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Neural dynamics of two players when using nonverbal cues to gauge intentions to cooperate during the Prisoner's Dilemma Game

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ABSTRACT

Social interaction is a fundamental part of our daily lives; however, exactly how our brains use social cues to determine whether to cooperate without being exploited remains unclear. In this study, we used an electroencephalography (EEG) hyperscanning approach to investigate the effect of face-to-face contact on the brain mechanisms underlying the decision to cooperate or defect in an iterated version of the Prisoner's Dilemma Game. Participants played the game either in face-to-face or face-blocked conditions. The face-to-face interaction led players to cooperate more often, providing behavioral evidence for the use of these nonverbal cues in their social decision-making. In addition, the EEG hyperscanning identified temporal dynamics and inter-brain synchronization across the cortex, providing evidence for involvement of these regions in the processing of face-to-face cues to read each other's intent to cooperate. Most notably, the power of the alpha frequency band (8–13 Hz) in the right temporoparietal region immediately after seeing a round outcome significantly differed between face-to-face and face-blocked conditions and predicted whether an individual would adopt a ‘cooperation’ or ‘defection’ strategy. Moreover, inter-brain synchronies within this time and frequency range reflected the use of these strategies. This study provides evidence for how the cortex uses nonverbal social cues to determine other's intentions, and highlights the significance of power in the alpha band and inter-brain phase synchronizations in high-level socio-cognitive processing.

Introduction

Social interaction is a fundamental part of our daily lives, and understanding how it is achieved provides a window into how our minds work. Sociality is beneficial when helping each other (i.e., cooperation) pays off more than either acting independently or competing with others. However, the willingness to cooperate entails a risk—the possibility of being exploited. Indeed, the potential to exploit a cooperator is available to everyone, producing a tradeoff between the utility (benefits versus costs) of cooperating and exploiting. At the same time, the decision to cooperate requires an assessment of what the other individual(s) will do—i.e., whether they will also attempt to cooperate or exploit. The Prisoner's Dilemma Game captures these fundamental issues in a formalized framework, and is therefore used to study the mechanisms underlying cooperative (and exploitive) behavior. In the game, two players decide whether to “cooperate” or “defect” and then receive a payoff based on the joint outcome, in which mutual cooperation pays off more than mutual defection, but a combined cooperation and defection leads to the highest payoff for the defector and the lowest for the exploited cooperator (see Fig. 1B). There is thus incentive to cooperate and to exploit. In the iterated version, the same choice is made over several rounds with both players seeing the outcomes (choices and payoffs) after each round, and we use “Prisoner's Dilemma Game” to denote the iterated version unless otherwise noted as the “single-shot” case (i.e., only one round conducted). When decisions are made over multiple rounds, individuals can potentially use verbal and nonverbal cues as well as past choices to gauge the other's intentions in future rounds. However, verbal communication is not always feasible, and moreover, since verbal cues are a chief avenue for deception, it is likely that people seek honest signals from nonverbal cues; yet how nonverbal cues influence social decisions in contexts such as the Prisoner's Dilemma Game remains unclear. Therefore, in the current study we sought to examine the effects of direct face-to-face interaction during the Prisoner's Dilemma Game on both the behavioral choices and on the underlying neural activity mediating the decisions.

Rilling et al. (2002) examined the brain via fMRI as participants played the Prisoner's Dilemma Game. The regions activated during

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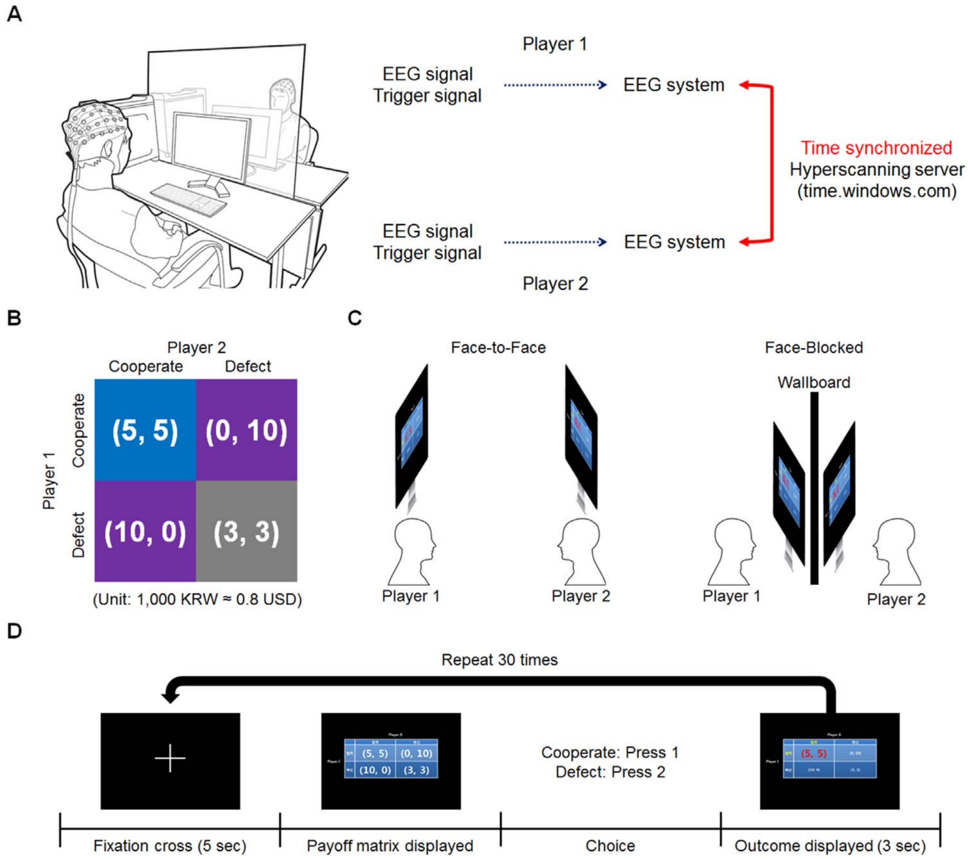

Fig. 1. Experimental setup and procedure. (A) The EEG data were simultaneously acquired using two EEG-recording systems that were synchronized using a hyperscanning server (time.windows.com) (note that the opaque barrier is depicted as transparent to see overall setup). (B) Payoff matrix of the iterated Prisoner's Dilemma Game. (C) For face-to-face groups, the wallboard was removed for the players to face each other during the game (with each participant sitting next to the other player's monitor, enabling each person to view both the other participant and the monitor adjacent to the other participant). For face-blocked groups, the wallboard remained in place so that the players could not see each other during the game. (D) At the beginning of every round, a white fixation cross appeared on the dark screen for 5 s, followed by the payoff matrix. The two players then made their choices by pressing either key 1 or 2 on the keyboard. After they made their decision, the outcome was presented for 3 s and the fixation mark appeared again, beginning the next round. The game was repeated 30 times.

mutual cooperation were largely areas known for reward processing, such as the caudate nucleus of the striatum and the anterior cingulate cortex (ACC), suggesting that cooperation may be driven by the rewarding effects it produces.

To characterize the brain mechanisms further, studies using electroencephalography (EEG) signals enable an examination of the neural activity of people more directly (i.e., electrical recordings vs. BOLD signal) and precisely, especially regarding the specific time and frequency ranges of the neural processing (Astolfi et al., 2009, 2010, 2011; Babiloni et al., 2007a, 2007b; Chiu et al., 2008; De Vico Fallani et al., 2010; Dumas et al., 2010; Kawasaki et al., 2013; King-Casas et al., 2005; Logothetis and Wandell, 2004; Müller and Lindenberger, 2014; Müller et al., 2013; Sänger et al., 2012, 2013; Tomlin et al., 2006; Yun et al., 2008, 2012). EEG studies also offer the opportunity to investigate more realistic social interaction, with the participants in the same room (rather than interacting with a partner via photos and choices displayed on a computer screen), and more details of the social interaction, including potential neural relationships across their brains (such as coherence), called *hyperscanning* (Montague et al., 2002). This is particularly advantageous given that people are known to behave differently when they are interacting with computers instead of with other people (Rilling et al., 2008; Rilling and Sanfey, 2011).

Astolfi and colleagues conducted a hyperscanning EEG study with two individuals playing the Prisoner's Dilemma Game (Astolfi et al., 2009, 2010, 2011; De Vico Fallani et al., 2010). Comparing cooperation and defection strategies during the time when the outcomes are shown to the individuals (i.e., both player's choices and their payoffs), they found greater activity in the theta (4–7 Hz) and alpha (8–13 Hz) bands of the orbitofrontal region during defection, but relatively little cortical activity during cooperation. This relative lack of neural activity associated with cooperation may reflect comparable findings to the Rilling et al. (2004) single-shot Prisoner's Dilemma Game study, in which deeper structures were implicated (i.e., the striatum and ACC). In contrast, the relatively weak relationship to cooperation may also reflect the fact that the cooperation strategy examined may have occurred relatively automatically and independently of the partner's behavior, and thus not requiring significant higher-level socio-cognitive processing, with the cooperation strategy defined as cases in which the individual either (a) cooperated in consecutive rounds regardless of the partner's choice or (b) chose to cooperate even when the partner defected on the previous round. At the same time, it remains unclear the degree to which the participants observed each other during the task and how much this may have influenced their choices. Their interesting results thus warrant further investigation.

Indeed, sociality evolved under face-to-face interactions, and a great deal of evidence shows that nonverbal cues (e.g., facial expressions) play a large role in the attempt to decipher other's intentions and predict their behavior (Conty et al., 2012, 2007; Emery, 2000; Kuzmanovic et al., 2009). Non-verbal communication conveys more detailed and subtle feelings that verbal communication alone has difficultly expressing. For example, it is known that the eyes reveal important social data of an individual such as gender, age, familiarity, emotional expression and intention (Emery, 2000). During social interactions, facial expressions, gaze direction, gaze duration, and