INTER-BRAIN SYNCHRONIZATION PATTERNS OF COOPERATION IN THE PREFRONTAL CORTEX DURING STAG HUNT GAME VIA FNIRS HYPERSCANNING

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ABSTRACT

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Cooperation in various tasks has been shown to increase synchronization between people's prefrontal cortices. In game theory, the Stag Hunt game is utilized as a model for social cooperation in the face of strategic uncertainty. In this thesis, we analyzed the synchronization of hemodynamic responses of 24 pairs of subjects under Functional Near-Infrared Spectroscopy (fNIRS) hyperscanning, playing ten rounds of repeated Stag Hunt games with each other. The data analyzed here were gathered for another thesis work (Aydoğan, 2019), partially replicating Schmidt et al.'s (2003) study that involves four types of Stag Hunt games with varying payoff and risk dominance levels. Wavelet Transform Coherence (WTC) increases were calculated for the same optode combinations between subjects to investigate inter-brain synchrony (IBS). Independent samples t-tests are performed to compare the IBS of subjects settling on the payoff dominant equilibrium (cooperation group) to other subjects (non-cooperation group). The cooperation group yielded significantly higher IBS between their dorsolateral prefrontal cortices than the non-cooperation group. This finding suggests that IBS synchrony might be an underlying neural mechanism for cooperation.

Keywords: fNIRS, inter-brain synchrony, Stag Hunt game, cooperation, hyperscanning

ÖZ

PREFRONTAL KORTEKSTE FNIRS HİPERTARAMA İLE GÖZLEMLENEN STAG HUNT OYUNLARINDAKİ İŞBİRLİĞİNİN BEYİNLER ARASI SENKRONİZASYON ÖRÜNTÜLERİ

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Bir çok işbirliği türünün insanların prefrontal korteksleri arasındaki senkronizasyonu arttırdığı gösterilmiştir. Oyun teorisinde, Stag Hunt oyunu, stratejik belirsizlik karşısında sosyal işbirliği için bir model olarak kullanılır. Bu tezde, Fonksiyonel Yakın Kızılötesi Spektroskopi (fNIRS) hiper taraması ile 24 çift deneğin hemodinamik tepkilerinin senkronizasyonunu, birbirleriyle on tur tekrarlanan Stag Hunt oyunları oynatarak analiz ettik. Burada analiz edilen veriler, Schmidt ve diğerlerinin (2003) farklı ödül ve risk baskınlık seviyelerine sahip dört tür Stag Hunt oyununu içeren çalışmasını kısmen adapte eden başka bir tez çalışması (Aydoğan, 2019) için toplanmıştır. Beyinler arası senkronizasyonu (BAS) araştırmak için denekler arasında aynı sensör kombinasyonları için Dalgacık Dönüşümü Tutarlılığı artışları hesaplandı. Ödül baskın dengesine (işbirliği grubu) yerleşen deneklerin BAS'ını diğer deneklerle (işbirliği olmayan grup) karşılaştırmak için bağımsız örneklem t-testleri yapıldı. İşbirliği grubu, işbirliği yapmayan gruba göre dorsolateral prefrontal korteksleri arasında önemli ölçüde daha yüksek BAS sergiledi. Bu bulgu, BAS senkronizasyonunun işbirliği için altta yatan bir nöral mekanizma olabileceğini imlemektedir.

Anahtar Sözcükler: fNIRS, beyinler arası senkronizasyon, Stag Hunt oyunu, iş birliği, hipertarama

To My Grandfather

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PFC	Prefrontal cortex
dlPFC	Dorsolateral prefrontal cortex
vmPFC	Ventromedial prefrontal cortex
FPC	Frontopolar cortex
IBS	Interbrain synchrony
WTC	Wavelet Transfer Coherence
SCA	Shared Cooperative Activity
fMRI	Functional magnetic resonance imaging
fNIRS	Functional near-infrared Spectroscopy
FDR	False discovery rate

CHAPTER 1

INTRODUCTION

There is a shifting trend in social neuroscience towards observing people in real-life scenarios. This shift is necessary to capture the unique qualities of human interaction that emerge only in these kinds of real-world scenarios (Schilbach et al., 2013). Since Montague et al. (2002), hyperscanning gained popularity as a method to capture the dynamic nature of human interaction. This method allows researchers to collect data from two brains simultaneously and investigate the nature of the relationship between subjects' brain signals which tend to synchronize during social alignment. Interbrain synchrony has been claimed to be an essential part of the neural mechanism of the human social attention system (Gvirts & Perlmutter, 2020). Therefore, it is desirable to utilize this tool to investigate social phenomena.

Cooperation is an innate trait that differentiates humans from other species and involves acting on a shared goal by sharing intentions (Tomasello et al., 2005). It is the essential skill that ensured the human species' survival and creation of culture (Tomasello et al., 2012). Given the significance of the subject, there has been a surge of hyperscanning studies that explored the interbrain synchrony of cooperating people utilizing different tasks, underscoring the relevance of prefrontal cortex synchrony for cooperation (Czeszumski et al., 2022). Functional Near-Infrared Spectroscopy (fNIRS) is a brain-imaging methodology that is non-invasive, portable and with a good balance of spatial and temporal resolution (Quaresima & Ferrari, 2019). Therefore, fNIRS has been heavily utilized in hyperscanning studies due to these qualities.

Behavioral economics, specifically Game Theory, has been a fruitful study of social decision-making and is being integrated with behavioral sciences more and more (van Dijk & De Dreu, 2021). In this vein, neuroeconomics research utilizes both Game Theory and neuroscience research for understanding the nature of humans in a more holistic manner. One of the heavily studied games in Game Theory is the Stag Hunt game. It is a game in which trusting the other player and coordinating one's action yields the best outcome. The Stag Hunt game has been suggested as a problem of trust and cooperation (Skyrms, 2001) and a model for human cooperation in the foraging history of the human species (Tomasello et al., 2012). The Stag Hunt game varies in characteristics of reward and risk, which allows researchers to investigate the effect of reward and risk on cooperation.

In this light, this study aims to explore the interbrain synchrony between cooperating players during the Stag Hunt Game and how interbrain synchrony changes with different game characteristics.

1.1 Research Questions and Hypotheses

In this study, we used the data collected for thesis work (Aydoğan, 2019). In the original study, people played four different kinds of Stag Hunt games, differing in payoff and risk. fNIRS measurements are used for activation analysis individually. In this study, we utilized the hyperscanning methodology to look at the same data from an interactive social neuroscience perspective. We assigned the pairs into two categories, cooperation, and non-cooperation, according to their history of play. We calculated Wavelet Transform Coherence increase values to observe interbrain synchrony among the pairs.

In this thesis study we investigated the following research questions:

1. Does cooperating while playing Stag Hunt games result in a higher interbrain synchronization than not cooperating?

2. How do the game characteristics affect the interbrain synchronization of pairs?

Human cooperation in different tasks yields interbrain synchrony among the prefrontal cortices of subjects (see Czeszumski et al., 2022 for a detailed review of the literature). Given the nature of the Stag Hunt game, we argued choosing the best collective outcome can be considered cooperation, similar to the conception of cooperation in the social neuroscience literature. That is why we hypothesized:

1. Cooperating pairs in the Stag Hunt game will have significantly more interbrain synchrony of the prefrontal cortex compared to pairs that are not cooperating.

Second, risk and payoff have been shown to affect coordination behavior in Aydoğan's (2019) work. On the other hand, the literature lacked investigation of these effects in the context of interbrain synchrony. Also, we thought the cooperation condition that we defined would interact with the effects of risk and payoff. So, in a more exploratory manner, we hypothesized:

2. Different game characteristics, both by themselves and combined with our construct of cooperation, will show significantly different interbrain synchronization levels.

CHAPTER 2

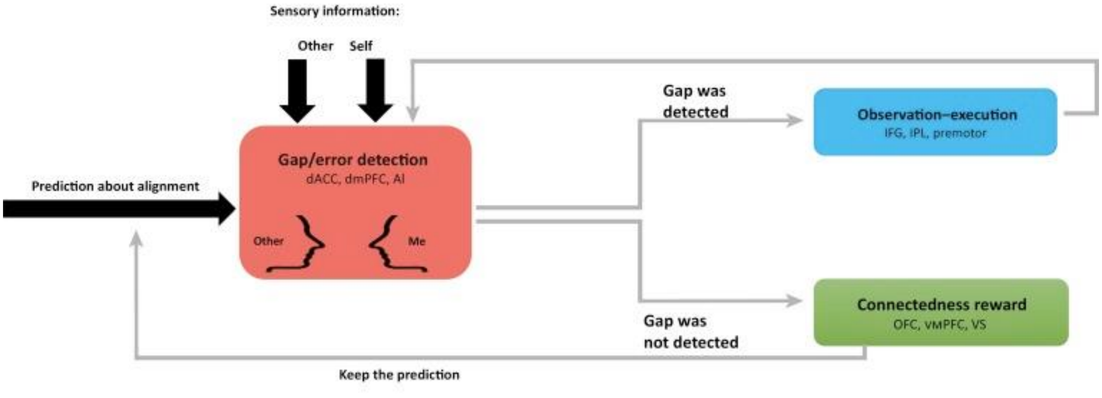
BACKGROUND

2.1 Cooperation

Cooperation is a fundamental part of human existence. We play team sports, sing together, collaborate on projects, or simply hold a conversation. With people around us, we strive toward common goals. Certainly, cooperating in activities is a big part of our social existence and makes us closer. It is argued that Homo Sapiens are evolutionarily selected for intragroup prosociality over aggression, increasing our capacity to cooperate and allowing unique human communicative skills to develop (Hare, 2017). According to Tomasello et al. (2012), the feat of human cooperation began in our evolutionary history, when humans had been forced to collaborate for foraging. This made humans interdependent on one another and allowed the development of joint intentionality. Sharing intentionality and goals is the critical ability that differentiates humans from other species, and it involves not only reading others' minds but also sharing psychological states and cognitive representations (Tomasello et al., 2005).

Bratman (1992) called this human experience Shared Cooperative Activity (SCA) and tried to characterize it with three features. First, humans participating in SCA have mutual responsiveness, which means they pursue to understand and reciprocate others' intentions and expect the same for themselves. Second, they commit to the activity despite having different reasons for doing so. A cooperation attitude in itself does not have to be the intention. However, committing to the joint activity is required. Third, humans need to commit to supporting the efforts of others. Successful SCA requires reciprocal help. These three requirements can be applied to even menial social interactions. For example, carrying a conversation can be said to involve the understanding of the mutual intention to keep talking with each other. Speakers understand the intention of what is being said and expect others to try to understand their intention of what they are saying. They can have different motivations for the conversation; for example, one might be trying to convince another of an idea that she does not believe in, yet they still commit to the mutual goal of talking. Lastly, people ask questions and carry the conversation by bringing different perspectives to the other speaker's intended message, so their intention is realized.

Shamay-Tsoory et al. (2019) introduced a neural and cognitive feedback-loop model explaining how social alignment is achieved. They defined three interrelated core components of social alignment, which are the synchronization of movement, sharing emotions, and lastly, the conformity that includes alignment of thought, beliefs, intentions, or attitudes. They indicated that these three components affect each other reciprocally. For example, dancing synchronously increased participants' perception of social closeness (Tarr et al., 2016). Another study showed that people show facial motor congruency while watching others showing emotions, and when their facial motor movements are inhibited, they reported lesser subjective shared emotions (Hawk et al., 2012). In addition, Páez et al. (2015) observed that people attending marches who reported higher perceived emotional synchrony scored higher on scales measuring social integration and beliefs compared to the lower perceived emotional synchrony group. These synchronizations across three domains create a sense of closeness and cohesion in groups. Shamay-Tsoory et al. (2019) postulated that this effect at the heart of social alignment is realized via three systems. First is the misalignment system, which monitors the expected movement, emotions, and beliefs and detects deviations between expectations and observations. Second, the observation-execution system executes the observed behavior, or if there is a discrepancy between expectations and reality, act accordingly. Finally, a third system rewards the alignment process, which makes social alignment satisfactory for people. The working of the system is depicted in Figure 2.1. Next, we will be focusing on another framework, building on Shamay-Tsoory et al.'s (2019) framework.



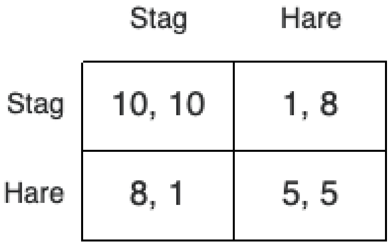
Trends in Cognitive Sciences

Figure 2.1: Feedback-loop model of social alignment. The image is taken from Shamay-Tsoory et al. (2019, p. 179).

Gvirts and Perlmutter (2020) suggested that interbrain synchrony (IBS) between people's prefrontal cortices (PFC) and temporal regions, in addition to individual activation patterns (Shamay-Tsoory et al., 2019), might be an essential part of the neural mechanism that produces social alignment. People achieve social connectedness with what they call the social attention system. Connectedness is significant because it is inherently rewarding for humans. They proposed there are key factors that make people deem certain social interactions significant, and those interactions lead to a mutual social attention system and higher IBS. Two factors that are irrelevant for this study are the setting of the interaction and the nature of the relationship. To exemplify the effect of the setting, people playing an economic exchange game face-to-face compared to those facing to a wall showed significantly greater IBS (Tang et al., 2016). For the nature of the relationship, one study showed higher IBS observed for romantic partners compared to strangers or friends during a cooperation task (Pan et al., 2017). The other factor influential in achieving significance in social interactions is the nature of the task. In a recent meta-analysis on fNIRS hyperscanning studies of cooperation, Czeszumski et al. (2022) observed that studies in the literature consistently showed IBS in PFC. Cooperating, by definition, involves shared intentionality because it involves a mutual goal. Hence, it can be considered conformity in which people share cognitive representations of the task and a mutual goal. It involves observing the other, executing necessary actions, checking for misaligned behaviors of others, and the intrinsic reward of cooperation. From the perspective of this framework, it is expected to observe IBS between PFC of people while cooperating as an underlying mechanism of the social attention system.

2.2 Stag Hunt Game

Game theory is a mathematical study of agents' decision-making under uncertain situations. It uses games of different kinds where agents' and other participants' actions affect the outcome of the game; hence it requires strategizing. In some games, agents make their choices simultaneously without knowing other participants' choices. One commonly studied version of the games in Game Theory is called Stag Hunt Game. It is a game derived from an example given in Jean-Jacques Rousseau's book "A discourse on Inequality" (Rousseau, 1985). In the hypothetical scenario, two hunters must decide whether to stay in their post and hunt for the stag. A successful hunt of the stag requires two hunters. Alternatively, one hunter can decide to leave her post and hunt the hare. In this case, the hunter will hunt the hare, which is a smaller prey compared to a stag. If one hunter goes for the hare, the other will not be able to hunt the stag. This creates a choice between cooperation and personal security or risk aversion. The game is sometimes aptly referred to as the assurance or trust game. For the best outcome, players need to trust the other player and cooperate because doing so is in their best interest.



	Stag	Hare
Stag	10, 10	1, 8
Hare	8, 1	5, 5

Figure 2.2: An example of a Stag Hunt game payoff matrix.

Nash equilibrium is a state of the game where two agents' actions are the same, and changing one's action always results in an inferior outcome for the agent. It might be considered the social norm everyone steadily benefits from, and deviating from it is undesirable (Osborne, 2004). The Stag Hunt game has two pure Nash equilibria. Those are (stag, stag) and (hare, hare) set of actions where changing one's action causes loss. The former is the payoff dominant equilibrium which involves the set of actions yielding the best possible outcomes for the agents. The latter is the risk dominant equilibrium which involves the set of actions that are least risky for the agents. The Stag Hunt games create this tension between trusting and cooperating or not taking the risk of another player not cooperating and opting in for the safe action. In repeated games, however, mixing choices can be another strategy. Game theory research operationalize human interactions as games and tries to understand why people select different strategies.

In his philosophical analysis of the Stag Hunt game, Skyrms (2001) describes the game as a problem of cooperation and trust and suggests whether the hunters choose to settle on risk dominant or payoff dominant equilibrium depends on their interaction dynamics and their history together. Clark and Sefton (2001) put this idea to test by comparing Stag Hunt games where participants played repeated games with the same person or alternatively, they played one-shot games, meaning they played the game each time with a random person. Consistent with the literature on the effect of repeated games, they observed that cooperation was more frequent compared to one-shot games. Interestingly, this effect was present in the initial games before any history was established. They suggested this could be a way of signaling their intention to cooperate. In another study, Bolton et al. (2016) tested the effect of social interaction during the Stag Hunt Game. In addition to a regular Stag Hunt game with another player, they included a version with a real person, but this person's choice depended on the chance factor. The third version of the game did not involve a real person but a computer program. Cooperation rates decreased when their partner's choice depended on chance and decreased, even more when they played it with a computer. They showed social context where they have a freely deciding intentional partner steered subjects towards cooperation.

In the paper mentioned in the previous section, Tomasello et al. (2012) suggested that humans' cooperation while foraging occurred in a Stag Hunt-like scenario, and the Stag Hunt game can be seen as a model for cooperation in other human collaborative activities too. It fulfills the three requirements of Bratman's (1992) Shared Cooperative Act (SCA) definition when players settle on the dominant payoff equilibrium. Participants understand that their partners intend to cooperate and go for the Stag. They intend to go for the Stag and expect their partner to understand it. Therefore, there is mutual responsiveness. Second, they might want to get the higher payoff, be afraid of not getting the higher payoff, or intend to cooperate with another person, which Bratman (1992) calls cooperatively loaded acts. Either way, they commit to the mutual goal of going for the stag, irrespective of their motivation to do so. Lastly, if in a repeated game, one participant goes for the hare and the other for the stag, in order for there to be cooperation, the hare hunter needs to see the intention and go for the stag next round supporting the other's goal. Not intending to cooperate and not reciprocating the intention of cooperation results in a coordination failure and can be considered not an SCA. Cooperation in the Stag Hunt game involves conformity as a core component of social alignment (Shamay-Tsoory et al., 2019). People align their intentions (We intend to go for the stag) and their beliefs (It is best for both of us, or the other player knows I know that she intends to cooperate and vice versa). From our review of the literature on cooperation, we argue that the nature of the Stag Hunt game yields cooperative (payoff dominant equilibrium) and non-cooperative (risk dominant or mixed-strategy equilibrium) strategies among players. Settling on a cooperative strategy of going for the stag seems to be a form of social alignment. Therefore, we expect the social attention system to be utilized and IBS between the PFC of participants to be observed.

2.3 Single Brain Studies

Although in this thesis work, we will focus on interbrain synchrony, it is still important to understand the relevant single brain regions for decision-making. In this section, we will be focusing on decision-making studies. We will be limiting the scope of the discussion to our experiment, i.e., to the discussion of regions that can be observed with fNIRS scanning.

The literature in neuroscience studied mostly simple decision-making scenarios due to limitations of brain imaging research, and they formed a picture of critical neural mechanisms for reward evaluation, value comparison, and risk management (Smith and Huettel, 2010). The ventromedial PFC (vmPFC) and neighboring orbitofrontal cortex have been shown to activate when subjects receive rewards, and these regions are associated with reward expectation (Knutson et al., 2005). Furthermore, Metereau and Dreher (2015) reported that these regions' activities are associated with the expectation of subjective value signals, whether the signal is positive or negative. In the real world, decision-making comes with uncertainty and risk. This is another parameter that factors into decision-making, changing the value attributed to a decision (Sanfey et al., 2006). Imaging studies involving risk and decision-making have shown activations in vmPFC, dorsolateral PFC (dlPFC), and orbitofrontal cortex (Smith and Huettel, 2010). This network (including unmentioned cortical and subcortical regions) is postulated to encode two aspects of the value signal, which are risk probability and expected value (Schonberg et al., 2012; Ogawa et al., 2014). Tobler et al. (2009) suggested these two aspects are integrated via medial and lateral PFC. Finally, although the dorsolateral PFC is not associated with subjective value as much as, say, medial PFC, it might be regulating the medial PFC (McClure et al.,2004).

PFC is extensively studied; however, because of its involvement in practically every cognitive task, it is hard to single out specific functions to its parts. To see a general account of what PFC does, Passingham and Wise's (2012) theory is reviewed. Here we included key subregions of the PFC. Orbital PFC has rich connections to sensory stimuli processing regions, forming representations for the outcome of an action. It is associated with assessment and selecting stimuli within perception as goals. With its connections to the amygdala, the goal's value is determined based on the information coming from the regions that code the organism's biological needs. Medial PFC, on the other hand, has connections to regions coding past actions and their results. This allows the organism to utilize its experience when settling on an action, comparing its memory to current sensory inputs. Lastly, the dorsal PFC has connections to parietal, temporal, and premotor cortices, which provide the organism with information regarding the spatial and temporal contexts. In turn, the dorsal PFC forms plans and manages goals. This is achieved via its connections with orbital PFC, which allows dynamic goal shaping and actions according to expected outcomes of goals and actions. It is important to stress that decision-making is highly complex and involves more regions than discussed here. However, this short coverage will suffice for the scope of this thesis work in terms of understanding the role of the PFC in the evaluation of goals and actions.

2.4 Social Neuroscience and Hyperscanning

Social cognitive neuroscience is a flourishing interdisciplinary field that tries to understand conscious phenomena from the lens of social cognition. According to Ochsner and Lieberman (2001), social cognitive neuroscience takes three perspectives into account when looking at human behavior. First is the social perspective, which approaches human behavior and experience as a social phenomenon. Second, the cognitive perspective sees cognition as information processing and tries to explain how these processes cause social phenomena. The third is the neural perspective, which is concerned with the underlying neurobiological phenomena. Ochsner and Lieberman (2001) postulate that this field is a necessary combination of cognitive neuroscience and social psychology, where the former is concerned with neural and cognitive perspectives, and the latter is concerned with social and cognitive perspectives. Bridging the two allows researchers to theorize more holistically.

Redcay and Schilbach (2019) differentiate between two approaches in neuroscientific literature regarding social cognition. The first one is the third-person approach that involves scanning a single individual's brain while observing non-interactive social stimuli such as looking at pictures of faces that are different from the subject's racial group under functional magnetic resonance imaging (fMRI) (Hart et al., 2000) or showing participants shapes that move in complex and intentional ways and scanning the brain with positron emission tomography to find the areas involved in mental state attribution (Castelli et al., 2000). The second approach is called second-person neuroscience, which involves real or perceived others in the experiment, which allows researchers to study the actual social interaction, not just observation of it. In this category, dual-brain approaches are getting more and more prevalent. As the name suggests, researchers observe two or more brains during social interaction. The second-person neuroscience view of social cognition is characterized by emotional engagement and interaction with others and aligns with the embedded and embodied view of cognition as opposed to the passive information processing of a spectator (Schilbach et al., 2013). Second-person neuroscience utilizes more ecologically valid experimental settings by observing people in more realistic scenarios.

Dual-brain approaches can be sequential, where subjects take turns performing a task. For instance, Schippers et al. (2009) asked romantically involved pairs to play a game of charades which is a game of describing a set of words with only gestures. Pairs took turns gesturing and guessing under fMRI while being recorded with a video camera. The aim of the study was to find the neural correlates of gestural communication. In this approach, brain images are taken at different points in time and are compared afterward. The other dual-brain approach involves recording from two brains simultaneously, which is also known as hyperscanning. Montague et al. (2002) introduced the hyperscanning technique as a new method to look for dynamic relations between two brains during social interaction. In the study, two persons played a simple competitive deception game under fMRI and were rewarded with a squirt of juice when they could correctly guess or successfully deceive. A single game had a period of 25 seconds, so they focused on the frequency band of 0.04 Hz and found temporal correlations of signals for particular voxels. Montague et al. (2002) suggested that these temporal correlations, or in other words, coherence of two datasets, quantifies the functional coupling of brain signals. Since then, hyperscanning studies have flourished in social neuroscience, looking for interbrain synchrony (IBS) of interacting subjects. As argued by Gvirts & Perlmutter (2020), IBS seems to be one of the mechanisms underlying the social attention system; thus, hyperscanning studies of interacting agents can provide us with unique and essential information on human interactions. In the next section, we will be focusing on hyperscanning studies on human cooperation and a few hyperscanning studies on economic games.

2.4.1 Hyperscanning Studies on Cooperation

IBS is suggested as a neural mechanism underlying social cognition, appearing in different aspects of social interaction like verbal and nonverbal communication, joint action and decision-making, and speech coordination (Hasson et al.,2012). In this section, some fNIRS hyperscanning studies from the literature on cooperation and economic game playing will be reviewed in no particular order.

In a study to understand the effect of IBS and synchronization of movements on prosociality, Hu et al. (2017) used the experimental paradigm of synchronized key pressing under fNIRS hyperscanning. Participants pressed a key after counting time in their minds in the cooperation condition. After each session, their performance was shown, and they tried to adjust to their partner's counting in their mind to get better. In the independent condition, two people coordinated their key pressing with a computer, still sitting across from each other. In addition to the task, they delivered subjective measurements of shared intentionality and perceived similarity to the subjects to understand these mechanisms' effects on human prosocial behavior. They measured prosociality by delivering a fictive scenario to the subjects. In the scenario, subjects had the option to help their partner in the experiment in varying degrees. The prosociality of the participants and their coordination were significantly higher in the cooperation group compared to the independent group. Furthermore, subjective perceived shared intentionality scores and prosociality effect were significantly correlated with the IBS of the cooperation group. IBS was observed in the left medial PFC in the participants.

Fishburn et al. (2018) investigated the neurobiological underpinnings of shared intentionality. They defined shared intentionality as attending to the same stimulus while engaging in a mutual goal of problem-solving. Participants, which consisted of triads, completed Tangram puzzles together. The task required a shared goal and coordination under fNIRS hyperscanning. They included a solo puzzle task to differentiate the intentionality of completing the puzzle from the shared intentionality of completing the puzzle together. They added two more control conditions in which participants observed people completing a puzzle or they watched a movie together. All task conditions were performed in a similar setting, seated side-by-side on a table. They found that when people engaged in the cooperative puzzle task, IBS occurred between their lateral PFC regions (they only measured the hemodynamic response of the lateral PFC) as opposed to other control conditions. They concluded that the IBS difference observed was due to interactively engaging in a common goal rather than being exposed to the same stimuli.

In an economic exchange study, Tang et al. (2016) examined the effect of shared intentionality on cooperation during ultimatum games under fNIRS hyperscanning. They predicted that shared intentionality and, in turn, cooperation would be increased during face-to-face condition compared to face-blocked condition. In this variation of the ultimatum game, a proposer is given a certain amount of money, and they truthfully or deceitfully tells the amount to the responder and proposes an offer. In the judgment stage, the responder accepts or rejects the offer, and the proposer tries to predict whether the responder will take the offer or not. Then, results are shown at the end of a round. Researchers used the evaluation of the participants during the judgment phase as a measure of shared intentionality and called it the Shared Intentionality Rate. Positive evaluations of accepting the offer and expecting the responder to accept to offer were taken as a positive appraisal of others' intention and trust. In line with their expectations, the face-to-face condition elicited more shared intentionality and mutual monetary gains than the face-block condition. They suggested that visual cues facilitate shared intentionality and cooperation. Accordingly, they observed significant IBS between different parts of the right temporoparietal junction in face-to-face conditions, a part of Mentalizing Network (Frith & Frith 2006). Another exciting study result was that participants in the face-to-face condition had significantly lower response times.

In another fNIRS hyperscanning study (Nozawa et al., 2016) on cooperative game playing, groups of four participants played a word-chain game in which they aimed to produce the longest word chain by adding words to the chain based on the previous word's last two syllables. In the communicating condition, people were allowed to interact naturally and discuss while playing the game. In the independent condition, they sit silently and avoid eye contact. Only when they thought of a word did they speak. They suggested that communication in a group is a highly dynamic act and includes moments where people do not take overt communicative action, which would require understanding others implicitly. They predicted that the mentalizing system would be essential for successful communication in this type of scenario. They expected to see IBS in the frontopolar cortex due to this demand. Comparing communicating and independent conditions, they observed higher averaged wavelet coherence transform (WTC) values among the frontopolar cortices of the participants.

In Li et al. (2020), researchers investigated the effect of playing team-based sports in cooperation with fNIRS hyperscanning. Participants were either basketball players or college students without team-based sports experience. They used a collaborative drawing task which is used for measuring cooperation. During the experiment, pairs controlled a digital brush with one person moving it horizontally and another vertically. In the control condition, they moved the brush individually. To control for previous relations, they asked participants to fill out an intimacy questionnaire which showed no significant difference between groups. Only the basketball players displayed IBS in dlPFC and frontopolar cortex in the cooperation condition but not in the control condition. Moreover, different pairs performed similarly, but basketball players reported higher subjective cooperation. They explained that the similar performances between groups were due to unfamiliarity with the task for both groups.

A very recent study (Zhou et al., 2022) examined the influence of social cooperation on reward allocation and responsibility attribution. They used the same synchronized key pressing task as Hu et al. (2017); however, in this study, after each button pressing, participants were asked whom did they think responsible for the result and how did they think the reward should be distributed. In the experiment, if their key pressing was close, they earned extra points and were paid according to the points they collected as a team. To account for the personal differences, participants filled out questionnaires relating to their personality traits and emotional states, and there was no difference between the control and cooperation groups. fNIRS hyperscanning results showed IBS in dlPFC in the cooperation group. The cooperation group attributed the responsibility of their performance to the group as opposed to the control group. Cooperation and control groups did not differ in their resource allocation. However, further correlation analysis of participants in the cooperative group with dorsomedial PFC (dmPFC) IBS demonstrated that this subset of the cooperation group allocated the reward in a more egalitarian manner. They concluded that dlPFC synchronization could function as a mechanism for interpersonal coordination and dmPFC as consideration for others in resource allocation.

CHAPTER 3

MATERIALS AND METHODS

This thesis is based on the data collected for Aydoğan's (2019) thesis work for the degree of master of science in the departments of Economics. The thesis title is Neural Basis of Decision Making in Stag Hunt Games: Effects of Change In Payoff and Dominance Level. Aydoğan (2019) focused on the individual hemodynamic response of individual participants while making decisions playing the Stag Hunt game. In this thesis, Interbrain Synchrony between pairs will be investigated and compared for different games with different characteristics.

3.1 Participants

Forty-eight (twenty-four pairs) right-handed voluntary undergraduate and graduate students from Middle East Technical University were participants in the experiment (6 female, 42 male, age range 19-30, $M = 23.8$). Participants who had a history of neurological or psychiatric problems were excluded from the study. After the verbal description of the task, written informed consent was obtained from all participants before the experiment. The study protocol was approved by the Middle East Technical University human subjects research ethics committee (Appendix A).

3.2 Experimental Setup and Devices

The study was conducted in METU Cognitive Science Optics Brain Imaging Lab. Each player had one computer to play the game and save their choices. In addition, a third computer was used as a server connecting the other two. Subjects were instructed on how the game works, both verbally and in a written format. They played a trial session before the actual experiment. Subjects were warned not to interact with each other and had a screen placed between them (Figure 3.1). By providing detailed instructions and preventing interaction, subjects were able to focus solely on the task and had no interaction with the experimenter or each other.

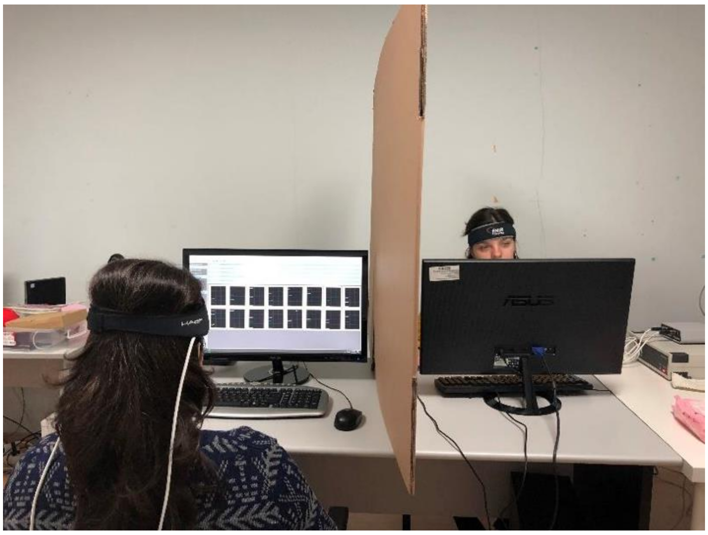


Figure 3.1: Experimental setup in METU Cognitive Science Optics Brain Imaging Lab.

An experiment software called Z-Tree 4.1 (Fischbacher, 2007) is used for programming the experiment. Markers at the beginning of every round were inserted via Python programming language. These markers split the experiment into a first phase consisting of ten blocks and a second phase consisting of four blocks. During the experiment, each subject had worn a sensor pad over their forehead that was connected to an fNIRS Imager 1000 device measuring their brain activity. The sampling rate was 2 Hz. Sensor pads in both devices had four light sources and ten detectors, collecting oxygenation data from 16 locations (optodes) on the prefrontal cortex. The pads were adjusted to a proper gap between sensors and the subjects' forehead for accurate measurement. An fNIRS device, the sensor pad, and detector-source distribution on the head can be seen in Figure 3.2. Finally, COBI Studio software (Ayaz et al., 2011) was used to record raw light intensity continuously.

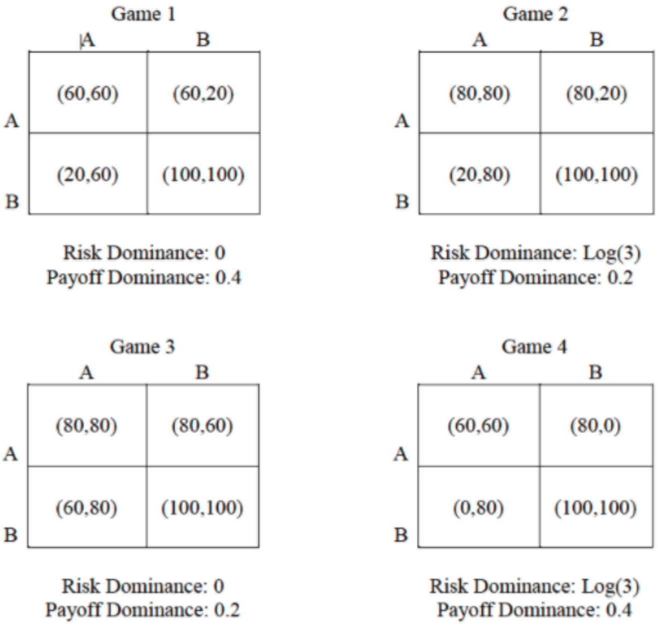
Figure 3.2: fNIRS device, sensor pad, and detector-source distribution.

3.3 Experimental Protocol

This section will briefly examine the original study used in Aydoğan's (2009) thesis work. Then, the flow of the experiment will be presented.

3.3.1 Experimental Game Design

The games played in the experiment are a replication of the work of Schmidt et al. (2003); therefore, it is essential to review their work first. In the experiment, there were four types of Stag Hunt games, differing in payoff and risk dominance levels. Games were two players games, and players had two options: A or B. The games and their payoff matrices can be seen in Figure 3.3 below.



Game 1

	A	B
A	(60,60)	(60,20)
B	(20,60)	(100,100)

Risk Dominance: 0
Payoff Dominance: 0.4

Game 2

	A	B
A	(80,80)	(80,20)
B	(20,80)	(100,100)

Risk Dominance: Log(3)
Payoff Dominance: 0.2

Game 3

	A	B
A	(80,80)	(80,60)
B	(60,80)	(100,100)

Risk Dominance: 0
Payoff Dominance: 0.2

Game 4

	A	B
A	(60,60)	(80,0)
B	(0,80)	(100,100)

Risk Dominance: Log(3)
Payoff Dominance: 0.4

Figure 3.3: Payoff matrices of the games and their risk and payoff dominance values. Image of the tables taken from Aydoğan (2009).

In the matrices, rows and columns are two different players, and the corresponding A or B option shows their choices. For example, in game 4, if the row player chooses B and the column player chooses A, the set of actions (B,A) results in (0,80) payoff where the row player gets 0, and the column player gets 80. In all game types, the set of actions (A,A) is the first Nash Equilibrium where players go for the less risky option. Set of actions (B,B) is the other Nash Equilibrium where players decide on cooperation. The former corresponds to hunters going for the hare individually, and the latter corresponds to hunters going for the stag collectively, as in Rousseau's (1985) example.

Schmidt et al. (2003) define payoff dominance as a measure of efficiency loss from both players choosing the risk-dominant equilibrium (A,A). It is calculated as P =

[u(B,B) − u(A,A)]/u(B,B)] which is essentially the percentage of lost utility not playing payoff dominant equilibrium (B,B). For example, game 4 is more payoff dominant than game 3 because (B,B) gives the outcome of 100 in both games, but (A,A) gives the outcome of 80 in game 4 and 60 in game 3. In this sense, cooperating and playing the (B,B) is more desirable.

In the study (Schmidt et al., 2003), risk dominance was another critical measure used to differentiate the games. It is a measure of riskiness in comparison to different equilibria. They used Selten’s (1995) measure to determine the risk dominance of the games, and its calculation in the context of this study is as follows:

$$R = Log(\frac{u_1(A,A) - u_1(B,A)}{u_1(B,B) - u_1(A,B)})$$

In Schmidt et al.’s (2003) study, the experiment had two phases. The first phase included eight Stag Hunt games where pairs always played one kind of game among the four kinds. At the end of each game, the payoff, therefore, other participant’s choice was revealed. The second phase of the experiment included four Stag Hunt games of each type. In the second phase, however, the results were not revealed until the end of the second phase. This study differs from the original study because there are ten rounds for the first phase. Our study only uses the first phase of the study.

Another aspect of this study that deviates from the original is the matching protocols. Schmidt et al. (2003) used three different matching protocols. First, random match protocol in which players do not play with others more than once. Second, one-shot protocol in which a participant plays only one game. Third, fixed match protocol in which two players always play with each other. In the experiment, only the fixed match protocol was implemented, meaning participants played the game with the same person, which allowed a building of history between them.

3.3.2 Experiment Flow

Before the beginning of the experiment, subjects were instructed on how to make a choice and how to interpret the results of the games played. In order to make the experiment more serious and realistic, subjects were paid money after the experiment. In addition to 5 Turkish Liras for participating, they gained varying amounts of money, determined by randomly selecting a single game from the experiment. In the random game among the fourteen games they played, if they played (B,B), they both earned 20 Turkish Liras. If they played (A,A), they both earned 10 Turkish Liras. Finally, if one played A and the other B, the subject who played A earned 10 Turkish Liras, and the subject who played B earned 15 Turkish Liras. Subjects were briefed on the payment method before and received their payment after the experiment.

In the first phase, after a welcome screen, a round is played. Payoff table was presented, and participants had the option to choose between playing A or B with their keyboards. After both participants made their choices, the results of the game showed for 10 seconds and 10 seconds of waiting screen followed. Game playing, results, and waiting period constructed a single block of gameplay in the first phase of the experiment. This was repeated ten times. Pairs only played one version of the Stag Hunt game ten times in this phase. The flow of phase one of the experiment can be visually inspected in Figure 3.4.

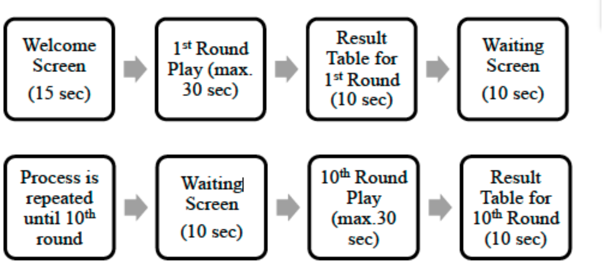


Figure 3.4: The flow of the experiment for the first phase

Overall, there were 24 experimental sessions where two people played the game in each session. The matching procedure was fixed match procedure; meaning pairs always played the game with each other. Every round, each player chose between A or B. For phase one, there was 480 decisions in total (2 subjects x 10 games x 24 sessions).

3.4 fNIRS Hyperscanning

First, this section presents the fNIRS methodology and its underlying principles. Second, the hyperscanning methodology will be presented. Finally, the processing of the neurological data will be described.

3.4.1. fNIRS

fNIRS is an optical imaging technique used for observing cortical activation. It capitalizes on the brain's need for oxygen when there is electrical activity in a region. Neurons, the basic building blocks for cognition in the brain, use glucose for energy. Glucose needs to be metabolized with oxygen to attain the energy needed. The body sends glucose and oxygen to tissue when there is demand, which is called the hemodynamic response. The body constantly maintains homeostasis by providing what is lacking in different tissues. The vascular system is utilized for sending the nutrients. When the neurons need these nutrients due to cognitive activity, there appears a temporal and spatial correspondence between the neuronal activation and cerebral blood flow, and this phenomenon is called neurovascular coupling (Phillips et al.,2016). The vascular system distributes oxygen via molecules called hemoglobin in the blood. They are called deoxyhemoglobin when they do not carry oxygen. Figure 3.5 shows the deoxy, oxy, and total hemoglobin change when there is a typical hemodynamic response in the brain tissue.

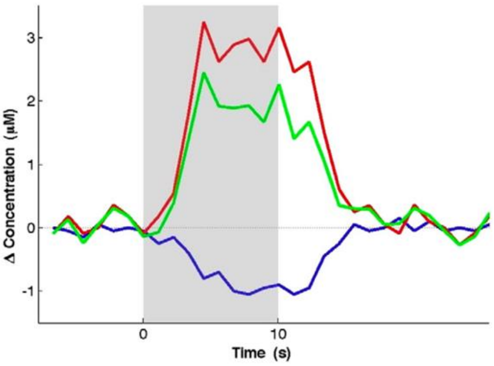


Figure 3.5: Representation of typical hemodynamic response captured with fNIRS. Shadow shows the stimulus duration. The red line is oxyhemoglobin, the blue line is deoxyhemoglobin, and the green light indicates total hemoglobin, which is also used as a proxy for total blood volume**.** The image is taken from Ferrari and Quaresima (2012, p. 925).

fNIRS systems use light sources that send photons. These photons penetrate the skull and cortical tissue. The photons follow a banana-like shape shown in figure 3.6 (left). Some of them are absorbed; some are scattered (Figure 3.6, right). The light detectors on the fNIRS device detect the scattered photons. The change in photons received by the sensors is determined by the hemoglobin and deoxyhemoglobin density along with other molecules present. By measuring the change in the photons received, the change in the total hemoglobin levels is derived indirectly. fNIRS also can detect hemodynamic responses from other physiological sources like blood pressure, heartbeat and respiration; however, these sources have characteristic rhythms that usually occupy different frequency bands and can be filtered out well (Ayaz et al., 2019).

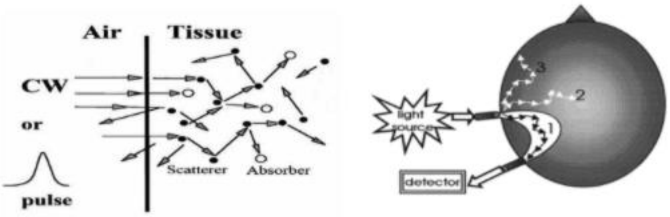


Figure 3.6: On the left is a depiction of the behavior of light sent. On the right, the shape of the path light travels from the light source to the detector.

fNIRS light sources send two different wavelengths of light. Tissues in the human body are mainly transparent to light within 700-900 nm which allows the detectors to catch scattered photons. Water is abundant in the body and has low absorption in this region, which makes this range of light desirable for imaging. In addition, the absorption characteristics of deoxy and oxyhemoglobin are relatively different in this region (Izzetoglu et al., 2007). This range of wavelength is called the optical window (Figure 3.7). Choosing two or more wavelengths of light from this region allows researchers to discover the relative change in deoxy and oxyhemoglobin levels in continuous fNIRS systems by using the Modified Beer-Lambert Law (Ayaz et al., 2012).

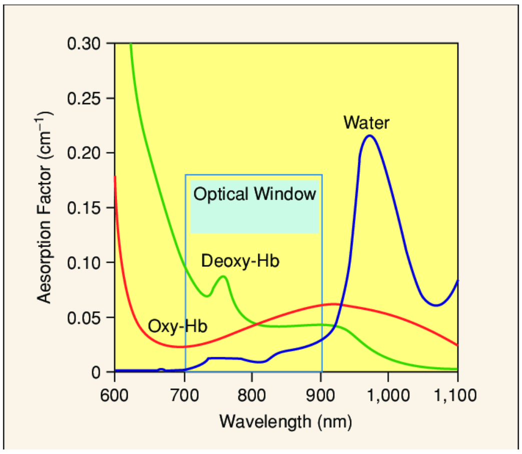


Figure 3.7: Optical window of light (Izzetoglu et al., 2007, p. 39).

The fNIRS methodology has its disadvantages and advantages. Some advantages are that it is a non-invasive, portable, low-cost modality that offers a high temporal resolution (in most cases, the sampling rate is between 1 and 10 Hz) as compared to other hemodynamics-based modalities such as fMRI and PET, and is tolerant of movements, allowing researchers to design more natural experiments. Some disadvantages are that it needs good contact with the skin, is easily affected by the hair, has a limited spatial resolution of around 1 cm, and deeper regions cannot be investigated with it. Also, continuous wave-based systems cannot provide absolute values of blood oxygenation (Quaresima & Ferrari, 2019). The fNIRS measures are compared to subjects' baseline values which yield relative oxygenation levels compared to the resting state when they do not perform any task. A comparison of spatial and temporal sensitivity of fNIRS to other neuroimaging techniques is illustrated in Figure 3.8:

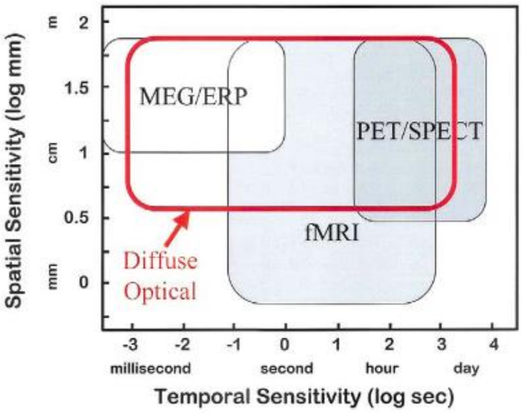


Figure 3.8: The spatial and temporal sensitivities of different neuroimaging modalities. The red rectangle Diffuse Optical represents optical imaging techniques' spatial and temporal sensitivity. The image is reprinted from Strangman et al. (2002, p. 680).

3.4.2 Hyperscanning and Wavelet Coherence Transform

As introduced before, hyperscanning is a neuroimaging technique for measuring two brains simultaneously, allowing researchers to compare and contrast two brain signals between subjects. This approach to neuroscience considers two brains as one exploratory unit. Within this approach, Wavelet Transfer Coherence (WTC) method gained popularity in recent years. WTC is used for analyzing the cross-correlation of two signals as a function of frequency and time, and it gives a coherence coefficient between 0 and 1 (Léné et al., 2019). The coherence value indicates a temporary correlation of specified frequencies in the data within a time window.

The Wavelet Transform Coherence Plot in figure 3.10 is an example from Cui et al.'s (2012) study of hyperscanning during cooperation. The WTC plot captures the time-frequency alignment among the wavelet transforms of two time-series signals, as illustrated in Figure 3.10. A simple correlation coefficient can be computed to measure the degree of the linear relationship between such two signals, but such temporal analysis inevitably misses information about relationships between those signals at different time-frequency scales. WTC analysis was proposed to explore such relationships that are difficult to capture with time-domain methods.

WTC is a method for expanding time series into time-frequency space and can therefore find localized intermittent periodicities (Grinsted et al., 2004). In this method, narrow rectangles are used for the high frequencies that give a precise localization in time, whereas large rectangles are used for the low frequencies that give a precise localization in frequency (Figure 3.9). This effect is achieved by convolving both time series with a range of wavelets (e.g., Morlet wavelets that are finite waves with a given frequency) that differ in their periodicities to achieve a time-frequency decomposition of the signals. In other words, the WTC method aims to balance accuracy in time and frequency by having different granularities at different time-frequency bands. The wavelet transforms computed for each signal are then compared to find those regions in time-frequency space where the two time series have a large common power and whether they have a consistent phase relationship.

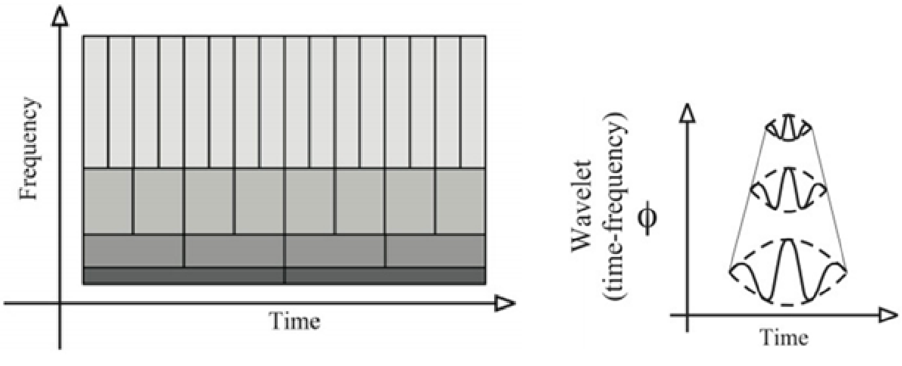


Figure 3.9: Convolution principles of the wavelet transform coherence method.

In the study, participants pressed a button in 6-7 seconds periods. The bar on the right indicates the coherence level. The horizontal and vertical axis represents time and frequency domains, respectively. The plot has a band of high coherence around period 8. The sampling rate of the fNIRS devices is 10 Hz, which means this band of high coherence shows synchronization for signals repeating every 1 second or so. It corresponds to the participants' heartbeat, indicating their heartbeats were in synch most of the time. Similarly, the coherent parts around period 64 correspond to the correlation of brain activity due to button pressing. In the end, this method gives us a matrix of coherence values, columns corresponding to time, and rows corresponding to respective periods or frequencies. Furthermore, it gives us a different perspective that would not be possible to see by looking at individual brain signals.

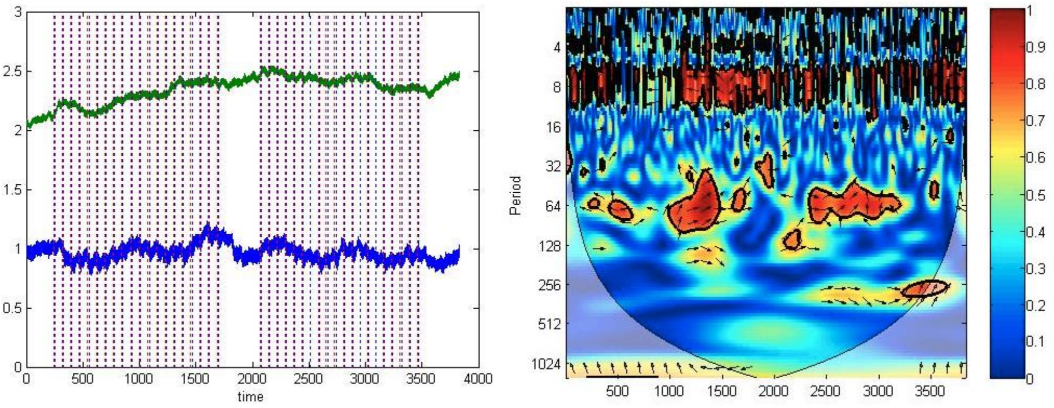


Figure 3.10: Wavelet Coherence plot of two subjects’ brain signals while performing a cooperative button pressing task (Cui et al., 2012).

The following examples further illustrate the types of time-frequency relationships that can be identified through WTC analysis. For instance, the example in Figure 3.10 includes two sinusoids that are in phase at an increasing frequency, which is depicted as a yellow band that represents common power, that is drifting to higher frequency bands. The example on the right shows that WTC is not sensitive to changes in the amplitude of the signals. This could be a desirable property in a hyperscanning study since signals may exhibit different amplitudes across pairs of participants due to physical and individual differences such as skin tone and hairline.

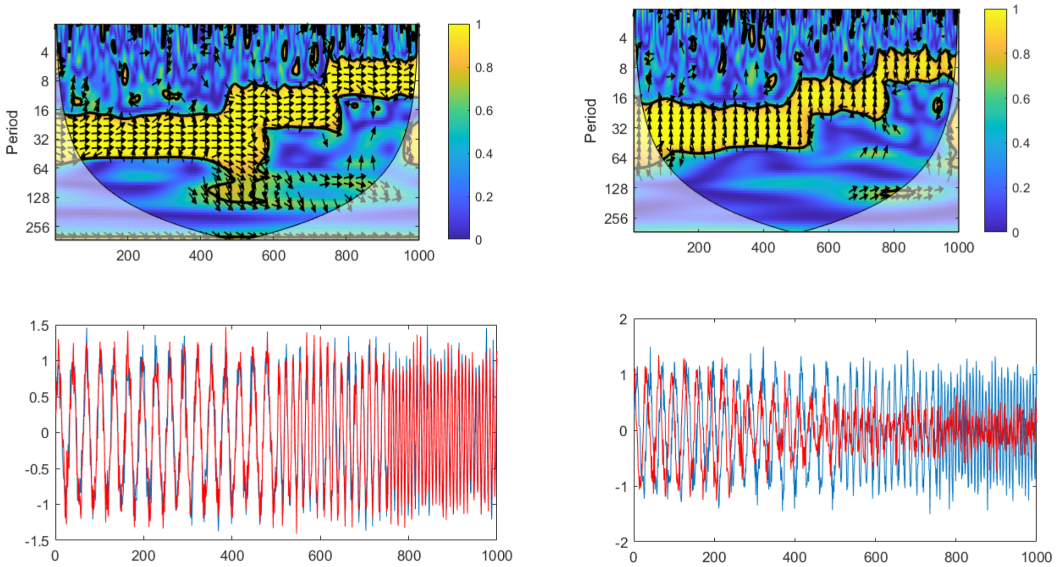


Figure 3.11: Effects of increased frequency (left), and amplitude (right) in WTC analysis.

The next example (Figure 3.11) presents two sinusoids that are initially phase synchronized but later become anti-phase. The initial in-phase stage is represented as a yellow band indicating high shared power, together with arrows pointing towards the right that signal phase alignment. As the signals switch to anti-phase, the yellow band briefly diminishes, and then it becomes visible again as the signals reach opposite phases. Note that the shift in phase is depicted with an arrow pointing towards the left. The example on the right shows the same example with two signals that also exhibit linear drift. The drift introduces a lower frequency component in the WTC plot, which does not affect the coherence around periods 32-128.

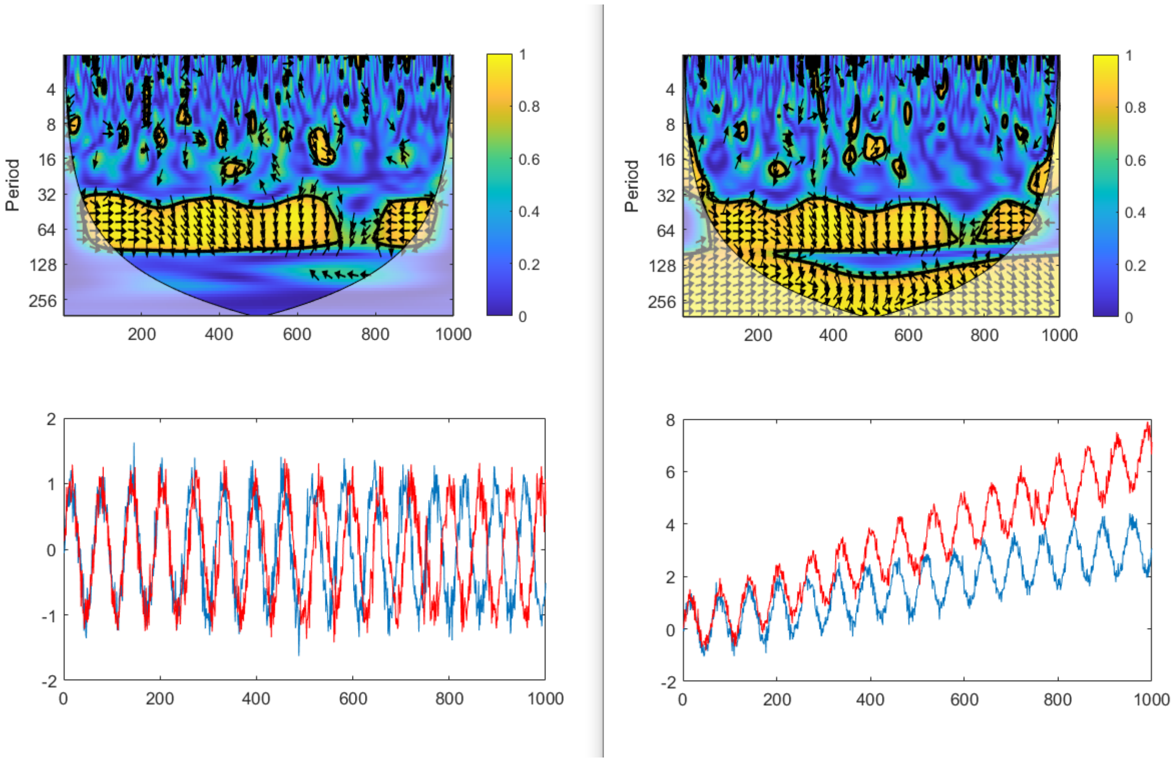


Figure 3.12: The effect of phase (left) and linear drift (right) on WTC analysis.

3.4.3 Neurological Data

During the Stag Hunt game, fNIRS devices were sampling at 2 Hz. The pads participants wore had 16 detectors collecting infrared light intensity data for the duration of the experiment. First, using fnirSOFT software, all of the participants' raw light data and the markers were inspected, and faulty channels that were oversaturated with light were discarded. For each participant's data, the markers are used to obtain a single block of data that starts 30 seconds before the first game and ends 30 seconds after the ending of the last game. 30 seconds of buffer zones were necessary due to WTC's tendency to not work accurately around the edges of the data. Then, in fnirSOFT software, Modified Beer-Lambert Law was applied to obtain relative oxyhemoglobin concentration, using the first 20 seconds as a baseline. Oxyhemoglobin data were detrended to remove the effects of any global trends in data. After these steps, every pair's oxyhemoglobin data were exported as a MATLAB file.

The fNIRS device used during data collection can monitor 16 different locations or optodes over the prefrontal cortex, which is under the forehead. These regions overlap with Brodmann areas 9, 10, 46, 45, 47, and 44 that are known to be associated with various higher-order cognitive functions. Optodes 1-4, 5-6, and 7-8 roughly cover the left dorsolateral, dorsomedial, and frontopolar regions in the PFC, whereas optodes 9-10, 11-12, and 13-16 cover the right frontopolar, dorsomedial and, dorsolateral PFC regions, respectively (Figure 3.12).

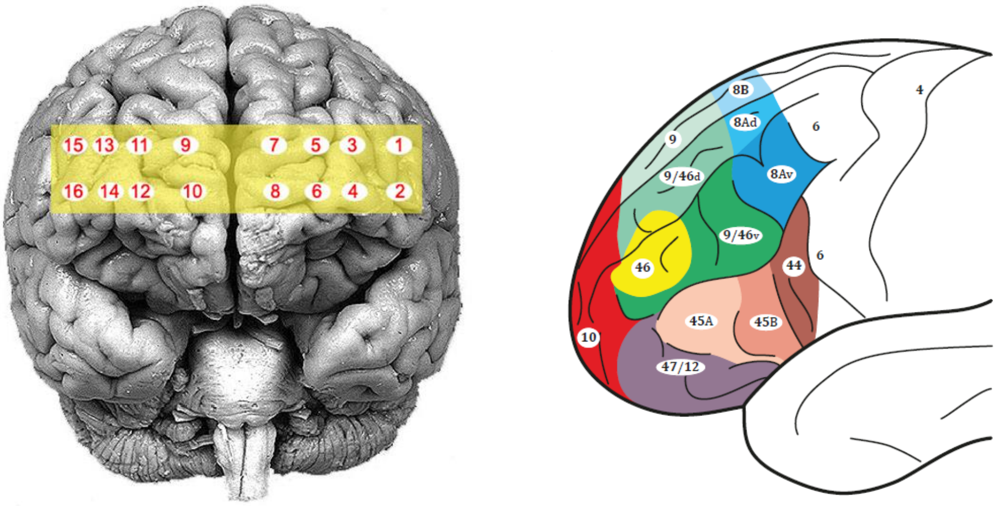


Figure 3.13: The correspondence between 16 measurement locations (optodes) monitored by the fNIRS device used during data collection (left) and the corresponding Brodmann regions associated with those optodes.

A MATLAB script was written for analysis, and coherence values were calculated using Grindset et al.’s (2004) MATLAB library. First, markers from the experiment were imported to determine the time periods of blocks in phase 1 and phase 2. Since the average period of a single game add up to approximately 30 seconds (average decision time of 10 seconds, 10 seconds of result screen, and 10 seconds of waiting screen), the period range of 18 to 33 seconds was chosen for the analysis. The coherence values of the periodic activity within the time frame of a single game collapsed into a single number by taking the mean twice so that we have a single metric for a single game. For the purpose of accounting for the coherence before the period of interest, the coherence of the previous 10 seconds was subtracted from the coherence of the block. This yielded a coherence increase value as a more accurate metric of the effect of playing the game.

Coherence increase values between oxyhemoglobin measures obtained from the same optodes for each partner were computed to measure the level of inter-brain synchrony among those optodes. The WTC analysis steps illustrated were applied to all 16 optode pairs across participants. WTC coherence values are then computed for each trial by calculating the mean of the time-frequency rectangle corresponding to the beginning and end of the trial block and the periods of 16-64, which correspond to a periodicity of 8 to 32 seconds that matches the duration of the trials. The raw coherence measures were subtracted by the coherence value observed during the rest period preceding each trial. These coherence increase measures are then subjected to a Fisher’s z-transform to aid the subsequent group level analysis. The mean z-transformed coherence increase measurements are then compared across conditions of the experiment via false discovery rate corrected independent samples t-tests. FDR- corrected critical thresholds are then used to produce topographical plots over the PFC to aid the interpretation of interbrain synchronization changes.

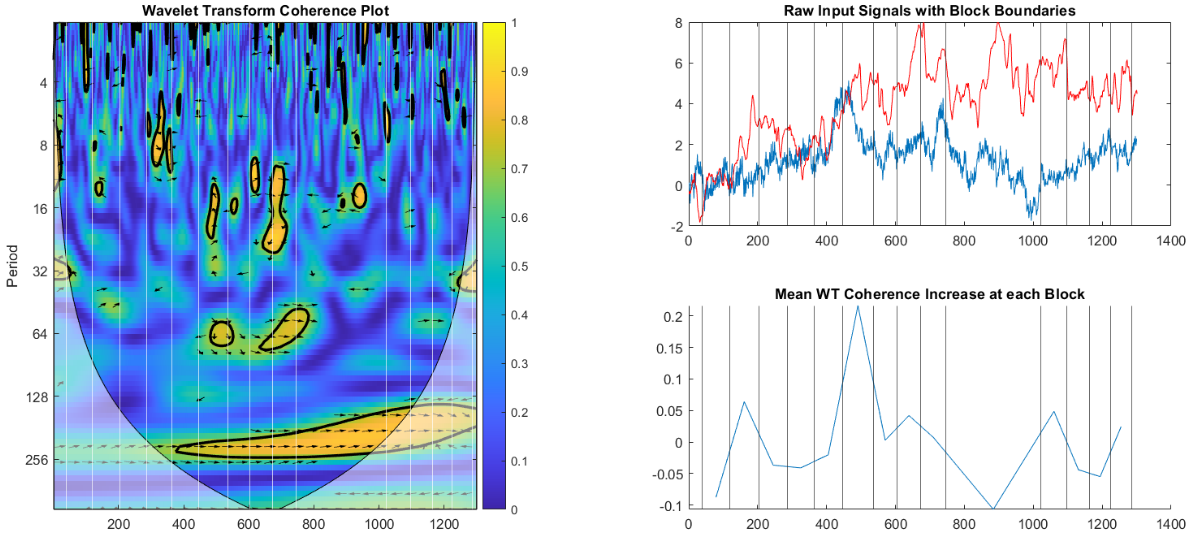


Figure 3.14: An example WTC plot for oxyhemoglobin signals obtained from a pair and the average WTC coherence increase values observed during each task block during the experiment.

CHAPTER 4

RESULTS

In this chapter the results of the main analysis of interbrain synchrony (IBS) between cooperation and non-cooperation conditions will be presented. Then in the second part, IBS analysis with respect to cooperation status and payoff/risk dominance of the game types will be explored.

4.1 Cooperation vs. Non-Cooperation

In this thesis work, we defined cooperation behavior as playing (stag, stag) in the majority of 10 rounds of play. If players played mixed strategies or settled on the risk-dominant equilibrium (hare,hare), they are considered not cooperating. The distribution of cooperation and non-cooperation cases according to payoff and risk dominance levels can be observed below:

Table 4.1: Cooperation frequencies according to payoff and risk dominance levels.

				Non-Cooperation Group	Cooperation Group
Payoff Dominance	Low	Risk Dominance	Low	2	4
			High	5	1
	High	Risk Dominance	Low	2	4
			High	3	3

As described in the method section, we calculated the WTC increase of every trial between the same optode pairs. Then, ten trials between each group are averaged to find the final WTC increase value between the same optodes. In the main analysis, the pairs were divided into a cooperation group and a non-cooperation group. We hypothesized that cooperation would cause higher IBS, so a series of one-tailed independent samples t-tests for each same optode pair was utilized to compare the IBS of the cooperation group to the non-cooperation group. Then, p-values derived from comparisons of mean coherence increase values are corrected by applying the false discovery rate (FDR) procedure (Benjamini & Hochberg, 1995). The alpha level of .05 was used as a significance level threshold. For the main analysis, optode pairs that differed significantly and relevant statistics can be seen in table 4.2.

These results indicate that the cooperation group had significantly more WTC increase between their optodes 1, 2, 3, and 4 compared to the non-cooperation group with large effect sizes. The topographic plot in Figure 4.1 shows the B-spline interpolated t-map over the prefrontal cortex contrasting the average wavelet transform coherence increase values observed among pairs cooperated or not by the end of the ten rounds.

Table 4.2: One-tailed t-test results of optodes showed significant WTC increase after FDR correction.

Optode Number	T-statistic (df)	Fdr-corrected P Value	Effect Size (Cohen's d)
Opt 1	t(22) = 1.97	*p* = .031	*d* = .84
Opt 2	t(22) = 2.32	*p* = .016	*d* = .99
Opt 3	t(22) = 2.40	*p* = .013	*d* = 1.02
Opt 4	t(22) = 2.94	*p* = .004	*d* = 1.26

The optodes that showed a significant positive IBS difference between cooperation and non-cooperation pairs are clustered around the left dorsolateral PFC. Other regions did not reach significance.

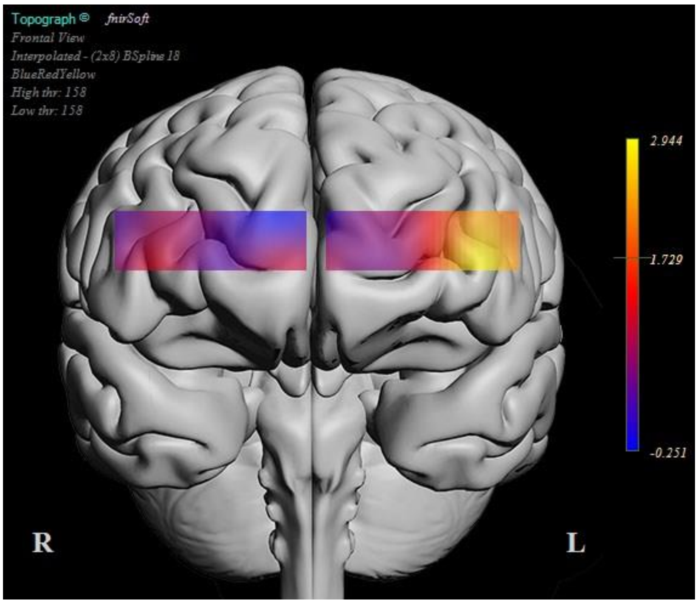


Figure 4.1: Bspline interpolated t-map contrasting the average wavelet coherence increase between cooperation and non-cooperation groups (the critical threshold for the one-tailed contrast was set as t=1.73 after FDR correction).

4.1.1 The Behavior and IBS Relation

To lay out the relation of cooperating and IBS of significant optodes, first, the frequencies of payoff dominant equilibria for each trial are calculated. Afterward, a series of Pearson correlation analyses are conducted between mean WTC coherence increase values of significant optodes and payoff dominant equilibria frequencies of cooperation and non-cooperation group across ten games.

Correlation analysis results at the alpha level of .5 were insignificant (*p* < *.5)* for all the optodes, both for the cooperation and non-cooperation groups. For the cooperation group, test statistics were *r*(8) = .51 (optode 1), *r*(8) = .44 (optode 2), *r*(8) = .57 (optode 3),and *r*(8) = .28 (optode 4), whereas for the non-cooperation group they were *r*(8) = .14 (optode 1), *r*(8) = .04 (optode 2), *r*(8) = .24 (optode 3),and *r*(8) = .03 (optode 4). Although the tests did not show statistical significance, possibly due to low sample sizes, correlation coefficients and visual inspection of the graphs (Figures 4.2 and 4.3) hint at a relationship between cooperation behavior and IBS of dlPFC for the cooperation group but not for the non-cooperation group.

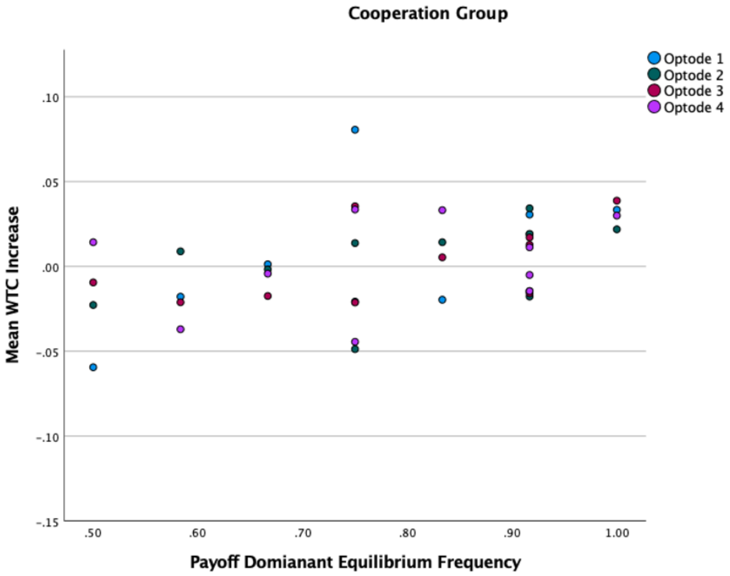


Figure 4.2: Correlation between WTC increase and payoff dominant equilibrium frequency for the cooperation group.

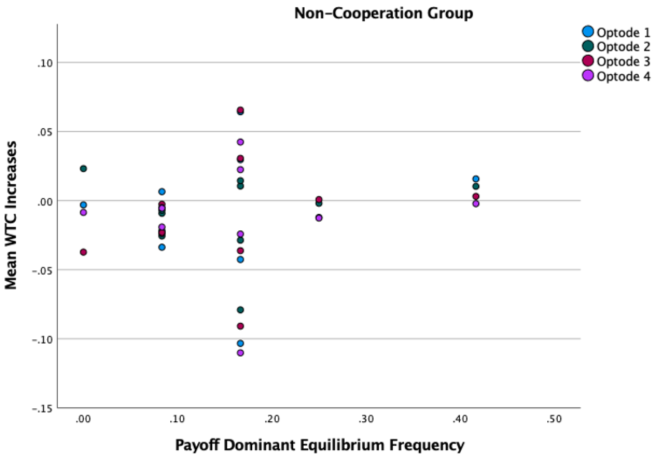


Figure 4.3: Correlation between WTC increase and payoff dominant equilibrium frequency for the non-cooperation group.

4.2 Effect of Game Characteristics on IBS

Since the pairs played four different types of games that differed in terms of their payoff and risk dominance levels, we wanted to explore the IBS patterns to see whether varying risk and dominance levels affect IBS. For the purpose of seeing the combined effect of cooperation behavior and game characteristics, further comparisons are carried out with cooperation and non-cooperation groups.

4.2.1 Effect of Payoff Dominance on IBS

Figure 4.4 shows the t-map obtained for the contrast between average WTC increase values observed across 16 optodes for high versus low payoff games. Since we only tested for differences among these conditions, two-tailed independent samples t-tests were conducted. After FDR correction, we observed a significant IBS difference for the high payoff group in optode 5, $t(22) = 2.37$, $p = .03$, Cohen's $d = 1.01$. This optode measures the hemodynamic response from the left dmPFC.

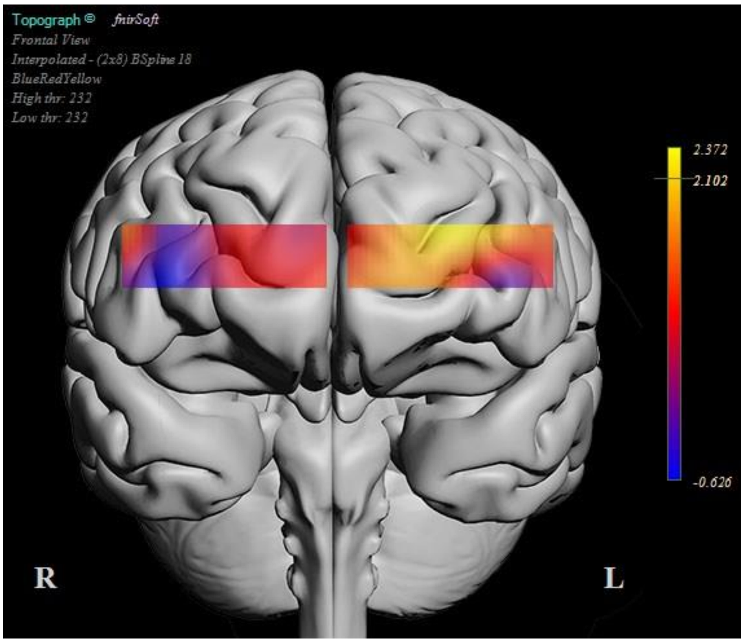


Figure 4.4. Bspline interpolated t-map contrasting the average wavelet coherence increase between high and low payoff games (the critical threshold for the two-tailed contrast was set as t=2.10 after FDR correction).

We followed this analysis further by focusing on pairs that exhibited cooperation and no cooperation. The t-map in Figure 4.5 contrasts the high and low payoff games for the cooperation pairs. After FDR correction, a significantly higher IBS was observed for the high payoff games in optode 15, which is on the right dlPFC, $t(10) = 2.40$, $p = .03$, Cohen's $d = 0.99$.

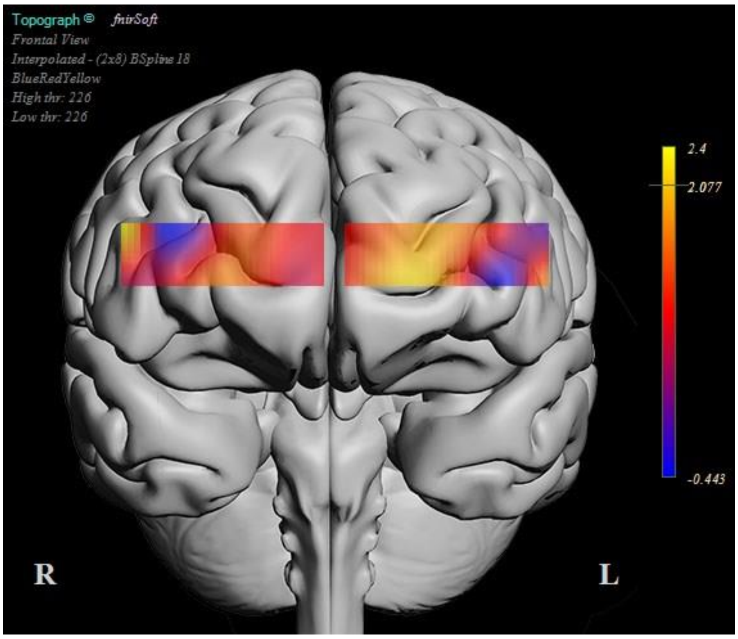


Figure 4.5. Bspline interpolated t-map contrasting the average WTC increase between high and low payoff games for the cooperation pairs (the critical threshold for the two-tailed contrast was set as t=2.08 after FDR correction).

When the analysis was restricted to non-cooperation pairs, no significant differences were observed between IBS levels (Figure 4.6).

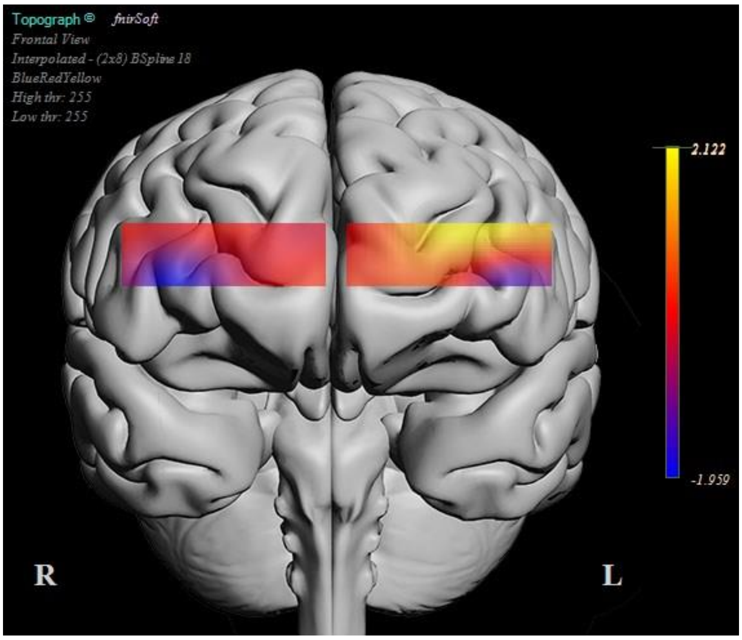


Figure 4.6. Bspline interpolated t-map contrasting the average WTC increase between high and low payoff games for the non-cooperation pairs (none of the contrasts exceeded the critical threshold).

4.2.2 Effect of Risk Dominance on IBS

The same analyses are carried out for risk dominance. The t-map in Figure 4.7 shows the contrast between IBS levels observed during high and low-risk games. After FDR-correction, none of the contrasts reached significance.

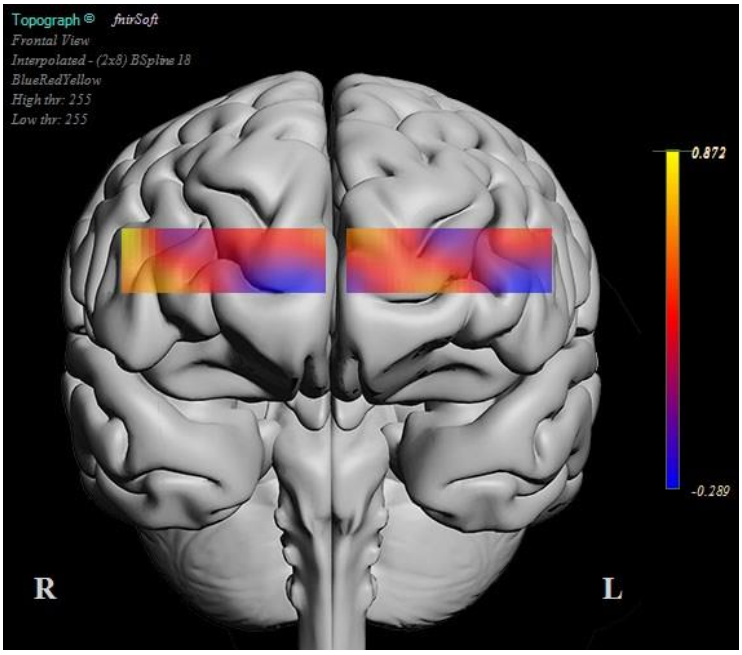


Figure 4.7. Bspline interpolated t-map contrasting the average WTC increase between high and low-risk games (none of the contrasts exceeded the critical threshold).

We followed this analysis by focusing separately on cooperation and non-cooperation groups. For the cooperation group, two-tailed independent samples t-tests revealed significantly higher IBS in high-risk games, for optode 3, *t*(10) = 2.25, *p* = .04, Cohen's *d*=1.11, optode 5, *t*(10) = 3.56, *p* = .002, Cohen's *d*=1.52 and optode 7, *t*(10) = 2.69, *p* = .01, Cohen's *d*=1.49. Figure 4.8 shows the t-map for the cooperation groups where we observed significantly higher levels of IBS around the left FC, left dmPFC, and left dlPFC regions.

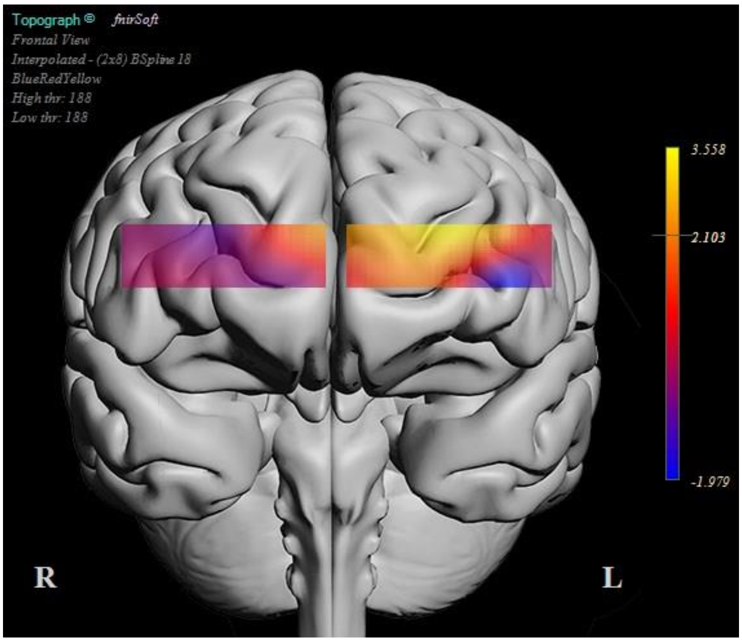


Figure 4.8. Bspline interpolated t-map contrasting the average wavelet coherence increase between high and low-risk games for the cooperation pairs (the critical threshold for the two-tailed contrast was set as t=2.10 after FDR correction).

The statistical test results were insignificant for the non-cooperation pairs (Figure 4.9).

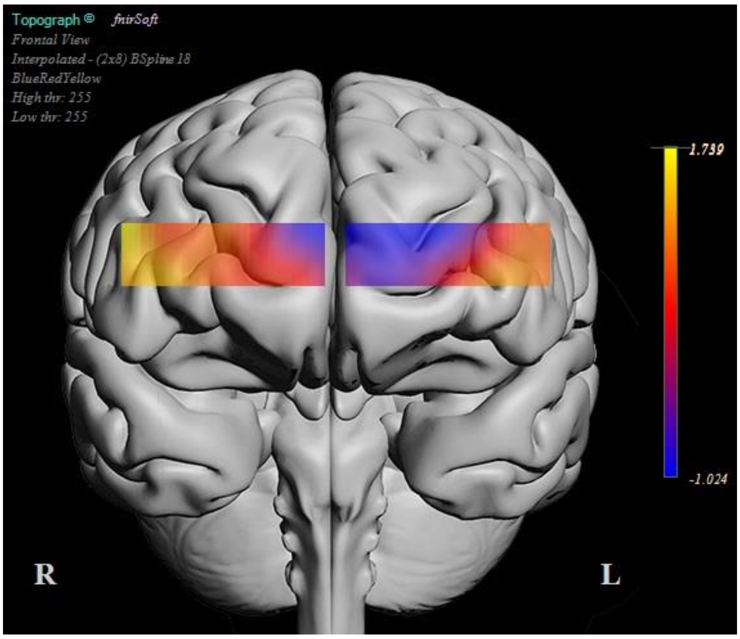


Figure 4.9. Bspline interpolated t-map contrasting the average WTC increase between high and low-risk games for the non-cooperation pairs (none of the contrasts exceeded the critical threshold).

CHAPTER 5

DISCUSSION

5.1 IBS and Cooperation

The fNIRS hyperscanning studies reviewed here differentiated cooperation and non-cooperation as two different experimental conditions. Contrary to the literature on cooperation, we did not have different experimental conditions. Instead, given the psychological nature of the task, we argued settling on the payoff dominant equilibrium can be considered as cooperation. The reasoning behind this decision can be summarised with two points. First, the relation between participants that settled on payoff dominant equilibrium has similar characteristics to Bratman's (1992) Shared Cooperative Activity. Second, achieving payoff dominant equilibrium requires shared intentionality, which is at the heart of human cooperation (Tomasello et al., 2005). This perspective allowed us to look at the heavily studied Stag Hunt game from a new perspective. Participants playing repeated games allowed us to characterize cooperation as a history of cumulative interactions whereas, in other Stag Hunt studies in the economics literature (Bolton et al., 2016; Schmidt et al., 2013), the frequency of individual play of stag is examined.

We expected cooperating in the task would involve social attention system (Gvirts & Perlmutter, 2019), and we expected to see higher IBS in the cooperation group compared to the non-cooperation group. We found significant IBS between left dlPFCs of the cooperation group, including all of the optodes 1,2,3 and 4. The fact that the cooperation group yielded significantly more IBS in dlPFC shows that results cannot be attributed to only the payoff and risk dominance levels. Although uncertainty and decision-making have been associated with dlPFC before (Smith and Huettel, 2010), every game type involved decision-making and, arguably, uncertainty due to not knowing what the other player's responses will be. The same argument can be reiterated for the function of dorsal regions of the PFC as planning and managing goals (Passingham & Wise, 2012).

These results make more sense in the context of hyperscanning studies of cooperation. For instance, in Zhou et al.'s (2022) study, IBS in dlPFC occurred in only the cooperation group. In addition to this, the cooperation group attributed the responsibility of results to the team, as opposed to attributing it to their partner. In another study, IBS in dlPFC was observed in the group that had team-based sports experience, and they reported higher subjective cooperation (Li et al., 2020). Fishburn et al.'s (2018) study examined the effect of shared intentionality on a cooperative puzzle-solving task. The cooperation group showed IBS in lateral PFC, and they reported higher subjective shared intentionality. This study involved control conditions of solving a puzzle individually with another person and watching another person solve a puzzle in order to control for being exposed to the same stimuli.

These studies suggest that IBS between dlPFC might be a mechanism for cooperating on a mutual goal as a team. Moreover, the level of synchronization of dlPFC seems to be unique to interacting in a cooperative manner in these studies. In our experiment, settling on the payoff dominant equilibrium resembles these qualities found in cooperation studies. The cooperation behavior observed in the experiment can be seen as an instance of Shamay-Tsoory et al.'s (2019) idea of conformity as a social alignment where people align their beliefs, intentions, and attitudes. This might be achieved via social attention system (Gvirts & Perlmutter, 2020), which includes IBS of interacting people.

5.2 Risk and Payoff Dominance's Effect on IBS

Risk and payoff have been shown to affect the choices of players in the Stag Hunt game (Aydoğan, 2019; Schmidt et al., 2003). Aydoğan's (2019) thesis work focused on activation analysis of brain regions and suggested the need for working memory and theory of mind mechanisms during gameplay. IBS synchrony, on the other hand, is suggested as a different mechanism combined with single brain activation to form social attention system (Gvirts & Perlmutter, 2020). Synchrony of brain regions is about transient dynamics of signals, not amplitude. That is why, the set of analyses in this section brings additional and unique explanations of cooperation in Stag Hunt games or possibly cooperating in general.

The first analysis that yielded significant results was payoff contrast between all participants. Higher IBS was observed in left dmPFC in the games with higher payoffs. Zhou et al. (2022) associated dmPFC IBS with the prosocial effect of more generous reward allocation. Another study showed the IBS between medial PFC correlated with prosocial behavior during a cooperative key pressing task. Aydoğan's (2019) study showed the positive effect of payoff for coordination. Also, monetary incentives have been demonstrated to increase cooperation (Tan & Bolle, 2007). In light of these studies, the IBS increase between dmPFC seems to be related to the motivation of people for cooperation.

The second analysis showed significant results compared to the payoff levels among cooperating players. IBS between right dlPFC was significantly higher for the high payoff group. The primary analysis and the literature consistently showed the emergence of dlPFC IBS in cooperation tasks. Higher payoffs increase the cooperation rates between subjects. Among the cooperating pairs, a higher payoff level might utilize the right dlPFC as well as the left dlPFC. After all, there are studies of cooperation that did not show a lateralization effect in dlPFC, as our results did (Zhou et al., 2022; Li et al., 2020).

Lastly, for the cooperating pairs, high-risk games resulted in higher IBS between three optodes, located on the left dlPFC, vmPFC, and FPC. In Stag Hunt games, high-risk dominance makes it harder to cooperate (Aydoğan, 2019; Schmidt et al., 2003). In the face of strategic uncertainty, it might be necessary to utilize every aspect of the social attention system in the form of IBS between PFCs to achieve cooperation. The prosocial effect of vmPFC is discussed for the first analysis in this section. The dlPFC is also associated with different cooperation tasks. On the other hand, Nozawa et al. (2016) created a scenario where people need to implicitly understand each other, utilizing the mentalizing system. They observed higher IBS between FPCs of participants compared to a control condition where they did not need to understand others' intentions. This is very similar to trying to decipher whether the other player will cooperate under higher uncertainty. It is easier to cooperate when there is no risk and high reward, but it is another thing to cooperate under high risk. When the participants in our study cooperated under such circumstances, it seems they are utilizing more of their social attention system. It might be the case that cooperating in even riskier situations can result in more utilization of this system.

5.3 Conclusions

In this study, we investigated the underlying interbrain synchrony of subjects playing the Stag Hunt game. We expanded on the experiment that was done by Aydoğan (2009) by analyzing the Wavelet Transform Coherence increase of hemodynamic responses between pairs. We focused on the cooperation aspect of the Stag Hunt game and its interbrain neural correlates, whereas the original study focused on activation patterns in single brains. We defined cooperation as playing the payoff dominant equilibrium collectively in the majority of ten trials of gameplay. For the first analysis, we observed significant interbrain synchrony among the left dlPFCs of the pairs. This result was consistent with the literature on hyperscanning on cooperation. Then we contrasted the couples based on the dominance characteristics of the games and cooperation behavior that we defined. The results of the second analysis were parallel to some of the observations in the literature.

Given the novelty of the field and lack of theoretic understanding of interbrain synchrony, this study can be considered an exploratory foray into the neural correlates of human cooperation behavior. In the literature, cooperation tasks utilized showed enormous variation. Cooperation and competition are studied heavily in behavioral economics. This study combines these two perspectives, bridging the gap between second-person neuroscience and Game Theory. This study suggests that the Stag Hunt game can be a viable addition to the tasks in social neuroscience of cooperation and can lead to fruitful research.

5.4 Limitations and Future Directions

The original study of Schmidt et al. (2003) involved random matching and one-shot protocols, but in this study, we could only observe the repeated games. Contrasting repeated games, which allowed players to build history and trust, and other game protocols could further differentiate the cooperation aspect of the game; however, playing random matching games under hyperscanning is methodologically untenable. Also, the effect of the payoff and risk dominance measures could be observed better in this way. This thesis work's investigation of the economic parameters of the game is lacking for two reasons. First, we lacked control in the form of other game protocols. Second, we collapsed so many games, hence so many observations, to a binary category, namely cooperation. We focused on the social cognitive aspect of the interactions, but by doing so, we could not focus on the effect of the economic metrics and their neuronal substrates as much. In future studies, a trial-by-trial analysis combined with the cooperation aspect of the game can reveal a better understanding of people, both as utility-maximizing agents and socially-driven beings.

The cooperation aspect could be explored further with questionnaires used in the literature on cooperation, measuring shared intentionality (Hu et al., 2017), the affective state of the individual (Zhou et al., 2022), or subjective cooperation reports (Li et al., 2020). In addition, in Shamay-Tsoory et al.'s (2019) framework, aspects of social alignment are argued to affect each other. Also, Gvirts and Perlmutter's (2020) framework suggested setting and nature of the relation are determinants in the social attention system, hence IBS. In the future, these parameters can be manipulated to see whether they affect the outcome of the Stag Hunt game.

Moreover, there is a plethora of various analyses that can unveil different qualities of the IBS. Taking the temporal aspect into consideration is mentioned above. Furthermore, phase synchrony can be informative in the context of hyperscanning, which is suggested as a possible mechanism for human verbal interaction (Jiang et al., 2021). Lastly, although the hyperscanning studies usually focus on the interconnection of the same brain regions, exploring intra-connections within brains and interconnections between different brain regions can yield a richer picture in the context of this study.

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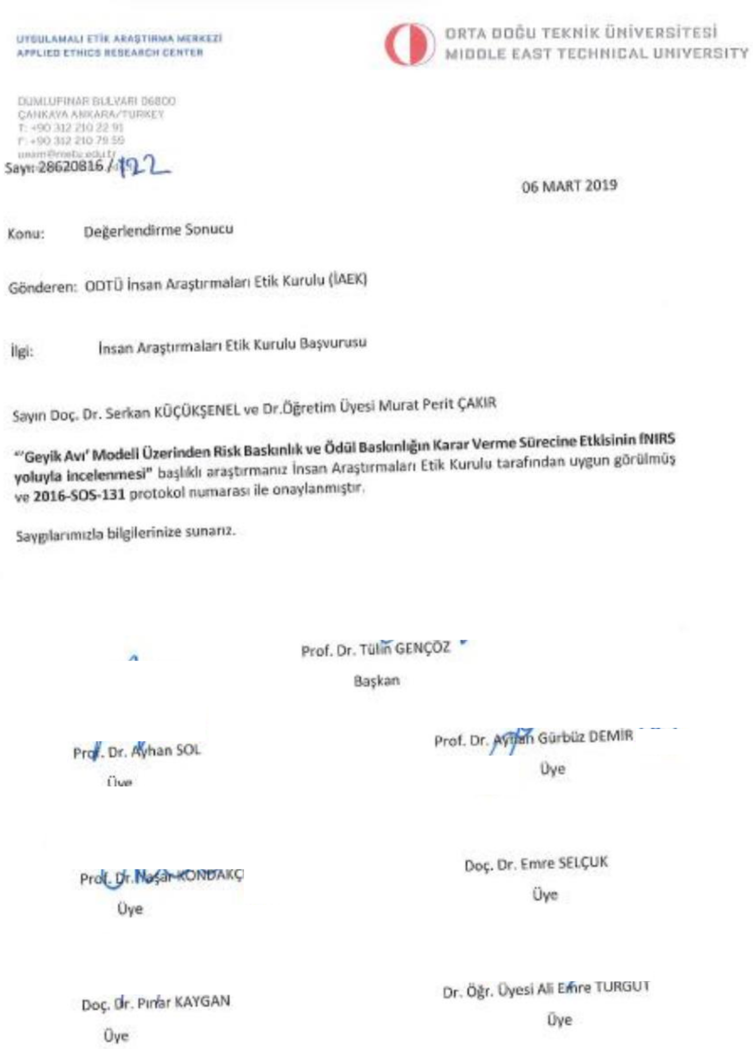
APPENDIX

ETHICS COMMITTEE APPROVAL



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06 MART 2019

Konu: Değerlendirme Sonucu

Gönderen: ODTÜ İnsan Araştırmaları Etik Kurulu (İAEK)

İlgi: İnsan Araştırmaları Etik Kurulu Başvurusu

Sayın Doç. Dr. Serkan KÜÇÜKŞENEL ve Dr.Öğretim Üyesi Murat Perit ÇAKIR

"'Geyik Avı' Modeli Üzerinden Risk Baskınlık ve Ödül Baskınlığın Karar Verme Sürecine Etkisinin fNIRS yoluyla incelenmesi" başlıklı araştırmanız İnsan Araştırmaları Etik Kurulu tarafından uygun görülmüş ve **2016-SOS-131** protokol numarası ile onaylanmıştır.

Saygılarımızla bilgilerinize sunarız.

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