often used in previous studies: heartrate and skin conductance level (Palumbo et al., 2017). These measures reflect activity in the autonomic nervous system (ANS). This system is part of the peripheral nervous system (as opposed to the central nervous system) and its function is to maintain homeostasis and adapt our body to changes in the environment. The ANS is an integral component of emotional experiences and has been shown to influence cognitive processes, among others social decision-making (Kreibig, 2010). The ANS is divided into two antagonistic, yet intertwined branches referred to as the sympathetic and the parasympathetic nervous system. The former prepares the body for a fight-or-flight response and activation of this system causes the pupils to dilate, the heart to beat faster, and the hands to sweat. The latter response is measured by changes in skin conductance which is elevated with sweat. Skin conductance responses have been associated with a range of processes such as activation, attention, and significance or affective intensity of a stimulus (Dawson, Schell, & Filion, 2000). The parasympathetic nervous system is also referred to as the "rest and digest" system pinpointing to its role in relaxation and recovery from the elevated activity of the sympathetic branch. Biologically, activation of the parasympathetic nervous system constricts the pupils, decreases heartrate and activates, among others, the digestion processes. A measure of parasympathetic nervous system activity is the Respiratory Sinus Arrhythmia (RSA) which reflects the high-frequency component of the general heartrate measure and reflects the respiratory cycle. Chapter 4 focuses on the global heartrate which is controlled by both sympathetic and parasympathetic nervous system activity and is therefore less specific in identifying distinct processes in the body than the skin conductance measure. Nonetheless, heartrate has been shown to influence psychological processes such as decision-making and emotional processing (Crone et al., 2004; Kreibig, 2010). With regard to the link between synchrony and cooperation, both measures have been shown to play a role, however, the findings were equivocal between studies. Most showed effects in one of the measures (Mitkidis et al., 2015; Mønster et al., 2016; Vanutelli et al., 2017), whereas others did not observe any effects (Järvelä et al., 2014). Therefore, by combining skin conductance level with heartrate measures, we could shed more light on the inconsistency in the literature and the role of the two branches of the ANS in social decision-making.

While conducting the study presented in the Chapter 4, I encountered a methodological challenge: how can we accurately quantify physiological synchrony? Despite the popularity across different disciplines to understand the phenomenon of interpersonal synchrony, no standardized guidelines have been developed on how to properly capture the dynamics between two individuals statistically. The method that I rendered most appropriate for our research question and type of data was the Windowed Cross-Correlation analysis (WCC; Boker, Xu, Rotondo, & King, 2002). The method incorporates two features that allows for dynamic changes over time: first, by segmenting the time series into smaller, overlapping windows and calculating the cross-correlation for each window, the strength of synchrony (i.e., the correlation estimate) can change throughout an interaction. This is important as two individuals most certainly do not establish the same degree of synchrony throughout an interaction, but rather show moments of weak and strong synchrony. Second, there is great intra- and interpersonal variation in the pace of (physiological) responses introducing varying time delays between the responses of two individuals. The method accounts for such variations by shifting the windows of the interacting people away from each other with increasing delays. Thus, this method offers a neat way to compute a quantification of the overall strength of synchrony throughout a conversation.

The challenge lies in tailoring the WCC analysis to the characteristics of the signal of interest by specifying parameters. There is great variation between studies on which parameters are used and researchers have proposed that the choice of parameters is arbitrary and does not change the relative results (McAssey, Helm, Hsieh, Sbarra, & Ferrer, 2013). For the study presented in Chapter 4, I applied a similar approach and based the choice of the parameters mostly on previous literature and the biological nature of the signals of interest. However, during a research visit to the lab of Steven Boker, who developed the statistical method, I had the opportunity to shed light on this issue in a data-driven manner, a project that is presented in Chapter 5. Particularly, I systematically investigated the influence of the parameters and developed guidelines for the best parameter configurations for four different physiological measures: heartrate, skin conductance level, pupil size, and facial expressions (the left zygomaticus major, a muscle associated with smiling). Such guidelines can guide other researchers to make informed choices about which parameters to use, thereby increasing the comparability between studies and contributing to solving the inconsistencies in findings between studies.

Chapter Overview

This dissertation is based on four empirical stand-alone research articles that are presented in Chapters 2 to 5. They build upon each other by holding a magnifying glass over one aspect of the previous study. However, as they are written as independent research articles, they contain some theoretical overlap. In the following, I will give a short overview of the studies presented in each chapter.

In **Chapter 2**, I investigated how six different prosocial behavior tasks relate to one another. To that end, 74 participants played all tasks in a within-subject design with three different partners. The games have been used previously to measure prosocial behavior and include three variants of the social dilemma game, an egg-hunt game, a puzzle, and a communication task. By means of a Principal Component Analysis, I examined whether these games measure similar behavioral tendencies (i.e., prosociality). Two of the examined games were used in Chapter 3 and 4 to measure cooperative behavior.

In **Chapter 3**, I investigated the effect of face contact and feedback on cooperative behavior. People played multiple rounds of the Prisoner's Dilemma game in a dyadic interaction setting ($N = 116$). In a mixed design I manipulated whether people could see each other or not (within-subject manipulation) and whether they received correct, random, or no feedback (between-subject manipulation). I was particularly interested in the interaction between the two manipulations, investigating whether the effect of face-to-face contact on cooperative behavior was moderated by how much information people received about each other's past behavior.

In **Chapter 4**, the aim was to dive deeper into the beneficial effect of face contact on cooperation. Specifically, I investigated whether physiological synchrony functions as a potential mechanism of such beneficial effect. To investigate this, I used a similar set-up to the previous study ($N = 152$). Additionally, participants' physiological responses by means of their skin conductance level and heartrate responses were measured throughout the experiment. I hypothesized that physiological synchrony would be higher when people could face each other compared to when they could not. Most importantly, I expected physiological synchrony to predict cooperative success in a dyad, particularly when participants interacted face-to-face.

In **Chapter 5**, I focused on the methodological challenge of properly quantifying synchrony. In particular, I advanced an existing analysis, the Windowed Cross-Correlation analysis, that has been used to measure synchrony by refining it to four physiological responses. The data I used for this methodological study was from a dyadic interaction study where people engaged in storytelling while their heartrate, skin conductance level, pupil size, and facial expressions (i.e., smiling) were measured ($N = 68$). I elaborated the analysis by investigating its sensitivity to discriminate the original dyads from dyads who participated in the same experiment, but never interacted. Such distinction is particularly important to draw conclusions about that synchrony is the result of interpersonal processes rather than artifacts deriving from the recurrent nature of the signals or the same structure of the experiment across dyads. Based on these outcomes, I could provide recommendations on how to tailor the analysis to each physiological measure.

In **Chapter 6**, I close the dissertation with a general discussion, where I highlight and integrate the key findings from the different chapters. I also pinpoint to new questions that this dissertation has provoked and propose ideas for future studies. I finalize the chapter and the dissertation with concluding remarks.

Finally, I want to emphasize that the empirical studies are the result of the collaboration with my co-authors as acknowledged by including them in the author list of each study and by writing these chapters using plural personal pronouns. However, Chapter 1 and 6 are based on my own thoughts which is why I use singular personal pronouns in these chapters.