Empathy and Inter-brain Synchrony During Online Collaboration

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Tiivistelmä – Referat – Abstract

Tavoitteet. Tutkimustietoa heikentyneistä empatiataidoista tietokonevälitteisen vuorovaikutuksen aikana on runsaasti. Myös empatiakykyjen neuraalisesta perustasta tiedetään jo melko paljon. Tietoa siitä, miten puutteet empatiataidoissa näkyvät aivotoiminnan tasolla ihmisten välisen tietokonevälitteisen vuorovaikutuksen aikana, on kuitenkin huomattavasti vähemmän. Aivojen sähköisen toiminnan on löydetty synkronoituvan kasvokkain yhteistyötä tekevien henkilöiden välillä, ja tämä synkronia näyttäisi olevan yhteydessä vuorovaikutuksen laatuun. Tämän tutkimuksen tarkoituksena onkin selvittää 1) löytyykö samanlaista sähköisen toiminnan synkronoitumista myös tietokonevälitteisen yhteistyön aikana, kun henkilöt eivät ole samassa fyysisessä tilassa 2) onko tietokonevälitteisen yhteistyön aikainen aivojen sähköisen toiminnan synkronoituminen yhteydessä vuorovaikutuksessa olevien henkilöiden empatiakykyihin.

Menetelmät. Tutkimuksessa oli mukana 21 paria, joista jokainen muodostui kahdesta koehenkilöstä, jotka tunsivat toisensa, ja päättivät osallistua tutkimukseen yhdessä. Parit suorittivat ensin yksilöllisiä empatiatestejä, jonka jälkeen he saivat tehtäväkseen pelata tietokoneen välityksellä yhdessä autopeliä, jossa toisen tuli säädellä auton ajonopeutta ja toisen auton ajosuuntaa. Tehtävän aikana koehenkilöiden aivojen sähköistä toimintaa mitattiin EEG:n avulla. Henkilöiden välistä aivojen toiminnan synkroniaa tutkittiin tarkastelemalla theta-, alfa-, beta- ja gamma-aktivaation voimakkuuden eroja koehenkilöiden välillä frontaali-, frontosentraali-, sentraali-, parietaali-, temporoparietaali- ja oksipitaalialueilta mitattuna.

Tulokset ja johtopäätökset. Koehenkilöiden väliseen yhteistyöhön liittyvää synkroniaa löytyi theta-taajuuden osalta frontaali-, frontosentraali-, sentraali-, parietaali- ja temporoparietaalialueilta; alfa-taajuuden osalta frontosentraalialueilta; beta-taajuuden osalta frontosentraali-, sentraali-, parietaali-, ja oksipitaalialueilta sekä gamma-taajuuden osalta frontosentraali- ja sentraalialueilta mitattuna. Synkronoitunut aktviaatio näillä taajuuskaistoilla, näiltä alueilta mitattuna näyttäisi olevan tietokonevälitteisen yhteistyön kannalta merkityksellistä. Tilastollisesti merkitseviä yhteyksiä löydetyn synkronian ja empatiataitojen välillä ei löytynyt.

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Objective. In cognitive neuroscience empathy is defined as a set of skills and tendencies that enables us to interpret and predict the mental states and actions of others and share emotional states and the experience of others. These skills and tendencies are important for successful interaction and in most situations rely heavily on natural social cues. In addition to verbal cues, these natural cues consist of for example facial expressions, bodily gestures, and prosody of speech. Also, a shared environment that enables for example eye contact and joint attention have previously been found beneficial for empathy. However, a growing percentage of our social interaction takes place in online environments where many of these features found important during face-to-face interaction are absent. A great body of evidence exists on the decrease in empathy skills during online compared to face-to-face interaction. A fair amount of research also exists on the neural foundation underlying empathy. Research on how this decrease in empathy processes during online interaction can be observed on the neural level is however limited. One phenomenon found to occur during face-to-face interaction is the synchronization of the brain's electric activity between collaborating individuals. Associations between this neural synchrony and the quality of interaction have also been found. The purpose of this study is to investigate 1) whether inter-brain synchrony occurs during online collaboration in the absence of natural social cues and 2) whether this synchrony is associated with the empathy skills of the collaborating individuals.

Methods. The subjects of the study consisted of 21 pairs, each in which the two subjects knew each other in advance and decided to participate in the study together. The subjects first completed individual empathy tests, after which their task was to play a collaborative online car game together in separate physical locations during which one of the subjects was to control the speed while the other was to control the direction of the car. During this task, the neural activity of each subject was measured with EEG. The inter-brain synchrony between the collaborating individuals was studied by investigating the associations of power in the theta, alpha, beta, and gamma frequency bands measured over the frontal, frontocentral, central, parietal, temporoparietal, and occipital regions between the two individuals.

Results and Conclusions. Inter-brain synchrony specific to collaboration was found in the theta frequency band over the frontal, frontocentral, central, parietal, and temporoparietal regions; in the alpha frequency band over the frontocentral region; in the beta frequency band over the frontocentral, central, parietal, and occipital regions; and in the gamma frequency band over the frontocentral and central regions. This suggests that the synchrony in these frequency bands measured over these regions is related to computer-mediated collaboration. No significant associations were found between the inter-brain synchrony and empathy skills.

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Foreword

The study presented in this thesis is part of the Natural Emotionality in Digital Interaction (NEMO) project. NEMO is a research project that strives to enrich digital interactions by finding new ways of conveying emotions and enhancing empathy online. The team - also responsible for the experimental design - consists of team leader Katri Saarikivi, Valtteri Wikström, Tommi Makkonen, PhD Mari Tervaniemi and the author. The game used in the experiment was designed and created by Valtteri Wikström (vatte.net).

I would like to thank everyone involved in the NEMO project. A special thank you to my supervisors Valtteri Wikström, Katri Saarikivi, and Docent Benjamin Cowley for the extremely helpful guidance and pleasant collaboration. Thank you also to Tommi Makkonen for the much appreciated help with everything from lab setups to data processing, as well as Silja Martikainen and Vesa Putkinen for your valuable insights.

Contents

1 Introduction

Interaction and collaboration are phenomena that to a large degree have defined the success of the human species. While the tools for interaction have transformed enormously in the past few decades due to technological advancements, the core requirements of successful interaction have remained more or less the same: in order to collaborate, we must be able to understand each other's mental states and be motivated to work towards common goals. The psychophysiological mechanisms that give rise to these abilities can collectively be called empathy. Empathy is a set of skills that allow us to understand and predict others' mental states, share their emotional states, and gain pleasure from helping them [1]. The functioning of these empathy mechanisms, and the successful interpretation of others' mental states, depend on receiving social, emotional, environmental and contextual cues [2].

Today's technology enables us to create and maintain social connections more effortlessly than ever before. However, the way we interact through this technology differs significantly from that in face-to-face settings. Many of the social cues present in face-to-face interaction are lacking online, meaning that mechanisms related to empathy may be disabled. For example, the lack of social cues in online interaction has been shown to cause challenges in communication [1]. To support our inherent tendencies and abilities during interaction, new ways to diminish the deficiencies of current online communication tools that prevent comprehensive interaction are needed. Better understanding of the psychophysiological mechanisms of empathy, and whether and how they function in online settings, could provide new ways of improving communication technologies.

Even though a wealth of research exists on differences related to the quality of interaction in online compared to face-to-face settings, what remains to be answered is how the neural patterns important for interaction differ during online compared to face-to-face interaction. One phenomenon found to occur during face-to-face interaction is neural synchrony between the interacting individuals. This synchrony also seems to be associated with a variety of social functions, including empathy. However, it is still unclear whether this synchrony occurs during online interaction and whether there is an association between empathy and this synchrony in the absence of natural social cues.

Hence, this thesis aims to uncover whether inter-brain synchronization of the brain's oscillatory activity occurs between individuals during online collaboration, and whether the empathy skills of individuals contribute to this synchronization.

In the following, I will first review prior research related to empathy and its role in interaction in both face-to-face and online communication. After this I will provide an overview of studies concerning behavioural, physiological, and neural inter-individual synchrony as they have been found associated with empathic tendencies and social interaction. Finally, I will present a novel electroenchephalography (EEG) study on inter-brain synchronization utilizing a collaborative online gaming setting, where two subjects in separate physical locations maneuver a car through different shaped tracks together without being able to communicate with one another in any other form than through playing the game.

The results of the study will shed light on the relationships between inter-brain synchrony and empathy during online collaboration.

1.1 Defining Empathy

Empathy is one of the core elements of human social cognition. It is, however, not a feature strictly limited to the modern human. Some forms of empathic processes can be found among also other mammals. For example, contagion of pain has been found to occur among rodents and this contagion can even be altered by social factors, such as familiarity [3]. Furthermore, primates tend to utilize social cues related to their fellows in rich ways. Chimpanzees have even been found to intentionally alter and induce mental states in others through their own actions, suggesting abilities of understanding others' mental states and the factors that influence them [4]. Empathy mechanisms can also be seen as an essential survival tool as predators and prey use information of the other's movements to predict motor intentions [5]. From an evolutionary perspective, it can be assumed that these skills have been similarly beneficial for humans in the past. However, due to evolutionary, societal and technological developments, empathy skills play a different type of role in today's society. The need for understanding and predicting the actions of predators or collaborating with others to hunt or fight against enemies to ensure survival have been replaced by different collaborative goals and needs. Therefore, these skills are still found crucial for successful interaction and collaboration.

As might be intuitively assumed, empathy skills and tendencies have been found to correlate strongly with competence related to different aspects of social interaction[5]. The lack of these skills are at the core of disorders in which social functions, such as understanding or being affected by social cues, are severely impaired [6]. What has only recently become a more common topic in research is the role of empathy skills and tendencies when it comes to collaborative success. Recent work has addressed the question on the relationship between empathy skills and team success. For example, Woolley et al. (2010) found in their study that groups of adults with higher average empathy scores performed significantly better across a wide range of different group tasks [7]. Research also suggests that empathy skills are connected to the quality of interaction in the form of, for example, social affiliation [8]. Furthermore, empathy skills have been found to predict successful cooperation in face-to-face [7], online text-based [9], and video-assisted [10] interaction. Hence, empathy seems to be important for the quality of interaction as well as successful performance in various collaborative contexts, including those taking place online.

There is however some considerable variance in how the term empathy is used in behavioral sciences [11]. In this chapter, I will describe the characteristics of empathy as defined by cognitive neuroscience. In this field, empathy is generally referred to as the set of skills and tendencies that enable successful interpretation of the mental states of others and sharing of emotional states between individuals. These components are nowadays often referred to as Cognitive Empathy and Affective Empathy, respectively [12]. A third component called Prosocial Behavior (Prosocial Concern, Prosocial Motivation or Empathic Motivation) is also sometimes included. However, according to many researchers, Cognitive Empathy and Affective Empathy are seen as strong predictors of Prosocial Behavior [11]. Thus, Prosocial Behavior is in general not seen as a component of empathy, but rather a separate function that follows from processes related to Cognitive and Affective Empathy [13]. When discussing empathy in this thesis, I will be referring to Cognitive Empathy and Affective Empathy as defined in the next paragraphs due to the consistent evidence on these two partially separate core components of empathy.

Being able to successfully interpret and predict the mental states of others requires the understanding that one's own mind is separate from those of others. In addition, one needs to possess a functioning model of how the human mind generally works and an ability to deliberately take another person's perspective. These abilities together form the essence of Cognitive Empathy - also referred to in literature as mentalizing, perspective taking or Theory of Mind - which usually develops around the age of 2-4 years [14, 12]. The interpretations and predictions related to the mental states of others can be made based on cues gathered from another person's behavior. These behavioral cues include verbal cues, bodily gestures, facial expressions, direction of gaze or tone of voice. If for example during a conversation we notice our friend suddenly glancing over our shoulder with excitement in their eyes, we will likely be quick to make an assumption that they have noticed something behind us that has sparked their interest. In these types of situations, simulation or imagination is used to infer the intentions, thoughts and emotions that likely explain the observed social cues (such as a sudden glance featuring excitement). In addition to using observable cues, information about circumstances, events and context can be enough to imagine another person's mental state. As an example, if a person with functioning empathy mechanisms hears a story about an individual tripping in front of a crowd, that person is able to automatically imagine how the individual in the story must have been feeling after this humiliating incident. As in this example, this type of perspective-taking and mentalizing is possible even though the person hearing the story may neither be observing nor in the same position as the story's individual. Similar perspective-taking and mentalizing is possible even when it comes to situations that involve a high complexity of mental states that we have never experienced ourselves. For example, we can imagine the approximate feelings of someone convicted for a crime they did not commit, even though we have never been in a similar situation ourselves. In these types of situations, imagination is used to simulate an entire person with behavioral and mental states of their own.

The tendency to automatically experience the same emotions that we observe in others is generally known as Affective Empathy - also referred to in literature as Emotional Empathy and Affective Responsiveness [15]. The mechanisms underlying this tendency is what cause emotion contagion between individuals. Emotion contagion occurs when observing cues related to the emotional states of others automatically evokes these same mental states in ourselves. For example, hearing happy laughter of others is likely to automatically make us feel amused even when we have received no clues related to the reason behind the laughter. Similarly, observing someone's misery is likely to bring our own mood down as well. This type of contagion of emotions can be observed even among newborns [15] when the sound of other children crying or the smile of a parent can quickly change the mood of an infant. This suggests the innate nature of Affective Empathy.

Although, Affective Empathy and Cognitive Empathy can be observed separately, they are also functionally related in many ways [16, 17]. For example, in order to feel affected by someone's pain (Affective Empathy) based on a story, one must first be able to take the other person's perspective (Cognitive Empathy). On the other hand, automatic contagion of emotions (Affective Empathy) is likely to help interpret the other person's mental states correctly (Cognitive Empathy) [18].

As mentioned earlier, in order to function appropriately, mechanisms related to both Cognitive and Affective Empathy often rely on sufficient social cues. Although one of the features that distinguishes humans from all other species is the ability to use rich language as a communication tool, much of the information required for successful interpretation of the mental states of others is nonverbal. The nonverbal cues used when interpreting others' thoughts, feelings, and intentions consist of many consciously visible physical and behavioral cues such as hand gestures, facial expressions, and the tone and volume of speech [19]. However, a large portion of the cues are processed subliminally and automatically. These types of cues include subtle changes in body language or facial expressions, the prosody of speech, the number and duration of blinks and even changes in the physiology of the body; for example, changes in heart rate, that appear as slight variation of skin tone. [5, 20]. Our empathy mechanisms have evolved to make use of even the slightest of these cues in order to understand the actions and mental states of others. As less social cues are generally available in online environments, it is important to consider the possible effects of the lack of these cues on empathy during online interaction. It is presumable that in the absence of social cues some limitations concerning our empathic abilities may occur. In order to address these potential limitations, research concerning empathy and its underlying neural patterns during online interaction is needed.

1.2 Measuring Empathy

The level of Cognitive Empathy and Affective Empathy, as presented above, can be measured in humans using questionnaires, neuropsychological tests, and to some extent even physiological measures [21, 22, 23]. Cognitive Empathy, that is, the skill to recognise and interpret the cognitive states of others correctly, can be examined using different neuropsychological tests designed to assess whether a person has an appropriate model of how the human mind functions. This type of model enables a person to make accurate predictions of the other person's mental states. For example, in the Theory of Mind subtest of the Developmental Neuropsychological Assessment for children (NEPSY), the subject is asked to look at pictures of a child in different emotion-evoking situations, and determine which one of the given mood words best describes the child's probable mental state in such situation [23]. Additionally, tests of Cognitive Empathy measure the ability of a person to recognize emotional states accurately based on emotional cues such as facial expressions or voices. In order to address whether the level of Cognitive Empathy is associated with inter-brain synchrony, one of these type of tests, namely the Reading the Mind in the Eyes (RME) test [22], will be used in the study of this thesis and will, therefore, be presented in more detail in the upcoming Methods section. Assessments of Affective Empathy as well as Prosocial Behavior are often carried out using self-report questionnaires. As an example, a person can be asked to what extent they generally feel affected by the moods of others, or how they react in different social situations. The commonly used Interpersonal Reactivity Index (IRI) is a questionnaire [24] that includes subscales for measuring Affective Empathy traits. In order to address whether the level of Affective Empathy is associated with inter-brain synchrony, IRI will also be used as a method in the study of this thesis and will be presented later on. Psychophysiological assessments of empathic tendencies based on biosignals related to (for example) electrodermal activity, heart rate, or neural activity are not (to date) reliable for assessments on the individual level. However, significant correlations between certain types of psychophysiological activity and empathy traits on a statistical level have been found. These types of phenomena will be discussed in the upcoming sections related to synchrony and social interaction.

1.3 Neural Correlates of Empathy

In this section, I will give an overview on the brain regions previously found important for the two empathy components (Cognitive and Affective Empathy) in order to provide context for the choice of methods and the results of our EEG study presented later. As mentioned in the previous section, Cognitive Empathy and Affective Empathy can to a considerable extent be seen as separate functions. Certain disorders and lesions may lead to an impairment of only one component, leaving the other at least partly intact [25]. For example, lesions in different parts of the brain seem to cause impairments in Cognitive Empathy leaving Affective Empathy intact, and vice-versa [6, 25]. Also atypical brain development may selectively influence the components of empathy. This is evidenced for instance in people with autism spectrum disorders who tend to struggle to accurately identify others' feelings, thoughts and intentions (Cognitive Empathy), although contagion of emotions (Affective Empathy) seems to in many cases occur at a typical, or only partially impaired, level [26, 27]. Conversely, people suffering from dissocial personality disorders lack the tendency to be emotionally affected by the mental states of others, while typically being well aware of the mental states of others [6]. This dissociation between the components is supported by multiple fMRI studies showing that the neural activity behind the two different empathy components does seem to employ partly separate regions [15, 18]. However, these same studies have also revealed significant interconnection between the brain regions. When controlling for the neural activity that is specific to Cognitive or Affective Empathy, similar neural architecture has been found during conditions evoking processes related to either one of these empathy components. These findings suggest a core system of empathy that is active during all types of empathy processes and enables the elementary understanding of other people's behavior [18].

Although many unanswered questions remain regarding the specific roles of different neural structures in empathic processes, certain brain regions seem to be crucial for intact empathy mechanisms. Regions that have received most attention within the field are the medial prefrontal cortex (mPFC), including the dorsomedial prefrontal cortex (dmPFC), ventromedial prefrontal cortex (vmPFC), orbitofrontal cortex, superior temporal sulcus (STS), inferior frontal gyrus (IFG), anterior cingulate cortex(ACC), insula and amygdala [14, 28]. In the temporal parietal region, the temporo-parietal junction (TPJ) has been found to be linked to the short-time estimation of others' intentions, goals and desires [29], and therefore is likely to play an important role in Cognitive Empathy. In addition to the temporo-parietal junction, vmPFC is seen to be associated with mechanisms specific to Cognitive Empathy, whereas the limbic area, insula and IFG have been more closely associated with Affective Empathy. In addition to the roles of specific brain regions, research has also examined how networks of brain regions relate to empathy [14]. The role of the mirror neuron system has been found to play an important part in social cognition, including empathy.

The mirror neuron system (MNS) is a network of neurons essential for understanding the behavior and intentions of others. The neurons of the MNS are activated in a similar manner both when carrying out body movements oneself as well as when only observing body movements of others. The same neural activity that is related to producing body movement has also been found to occur when one is merely imagining someone carrying out the movement [30]. Many theories suggest that understanding others relies on this automatic adaptation to the neural states of the observed (or imagined) individual. This automatic matching of neural activity is called neural resonance and it is seen to represent the simulation of the other person's states in one's own brain. The activity of the MNS has been found to correspond with several functions related to social cognition [18]. However, there is little understanding on how the MNS functions in situations with a lack of nonverbal cues, such as during online collaboration. Due to this the possible role of the MNS will also be considered in our study.

Mirror neurons were first found in the premotor cortex of macaque monkeys through single neuron recordings in 1992 by Rizzolatti et al. (1992) [31]. Although single neuron recording studies on humans are limited [32], evidence from EEG, Magnetoencephalography (MEG), Transcranial Magnetic Stimulation (TMS) and functional Magnetic Resonance Imaging (fMRI) studies confirm that mirror neurons can also be found in the human brain. The rostral part of the inferior parietal lobule, the lower part of the precentral gyrus, the posterior part of the IFG, the ventral premotor cortex (PMv) and the dorsal premotor cortex (PMd) seem to form the core of the human MNS [14]. Activity of the MNS in humans can, measured by EEG, be observed as neural oscillations at the frequency of approximately 7-13 Hz in the motor cortex when producing movement, imagining movement, and watching other people's movement. These oscillations are generally called mu waves or mu rhythms and differences in the occurrence of these oscillations have been found between different groups [33]. The decrease of these oscillations, often referred to as mu suppression, has been associated with for example joint attention and social mirroring [33].

Recently, Lachat et al. (2012) investigated subjects' neural oscillatory activity during face-to-face interaction in conditions that either included or did not include joint attention. Comparing the joint attention and no-joint attention conditions, they found a decrease in mu oscillations over the centro-parieto-occipital region during the conditions involving joint attention. This decrease in mu oscillations was seen to reflect processes of attention mirroring, joint attentiveness and social coordination [33].

In addition to these regions related to motor functions, evidence suggests that mirror neurons can also be found in the IFG, STS, and the inferior parietal lobule (IPL) [34]. These findings indicate that the MNS covers a large portion of cortical areas, some of which are found essential for both Cognitive and Affective Empathy functions. Accordingly, the MNS has been found to encode and thereby contribute to the understanding of intentions and emotions in addition to motor functions [34]. It is, hence, plausible that the MNS enables the activation of empathy mechanisms through the interpersonal resonance of neural states. On the other hand, the activation of the MNS may be enhanced by empathy processes, for example, as a result of deliberate perspective taking. Dysfunction of the MNS has also been associated with social deficits such as those related to ASD. However, in some studies MNS has been found more closely associated with Affective Empathy [18], which as mentioned previously is not always seen to be impaired in ASD.

Although there is a broad range of different partly contradicting findings related to the specific role that the MNS plays in different cognitive processes, there seems to be a wide consensus that MNS is crucial for action understanding, imitation [35] and the two components of empathy [18]. Naturally, activity of the MNS results in neural resonance between individuals, as similar neural activation occurs in both the observer and the individual being observed. Furthermore, the MNS facilitates understanding others' actions and mental states. As these social and neural functions are extremely relevant to empathy, the MNS is seen to strongly serve the processes necessary for both Cognitive and Affective Empathy. Understanding whether and how this system functions in situations with scant or no direct information on the motor operations of others is needed to understand how empathy functions during online collaboration.

As neural activity related to empathy seems to be broadly represented in different parts of the brain, some considerations should be made when choosing methods for investigating these partly overlapping neural mechanisms. Even though some of the brain regions specific to Affective Empathy are subcortical (limbic area, insula), most of the core regions responsible for processes related to empathy are cortical (eg. mPF, TPJ, ACC and MNS) which makes it possible to capture activation stemming from these regions with EEG. For this reason EEG can be seen as a suitable method for investigating neural activity related to Empathy, as is also done in our current study.

While suitable, there are limitations to using EEG (or any other imaging methods) when seeking to differentiate correlates of Affective and Cognitive Empathy processes [18, 14, 29]. Regarding the MNS, it may in some cases be difficult to differentiate between the type of automatic neural resonance directly resulting from perceived actions of others and the type of neural resonance that occurs as a result of more complex cognitive processes of predicting others' intentions (such as those resulting from processes related to Cognitive Empathy) [2]. In order to investigate neural resonance that only pertains to intention understanding and not direct observation of movement, the functioning of the MNS should be investigated in nonface-to-face situations. In order to take this into consideration in our current study, participants were seated in separate rooms with no visual contact with one another. Therefore no neural resonance should result from directly observing the other person or their movements. This enables ruling out automatic neural resonance resulting from motion observation as an explanation behind possible inter-brain synchrony.

Additionally, certain differences found in studies between the activity related to Affective Empathy and Cognitive Empathy may partly result from systematic differences in the type of stimuli processed during the experimental tasks [29]. For example, tasks designed to measure Cognitive Empathy often require more reasoning than tasks designed to measure Affective Empathy. As reasoning skills are indeed important for empathy processes in many contexts, the neural activity related to reasoning does not necessarily reflect the activity that is of interest when seeking to specify the activity specific to Cognitive Empathy. For example, the temporoparietal junction seems to consistently be engaged in Cognitive perspective-taking [15, 36]. Some findings suggest however that this activity may not be specific to empathy [37]. In order to be able to distinguish between activity related to Cognitive Empathy and activity related to mere reasoning, using experimental settings that do not require high levels of basic reasoning would be beneficial. This has been considered in the design of the task used in our EEG study. During the task extensive reasoning should not be necessary, as only short-time estimations related to the other person's intentions are needed in order to succeed in the task. For this reason, in case differences between the neural patterns of Cognitive Empathy and neural patterns of Affective Empathy were to be found, there should be no reason to presume that these differences were due to general reasoning.

These among other limitations have added to the challenges of specifying the exact roles of the different regions and networks in different empathy processes. Although the precise roles of different neural structures are not yet clear, there is strong evidence supporting the significant involvement of the neural structures and networks mentioned above in the two partly separate empathy components. While these neural structures are found essential for successful interaction and collaboration, another vital element consists of the cues of the environment that are used for making the assumptions and predictions of others' intentions and behavior.

In online environments, the number of social cues is often limited which can affect the extent to which Empathy mechanisms are activated. In the next section, I will present prior findings related to the association between online environments and empathy.

1.4 Empathy and Virtual Environments

In online settings, empathy skills seem to be related to similar social phenomena as in face-to-face settings. For instance, performance in the RME test that reflects Cognitive Empathy skills has been associated with joint task-performance, in the case of both face-to-face and online collaboration [9]. However, evidence suggests a reduction in empathy skills during online interaction compared to similar interaction carried out face-to-face [9]. Empathy and collaborative performance have been found to decline in digital environments [11, 9, 1]. In these studies the authors suggest that the decline may result from the lack of efficient cues for correctly interpreting the intentions and mental states of others, inhibiting the activation of processes crucial for Cognitive Empathy. Additionally, the lack of these cues may lead to the absence of sharing the mental states of others by preventing emotion contagion. Due to these issues, there is growing concern that increased use of technology may adversely influence the development and functioning of empathy in real life settings.

A study by Konrath et al. (2011) shows a significant reduction in empathy scores among American adolescents since the beginning of the 1980's. The possibility that this could result from the increase in the use of technology has been suggested by many [11, 38], although direct causal evidence is lacking. In case of a direct association between the increased use of technology and decreased empathy skills, it could be that the tools used for online interaction do not support the development of empathy mechanisms. With the existing data, conclusions about the long-lasting relationship between empathy and use of technology are impossible to draw. However, while the effects of technology usage on empathy in the long run are unclear, the traditional tools used for online interaction have been found suboptimal for supporting empathic behavior [9]. For these reasons, better ways of communicating online are needed in order to help activate the mechanisms that are vital for successful interaction. There is also a possibility that improvement in online environments could be beneficial for individuals' empathy skills in the long run, as these improved environments could potentially better support the development of empathy mechanisms of individuals. Through rapid technological advancements more novel tools such as those utilizing virtual reality technologies offer new possibilities for better remote communication. However, more knowledge related to the neuroscience of online interaction is needed in order to be able to develop optimal tools that best support our inherent social competence.

There is a growing body of research regarding the differences in quality between digital and face-to-face interaction and a consensus on why these differences occur on a behavioral level [9, 1]. New tools for communication are also being developed constantly. However, questions regarding the underlying psychophysiological patterns that play a part in this variation have only recently been brought up in the field of cognitive neuroscience. Advancing the understanding of how empathy-related mechanisms function in the absence of natural social cues is extremely important and is therefore also the main question addressed in our current study.

1.5 Synchrony and Social Interaction

Behavioral and physiological synchrony between individuals has been found to emerge during social interaction [39, 40, 41]. In the following paragraphs, I will present studies exploring the connections between inter-subject synchrony and different factors related to social interaction, such as empathy, social affiliation and collaborative success. Evidence of these types of connections support the importance of behavioral and physiological synchrony for success of social interaction.

1.5.1 Behavioral Synchrony

Inter-subject synchrony of behavior has in several studies been found to increase spontaneously during interaction [42]. For example, people's steps tend to unintentionally synchronize when walking. Similarly, unintentional synchrony tends to emerge during face-to-face interaction when two or more people automatically align their posture in accordance with the postures of others [42]. Furthermore, deliberately increasing behavioral synchrony has been found to positively affect success of collaboration, ratings of social closeness and the will to collaborate between individuals [43]. In a study by Tarr et al. (2016), elevated self-reported levels of social closeness between subjects were found among those dancing together in synchrony, compared to those dancing together asynchronously [44]. In another study, rocking in synchrony prior to a collaborative joint-action task was found to decrease the overall time it took pairs to complete a collaborative task, compared to the time it took for pairs that had been rocking asynchronously [45]. Similarly, increase of spontaneous synchrony of fingertip movement was found to negatively correlate with individual social anxiety levels in a study by Yun et al. (2012) [46]. These findings on synchronization of movement have employed dance and simpler movement coordination in face-to-face settings. There are of course several kinds of possibilities for synchronization and also in other than physical environments. Recently, attempts have been made to create online group activities that intentionally enhance behavioral synchrony, and therefore potentially also Prosocial Behavior online [47].

Many explanations have been proposed for the link between behavioral synchrony and the quality of interaction. The formerly mentioned mirror neuron system is seen as one plausible cause of this automatically emerging behavioral synchrony [35]. Behavioral synchrony may, on the other hand, create shared cognitive states through matched behavioral states and further facilitate mutual understanding and communication [48]. Behavioral synchrony may hence both result from and also support physiological synchrony and empathic understanding [48, 41].

1.5.2 Synchrony of Biosignals

In addition to behavioral synchrony, the synchrony of biosignals has been found to correlate with different features of social functions, such as those related to the quality of interaction. Such findings have utilized measures of heart rate and heart rate variability captured by electrocardiography (ECG) [49], and changes in electrodermal activity (EDA) [50]. In an early study [49] related to the topic, increased inter-subject synchrony of heart rate and electrodermal activity was found among distressed married couples, compared to non-distressed married couples. This study also found that the level of physiological synchrony was related to the level of conflict during conversation. More recently, Pijeira-Diaz et al. (2016) found that physiological synchrony indices of EDA between students predicted better collaborative learning outcomes and were positively associated with different collaborative learning features, such as collaborative will in a classroom setting [50]. In another study carried out in a classroom, Ahonen et al. (2016) found that synchrony of heart-rate variability occurred between collaborating programmer students, and that this synchrony was associated with a lower perceived workload of the individual [40]. Synchrony of cardiac measures and self-reported social presence evaluations among pairs was also found during chat-based interaction [41].

Cardiac synchrony has also been studied among infants and their mothers. Synchrony of heart rate was found to increase between the mother and infant during social interaction, especially during moments of synchronized vocal and emotional expressions [51]. Synchrony of heart rate has even been studied during a firewalking ritual, where synchrony was found to emerge between the heart rate of the person taking part in the ritual and the audience viewing the ritual [52]. The extent of synchrony of cardiac measures between individuals has also been found to correlate with measures of Affective Empathy. Järvelä et al. (2014) found that synchronization of ECG activity between individuals was associated with the level of self-reported empathy related to interaction during a turn-based gaming session [41]. Subjects that had higher level of physiological synchrony with the counterpart perceived more similarity of emotional states and comprehension between themselves and the other player. This result was suggested to reflect the activity of the MNS and to support the theory that mutual understanding is at least partly gained through sharing similar emotional states [41].

These findings strongly imply that biological synchronization is associated with several aspects of social cognition and social behavior, including empathy, quality of interaction, and collaborative success. It seems that increased synchrony does not always reflect specifically positive interactions. Rather, synchrony increases in situations in which the need for perspective taking and efforts to understand one another are heightened. Similarly, synchrony seems to increase during emotion contagion. For these reasons, it seems likely that physiological synchrony both reflects empathic processes as well as supports them. Understanding whether this physiological synchrony that likely supports empathy occurs in online situations would therefore be important. In case synchrony does not occur at the same level as face-to-face, new ways of attaining synchrony in online situations could be explored in the future.

In addition to inter-subject synchrony of biosignals related to EDA and cardiac measures, interesting findings on the inter-individual synchrony of biosignals related to the central nervous system have been made [29]. In the following section, I will present some findings related to this type of inter-brain synchrony.

1.6 Inter-brain Synchrony

Inter-brain synchrony in various brain regions measured with functional near-infrared spectroscopy (fNIRS), fMRI and EEG has been found to correspond to several social functions, such as: social gaze [53, 54], turn taking [55], facial communication of emotions [56] and feelings of social closeness [57] during different forms of interaction; different phases of collaborative tasks [29], decision making [58], collaboration [59] and level of competition [60] during gaming; degree of pain relief during hand-holding [61]; and coordinated actions [62] as well as empathy levels [63] during music production. The direction of synchronization, such as Granger causality that examines causal relationships between neural signals of individuals, can also be investigated. This means exploring possible factors that contribute to determining which one of the interacting individual's neural activity is likely to adapt to those of the other (instead of vice versa). For example, findings suggest that neural activity, measured with fNIRS, of individuals with better communication skills is more likely to become synchronized with the activity of others [64]. In another study investigating activation of brain regions with fNIRS, it was found that the brain activity of females in a romantic dyad synchronized more with the activity of their male counterparts than vice versa [65]. To conclude, measuring inter-brain synchrony has been found to be a valid method for investigating the neural processes related to different social phenomena between interacting individuals.

It should be noted that in the literature of inter-brain neuroscience different terms such as connectivity, coupling and linkage are interchangeably used to refer to synchrony. Additionally, these terms (e.g. synchrony, linkage, coupling, connectivity) are used in the literature when describing various different measures of synchrony, such as spatial distribution of neural activity or similarities in specific temporal patterns of neural signals. Due to the variety of terms used for the same concepts as well as the variety of different concepts described using the same term, it is important to consider the details of the findings when reviewing the literature related to inter-brain synchrony. In this as well as in upcoming chapters, synchrony is used as a term to more generally describe temporal or spatial similarities that have been found in neural activity between two or more subjects. Differentiation between distinct measures of synchrony will be made and more specific definitions will be provided, when relevant.

1.6.1 Inter-brain Oscillatory Synchrony

EEG is one of the most commonly used methods in research related to inter-brain synchrony. This is due to the temporal accuracy and non-invasiveness of the method as well as the convenience and availability of the required equipment. Compared to some of the other methods such as fMRI and PET, EEG lacks in spatial accuracy but is less obtrusive, which enables measurements in more ecologically valid settings [2, 66]. When studying neural synchrony during online interaction - as in the study of this thesis - these advantages of EEG are particularly important. This is due to the fact that looking at any type of more specific temporal synchrony requires high temporal precision. Additionally, as online interaction already lacks most natural social cues, any additional unnatural features of the experiment, such as extremely strict restriction of movement or high levels of noise, caused by some of the other methods(eg. fMRI) may diminish the remains of the social nature of the experiment. In the following paragraphs I will present the EEG method in more detail along with literature concerning previous EEG studies related to social cognition and inter-brain synchrony.

EEG is used to record signals that consist of rhythmic patterns produced by the relative changes in electric activity of neural populations in different parts of the brain as a function of time. These rhythmic patterns are more commonly referred to as brain waves, or oscillations. The EEG signal consisting of these oscillations can be further decomposed into several signals that represent the oscillations as composed of different frequencies. Frequencies of EEG signals can vary from 1Hz to 150Hz [67]. Frequency bands are most commonly categorized as delta (0,5-4Hz), theta (4-8Hz), alpha (8-13Hz), beta (13-30Hz), gamma (30-45Hz) and high gamma (45-70Hz).

Due to the typical occurrence of theta, alpha, beta and gamma frequency during wakefulness, these frequency bands are of most interest when it comes to social neuroscience. Oscillatory changes in these different frequency bands have been associated with various cognitive processes such as perception, attention and memory during one-person recordings [68]. Features of the alpha and gamma frequency band have particularly been associated with social cognition, as mentioned previously in connection to studies on mu oscillations [53, 33]. A large number of studies on brain activity and social cognition have been made with experiments investigating subjects' responses to socio-emotional and other social stimuli. However, in most cases, social interactions consist of a constant loop of two or more people producing social cues as well as interpreting and adapting to those of others [5]. Due to this nature of social interaction, there is now a common understanding that investigating neural activity related to social interaction requires looking at the behavior and biosignals of two individuals simultaneously instead of one individual at a time [2]. As a result of this consensus and the improved methods for measuring the activity of several brains at once, the amount of inter-brain research related to social interaction has grown since the first known two-brain measurement in the 1960's [69]. The technique of simultaneous measurement of the activity of two brains using different methods such as EEG, fMRI, MEG and positron emission tomography (PET) has come to be called hyperscanning or 2PN imaging [2].

As EEG is used to record the electric oscillations produced by neural activity, the inter-brain EEG studies related to social interaction focus on the oscillatory neural synchrony between two or more subjects during interaction. Evidence suggests that this type of synchrony plays an essential role in social interaction. Increased inter-brain synchrony of brain oscillations has been found to occur in a variety of social situations among several frequency bands [55, 60, 63, 62]. Different settings in which this synchrony has been studied include several gaming settings [60, 58, 70], interactive motion and music production [55, 62], and natural interaction [53, 49].

To date, two types of measures commonly used to study oscillatory synchrony in inter-brain research can generally be defined as phase-specific (also referred to as phasic synchrony) or power-specific measures. The phase-specific measures consist of indices related to the synchrony between the temporal structures of neural signals. Within this definition, two signals are seen as synchronous if the patterns related to the signals' phase angles coincide [71, 63]. The power-specific measures which have only more recently been applied to inter-brain studies involve comparing patterns related to the power or amplitude of the signals within a given time series [53, 60].

In the next section I will describe two synchrony measures: phase locking value (PLV) and covariance in frequency-specific power that are specific measures relating to the previously mentioned phase-specific and power-specific measures, respectively.

1.6.2 Inter-brain Phase Synchrony

Methods used for estimating phase-specific synchrony of oscillations tend to consist of measures related to the phasic patterns of signals in the time frequency domain. One commonly used phase-based synchrony measure in the field is the phase locking value (PLV). PLV represents the phase angle differences between two signals over time.

In a study conducted by Hu et al. (2017) inter-brain synchrony was measured as the PLV between the interacting subjects' spatially corresponding EEG signals band-filtered to different frequency bands (theta, alpha, beta, gamma) [72]. Inter-brain synchrony was found to increase in conditions of high collaboration compared to low collaboration during a game that involves interactive decision making. More specifically, larger centrofrontal theta-band and centroparietal alpha-band synchrony was found in tasks set for high cooperation compared to tasks set for low cooperation.

Using similar methods Dumas et al. (2010) found higher synchrony between two subjects during synchronized compared to non-synchronized actions. This study involved a task during which subjects were to spontaneously create hand movements and take turns in imitating each other [55]. In this study, synchrony calculated for all electrode site combinations (not only corresponding sites) between the two subjects were considered. Differences in neural synchrony between synchronized versus non-synchronized movement was found in the alpha-mu, beta, and gamma frequency bands. In another study that included an imitation task, Yun et al. 2012 found that cooperative training before the task increased not only task performance, but also inter-brain synchrony.

Inter-brain synchrony has also been studied during natural verbal interaction. Similarly to Dumas et al. (2010), Perez et al. (2017) calculated PLV for all electrode combinations and found increased synchronization between the neural activity of listeners and speakers in the delta, theta, alpha and beta frequency bands [55, 73]. Synchrony was found even when EEG channels that were expected to measure activity related to processing auditory speech information were excluded from the inter-brain synchrony analysis.

The idea behind the PLV measure used in the studies described above, and other phase-specific synchrony measures, originate from intra-brain studies related to regional connectivity of the brain [2]. Phase synchrony measured between two regions reflects different neural populations interacting in a way that facilitates the information flow between these populations through temporally optimal states of the interacting neurons within a brain [74]. Many findings, some of which are presented above, have been made by utilizing these methods in also inter-brain studies. However, the theoretical approach behind the measures does not quite apply when looking at two brains at once, as the original theory relies on the assumption that the synchronized neural populations are in some manner physically connected. Although the findings that utilize phase-specific measures are undoubtedly valuable, the theoretical background leaves room for exploring other types of measures in the field to complement these previously presented findings related to phase synchrony. Novel settings and approaches have been welcomed in the field in order to gain more understanding about the significant neural phenomena underlying interaction [60]. Based on findings from recent studies, synchrony measured as covariance of power has been suggested as an alternative measure of inter-brain synchrony [53, 60, 75]. In the next section I will present some findings related to this more novel approach that may provide new insights in the future [60].

1.6.3 Inter-brain Synchrony as Covariance in Power

As differences in the power of specific frequency bands in the EEG signal seem to reflect different cognitive functions [76], comparing the patterns related to the power spectra of EEG signals between two subjects has recently been investigated in social neuroscience as a potential measure of synchrony specific to social interaction. One power-specific measure used in research as an index of inter-brain synchronization is the correlation coefficients between the power values of two signals in specific frequencies. Although the number of studies related to this type of synchrony is still limited, preliminary findings have been encouraging, motivating further research utilizing these indices.

Spapé et al.(2013) studied synchrony of signal power in the context of video gaming. In this study, correlation coefficients of power in five frequency bands (theta, alpha, beta, gamma and higher gamma) between subjects was studied during a computer-mediated gaming setting that took place face-to-face [60]. Increased synchrony of power fluctuations in the beta frequency band was found between subjects during interactive gaming. Furthermore, this synchrony was higher during competition compared to during collaboration. The authors suggest that this finding could result from the heightened need to predict the other person's moves and intentions when competing against, as opposed to collaborating with, someone else. This synchrony was found mostly over the motor cortex, which could support views on the importance of this area and the MNS in understanding and predicting the behavior of others [60]. Kawasaki et al. (2018) also found increased synchrony measured as covariance of amplitudes over the motor region during a collaborative finger tapping task [75]. In this study, synchrony was instead found in the alpha and beta frequencies. This synchrony was also associated with the pair's performance in the task, and increased synchrony was found among pairs that performed well, compared to pairs that performed poorly.

In a study comparing inter-brain synchrony between romantic couples and strangers, Kinreich et al. (2017) found that gamma power correlations in the temporoparietal region were significantly higher for couples than for strangers [53]. This finding supports the link between social affiliation and inter-brain synchrony. In addition, synchrony was higher during moments that included social gaze (looking at the partner's face) compared to moments that did not include social gaze. This finding highlights the role of natural social cues - often absent in online interaction - in neural synchrony. These findings are intriguing also due to the fact that the temporoparietal region covers a subset of brain regions important for functions related to Cognitive Empathy, including the temporo-parietal junction. As a result of these findings that support the significance of this type of power-specific synchrony in social interaction, demand for these types of analyses in social neuroscience has emerged [60].

It should be noted that when considering the role of any kind of synchrony in social interaction, it is important to differentiate between the inter-individual synchrony that stems from the similarities of the shared environment and the type of synchrony that is in fact uniquely related to the particular social interaction. Some form of synchrony can and is most likely to be caused by for example the stimuli originating from the shared surroundings. For example, if subjects are in the same physical environment, these stimuli include the sounds and visual characteristics of the environment, among other things. Although some of these shared stimuli do not concern subjects collaborating remotely, many shared stimuli that may cause effects on synchronization unrelated to those concerning social interaction still remain. These include, for example, emotional states that are related to unusual experimental situations, and processes related to or even required for the success of the given experimental task. For example, if increased inter-brain synchrony is found to correlate with task performance during tasks in which success depends heavily on synchronous timing of movement, it is important to consider weather this correlation actually represents something more than synchronised motoneuronal activity or even artefacts caused by successfully moving in synchrony. Tackling this issue becomes increasingly important when investigating, for example, MNS-related activity of the motor cortex that has sparked interest due to previous findings related to both one-person and inter-brain neuroscience.

It is often difficult to differentiate between the investigated synchrony and the synchrony emerging as a side product, as it requires well designed experiments and paradigms, carefully chosen analysis techniques, and broad consideration of research limitations when drawing conclusions. This issue is widely considered and addressed in prior research. These considerations include using appropriate baseline measurements to control for neural activity that is not of interest in the study, using more than one experimental condition in order to specify the conditions in which synchrony emerges, and exploring the level of synchrony in relation to different factors that may affect the level of synchrony. These among other considerations allow the interpretation of the previously presented findings as support for the existence of inter-subject synchrony specific to social functions.

However, what is not always considered in prior research, is the evidence that supports the fundamental role of empathy in psychophysiological, including neural synchrony. Due to the strong evidence of this association [60, 62], not considering empathy levels as a plausible explanatory factor in studies related to inter-subject synchronization may in some cases lead to incomplete conclusions. For example, in separate studies, connections have been found between 1) empathy and perceived quality of interaction, 2) empathy and level of synchronization of biosignals, and 3) synchronization of biosignals and perceived social closeness. As high empathy levels may result in higher ratings of social closeness, the association between synchronization of biosignals and perceived social closeness may in fact result from the effects of level of empathy on both of these variables separately. For this reason, including measures of empathy in studies related to inter-subject synchrony would appear highly important.

In our study presented in this thesis, the general challenges related to studying inter-subject synchrony specific to social interaction are considered. Additionally, the potential relationship between this synchrony and empathy levels of the subjects are investigated.

2 The Current Study

Previous evidence suggests that inter-brain synchrony measured using indices such as PLV and covariance of power is associated with various social functions. Prior findings also suggest that empathy mechanisms are not activated to their full potential during online interaction [9]. What has yet to be answered, however, is whether inter-brain synchrony can be observed during collaboration taking place purely online, and whether empathy plays a part in this synchrony. In order to address these questions related to inter-brain synchrony and online collaboration, I seek to answer the following:

1. Does inter-brain synchrony, indexed by correlations of relative power values between EEG signals of interacting individuals, occur during collaborative online gaming?
2. If so, is there an association between this synchrony and the highest level of A) Cognitive or B) Affective Empathy of the collaborating pair?

Through the findings of this study, I hope to advance an understanding of the relationship between empathy and power-specific inter-brain synchrony during online collaboration.

The experimental setting of this study was designed to capture the dynamic nature of social interaction. The experimental task entails a constant loop of the subjects interpreting and predicting each other's intentions and actions, as well as reacting to those of the other. The setting also includes the lack of social cues that is typical for online interaction.

By comparing the measured inter-brain synchrony to the subjects' level of both Cognitive and Affective Empathy, I hope to provide more specific insights on which type of empathy mechanisms the potential synchrony may be related to and which type of empathy mechanisms therefore may be activated in these types of settings that so prominently lack natural social cues.

A better understanding of the neural mechanisms underlying interaction in the absence of social cues could open up new possibilities for developing improved online tools. Understanding which empathy mechanisms are active during online collaboration would enable seeking ways to enhance the activation of these mechanisms. Similarly, understanding which empathy mechanisms are not activated online could help determine the requirements for improved online tools that may help activate these mechanisms or compensate for their absence.

2.1 Methods

2.1.1 Subjects

Due to the evidence suggesting positive associations between social closeness and inter-brain synchrony [57], pairs who knew each other in advance were recruited in order to increase the chances of capturing the phenomenon of inter-brain synchrony despite the absence of social cues. Twenty-two pairs of friends or other acquaintances volunteered to take part in the study. Subjects were recruited via the university's student mailing lists and social media. Participants were right-handed, Finnish-speaking adults and had normal or corrected-to-normal vision. One pair was excluded from all analyses due to an equipment failure during the EEG measurement. This resulted in 42 subjects (9 female-female, 5 female-male and 7 male-male pairs). The participants' age varied between 20 and 45 years with the average age of 27 years. Each subject filled in a consent form and a background questionnaire. Subjects also completed tests designed to measure individual IQ and empathy. These tests are presented in the following paragraphs. The experiment protocol was approved by the Ethical Committee of the Faculty of Behavioural Sciences at the University of Helsinki, Finland.

2.1.2 Empathy Measures

Empathy scores were collected using the Reading the Mind in the Eyes (RME) test and two subscales of the Interpersonal Reactivity Index (IRI) questionnaire [77, 22]. RME is a widely used test developed for measuring an individual's ability to recognize emotions from the faces of strangers using only information gathered from the person's eyes. The test items are 36 pairs of eyes of actors portraying a specific emotion. For each item (i.e. pair of eyes), the subject is given four words that describe an emotion as response options and has to decide which of the suggested emotions best describes the emotional state of the person in the picture. The score of this test was used as an index of Cognitive Empathy skills [22]. IRI is a self-report questionnaire that is used to measure different components related to dispositional empathy. In the questionnaire the subject is asked to answer questions regarding their behavioral tendencies. The questionnaire consists of the following subscales: perspective taking, which is the tendency to adopt the psychological point of view of others; fantasy, which is the tendency to spontaneously transpose themselves imaginatively into the feelings and actions of fictional characters in books, movies and plays; empathic concern, which is the tendency to experience other-oriented feelings of sympathy and concern for others facing misfortune; and personal distress, which is the self-oriented feeling of anxiety and unease in tense interpersonal settings [24]. The two subscales, empathic concern and personal distress, are commonly considered to measure levels of Affective Empathy [78, 79, 80], and will also be used to investigate Affective Empathy in the current study.

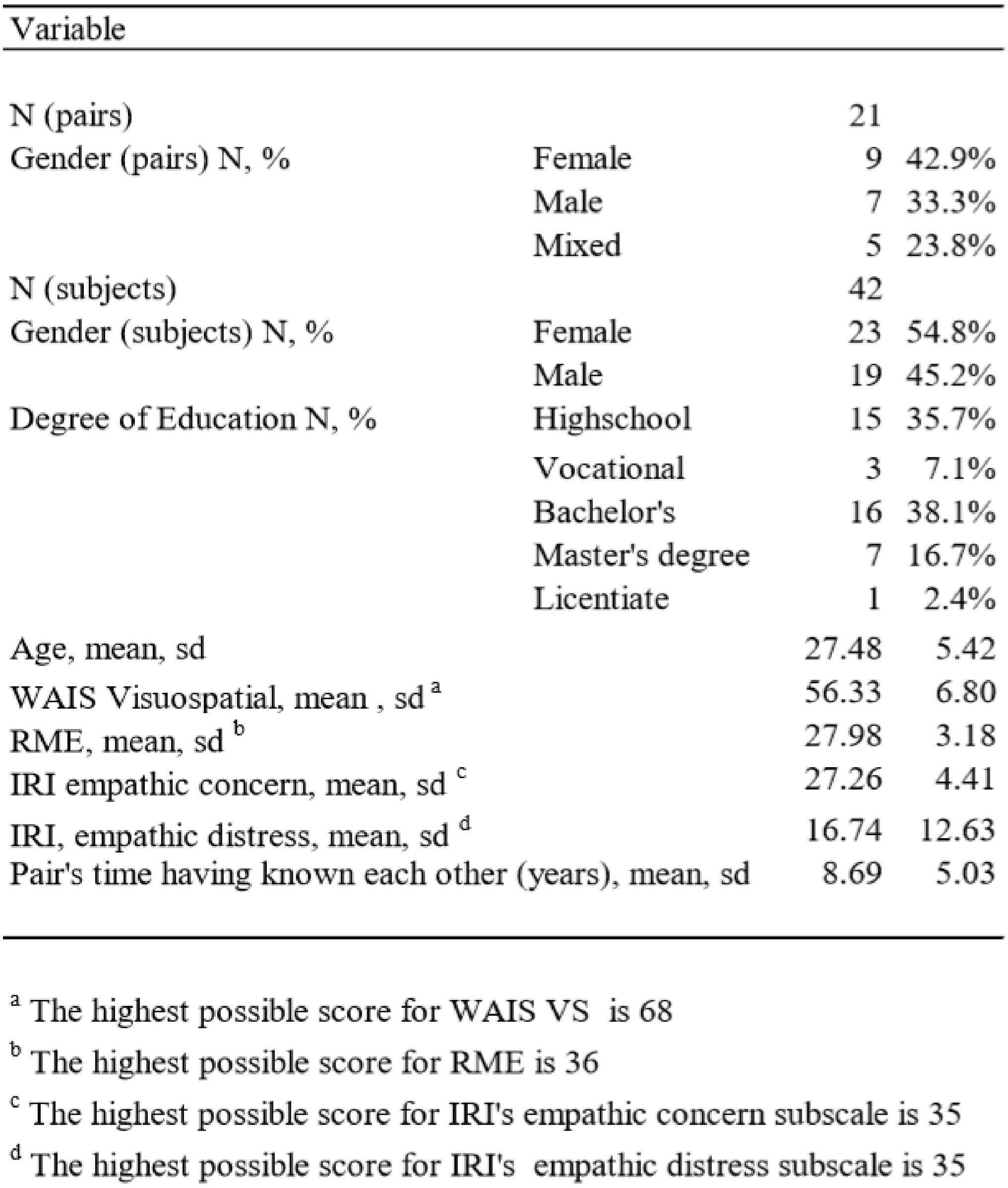
2.1.3 Visuospatial Skills

Visuospatial IQ was measured using the Block design subtest of the Wechsler's Adult Intelligence Scale's fourth edition (WAIS-IV) [81]. In this test the subject is given a set of cube-shaped blocks that consist of two white surfaces, two red surfaces and two surfaces that are half red and half white. The subject is then shown pictures of two-dimensional red and white figures and must construct the blocks within a certain time frame so that the surfaces of the blocks that are facing up match the two-dimensional figures presented in the pictures. WAIS is a widely used method for measuring individual IQ. The subtest used in this study was chosen due to its relevance concerning the experiment.

2.1.4 Background Factors

With the background questionnaire, information regarding age, gender, level of education and relationship with the other subject was collected. Group statistics on the background information as well as visuospatial IQ and empathy scores can be found in Table 1.

Table 1 *Descriptive statistics of participants' background factors*



Variable			
N (pairs)		21	
Gender (pairs) N, %	Female	9	42.9%
	Male	7	33.3%
	Mixed	5	23.8%
N (subjects)		42	
Gender (subjects) N, %	Female	23	54.8%
	Male	19	45.2%
Degree of Education N, %	Highschool	15	35.7%
	Vocational	3	7.1%
	Bachelor's	16	38.1%
	Master's degree	7	16.7%
	Licentiate	1	2.4%
Age, mean, sd		27.48	5.42
WAIS Visuospatial, mean , sd [a]		56.33	6.80
RME, mean, sd [b]		27.98	3.18
IRI empathic concern, mean, sd [c]		27.26	4.41
IRI, empathic distress, mean, sd [d]		16.74	12.63
Pair's time having known each other (years), mean, sd		8.69	5.03

[a] The highest possible score for WAIS VS is 68

[b] The highest possible score for RME is 36

[c] The highest possible score for IRI's empathic concern subscale is 35

[d] The highest possible score for IRI's empathic distress subscale is 35

2.1.5 The Task

In order to investigate inter-brain synchrony during online collaboration, a two-person online interactive racing game was created by the researchers of the Natural Emotionality in Digital Interaction (NEMO) project in the University of Helsinki. In this custom-built game, the goal of the pair is to drive a car along a track, while one of the subjects controls steering and the other controls speed. In this study, each pair completed two game sessions. One game session consisted of 8 runs which each lasted for 90 seconds. During this 90-second run, the task of the pair was to complete as many laps as possible. After each complete run, there was a 12-second pause during which the subjects' roles (steering vs speed) switched. This way each subject completed the same track playing both roles. After two runs of the same track, the track would change as a new run began and the roles of the subjects would switch back to the original ones. All-in-all, there were four different tracks that were each played as described. With four tracks, and each track being played in two different roles, this amounted to eight runs per session. After finishing the first session, the subjects were given a 10-minute break. Another identical session, where the subjects alternated roles in the exact same order through the 4 different tracks, was held thereafter. Other than driving the car together, the subjects had no other interaction during the task. An example track from the game is presented in Figure 1. The screen view was identical for both participants.

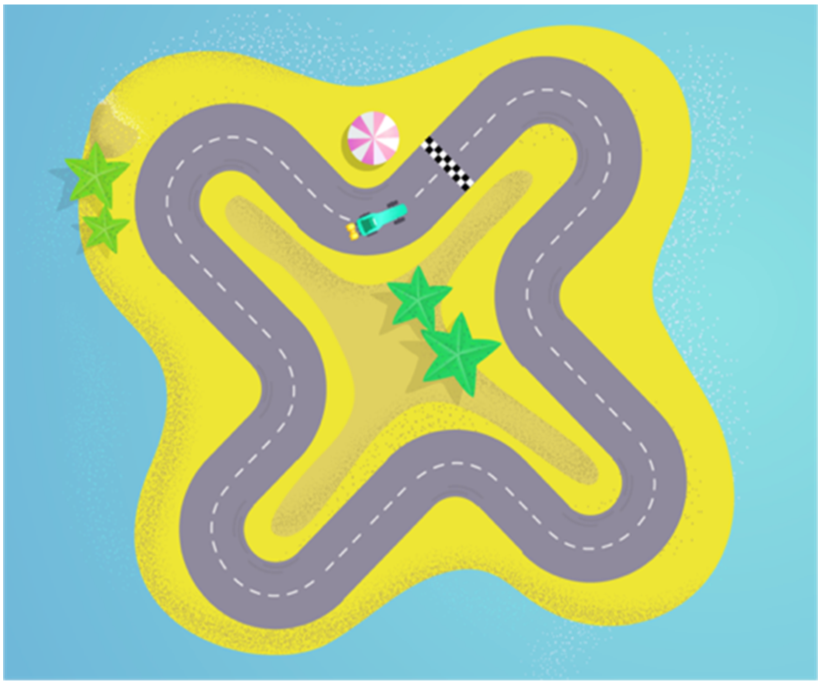


Figure 1: An example track of the online game used in the study.

2.1.6 Procedure

Upon arrival to the experiment, the two participants were asked to fill in a consent form. The subjects were informed about the course of the experiment and were informed that they could withdraw from the study at any time upon request without needing to provide a reason. After filling in the consent form, the subjects were separated and no longer able to communicate with one another. Two members of the research group were present conducting the EEG measurement separately for each participant. The participants were able to communicate with their respective researchers throughout the experiment. The subjects were randomly assigned to either first complete the IQ tests run by a member of the research group and then fill in the background, RME and IRI questionnaires while the other subject was assigned to carry out these tasks in the opposite order.

After this, preparations for the EEG measurements were made in the laboratory room where participants were seated in separate spaces with no visual contact with one another. An EEG cap with 64 electrodes was placed on the participant's head, two facial electrodes were placed to measure eye movements and two ECG electrodes were placed on the subject's upper body (for details see below).

During the experiment, subjects were seated in separate electromagnetically shielded rooms. The subjects were then individually introduced to the custom-built racing game described above. Subjects were informed about the setting and their goal regarding the task. As a result, they were aware that they would be playing the game with their partner and that they would not able to interact with each other, except in the form of playing the game. They were instructed to collaborate and finish as many laps as possible. During the experiment, the subjects used two keys of a regular key board at a time. The functions of the keys depended on (and changed according to) the subject's role and were used either to control speed (accelerating and decelerating) or steering (turning left or right). Both subjects sat approximately 80 cm in front of an identical (size: 19 x 19 inch, resolution: 1280 x 1024 resolution) computer screen used during the task. The course of the experiment is presented in Figure 2.

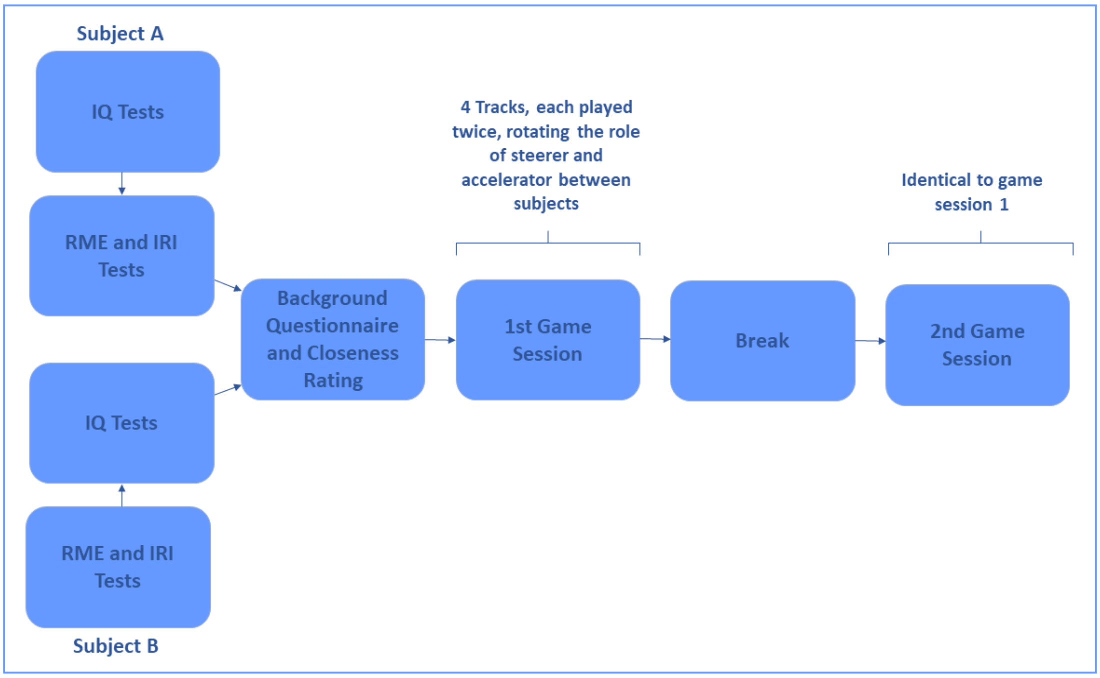


Figure 2: The course of the experiment.

2.1.7 EEG Recording

During the task, the brain activity of the subjects was simultaneously recorded in the separate shielded rooms using two EEG systems (BioSemi Active-Two systems, BioSemi, Inc.) with 64 active scalp electrodes at a sampling rate of 512 Hz. Information regarding subjects pressing the keys was stored in a log file and triggers from the coordinates of the car on (or off) the track were sent simultaneously to both of the subjects' EEG data, enabling precise temporal matching of the two EEG datasets. Reference electrodes were placed on the right and left mastoid. Two electrodes for measuring electrooculography (EOG) were placed beside and under the left eye in order to identify artefacts from vertical and horizontal eye movements. This number of EOG electrodes was found sufficient as the placement of the most frontal electrodes of the EEG caps used in this study also detect eye movements. In addition, ECG was measured with electrodes placed on the subject's upper body but ECG will not be included in the analyses of this thesis. The data for each gaming session was saved as separate datasets, resulting in two datasets per subject, and four datasets per pair.

2.1.8 Preprocessing

The preprocessing of the EEG data was carried out using EEGLAB [82] and custom MATLAB (MathWorks Inc.) scripts. Each dataset was set to begin from the starting point of the first race track and end 5 seconds after the endpoint of the last track of the session. Based on the EEG caps used, channel locations were added using the standard Biosemi 64 electrode 10/20 layout. The locations of the two EOG channels were added in accordance to the locations of the electrodes described above. Data from all channels was visually inspected, and flat or highly noisy channels were marked in order to be excluded in the following steps. Due to the inconsistent quality of the data recorded using the mastoid electrodes, resulting from mastoid electrodes having detached during some of the measurements, the data was referenced to channel Cz. After this, a low-pass filter of 0,5 Hz was first applied, followed by the application of a high-pass filter of 48 Hz.

The data was then segmented into three-second segments for exclusion of segments with significant artefacts. The segmenting resulted in 270 segments per the dataset concerning session 1 and 270 segments per the dataset concerning session 2, equalling 540 segments over all. The threshold for segment rejection was set to 500 uV. Prior to rejection, segments set for removal as well as segments set for inclusion in the data were visually inspected. This process resulted in a minimum number of 0 (0%) and a maximum number of 43 segments (16%) being removed from one dataset. In 35 out of 42 datasets, less than 10 segments (<4%) were removed, and all but one had less than 20 removed segments (<8%). In order to remove EOG artefacts from the data, Independent Component Analysis (ICA) was run for each dataset consisting of the remaining segments including data measured with the EEG as well as EOG channels. EEGLAB's IClabel tool was used to support the identification of these artefacts. As a result of initial inspection, components labeled as ocular artefacts with the probability of 90 percent or higher, according to IClabel, were removed from the data. Prior to the removal of each component, the components' spectral map and the effects of the removal of the component on the dataset were visually inspected. This IClabel criterion was found highly suitable for the removal of EOG artefacts throughout the datasets, as all components suggested for rejection based on IClabel were found to reflect ocular artefacts also based on visual inspection. Additionally, no components that were not suggested for rejection based on IClabel were found likely to reflect ocular artefacts based on visual inspection. The bad channels excluded from the previous steps of preprocessing were then interpolated.

After this the data was re-referenced to the common average in order to preserve data from Cz and prevent affecting the amplitudes of some channels more than others. Finally, the data included in the analyses was temporally matched for each pair. Segments rejected from one subject's data were also removed from the data of their partner. Concerning the pair's entire data, including both gaming sessions, this resulted in a minimum of 0 segments (0%), maximum of 45 segments (8%) and an average of 7.7 segments (2%) removed from a pair's data, leaving an average of 532 segments (98%) per pair for analysis.

2.2 Analysis

All 42 subjects (21 pairs) were included in each analysis. Due to the fact that the pairs taking part in the study consisted of individuals who had selectively chosen to participate together, independence of variables such as empathy scores and visuospatial scores between the subjects of each pair could not be assumed. As the number of pairs was lower than 35, which is seen as the minimum number of pairs required for reliable testing for the independence of the individual variables between the subjects, factors could not be reliably tested for and, hence, all analyses were carried out using pair instead of individual variables [83].

2.2.1 Inter-brain Synchrony During Collaboration

Between-subject correlations of relative power values for different frequencies and regions of interest (ROI) were calculated and used as an index of inter-brain synchrony among pairs. Due to and based on the variety of different brain regions and frequency bands found relevant in previous studies related to inter-brain synchrony and interaction, six regions (frontal, frontocentral, central, parietal, temporoparietal and occipital) and four frequency bands; theta (4-8Hz), alpha (9-13Hz), beta (14-30Hz) and gamma (31-45Hz), were considered in the synchrony analysis of this study. The EEG channels included in each ROI are presented in Figure 3.

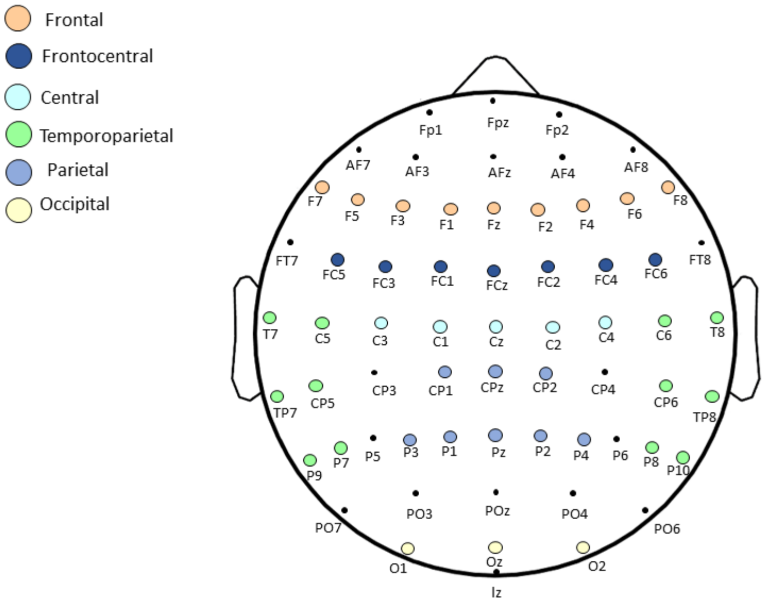


Figure 3: Electrodes included in each region of interest (ROI).

Correlation coefficients were calculated between relative power values of the EEG from subjects in each pair for each frequency band and ROI combination. These correlation coefficient values were used as an index of synchronization similarly as in the studies by Kawasaki et al. (2018) and Kinreich et al. (2017) [53, 75]. In order to examine whether synchrony was specific to collaboration, correlation coefficients between pairs were compared to correlation coefficients calculated between the data of two selectively chosen subjects that were not playing together. These false pairs were selected by matching two pairs in the study based on their level of performance in the task, so that the difference in the mean lap speeds during the two gaming sessions was as low as possible. Due to the uneven number of pairs, one of the pairs was included in two of the false pairs. Within these matched pairs, the subjects' data was matched to correspond with the reverse order of the roles (speed or steering) between subjects during the actual game session. The same temporal matching and segment rejection approach was applied as for real pair. Concerning the false pair's entire data, including both gaming sessions, this resulted in a minimum of 0 segments (0%), maximum of 45 segments (8%) and an average of 7.5 segments (1.5%) removed from a pair's data, leaving an average of 532 segments (98.5%) per false pair for analysis.

A multitaper spectral analysis was applied for the signal measured by each EEG channel to calculate the Time-Frequency Representation of the signal for each three second segment using DPSS tapers. The MNE multitaper tool was used with decimation resulting in 12 time points per each segment, thus a 4 Hz resolution. The relative power values (power of frequency bin / power of all frequency bins) for each frequency band concerning each EEG signal were then calculated for each segment.

After this, correlations of power in each frequency-band at each channel were calculated between each subject-pairs' temporally matched EEG segments separately for the two sessions. Then, the corrections were averaged across the channels within each ROI separately for each frequency-band. Finally, these frequency-band specific correlations were averaged across the two sessions resulting in 24 correlations for each subject-pair (4 frequency-bands x 6 ROIs).

In order to investigate whether some of the synchrony was specific to collaboration, t-tests were conducted for the correlations between pairs and false pairs after testing for normality of the variables. T-tests were carried out between the groups for each frequency band and ROI. In order to avoid type 1 errors, the *p*-values were tested at level 0.05 by applying a false discovery rate (FDR) correction [84] including all *p*-values. The significance of each mean synchrony index among both groups was also investigated by comparing the group mean regarding each synchrony index to zero.

After this, the significance of each synchrony index that was found to differ between the groups of pairs and false pairs was tested. One sample t-tests were conducted for each synchrony index among each group to see whether the group mean of the synchrony index differed significantly from zero.

2.2.2 Inter-brain Synchrony and Empathy

Those correlations that were significantly higher among pairs than false pairs were included in the analyses of inter-brain synchrony and empathy. The RME scores reflecting Cognitive Empathy and the scores of the two dimensions of IRI reflecting Affective Empathy were investigated separately. Due to previous findings [64] suggesting that the emergence of synchrony is associated with the highest level of social skills among the interacting individuals, the maximum levels of empathy within each pair was used in the analyses.

In order to assess the possible relationship between inter-brain synchrony and Cognitive as well as Affective Empathy, correlations between the subjects' level of frequency-band-specific regional synchrony and the separate empathy scores were calculated among pairs. An FDR correction at level 0.05 was applied for all correlations at once.

3 Results

3.1 Inter-brain Synchrony and Collaboration

The results of the t-tests on the difference in synchrony between pairs and false pairs can be seen in Table 2. The levels of synchrony are also presented in Figures 4 - 7. Significant differences in the correlations of relative power between pairs compared to false pairs was initially found for the theta frequency band in the frontal (t=3.269 , p=0.002), frontocentral (t=4.834, p<0.001), central (t=5.437 , p<0.001), parietal (t=4.455 , p=0.001), and temporoparietal (t=2.404 , p=0.021) regions; for the alpha frequency band in the frontocentral region (t=2.79, p=0.008); for the beta frequency band in the frontocentral (t=2.607 , p=0.013), central(t=3.531, p=0.001), parietal (t=2.678 , p=0.011) and occipital (t=2.474, p=0.018) regions; and for the gamma frequency band in the frontocentral (t=2.806 , p=0.008) and central regions (t=2.804 , p=0.008). The difference concerning beta power correlations in the temporoparietal region was also initially found significant (t=2.159, p=0.037) but the significance did not survive the FDR correction.

Table 2 *Sample Statistics and p Values for Independent Samples T-tests*

	Collaboration factor					
	Pair (n = 21)		False pair (n = 22)			
	M	*SD*	*M*	*SD*	Absolute mean difference	t-test p value
Alpha synchrony[a]						
Frontal	.009	.031	-.002	.030	.011	.249
Frontocentral	.033	.036	.007	.025	.026	.008**
Central	.017	.031	.005	.026	.012	.176
Parietal	.010	.030	.009	.021	.001	.904
Temporoparietal	.091	.067	.074	.060	.018	.372
Occipital	.014	.028	.006	.026	.008	.340
Beta synchrony[a]						
Frontal	.031	.069	-.002	.062	.033	.109
Frontocentral	.034	.050	-.001	.037	.035	.013**
Central	.049	.038	.010	.035	.039	.001**
Parietal beta	.025	.031	.002	.025	.023	.011**
Temporoparietal	.078	.064	.035	.066	.043	.037
Occipital	.027	.034	.004	.028	.023	.018*
Gamma synchrony[a]						
Frontal	.014	.107	-.017	.088	.031	.312
Frontocentral	.087	.103	.008	.081	.079	.008**
Central	.086	.074	.029	.059	.057	.008**
Parietal beta	.056	.058	.030	.044	.027	.095
Temporoparietal	.147	.129	.109	.110	.039	.293
Occipital	.026	.061	.017	.076	.009	.663
Theta synchrony[a]						
Frontal	.027	.028	-.007	.040	.034	.002**
Frontocentral	.052	.033	.001	.036	.051	.001***
Central	.041	.030	-.003	.022	.044	.001***
Parietal beta	.030	.023	-.002	.025	.032	.001***
Temporoparietal	.117	.091	.054	.080	.063	.021*
Occipital	.022	.042	.012	.036	.010	.420

[a] Inter-brain synchrony indices calculated between each pair and falsepair

*p < .05. **p < .01. ***p < .001.

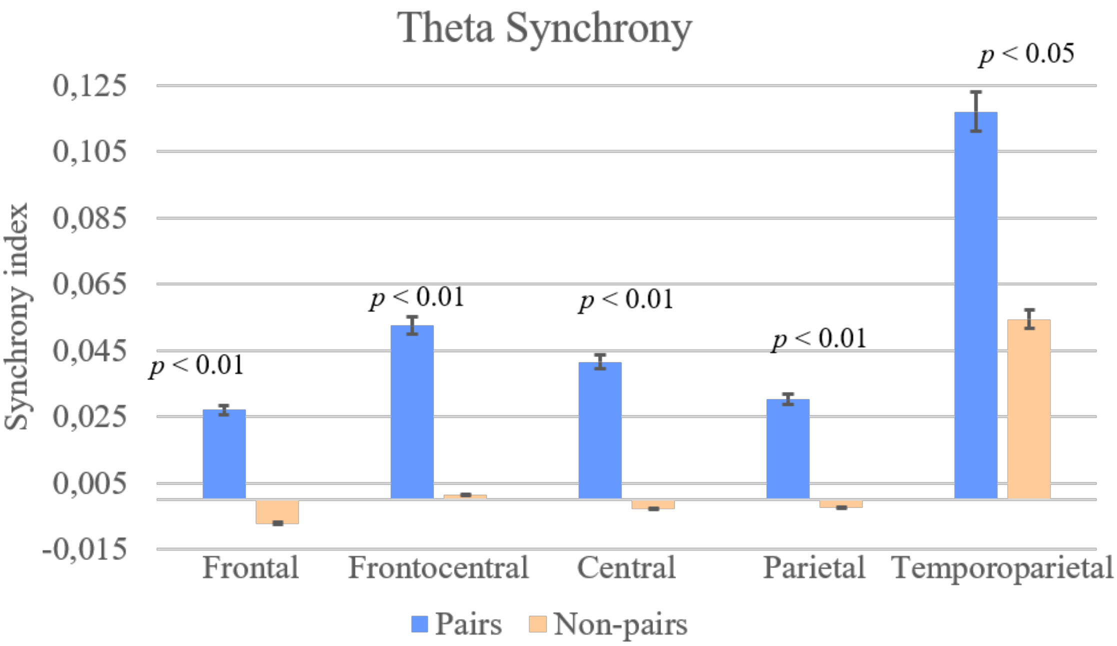


Figure 4: Differences in theta synchrony index means between group of pairs and group of false pairs.

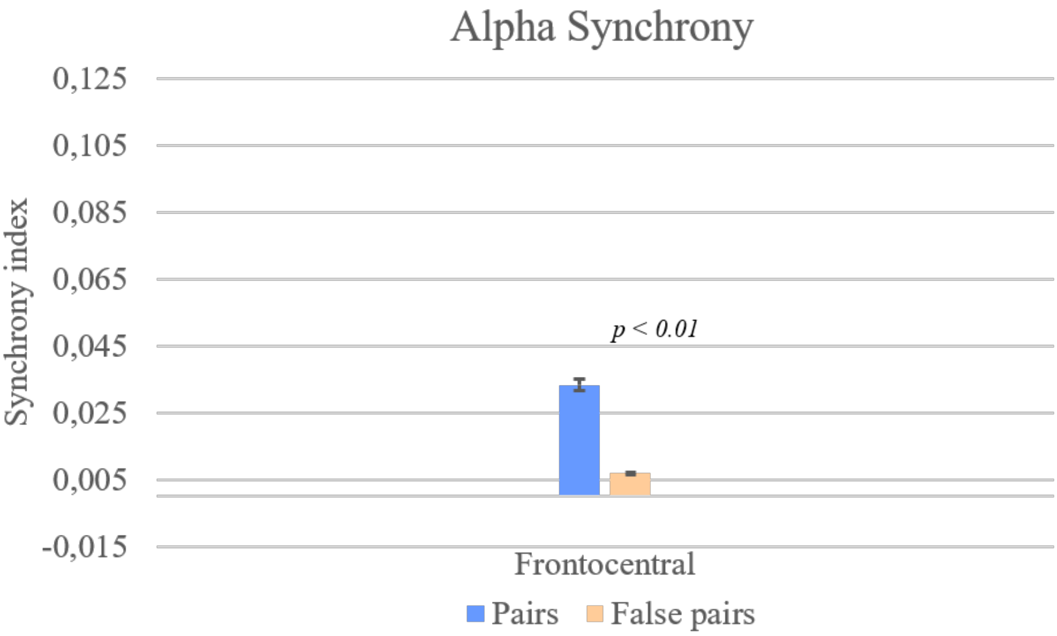


Figure 5: Differences in alpha synchrony index means between group of pairs and group of false pairs.

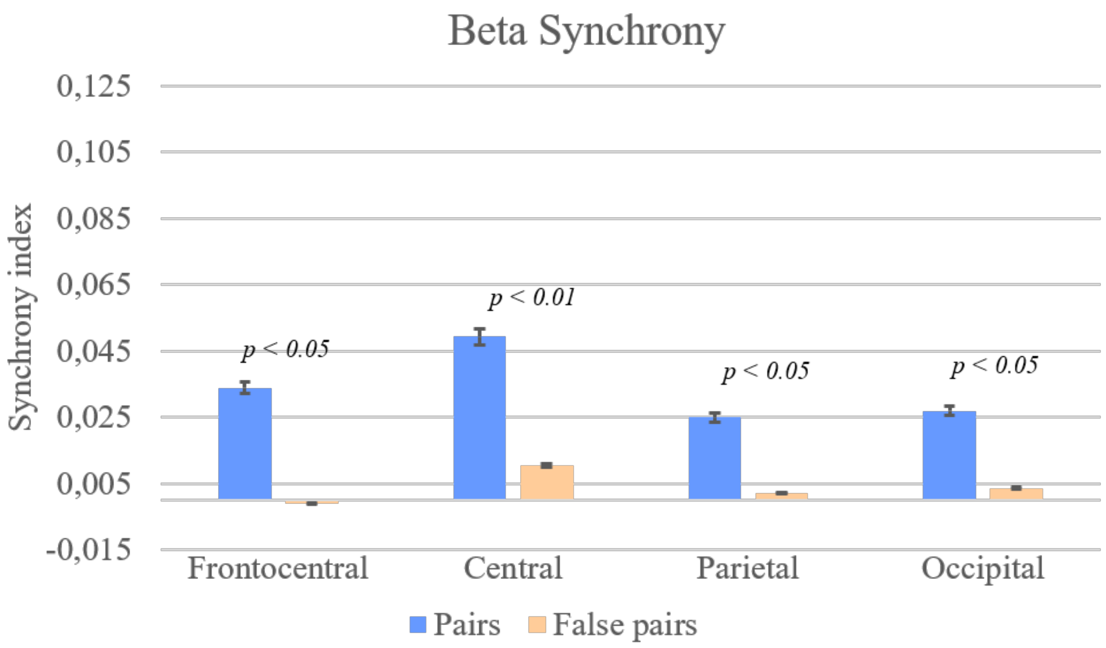


Figure 6: Differences in beta synchrony index means between group of pairs and group of false pairs.

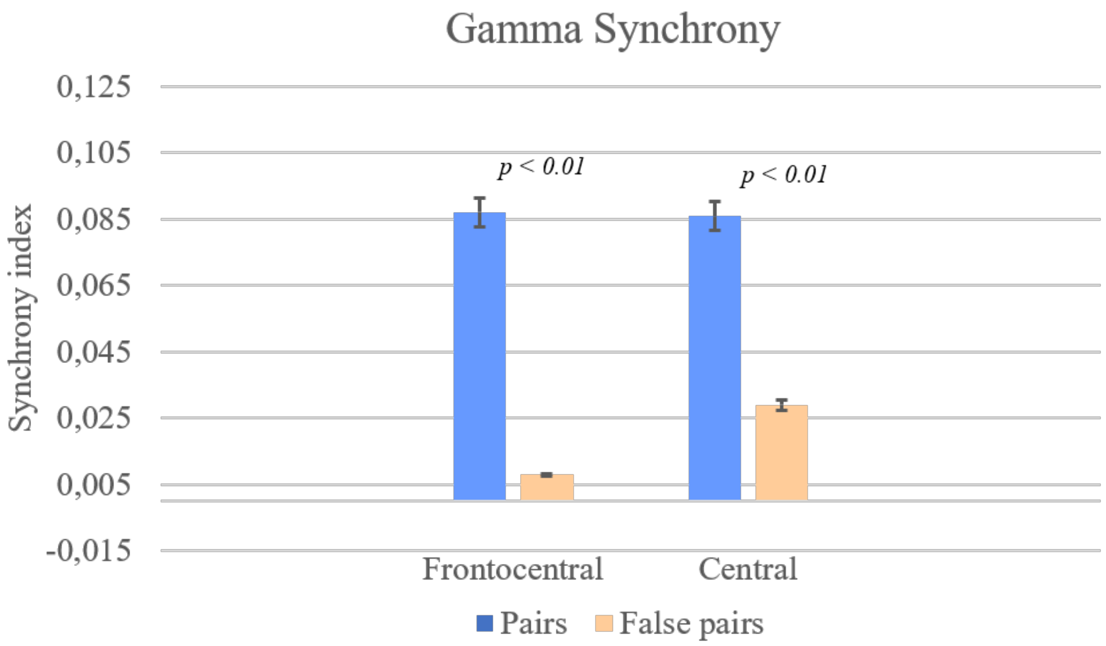


Figure 7: Differences in gamma synchrony index means between group of pairs and group of false pairs.

To test whether the mean of the synchrony index that differed significantly between pairs and false pairs differed significantly from zero, one sample t-tests within both the pair and false pair groups were performed for all 12 synchrony indices that remained significant after the FDR correction. The results of the independent sample t-tests can be found for pairs in Table 3 and false pairs in Table 4. At the group level, all of the correlation means were found to differ from zero for the group of pairs. For the false pairs, two of the correlation means were found to differ from zero (temporoparietal theta and central gamma). As the synchrony between false pairs can be assumed to reflect activity that is not specific to interaction (such as synchrony due to similar visual processing during the game), this synchrony was not included in the following analysis steps.

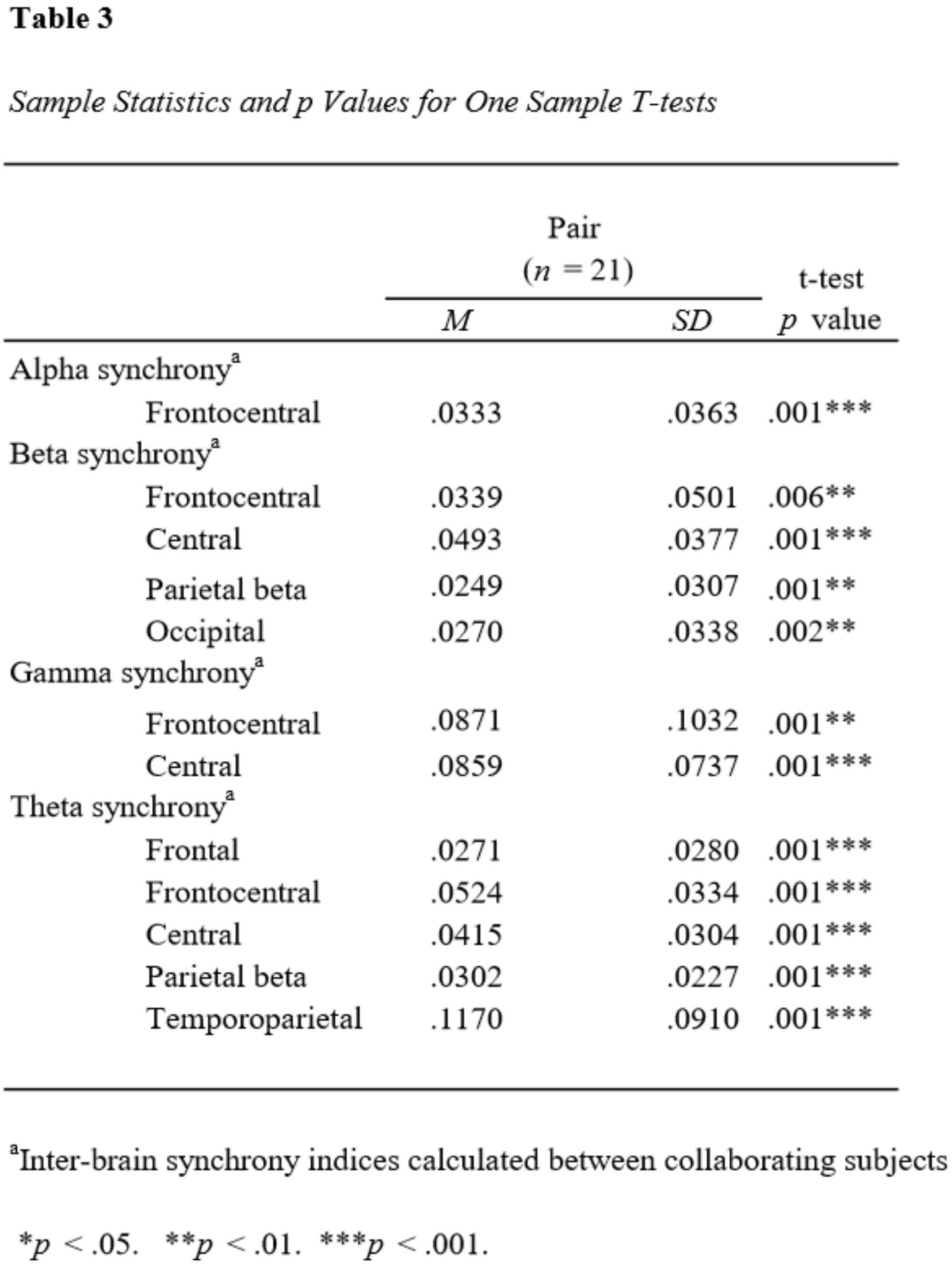


Table 3

Sample Statistics and p Values for One Sample T-tests

	Pair ($n = 21$)		t-test
	M	*SD*	*p* value
Alpha synchrony[a]			
Frontocentral	.0333	.0363	.001***
Beta synchrony[a]			
Frontocentral	.0339	.0501	.006**
Central	.0493	.0377	.001***
Parietal beta	.0249	.0307	.001**
Occipital	.0270	.0338	.002**
Gamma synchrony[a]			
Frontocentral	.0871	.1032	.001**
Central	.0859	.0737	.001***
Theta synchrony[a]			
Frontal	.0271	.0280	.001***
Frontocentral	.0524	.0334	.001***
Central	.0415	.0304	.001***
Parietal beta	.0302	.0227	.001***
Temporoparietal	.1170	.0910	.001***

[a] Inter-brain synchrony indices calculated between collaborating subjects

*$p < .05$. **$p < .01$. ***$p < .001$.

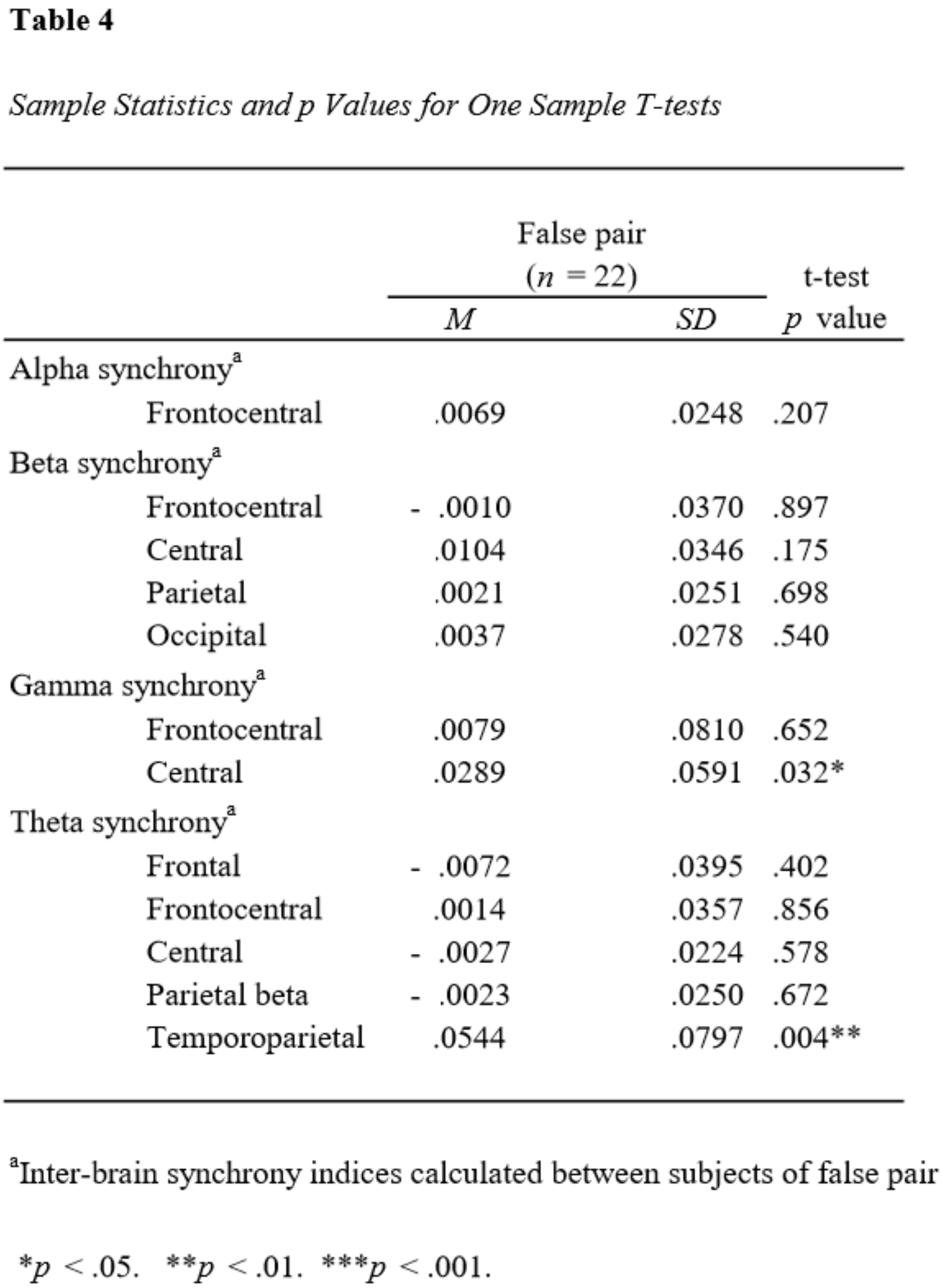


Table 4

Sample Statistics and p Values for One Sample T-tests

	False pair ($n = 22$)		t-test
	M	*SD*	*p* value
Alpha synchrony[a]			
Frontocentral	.0069	.0248	.207
Beta synchrony[a]			
Frontocentral	- .0010	.0370	.897
Central	.0104	.0346	.175
Parietal	.0021	.0251	.698
Occipital	.0037	.0278	.540
Gamma synchrony[a]			
Frontocentral	.0079	.0810	.652
Central	.0289	.0591	.032*
Theta synchrony[a]			
Frontal	- .0072	.0395	.402
Frontocentral	.0014	.0357	.856
Central	- .0027	.0224	.578
Parietal beta	- .0023	.0250	.672
Temporoparietal	.0544	.0797	.004**

[a] Inter-brain synchrony indices calculated between subjects of false pair

*$p < .05$. **$p < .01$. ***$p < .001$.

3.2 Inter-brain Synchrony and Empathy

A one-way ANOVA was performed for each measured variable to investigate whether there were differences in any of the measured synchrony, maximum empathy levels (Cognitive and Affective) or visual IQ (min, mean or max) between pairs of different genders (female, male or mixed). No differences between the three groups were found for any of the tested variables. These groups were therefore all included in the same analyses.

No significant correlations were found between synchrony and the pair's maximum RME score, maximum empathic concern score, maximum empathic distress score or any of the pair's visual IQ scores (pair min, pair mean or pair max) after the FDR correction.

Prior to the FDR correction, significant positive correlations were found between the pair's maximum RME score and the pair's theta synchrony in the temporoparietal (r=0.465, p=0.034) region as well as gamma synchrony in the frontocentral (r=0.457, p=0.030) and central (r=0.5411, p=0.011) regions. An initial significant positive correlation was also found between beta synchrony in the occipital region and empathic distress (r=0.512, p=0.018).

4 Discussion

The aim of this study was to investigate the occurrence of inter-brain synchrony during online collaboration and explore the relationship between this synchrony and the levels of Cognitive as well as Affective Empathy of interacting individuals.

To this end, inter-brain oscillatory synchrony was calculated between individuals who were playing a collaborative online driving game together without being able to communicate with one another in any other form but through playing the game. The inter-brain synchrony between subjects who were playing together was compared to synchrony between subjects of false pairs who were not playing together.

To the author's knowledge, this study is the first attempt to investigate inter-brain oscillatory synchrony and its associations with empathy using a collaborative gaming setting that takes place purely online.

Due to previous evidence on the association between inter-brain synchrony and face-to-face collaboration, we expected that synchrony might also occur during online collaboration. We also expected that the subjects' empathy skills may be associated with the level of this synchrony.

As expected, inter-brain oscillatory synchrony specific to interaction was found between the subjects collaborating together online. However, significant associations between this synchrony and the investigated empathy levels of the subjects were not found.

Significant differences in the inter-brain synchrony measured over multiple regions and frequency bands were found when comparing pairs who were collaborating together to false pairs who were not collaborating together. This finding suggests that processes specific to interaction seem to account for some of the observed synchrony. Significant synchrony that differed between the group of pairs and false pairs was found for the theta frequency band measured over the frontal, frontocentral, central, parietal and temporoparietal regions; for the alpha frequency band measured over the frontocentral region; for the beta frequency band measured over the frontocentral, central, parietal and occipital regions; and for the gamma frequency band measured over the frontocentral and central regions.

It should be noted that when investigating the significance of the synchrony indices, only the synchrony for which a significant difference between the groups of pairs and false pairs was found was considered. Therefore, no presumptions should be made concerning the relative amount of synchrony that is specific to collaboration compared to synchrony that is not specific to collaboration.

4.1 Inter-brain Synchrony During Collaboration

The findings of our current study suggest that synchrony in the theta frequency band measured over the frontal, frontocentral, central, parietal and temporoparietal regions; in the alpha frequency band measured over the frontocentral region; in the beta frequency band measured over the frontocentral, central, parietal and occipital regions; and in the gamma frequency band measured over the frontocentral and central regions might reflect processes specific to the type of collaboration required in the experimental online gaming setting of the current study. These processes include predicting the other's intentions and motor actions of either accelerating, decelerating or steering the car as well as adjusting one's own actions to those of the other. Correlation coefficients of the regional synchrony in frequency-specific power between the two subjects were used as an index for synchronization. It should be noted that the correlation coefficients used as indices of inter-brain synchronization were very modest in themselves and also when compared to previous findings [53, 60]. However, due to limited knowledge concerning the studied phenomenon, restrictions concerning the scale of potentially meaningful synchrony were not set for this study. Thorough efforts for preventing type 1 errors were also made by conducting FDR corrections. Therefore, the significance of each synchrony value and the differences in these values between pairs compared to false pairs can be assumed with reasonable levels of confidence. Hence, it could well be that as synchrony does occur during online interaction, it is not as strong as during face-to-face interaction. This may be a result of the lack of natural social cues that play a role in inter-individual synchronization.

There are different possible explanations as to why the lack of social cues may decrease synchronization. First, the fact that the subjects were not in visual contact with each other may prevent the type of automatic neural resonance that occurs due to simply observing the other person during face-to-face interaction. Second, the absence of social cues may prevent more controlled processes, such as those related to interpreting the other person's intentions and actions.

Similarly measured gamma synchrony has also previously been associated with social functions, specifically social connectedness and social gaze, during face-to-face interaction [53]. However, in the study in which such associations were found [53], the increased gamma synchrony was found over the temporoparietal region instead of the frontocentral and central region as was the case in our current study. In the same study [53], subjects were seated together in the same room, and their task included communicating with one another. Due to the difference in the setting of this previous study compared to our current study where participants were collaborating purely online, the differences in the findings could at least partly reflect the differences of the cognitive processes related to collaboration during the presence, versus the absence, of natural social cues. It is possible that gamma synchrony in the temporoparietal regions reflects some processes specific to face-to-face interaction, such as processing natural social cues and adapting one's actions and mental states according to these cues. Not having access to these cues online might result in the activation of alternative processes when trying to predict or adapt to the actions of others. These alternative processes could be reflected as other types of synchrony - such as the type found in our study - between the subjects.

Additionally, similarly measured beta synchrony has previously been found during a computer gaming study where participants were playing together while sitting next to each other [60]. In this previous study, increased beta power synchrony was found only over the central electrode sites, as opposed to over a broad range of electrode sites as in our current study. In our study, the success of the pair relied highly on collaborative efforts between the subjects and did not include competition. Hence the synchrony found in our current study should not represent any factors related to competition. Conversely, the previous study found that synchrony was higher during competitive compared to collaborative conditions. As suggested by the authors of the previous study [60], the finding that central beta synchrony was altered by level of competition may have resulted from emphasized motivation for predicting the intentions of others during competition as compared to collaboration. This could explain the difference in the level of beta synchrony measured over the central region which was lower in our current study than in the previous study. Another explanation for the differences between the findings of the previous and our study concerning beta synchrony could also be related to the natural social cues that were present in the previous but not in our current study, similarly as in the case of the previously discussed gamma synchrony.

In another study, the level of alpha power correlations in the visual and motor areas between collaborating individuals was found to be associated with better success in a task requiring adapting to each other's rhythmic behavior [75]. In our current study, alpha synchrony was found in the frontocentral region, which may similarly reflect synchrony in the motor areas. In the study by Kawasaki et al. (2018), the task required subjects to produce simultaneous behavior that was identical for both of the subjects, as their goal was to tap their finger in the same rhythm with their counterpart [75]. In the task of our current study, subjects also produced similar movements as they were both pressing keys on a keyboard. However, in the current task the subjects had distinct roles as one steered while the other controlled speed. Additionally, although temporally well-orchestrated coordination of behavior between the subjects was required for successful performance in the current task, the task did not require identical timing of behavior. In fact, systematically identical timing of pressing keys could be expected to result in exceptionally poor performance in this type of a task. The findings from the previous and current study together suggest that alpha synchrony measured over the frontocentral region could reflect processes related to adapting to the movements of each other. This neural synchrony could also reflect the type of synchrony of movement that is not specific to identical timing. Furthermore, the core of the MNS has been found to include the posterior part of the IFG, the PMv and the PMd. As the activity of these areas is likely measured from the frontocentral and central electrode sites, it could well be that the synchrony measured over the frontocentral region reflects activation of the MNS, as activity of the MNS has generally been found represented in alpha frequencies. This might suggest that the current task (i.e. animated car known to be partially controlled by the partner) could be enough to cause some sort of mirroring of the other person's states. It should, however, be emphasized that without source localization of the EEG signal, information regarding the location sites on the scalp only provides vague estimations of the sources of the signals. Therefore conclusions about the precise location of the measured synchrony can not be made.

In our current study, collaboration through the online task seems to have been enough for the emergence of some level of synchrony specific to interaction. However, as the significant synchrony values found in this study were weaker compared to similar synchrony values found in various previous studies investigating synchrony in face-to-face settings, it may be that the absence of social cues causes decreased synchronization of brain activity. This could also be a result of other differences in the experimental settings, such as the task. In addition, the frequency bands and electrode sites in which synchrony related to interaction was found differed to some extent from those of previous studies. This variation may reflect differences in the processes that are active during interaction in face-to-face versus in online settings. As synchrony in the theta frequency band measured over the frontal, frontocentral, central, parietal and temporoparietal regions; the alpha frequency band measured over the frontocentral region; the beta frequency band measured over the frontocentral, central, parietal and occipital regions; and the gamma frequency band measured over the frontocentral and central regions seem to reflect processes specific to collaboration (as defined by the task of the current study) synchrony in these regions and these frequency bands should be considered in future studies related to interaction. The specific role of synchrony measured over these various regions and frequency bands should be further investigated. These investigations could include exploring synchrony in relation to various factors that may alter the level of synchrony, such as task performance and social closeness.

The setting of the current study allowed examination of synchrony in relation to Cognitive and Affective Empathy levels. No significant associations between the synchrony indices and empathy levels were found after FDR correction.

As a downside of the FDR method used in order to prevent type 1 errors, the risk of type 2 errors was increased. It is therefore possible that some associations that were not captured by the chosen statistical methods nevertheless exist. The initial findings that did not survive the conservative methods concern the associations between RME scores (Cognitive Empathy) and temporoparietal theta as well as frontocentral and central theta synchrony. Although no conclusions should be made based on these initial findings between synchrony and empathy levels, these results may be considered with caution and used for guiding future studies.

In our current study, inter-brain synchrony specific to collaboration was found over the electrode sites in the theta frequency band in the frontal, frontocentral, central, parietal and temporoparietal regions; for the alpha frequency band in the frontocentral region; for the beta frequency band in the frontocentral, central, parietal, temporoparietal and occipital regions; and for the gamma frequency band in the frontocentral and central regions. Many different explanations for the occurrence of synchrony in these frequency bands and regions can be considered. These include processes specific to predicting the intentions of others in the absence of social clues. However, specifying the underlying reasons for the emergence of this synchrony must be left for future research.

Our findings suggests that inter-brain oscillatory synchrony, measured as the covariance in frequency-specific power, specific to interaction occurs during collaboration that takes place purely online and is thus not limited to face-to-face interaction. This means that the emergence of inter-brain synchrony does not necessarily require natural social cues. Synchrony in certain frequency bands measured over certain regions may occur in both face-to-face and online settings. However, some synchrony concerning specific regions and frequency bands was found in the current study but not in previous ones using similar synchrony indices and vice versa. Although the current study is not directly comparable with the previously discussed studies, some of the differences in the findings of our current study compared to previous findings could result from the lack of social cues during the experiment used in the current study.

Initial findings related to the relationship between inter-brain synchrony and levels of Cognitive and Affective empathy were also found but these findings did not survive the methods used for controlling for false discoveries. The possible significance of these preliminary findings between synchrony and empathy should not be assumed but they may be considered with caution in relation to planning future studies.

4.2 Limitations

A number of limitations concerning the current study should be addressed. Due to the limited knowledge concerning inter-brain synchrony, various other potential explanations behind the synchrony found between pairs compared to false pairs should be considered. Although the false pairs were formed by matching the datasets that were temporally most consistent with one another, the matching of the game phases and behavioral processes among the false pairs can not be assumed to correspond with the same precision as among the pairs. This is particularly relevant when considering synchrony regarding neural activity that is more likely than others to stem from the motor areas.

Additionally, although most EEG measurements were conducted during the same time of day, there was some variation in the time of day of the measurements. This means that the time of the EEG measurement might have differed between the false pair subjects, whereas the measurement of the actual pair subjects was always simultaneous. As systematic variation of activity in each frequency band is likely to occur throughout the day, this can be seen as an issue that needs to be controlled in future studies. In addition, appropriate baseline measurements conducted during resting state conditions as well as during individual game play would have been beneficial in order to control for, for example, individual differences in the power distribution in different frequency bands. Furthermore, these baseline measurements would have diminished some of the issues relating to the comparisons between actual pairs and false pairs by providing more optimal ways of controlling for the portion of synchrony that is not specific to collaboration. Lastly, as all pairs consisted of friends or acquaintances, some similarities in the brain functions of actual pairs compared to false pairs could have occurred due to, for example, common traits that result in selection of acquaintances.

In the analyses of our current study, synchrony was represented as the correlation coefficients of frequency specific relative power values. As mentioned previously, the index used as a representation of synchrony in this study has been used in previous research. However, power-specific synchrony methods have also been criticized by some [85]. More research is needed in order to further understand the significance of the emergence of these common patterns related to the fluctuation of frequency-specific relative power values. Similar studies using multiple measures of phase and power synchrony at once would also be extremely useful.

Initial significance of associations between the measure of Cognitive Empathy and the level of inter-brain synchrony was found, although these associations did not survive FDR corrections. Future research should, hence, address more questions related to possible additional factors that may affect the emergence of inter-brain synchrony and/or play a part in the relationship between this synchrony and Cognitive Empathy during online collaboration of this sort. It is possible that any potential associations between RME scores and increased synchrony are caused by some third factor that is associated with both synchrony and RME scores.

While EEG as a method can be found appropriate for the current study by enabling investigation of neural activity measured for different frequency bands and allowing an ecologically valid experimental setting, more precise spatial resolution would enable more accurate localization of the measured activity. Furthermore, for a broader view and for controlling the number of statistical tests, the activity recorded from the EEG channels used in this study was combined and averaged over six regions of interest, which makes localizing the synchrony increasingly challenging.

Finally, although the amount of EEG data allows comprehensive statistical analyses at the individual and pair level, the statistical power of the group level analyses and the external validity of the findings would have benefited from a larger number of subjects. Additionally, further research including a larger sample size would be beneficial for considering all variables on the group as well as individual level and distinguishing the associations specific to the features of the pair and the individual.

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