

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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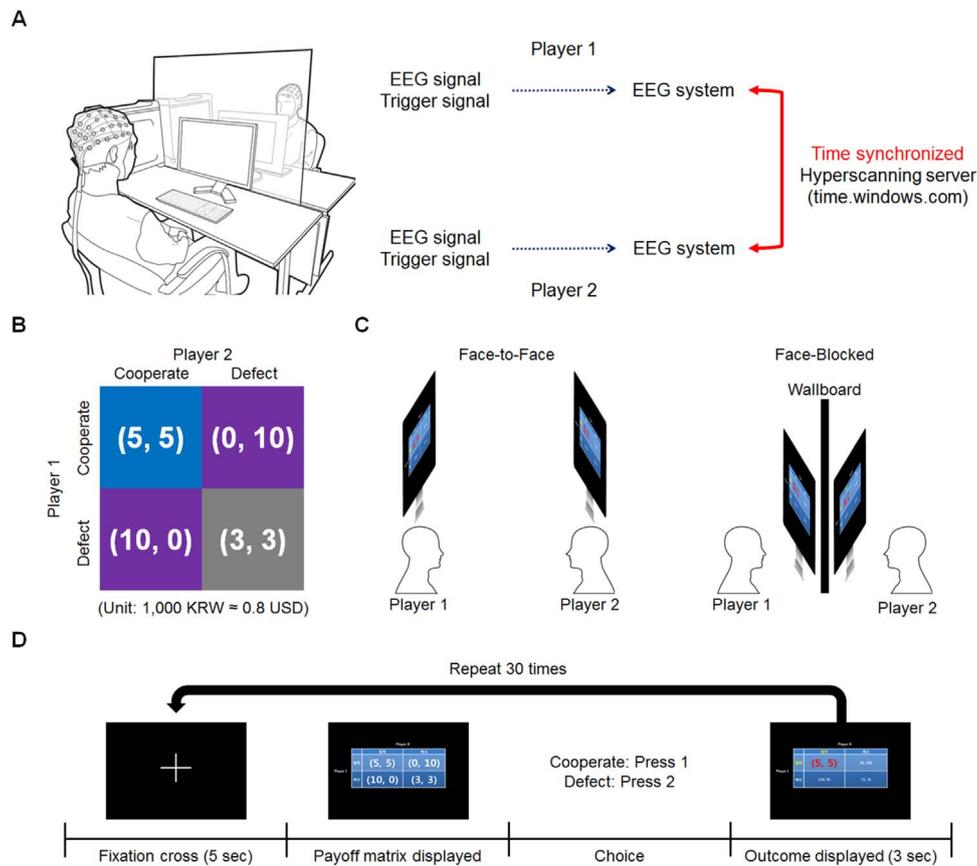


Fig. 1. Experimental setup and procedure. (A) The EEG data were simultaneously acquired using two EEG-recording systems that were synchronized using a hyperscanning server (time.windows.com) (note that the opaque barrier is depicted as transparent to see overall setup). (B) Payoff matrix of the iterated 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; Sängner 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 difficulty 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

gestures are known to be crucial visual cues of communicative intentions (Conty et al., 2012, 2007; Kuzmanovic et al., 2009). It also appears that direct eye contact activates regions of the brain related to social cognition including the ventral and medial prefrontal cortex, superior temporal gyrus, fusiform gyrus, cingulate gyrus and amygdala (Senju and Johnson, 2009). Indeed, by virtue of their more automatic and universal nature, nonverbal cues also can provide more reliable and honest signals that should also help to reduce social exploitation—i.e., used for ‘cheater detection’.

To examine the effects of face-to-face contact on the behavior and neural mechanisms of social interactions in a more formal game theory framework, a recent study examined face-to-face effects using another classic game used to study sociality: the Ultimatum Game, in which two people (a proposer and responder) are presented with a sum of money, the proposer decides how to split it between them, the responder subsequently decides whether to accept the proposal, with acceptance resulting in both receiving the proposed split, and rejection resulting in both receiving nothing (Tang et al., 2016). A prior neuroimaging study using the Ultimatum Game without face-to-face interaction found heightened activity for unfair offers versus fair ones that suggested cognitive processing (the dorsolateral prefrontal cortex) and the involvement of negative social emotions comparable to disgust (the anterior insula) (Sanfey, 2007). Examining face-to-face effects more directly (versus a face-blocked condition), Tang et al. (2016) used a modified Ultimatum Game in conjunction with functional near-infrared spectroscopy (fNIRS) to examine the effects on the dorsolateral prefrontal cortex and the temporoparietal junction (TPJ). That latter region was also studied given that the TPJ has been implicated in socio-cognitive processing in several studies, particularly regarding the assessment of what others are thinking (Adolphs, 2003, 2009; Pavlova et al., 2006; Puce and Perrett, 2003; Saxe, 2006; Saxe and Kanwisher, 2003; Tankersley et al., 2007). In their modified Ultimatum Game, only the proposer saw the actual total amount and could therefore lie about the total to the responder. Both the proposer and responder were then queried about the other’s expected behavior: was the proposer honest; will the responder accept the offer. In the face-to-face compared with the face-blocked condition, the researchers found both (a) a higher percentage of rounds in which both the proposer and responder expected positive responses (honest proposer and offer acceptance) and (b) increased interpersonal brain synchronization in the TPJ, suggesting further involvement of this area in the processing of nonverbal cues to assess proposer honesty, fairness and the responder’s subsequent expected response.

How the nonverbal cues afforded by face-to-face interactions affect decisions focused more directly on cooperation as examined in the Prisoner’s Dilemma Game, however, are unknown. To examine this, we used the EEG hyperscanning approach to leverage its ability to investigate more naturalistic social interactions, as well as the specific timing, frequency bands, and brain synchronizations involved in the social decision-making. On the behavioral level, we hypothesized that the nonverbal cues from face-to-face contact would encourage the players to cooperate more during the Prisoner’s Dilemma Game. On the neural level, we further assumed that we may find greater involvement of higher-level socio-cognitive areas, such as the temporoparietal region, in the use of face-to-face information to determine the partner’s intentions; and if so, we could characterize the temporal dynamics and between-brain neural features underlying this process.

Material and methods

Participants

64 healthy male participants (aged 23.08 ± 2.54 years, mean \pm SD) were recruited from a local university (Chungnam National University, Daejeon, South Korea). All participants were right-handed and had no history of neurological or psychiatric disorders. Written

informed consent was obtained from all participants after an explanation of the experimental procedures. The Institutional Review Board (IRB) of KAIST approved all experimental procedures for this study. Participant pools were restricted to men because sex differences during the Prisoner’s Dilemma Game have been reported both on the behavioral and neural levels (Frank et al., 1993; Krach et al., 2009; Ortmann and Tichy, 1999; Rapoport and Chammah, 1965). Groups of two strangers were formed, resulting in 32 groups. They played the game in one of two conditions: either *face-to-face* or *face-blocked*. 16 face-to-face and 16 face-blocked pairs in total were recruited. We first recruited 7 pairs per condition to record behavior only. 2 pairs from each condition (total of 4 participants) were excluded because of inappropriate behavior during the task (i.e., admittedly inattentive and simply pressing the same key without thinking even after the detailed instructions or dozing off due to sleep deprivation the previous night). This yielded 5 initial pairs per condition for behavioral testing. We then recruited 9 more pairs per condition for EEG recordings. Of these 9 initial EEG pairs, however, the EEG data from 4 pairs per condition (8 total participants) could not be analyzed due to the EEG amplifiers of the pair inadvertently having different settings, producing EEG signals recorded under different conditions, potentially compromising the integrity of the results. For these 4 pairs removed from EEG analysis, their behavioral data could still be analyzed, yielding 9 total pairs per condition for behavior alone, and 5 total pairs for behavior and EEG signal analysis. Because 5 pairs of participants have been used in other successful hyperscanning studies, we determined that this was a sufficient number to use for our EEG analyses (e.g., Astolfi et al., 2009, 2010, 2011). Thus, for the first behavioral analysis that included all participants, a total of 56 were included (14 face-to-face and 14 face-blocked pairs, aged 22.91 ± 4.36 years), and for the second behavioral analysis that examined only the EEG participants, 20 of the 56 were included (5 face-to-face and 5 face-blocked pairs, aged 23.20 ± 2.65 years).

Iterated Prisoner’s Dilemma Game

The participants were comfortably seated and a wallboard was placed between the two participants to prevent them from seeing each other prior to playing the game (Fig. 1A, with opaque barrier depicted as transparent to see overall setup). They were given a detailed explanation of the rules of the iterated Prisoner’s Dilemma Game by the instructor. To distinguish the participants, they are referred to as player 1 and player 2. The game was played 30 times, although the number of iterations, i.e., rounds, was unknown to the participants (they were told that there would be several rounds). This open-ended description of game length was intended to simulate real-world situations in which the actual ultimate number of interactions with particular individuals is often unknown. In each round, they were able to choose either to cooperate or to defect. As shown in the payoff matrix in Fig. 1B, they were told that on every round they would both earn 5000 KRW (approximately 4 US dollars) if they both chose to cooperate but only 3000 KRW (approximately 2.5 US dollars) if they both chose to defect. They were also told that if one chose to cooperate and the other chose to defect, only the defector would earn 10,000 KRW (approximately 8 US dollars) while the cooperator would earn nothing. It was emphasized that they would receive the mean amount of what they earned over the entire game as a reward and that they should aim to maximize their earnings. The game began after the instructor made sure both participants understood the rules. For participants in the face-to-face condition the wallboard was removed to allow them to face each other; whereas for participants in the face-blocked condition the wallboard remained in place (Fig. 1C). In the face-to-face condition, each participant sat next to the display monitor of the other participant—in this way, each participant could observe the other fully and also observe the monitor adjacent to their partner. Except for eye contact in the face-to-face condition, any other interactions in either

condition such as conversation between players were forbidden throughout the experiment.

As illustrated in Fig. 1D, when the game began, a white cross appeared in the center of the black screen for 5 s as a fixation point, followed by the payoff matrix. Participants made their choices by pressing a keyboard: key 1 to cooperate, key 2 to defect. Thus, the length of the decision period was not fixed, with the two players taking approximately 5–10 s to make their choices. After the players pressed a key, the outcome was presented on the screen for 3 s. Participants could therefore see both how much money each player earned and their partner's choice. Then the fixation mark appeared again beginning the next round until the game ended. Thus, once set up, it took approximately 10 min to complete each game. MATLAB R2012b (Mathworks, USA) was used for the task execution.

For analysis, we examined player choices based on both (a) the round-by-round *outcomes* (i.e., whether each player chose to cooperate, C, or defect, D) and (b) player *strategies*. To provide the most flexible and dynamic measure of possible strategy-use we identified strategies based on two consecutive rounds, i.e., by examining the pattern of outcomes on the k -th and $(k+1)$ -th rounds. We classified three basic possible *strategies* on each round (De Vico Fallani et al., 2010). The first was a *Cooperation strategy* (C_S), in which a player chooses to cooperate after previously cooperating, or when a player chooses to cooperate even after his/her partner defected. The second was a *Defection strategy* (D_S), in which a player defects continuously, or when a player who was cooperating starts to defect as soon as the other player cooperates. Finally, the third was a *Tit-for-tat strategy* (T_S), in which a player switches their choice to be the same as the other player's previous decision. Thus, for every round there would be 6 possible combinations of strategies of the two players: $C_S C_S$, $C_S D_S$, $C_S T_S$, $D_S D_S$, $D_S T_S$, and $T_S T_S$. The Supplementary material contains a more detailed definition and illustration of each strategy type.

EEG data acquisition and hyperscanning setup

EEGs were simultaneously recorded using two Neuroscan EEG-recording systems (Compumedics Neuroscan, USA) with two Ag/AgCl sintered electrode caps (Quik-cap, Compumedics Neuroscan, USA). EEGs were recorded from 62 scalp positions (FP1, FPZ, FP2, AF3, AF4, F7, F5, F3, F1, FZ, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCZ, FC2, FC4, FC6, FT8, T7, C5, C3, C1, CZ, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPZ, CP2, CP4, CP6, TP8, P7, P5, P3, P1, PZ, P2, P4, P6, P8, PO7, PO5, PO3, POZ, PO4, PO6, PO8, CB1, O1, OZ, O2, and CB2) mounted in a cap using what is termed a modified extended 10–20 electrode system (Jasper, 1958). Two electrodes were placed above and below the right eye for recording vertical ocular movements (vertical electrooculogram: VEOG), and another two were placed at the outer side of each eye for horizontal ocular movements (horizontal electrooculogram: HEOG). An additional two electrodes were placed below each mastoid (M1, M2). An electrode between CZ and FCZ was used as a reference and the one between FPZ and FZ was used as a ground. Electrode impedance was kept under 15 k Ω for all recordings. EEGs were continuously recorded and digitized at a sampling frequency of 1000 Hz with DC high-pass and 200 Hz low-pass system acquisition filter settings using Scan 4.5 (Compumedics Neuroscan, USA). The signal was amplified with a 64-channel SynAmps² amplifier (Compumedics Neuroscan, USA). Overall, the preparation for EEG acquisition for each participant pair took approximately an hour.

Before data acquisition, the times of the two EEG recording systems were synchronized according to a common time server (time.windows.com), providing millisecond-range synchrony between the two EEG systems (Fig. 1A).

EEG data processing

EEG data analysis was conducted using EEGLAB 12.0.2.6b, an

open source toolbox operated in MATLAB (<http://sccn.ucsd.edu/eeqlab>) (Delorme and Makeig, 2004). ADJUST (an Automatic EEG artifact Detector based on the Joint Use of Spatial and Temporal features) plug-in 1.1 was also used together with EEGLAB to remove EEG artifacts (<http://www.unicog.org/pm/pmwiki.php/MEG/RemovingArtifactsWithADJUST>) (Mognon et al., 2011). In the EEG data preprocessing, we applied a 0.5 Hz high pass filter, a 120 Hz low pass filter, and a 55–65 Hz notch filter consecutively to remove 60 Hz AC noise. After filtering, signals were re-referenced to a linked mastoid reference (M1, M2) to avoid the possibility of brain activity inflation in one hemisphere and thus to prevent a laterality bias (Teplan, 2002). We then extracted the rounds from the EEG recordings based on the time period ranging from -1 to $+3$ s with reference to the outcome presentation. We call these extracted recording segments *epochs*, with one per round per electrode. One second prior to the outcome presentation was removed as the baseline correction to detrend the data. Epochs whose maximum magnitude exceeded 150 microvolts were excluded (a widely-used threshold for gross artifact removal). If the round contained at least one excluded epoch (i.e., from any electrode), we removed the entire round from the EEG dataset (i.e., for all electrodes). Overall, 10 rounds and 5 rounds were excluded from the EEG dataset of the face-to-face and face-blocked conditions respectively, with Tables S2 and S3 listing the number of rounds collected and those that needed to be removed. Then to remove ocular artifacts (eye blinks, vertical eye movements, and horizontal eye movements) and muscular artifacts, independent component analysis (ICA) was first applied to the epoched data (as implemented in the EEGLAB toolbox) (Delorme and Makeig, 2004), and then the ADJUST plug-in was used to remove the ICA components that contained the artifacts according to the plug-in's default criteria (Mognon et al., 2011). For outcome analysis, the EEG epochs were divided into 6 types according to the 3 possible outcome combinations of the two players (CC, CD, DD) for both the face-to-face or face-blocked conditions. For strategy analysis, the EEG epochs were divided into 12 types according to the 6 possible outcome combinations of the two players ($C_S C_S$, $C_S D_S$, $C_S T_S$, $D_S D_S$, $D_S T_S$, and $T_S T_S$) for both the face-to-face or face-blocked conditions. For further EEG analyses, we clustered the scalp electrodes according to 6 corresponding brain regions: (1) frontal (FP1, FPZ, FP2, AF3, AF4, F7, F5, F3, F1, FZ, F2, F4, F6, F8), (2) fronto-central (FC3, FC1, FCZ, FC2, FC4, C3, C1, CZ, C2, C4), (3) parietal (CP3, CP1, CPZ, CP2, CP4, P5, P3, P1, PZ, P2, P4, P6), (4) left temporoparietal (FT7, FC5, T7, C5, TP7, CP5, P7), (5) right temporoparietal (FC6, FT8, C6, T8, CP6, TP8, P8), and (6) occipital (PO7, PO5, PO3, POZ, PO4, PO6, PO8, O1, OZ, O2).

EEG time-frequency analysis

Two general procedures were necessary to evaluate the EEG time-frequency data: (1) we first obtained the proper signals for analysis and then (2) we evaluated whether the signals in each of the 6 brain regions were related to the effect of face-to-face contact on cooperation. The first procedure required three steps. First, to obtain the amplitude of the EEG spectra at each frequency as a function of time, we calculated the event-related spectral perturbation (ERSP) of the artifact-free epochs using EEGLAB (Delorme and Makeig, 2004):

$$\text{ERSP}(\mathbf{f}, \mathbf{t}) = \frac{1}{n} \sum_{k=1}^n |F_k(f, t)|^2$$

where, for n rounds, $F_k(f, t)$ is the spectral estimate of round k at frequency f and time t . Second, we then calculated the spectral powers for all epochs based on a wavelet transformation using a default wavelet cycle setting of [3 0.5] (Delorme and Makeig, 2004) with reference to the baseline, which was 1 s prior to the outcome presentation. The frequency range was determined to be from 5.86 to 50.00 Hz, the pad ratio was set to 8 (related to frequency resolution),

and the frequency bin width was 0.25 Hz. Third, to use only the amplitudes significantly higher than baseline, a bootstrap method with alpha level set to 0.001 was conducted, with statistically insignificant results set to zero (Delorme and Makeig, 2004).

For the second procedure, because the main goal of the study was to examine the neural mechanisms that mediated cooperation during face-to-face contact, we looked to isolate signals that were related to both face-to-face contact and mutual cooperation during face-to-face contact. This evaluation required three steps. First, we evaluated whether the signals were related to the experimental conditions (face-to-face vs. face-blocked). Second, we evaluated whether the signals exhibited differences between mutual cooperation (CC or C_SC_S) and the other joint outcomes (i.e., CC vs. CD or DD) or joint strategies (i.e., C_SC_S vs. the five others) during the face-to-face condition. Third, we determined whether any signals were related to both condition differences (face-to-face vs. face-blocked) and differences between mutual cooperation and the other outcomes or strategies (e.g., C_SC_S vs. D_SD_S).

To conduct steps one and two of this evaluation – (1) to determine whether the resulting ERSP values for each of the 6 brain regions were related to the experimental conditions (face-to-face vs. face-blocked) and (2) related to mutual cooperation in the face-to-face condition (versus the other behavioral outcomes and strategies) – the same three methodological steps were required. First, at every frequency f by time t point we conducted a Wilcoxon rank sum test ($p < 0.05$) to compare the conditions, outcomes or strategies by using the ERSPs for each participant on each electrode of the brain region (e.g., for face-to-face vs. face-blocked at a given f , t point, if 10 participants per condition and 3 electrodes for the brain region: 10 vs. 10 ERSP values averaged over the region compared). Note that the nonparametric test was utilized since the ERSP data did not meet normality assumptions, and the p value was set to 0.05 given that the subsequent step (region of interest identification) provided strict criteria to eliminate possible spurious results. Thus, for the second step, we collated these results by identifying clear ‘hot spots’ of significance. We defined significant *time and frequency regions of interest (time-frequency ROIs)* based on two criteria that were designed as stated to be strict enough to eliminate potential spurious findings and at the same time provide enough overlap in the time and frequency domains to be interpreted as a time-frequency range of interest: (1) at least five consecutive frequency points showed significant differences at two (or more) consecutive time points, with at least one of the two consecutive time points being the same time point for all five frequency points (thus, all five frequency points held at least one significant time point in common); and (2) of these five frequency points, at least two consecutive frequency points had significant differences for at least ten consecutive time points (rather than just two consecutive). Third, we then examined how the time-frequency ROI results related to specific frequency bands: i.e., theta (4–7 Hz), alpha (8–13 Hz), beta (14–30 Hz), and gamma (31–50 Hz). Finally, we examined whether any time-frequency ROIs were related to both condition differences (face-to-face vs. face-blocked) and differences between mutual cooperation and the other outcomes or strategies.

Brain synchronization analysis

We first note that although the synchrony analysis inherently contains half as many data points as the time-frequency analysis (given that the former is a pairwise measure of the latter), and although more participants and rounds of the game per condition are always preferred, previous research suggests that the number of EEG participants and rounds conducted should be sufficient to properly examine the behavior, neural time-frequency dynamics, and neural synchrony (e.g., Astolfi et al., 2009; Astolfi et al., 2010;

Astolfi et al., 2011). Evaluation of inter-brain synchronization also required two general procedures: (1) obtaining the proper inter-brain phase synchronies and (2) examining their relationship to the experimental conditions (face-to-face vs. face-blocked) and response strategies, focusing on the time-frequency ROIs identified by the previous analysis (described in *EEG time-frequency analysis*) as those associated with the face-to-face influence on cooperation. (Note that, as reported in *EEG time-frequency results*, no results were found for response *outcomes* and thus, for behavior, only *strategies* were examined here.) The first procedure entailed calculating and evaluating the time-varying phase-locking value (PLV) (Lachaux et al., 1999) for all possible pairs of electrodes between the two brains at specific time and frequency ranges of interest: i.e., 4 frequency ranges (theta, alpha, beta, and gamma) and 5 time ranges subsequent to the outcome presentation (0–0.5 s, 0.5–1 s, 1–1.5 s, 1.5–2 s, and 2–2.5 s). This required four steps. We first computed the *phase* at a given frequency f and time t as:

$$\varphi(f, t) = \tan^{-1} \left(\frac{C(f, t)_i}{C(f, t)_r} \right)$$

where $C(f, t)_r$ and $C(f, t)_i$ are the real and imaginary Fourier coefficients, respectively. Second, we then computed the phase difference between the epochs of electrode i and j , denoted as $\varphi_{ij} = \varphi_i - \varphi_j$, for all time and frequency points within the specified time and frequency range. Third, the PLV between electrodes i and j at the given time and frequency range was given by:

$$PLV_{ij} = \left| \frac{1}{N} \sum \exp^{i\varphi_{ij}} \right|$$

where N is the number of samples of the data set and “ $| \cdot |$ ” the complex modulus. The PLV has values between 0 and 1, where 1 means perfect phase synchrony between two signals. To examine brain synchronization for the face-to-face versus face-blocked conditions as well as across strategies (i.e., C_SC_S vs. D_SD_S), the PLVs were calculated for all epochs and electrode pairs between participants (for the 4 frequency and 5 time ranges).

The final step of the first procedure was conducted to provide only significant synchronies that would be used for further brain-connectivity analyses. This step thus required determining the significance of the phase synchronizations, in which we tested the null hypothesis (H_0) that the two sets of phase values for electrodes i and j , φ_i and φ_j , recorded on a given round were independent. This test was conducted in four steps. First, for each successfully recorded round with electrodes i and j , we compared the actual PLV_{ij} with 200 values obtained from shuffling the electrode j epochs (i.e., all successful rounds) 200 times and computing the phase $\varphi_{j_{shuffle}}$, phase difference $\varphi_i - \varphi_{j_{shuffle}}$ and corresponding $PLV_{ij_{shuffle}}$ each time. Second, we defined the proportion of surrogate $PLV_{ij_{shuffle}}$ s exceeding the original PLV_{ij} as the phase-locking statistic (PLS) for the test of the original PLV_{ij} (Lachaux et al., 1999). Third, we then set the PLV_{ij} to 0 if the corresponding PLS_{ij} was less than 0.05. This statistical procedure (steps 1–3) was conducted for all PLV_{ij} s (i.e., all successful rounds of all possible pairs of electrodes), thus leaving only significant synchronies for the further brain-connectivity analyses. Finally, for PLV_{ij} with electrodes i and j from the two different players, the two values $PLV_{i_{player1}j_{player2}}$ and $PLV_{i_{player2}j_{player1}}$ were averaged and defined as the inter-brain synchrony between electrodes i and j .

Now in position to carry out the second procedure, we used repeated measures one-way analysis of variance (RMANOVA) with the condition (face-to-face and face-blocked) as a between-participant factor and the electrode pair (1953 pairs for inter-brain phase synchrony) as a within-subject factor (condition×electrode pair), as well as subsequent t-tests to examine the effects of condition and strategies on the synchronization values (significant PLV_{ij} s).

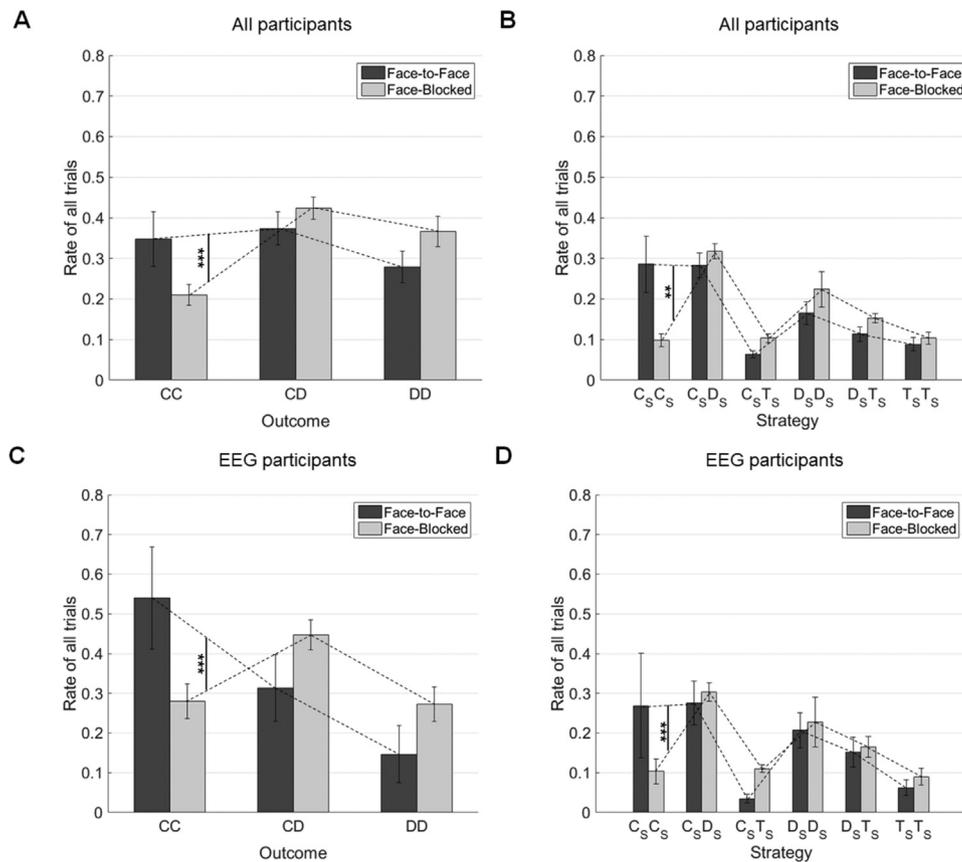


Fig. 2. Behavioral results of EEG participants. (A) Rate of each joint outcome (CC, CD, and DD) and (B) joint strategy ($C_S C_S$, $C_S D_S$, $C_S T_S$, $D_S D_S$, $D_S T_S$, and $T_S T_S$) in the face-to-face and face-blocked conditions for all participants tested (56 participants, 14 face-to-face and 14 face-blocked pairs). (C) Rate of each joint outcome and (D) joint strategy in the face-to-face and face-blocked conditions for the participants whose EEG recordings could be subsequently analyzed (20 participants, 5 face-to-face and 5 face-blocked pairs). For both the entire sample and the EEG subset, the distribution of outcomes and strategies differed significantly between the face-to-face (shifted left, and thus toward greater cooperation) and face-blocked (shifted right) conditions (all participants' outcome distributions: $\chi^2(2) = 20.590$; all participants' strategy distributions: $\chi^2(5) = 49.781$; EEG participants' outcome distributions: $\chi^2(2) = 21.605$; EEG participants' strategy distributions: $\chi^2(5) = 17.576$). **: $p < 0.005$, ***: $p < 0.001$. Error bars refer to the standard error of the mean.

Results

Behavioral results

For behavior, we examined both the entire participant sample (56 participants, 14 face-to-face and 14 face-blocked pairs) and the subset of participants whose EEG recordings could be subsequently analyzed (20 participants, 5 face-to-face and 5 face-blocked pairs) (see *Participants* for more information). For both data sets we tested the hypothesis that face-to-face contact would lead to a greater rate of cooperation. We first classified the behavioral results according to the three possible joint *outcomes* (CC, CD, and DD) and six possible joint *strategies* ($C_S C_S$, $C_S D_S$, $C_S T_S$, $D_S D_S$, $D_S T_S$, and $T_S T_S$), and then tested the hypothesis by comparing the face-to-face and face-blocked distributions for both the joint outcomes and the joint strategies (using IBM SPSS Statistics Version 20). Fig. 2A & B shows the results for the entire participant sample and Fig. 2C & D for the EEG participant subset. Both the entire sample and EEG subgroup exhibited significantly different distributions of joint outcomes and joint strategies, with the face-to-face distribution shifted toward greater cooperation in all cases (all participants' outcome distributions: $\chi^2(2) = 20.590$, $p < 0.001$; all participants' strategy distributions: $\chi^2(5) = 49.781$, $p < 0.001$; EEG participants' outcome distributions: $\chi^2(2) = 21.605$, $p < 0.001$; EEG participants' strategy distributions: $\chi^2(5) = 17.576$, $p = 0.0035$). Moreover, examining the direction of effect, the face-to-face rate was higher than the face-blocked rate for only joint cooperation (i.e., for CC and $C_S C_S$) and lower than the face-blocked rate in all other joint outcomes and joint strategies in all four instances (i.e., for both

entire participant pool and EEG subgroups, outcome and strategy). At the same time, an examination of the individual scores (Tables S2 and S3) revealed fairly large individual differences, suggesting that the different relevant factors, such as actual behavioral outcomes vs. nonverbal cues, influenced individuals to varying degrees. Nonetheless, inspection of the individual scores revealed an apparent shift toward more cooperation in the face-to-face condition and a shift away from it in the face-blocked condition, which was detected by the χ^2 distribution tests. Thus, face-to-face interaction appeared to shift the participants' decision to cooperate more frequently, yielding higher mutual cooperation with respect to both outcomes chosen and strategies adopted.

EEG time-frequency results

The main goal of our neural investigations was to identify and characterize the neural activity and brain regions that mediate cooperation during face-to-face contact. To do so, we first conducted a time-frequency analysis via three main steps. First, we identified neural activity related to condition (face-to-face vs. face-blocked). Second, we sought to identify neural activity during the face-to-face condition that mediated mutual cooperation. To do this, we identified neural activity that showed differences between mutual cooperation (CC or $C_S C_S$) and the other joint outcomes (i.e., CC vs. CD or DD) or joint strategies (i.e., $C_S C_S$ vs. others). As described further below, we did not find activity during the face-to-face condition that exhibited significant differences between the mutual outcome CC and CD or DD, but did so for strategy.

Third, we examined both sets of results in steps one and two to identify the neural activity that showed differences for *both* condition *and* the mutual cooperation strategy (C_SC_S) versus other strategies.

To conduct these three main steps, we first needed to assess whether there were a sufficient number of rounds recorded. That is, because the number of rounds per condition, outcome, or strategy varied due to removal of rounds with gross artifacts (described in *EEG data processing* and shown in [Tables S2 and S3](#)) or simply the choices made by the participants, we first assessed these differences in the number of rounds recorded prior to subsequent analyses. We first tested if the number of rounds recorded for the face-to-face and face-blocked conditions significantly differed from each other for both outcome and strategy: e.g., for outcome, we summed the first ten rows of [Table S2](#) (giving 10 values for the face-to-face condition) and the first ten rows under the face-block condition (giving 10 values) and compared these values with a two-sample t-test. For the face-to-face and face-blocked conditions, the number of rounds of outcome and strategy used for analysis did not differ significantly between the conditions (showing mean ± SEM, face-to-face pairs: 29.00 ± 0.54 rounds of outcome, 28.00 ± 0.54 rounds of strategy; face-blocked pairs: 29.50 ± 0.34 rounds of outcome, 28.50 ± 0.34 rounds of strategy; two-tailed $t(18) = -0.7851$, $p = 0.4426$, with identical statistical values for both outcome and strategy).

In addition, because the number of rounds recorded per outcome or strategy may have differed among the different joint outcomes or strategies, we also tested whether these difference were significant. Because our subsequent analyses attempted to isolate neural activity related to mutual cooperation (CC or C_SC_S) in the face-to-face condition, we compared the number of rounds of CC or C_SC_S versus the others in this condition. For outcome, the number of rounds of mutual cooperation (CC) did not differ from the others (CD or DD) in the face-to-face condition (CC: 8.90 ± 3.61 rounds, CD: 9.50 ± 1.83 rounds, DD: 10.60 ± 1.81 rounds; $t(18) = -0.1482$, -0.4207 , $p = 0.8838$, 0.6789 , respectively — thus both comparisons insignificant whether using the Bonferroni correction factor of two or not: $p > 0.05 > 0.05/2$). For strategy, we also found no significant differences in the number of rounds between mutual cooperation (C_SC_S) versus the others in the face-to-face condition (C_SC_S: 7.70 ± 3.61 rounds, C_SD_S: 7.70 ± 1.48 rounds, C_ST_S: 0.90 ± 0.28 rounds, D_SD_S: 5.80 ± 1.18 rounds, D_ST_S: 4.20 ± 1.00 rounds, T_ST_S: 1.70 ± 0.52 rounds; C_SC_S vs. C_SD_S, C_SC_S vs. C_ST_S, C_SC_S vs. D_SD_S, C_SC_S vs. D_ST_S, C_SC_S vs. T_ST_S: $t(18) = 0$, 1.8788 , 0.5004 , 0.9348 , 1.6458 , $p = 1$, 0.0766 , 0.6229 , 0.3623 , 0.1172 , respectively — thus all comparisons were insignificant whether using the Bonferroni correction factor of five or not: $p > 0.05 > 0.05/5$).

To identify the neural activity underlying the face-to-face influence on cooperation, we next conducted the first two analysis steps of evaluating whether the neural signals were related to (a) the experimental conditions (face-to-face vs. face-blocked), and (b) the behavioral outcomes and strategies. *EEG time-frequency analysis* describes how the EEG signals were first converted into ERSPs (event-related spectral perturbations), and then how we tested the ERSP values for differences between the face-to-face versus face-blocked conditions as well as between joint cooperation (for outcome or strategies) versus the other joint responses (e.g., for strategy, C_SC_S versus D_SD_S) for each of 6 brain regions (frontal, fronto-central, left temporoparietal, right temporoparietal, parietal, and occipital). The tests were conducted via two steps: (1) using a Wilcoxon rank sum test ($p < 0.05$) to compare the conditions, outcomes or strategies; and (2) collating these results by defining significant *time and frequency regions of interest (time-frequency ROIs)*. For *outcome*, again we found no significant time-frequency ROIs in the comparisons of CC to CD or DD, so in what follows, all relationships of neural activity to behavior are with the behavioral *strategies*. Results are shown for the right temporoparietal region in [Fig. 3](#), and the other five brain regions in [Figs. S1 and S2](#) (see [Supplementary material](#)). [Fig. 3A](#) shows the ERSP magnitudes for the face-to-face and face-blocked conditions, as well as the difference

between them. Although these average heat maps suggest multiple potential differences between the two conditions, actual statistical differences are shown in the far right panel, with the identified time-frequency ROIs outlined in red rectangles (see *EEG time-frequency analysis* for criteria to identify the time-frequency ROIs). [Fig. 3B](#) shows the same results comparing the C_SC_S and D_SD_S strategies within the face-to-face condition.

Finally, since the main goal of the current study was to investigate how face-to-face contact affected the willingness to cooperate, we examined whether any time-frequency ROIs were related to *both* visual condition differences (face-to-face vs. face-blocked) *and* differences between mutual cooperation and the other strategies (e.g., C_SC_S vs. D_SD_S). Three time-frequency ROIs exhibited these effects: (1) alpha band, 0–0.5 s, in the right temporoparietal (RTP) area (face-to-face > face-blocked and C_SC_S > D_SD_S); (2) alpha band, 1–1.5 s, in the parietal area (face-to-face > face-blocked and C_SC_S > C_ST_S); and (3) beta band, 1.5–2 s, in the occipital area (face-to-face > face-blocked and C_SC_S > D_SD_S). We note that in all three cases, *greater* activation within these time-frequency ROIs reflected both the influence of face-to-face contact and the decisions of both players to follow the cooperation strategy.

Inter-brain synchronization

We used phase locking values (PLVs) to measure potential inter-brain synchrony, which scales between 0 and 1, where 1 means perfect phase synchrony between two signals (see *Brain synchronization analysis*); and we examined the frequency and time ranges of the three time-frequency ROIs found to be associated with the face-to-face influence on cooperation, i.e., where both condition (i.e., face-to-face > face-blocked) and strategy (i.e., C_SC_S > others) effects were found as reported in the previous section: (1) alpha band, 0–0.5 s; (2) alpha band, 1–1.5 s; and (3) beta band, 1.5–2 s. Using these frequency and time ranges, we first investigated whether synchronization between the brains of the two players depended on the presence of face-to-face interaction and scalp positions. To do so, we used repeated measures one-way analysis of variance (RMANOVA) with the condition (face-to-face and face-blocked) as a between-participant factor and the electrode pair (1953 pairs for inter-brain phase synchrony) as a within-subject factor (condition×electrode pair). Significant effects of the between-subject factor were found in the inter-brain phase synchronies of the alpha band, 0–0.5 s and 1–1.5 s ($p < 0.05$). In addition, significant interactions of condition×electrode pair were also found in the inter-brain phase synchronies of all three time-frequency ROIs ($p < 0.05$) ([Table 1](#)).

We then performed independent two-sample t-tests for every electrode pair in the alpha band at 0–0.5 s and 1–1.5 s where significant between-group effects were shown, and we found pairs that showed significant condition differences. Because the EEGs were recorded at 62 electrode sites, the threshold of significance was set to $p=0.05/62$. For these electrode pairs, we performed one-way ANOVAs and post-hoc tests to further identify pairs that might account for the strategy differences within the face-to-face condition. Two-sample t-tests were conducted as the post-hoc tests: 5 vs. 5 PLVs were compared between strategies per each electrode pair. As a result, only 11 inter-brain synchronies were found to be significantly different between strategies in the face-to-face condition, with all showing a difference between C_SC_S and D_SD_S in the alpha band at 0–0.5 s: FZ-P8, FCZ-P8, C3-P6, CP6-P2, CP6-PO6, TP8-PZ, TP8-P2, PZ-PO6, P2-PO6, P4-PO4, and PO4-PO6 ($p < 0.05/62$, where 62 is the Bonferroni correction factor) ([Fig. 4](#)).

From these results, we see that significant inter-brain synchronies for C_SC_S vs. D_SD_S strategy selection in the face-to-face condition involved right temporoparietal (6/22×100 = 27.3% of synchronization participation), right parietal (31.8%), right occipital (27.3%), fronto-central (9.1%), and frontal (4.6%). The high participation rate of the RTP area is consistent with that found for the ERSPs of the RTP area in

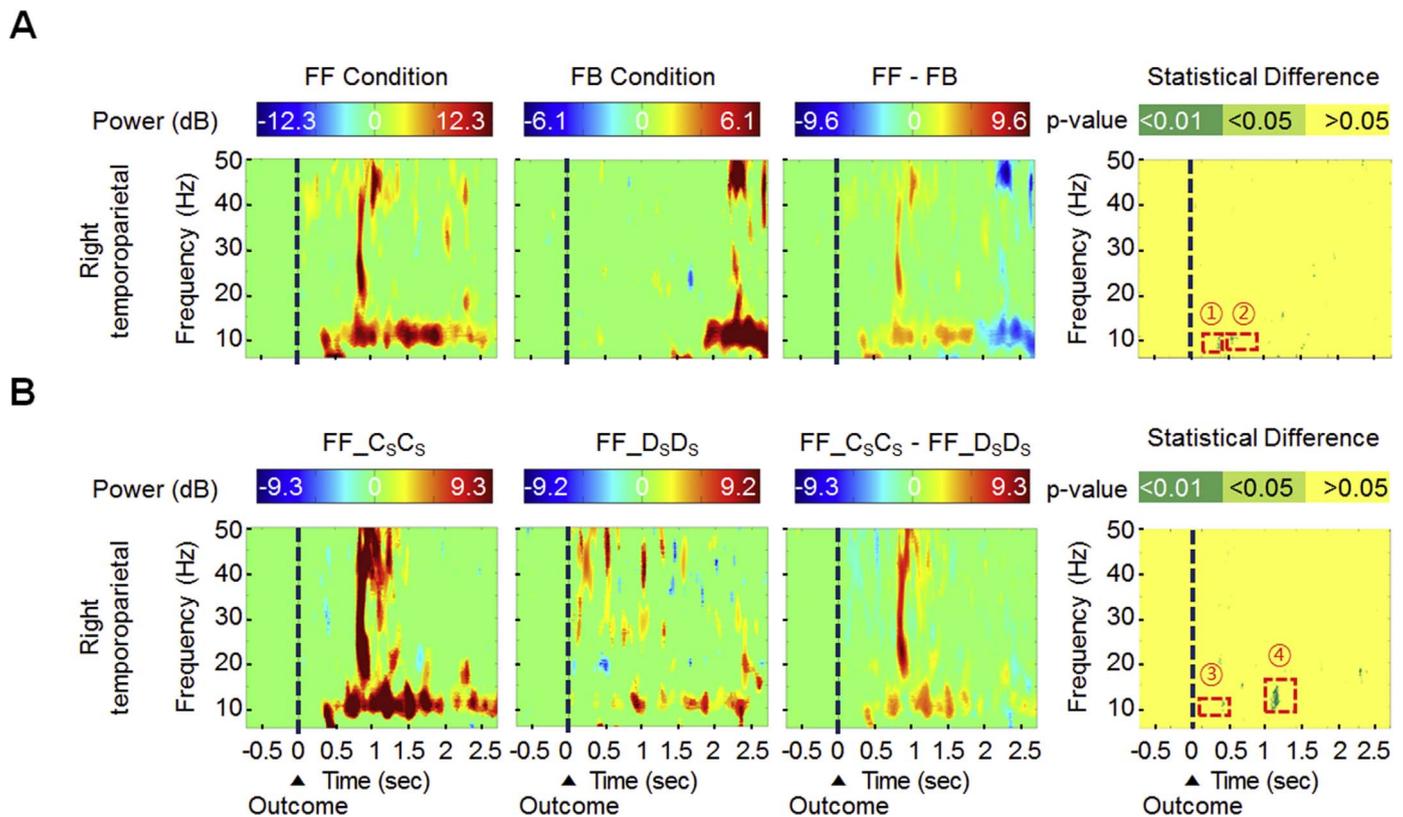


Fig. 3. Time-frequency results for the right temporoparietal area. (A) ERSP magnitudes for the two conditions (face-to-face, FF, and face-blocked, FB), the differences between them, and the statistical results. (B) ERSP magnitudes in the face-to-face condition when C_sC_s and D_sD_s were used, the differences between them (FF_C_sC_s vs. FF_D_sD_s), and the statistical results. Significant time-frequency ROIs (see *EEG time-frequency analysis*) are denoted as red dashed rectangles labeled ①–④ on the statistical difference plots. ① and ② are in the alpha band at the [0 0.5] sec time interval. ③ is in the alpha band at [0.5 1] sec, and ④ is in the alpha band at [1 1.5] sec.

Table 1.

Between-subject effects and interactions of condition×electrode pair of inter-brain phase synchronies for the frequency and time ranges implicated in the EEG time-frequency results. Condition (face-to-face and face-blocked) was a between-subject factor and electrode pair was a within-subject factor.

Frequency range	Time range	F-value	p-value	η_p^2
Between-subject effects: Inter-brain phase synchronies				
Alpha (8–13 Hz)	0–0.5 s	32.132	3.5589×10^{-8}	0.1064
Alpha (8–13 Hz)	1–1.5 s	3.8931	0.0495	0.0189
Beta (14–30 Hz)	1.5–2 s	1.3154	0.2524	0.0055
Interactions of condition×electrode: Inter-brain phase synchronies				
Alpha (8–13 Hz)	0–0.5 s	1.5385	8.8639×10^{-48}	0.0054
Alpha (8–13 Hz)	1–1.5 s	2.3351	7.2659×10^{-208}	0.0082
Beta (14–30 Hz)	1.5–2 s	1.1074	5.8378×10^{-4}	0.0039

the alpha band at 0–0.5 s, showing significant condition (face-to-face > face-blocked) and strategy (C_sC_s > D_sD_s) differences. Interestingly, the magnitudes of the synchronies between FZ-P8, FCZ-P8, and C3-P6 were found to be greater when both participants were cooperating versus when they were defecting (i.e., C_sC_s > D_sD_s) (Fig. 4A blue lines and Fig. 4B for magnitudes), thus implicating synchronization between the RTP and frontal cortical areas (i.e., frontal and fronto-central) during mutual cooperation with face-to-face contact. In contrast, the other pairs were found to be greater when both participants were defecting (i.e., D_sD_s > C_sC_s) (Fig. 4A red lines and Fig. 4B), implicating synchronization between RTP and right parietal and occipital regions when defecting.

Discussion

Sociality is a critical aspect of our lives and what our brains process,

and the Prisoner's Dilemma Game provides a formal framework to examine the critical tradeoff of when to work with others, i.e., cooperate, or attend to one's self interests, i.e., defect. The payoff also depends upon what the other person decides to do, and thus sociality also requires that individuals accurately predict the intentions of others. To do so, one may use their partner's previous behavior as well as other social cues, such as facial expressions. In the current study, we used the EEG hyperscanning approach to investigate (a) how face-to-face interactions influence choices in the Prisoner's Dilemma Game and (b) the corresponding brain mechanisms that mediate this process.

To evaluate the effects of face-to-face interaction, we examined both *outcome* (the mutual choices and reward payoff on the given round) and *strategy*, which captured three key patterns of behavior, measured across every two consecutive rounds: (1) *cooperation* (either consecutive cooperation choices by a player or cooperation after the partner has defected—reflecting either a stable cooperation strategy or some belief that the partner will change to cooperation), (2) *defection* (either consecutive defections by a player or as an attempt to exploit the partner when they cooperated), or (3) *tit-for-tat* (matching the partner's previous choice) (Astolfi et al., 2009, 2010, 2011; Rilling et al., 2002). Thus, *tit-for-tat* is based more strictly on using the partner's previous choice to maximize longer-term reward; whereas, for both *cooperation* and *defection* additional factors are involved, such as using additional external cues to determine the partner's intentions. In the current study, we first note that we did find fairly large individual differences among the participants overall, which suggests that individuals likely use different factors, such as actual behavioral outcomes vs. nonverbal cues, to varying degrees when attempting to predict their partner's behavior. Nonetheless, overall we found that face-to-face contact shifted the joint outcome and the joint strategy distributions toward cooperation. This result was

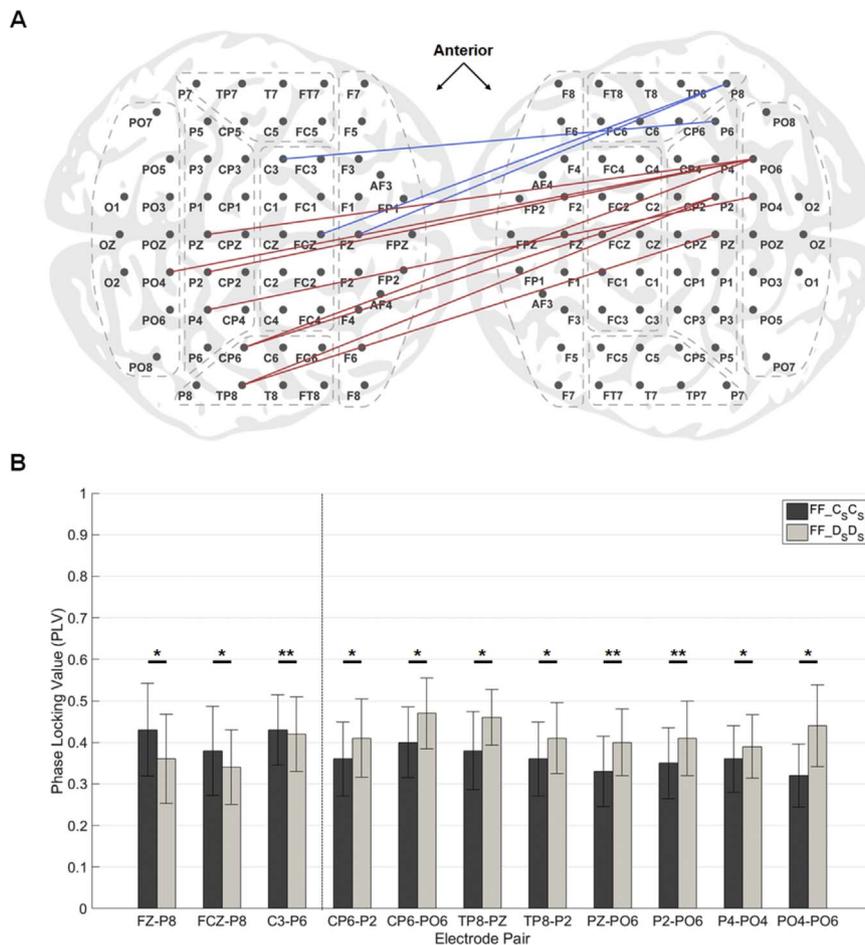


Fig. 4. Brain synchrony results. (A) Dorsal view of the inter-brain phase synchronies in the alpha band in the [0 0.5] sec. time interval. Links between electrodes means that the phase activities were synchronized (note the dot placed at the top of each electrode name, which the lines connect). All synchronies were higher in the face-to-face (FF) than in the face-blocked (FB) condition. Blue lines denote the synchronies that were higher in the C_SC_S rounds compared to the D_SD_S rounds in the face-to-face condition (C_SC_S > D_SD_S); whereas red lines denote the synchronies that were higher in the D_SD_S rounds compared to the C_SC_S rounds in the face-to-face condition (C_SC_S < D_SD_S). (B) Magnitudes of phase synchronies that showed significant C_SC_S and D_SD_S joint strategy differences in the face-to-face condition, which correspond to the links depicted as blue and red lines in (A). *: p < 0.05, **: p < 0.01, Bonferroni corrected. Inter-brain synchronies represent the average phase locking value (PLV) of the inter-brain analyses conducted for both brains (Player 1 electrode *i* to Player 2 electrode *j* and vice versa) (see *Brain synchronization analysis*). Error bars refer to the standard error of the mean.

obtained for both the entire sample of participants as well as for the smaller EEG participant subgroup. Thus, face-to-face interaction did appear to produce a higher degree of cooperation among the participants, yielding a higher degree of mutual cooperation both in terms of specific round-by-round choices and the strategies employed. Given that cooperation is a poor strategy if one's partner is expected to defect, our results suggest that individuals used nonverbal cues to successfully gauge the intentions of their partner to cooperate.

Mutual cooperation is achieved when each player has enough trust that the other player would share the ‘best for both’ motivation. Players in the face-to-face condition appeared to use external visible cues to infer their partner's intentions, resulting in a greater number of decisions to cooperate. These cues provided by face-to-face interaction could (a) contribute to a socio-cognitive assessment of what the other will do (based on what the other is thinking: i.e., ‘mind reading’) or (b) lead to heightened socio-emotional processing, e.g., from the potential social punishment (reflected in the partner's face and body language) (Cromwell and Schultz, 2003; De Quervain et al., 2004; Decety et al., 2004; Knutson and Cooper, 2005; McCabe et al., 2001; Moll et al., 2006; O’Doherty, 2004; Rilling et al., 2002; Sanfey, 2007; Spitzer et al., 2007). The neural findings can help shed light on the type of processing promoted by the face-to-face condition.

Being mindful that more participants per condition are always preferable, we also note that the EEG hyperscanning methodology remains a relatively new approach, requiring a great deal of precision to

achieve reliable results, and we hope our study will encourage others to adopt and help advance the approach in the future. Nonetheless, our study was able to collect a comparable amount of data to other recent hyperscanning studies (e.g., Astolfi et al., 2009, 2010, 2011). Moreover, our statistical analyses were able to identify neural activity significantly related to the behavioral findings of face-to-face contact promoting cooperation. With respect to our main manipulation of face-to-face versus face-blocked, five of six recorded brain regions (except left temporoparietal) showed differences between the face-to-face and face-blocked conditions, suggesting that face-to-face interactions have a marked influence throughout the brain, even though apparently not on social processing conducted in the left temporoparietal region (discussed further below).

To investigate how face-to-face contact affected the willingness to cooperate in the Prisoner's Dilemma Game, we identified the brain regions that showed *both* condition differences (face-to-face vs. face-blocked) and differences between mutual cooperation and the other outcomes or strategies. For outcome, we in fact found no cases in which the neural activity for CC was significantly different from either CD or DD, suggesting that either (a) the relevant brain regions were outside of the recording area (such as deeper structures) or (b) the outcome results were driven by the behavioral strategies of the participants. For strategy, we found three regions that exhibited differences in activity between face-to-face and face-blocked as well as between C_SC_S and another joint strategy; and in all three cases there was greater activity in the face-to-face condition (face-to-face >

face-blocked) and for $C_S C_S$ over the other joint strategy: for $C_S C_S > D_S D_S$, the occipital and RTP regions; for $C_S C_S > C_S T_S$, the parietal region.

High resolution of the temporal dynamics enables precise pinpointing of the neural changes with respect to round events. The significant activity in the RTP region occurred at 0–0.5 s, in the parietal region at 1–1.5 s, and in the occipital area at 1.5–2 s, perhaps implying a top-down progression from the temporoparietal to the occipital region, which would require further investigation to verify. In any case, the results of the current study show that the neural activity correlated with the decisions did not occur just prior to choice, but rather occurred just after the outcomes were revealed, implicating the activity at this time in the round in the assessment of the prior choices and outcomes as well as the following choices. The temporal dynamics thus suggest that previous choices and outcome played important roles in the future decisions, that the face-to-face cues used for decision-making appeared to be processed during this period, and that the RTP region was the main driver underlying this processing.

The face-to-face condition also led to increased synchronization between the player's brains; and the RTP area played a prominent role in the brain-to-brain synchronizations: inter-brain synchronies between the RTP and frontal areas (FZ-P8 and FCZ-P8) were greater when both players chose cooperative strategies ($C_S C_S > D_S D_S$), whereas those between the RTP and parieto-occipital areas (CP6-P2, CP6-PO6, TP8-PZ, and TP8-P2) were greater when both players chose defection strategies ($D_S D_S > C_S C_S$). These findings again provide evidence for RTP involvement in the decision to cooperate or defect during face-to-face interactions, and further suggests that these inter-brain synchronizations are key neural features associated with the intention to either cooperate or defect by both partners. Moreover, given that phase synchronization in the ' $C_S C_S$ ' case occurred between one's RTP and the partner's sensorimotor areas, one possibility is that the synchronization underlies the actual use of nonverbal cues to predict the other's intentions. For the ' $D_S D_S$ ' case, the phase synchronization actually appears to be more broadly distributed, although here, in posterior areas (Astolfi et al., 2009, 2010, 2011; Decety et al., 2004; Fukui et al., 2006). In any event, further examination of nonverbal processing in future studies is warranted, focusing on the relationship between socio-cognitive processing and sensorimotor areas (Adolphs, 2003, 2009; Saxe, 2006).

Whether the implicated brain regions such as RTP reflect socio-cognitive assessment of what the partner will do (based on what the other is thinking: i.e., mind reading) or socio-emotional processing, e.g., from social punishment, our results leave open the possibility for socio-emotional processing, particularly given that we did not examine deeper structures that have been linked to social processing, including in the Ultimatum Game and Prisoner's Dilemma (both iterated and single-shot) Game (Lee, 2008; Rilling et al., 2008, 2002, 2004; Rilling and Sanfey, 2011; Sanfey, 2007). However, according to previous studies, the right temporal lobe also has been implicated in social cognition such as visual processing of bodily motion (Pavlova et al., 2006), perception of agency (Tankersley et al., 2007), perception of the intentions and dispositions of others (Adolphs, 2003; Puce and Perrett, 2003), and theory of mind (Siegal and Varley, 2002). Specifically, the right temporoparietal junction (rTPJ) has been implicated as a key site that performs computations related to others' mental states (Adolphs, 2009; Saxe, 2006; Saxe and Kanwisher, 2003; Tang et al., 2016). At the same time, other neuroscience studies using game-theoretic frameworks have largely found different brain regions underlying the social processing, especially those that mediate outcome (reward and punishment) processing (Cromwell and Schultz, 2003; De Quervain et al., 2004; Decety et al., 2004; Knutson and Cooper, 2005; Lee, 2008; McCabe et al., 2001; Moll et al., 2006; O'Doherty, 2004; Rilling et al., 2002; Sanfey, 2007; Sharp et al., 2012; Spitzer et al., 2007). As described in the introduction, Astolfi and colleagues also conducted a hyperscanning study using the Prisoner's Dilemma Game and found greater activity in the theta and alpha bands of the orbitofrontal region

during defection, but relatively little cortical activity during cooperation (Astolfi et al., 2009, 2010, 2011; De Vico Fallani et al., 2010). Exactly why little was seen in the surface recordings with cooperation remains unclear (e.g., whether activity was mostly occurring in deeper structures). Taken together, the previous findings and ours suggest that face-to-face contact provided additional cues besides previous behavior and outcome to anticipate the future intentions of the partner to determine whether to cooperate or defect.

Indeed, the Tang et al. (2016) study using the fNIRS hyperscanning approach also reported evidence for RTP region involvement during face-to-face contact in the Ultimatum Game (more specifically, in the right TPJ). The fact that both their study and ours implicated the RTP region in face-to-face interactions with both the Ultimatum Game and Prisoner's Dilemma Game suggests that this region may mediate factors common to both game scenarios (Lee, 2008; Rilling et al., 2004; Yun et al., 2008); and other related studies help to clarify what these common factors may be. Jiang et al. (2012) examined the influence of face-to-face contact on communication, comparing the changes in the inter-brain synchronies during a face-to-face dialog, a back-to-back dialog, a face-to-face monologue, and a back-to-back monologue using fNIRS hyperscanning. They found a significant increase in between-brain synchronization in the left inferior frontal cortex during the face-to-face dialog (versus the other conditions), implying that the degree of social interaction indeed affects the neural synchronization, which may in turn promote successful communication. Nonetheless, the implicated brain region (left inferior frontal cortex) appears to be a more dedicated language region and thus different from our findings. Thus, the RTP activity does not appear to derive from face-to-face contact alone nor apparently from potential (nonverbal) communication or simple coordination aspects of the social interaction. Indeed, with respect to potential lower-level coordination, such as coordinating hand or finger movements, other hyperscanning studies have implicated other brain regions, such as the centroparietal (Dumas et al., 2010; Naeem et al., 2012; Tognoli et al., 2007), superior frontal (Cui et al., 2012), and ventrolateral frontal (Babiloni et al., 2012) areas. One study examined the coordination of speech rhythm using an alternating speech task, and did find activation in the temporal and lateral parietal regions (Kawasaki et al., 2013); however, whether this activity reflects auditory and language specific processing versus higher-level social processing remains unclear. Thus, the similarity of our findings to that of the Tang et al. (2016) study suggests that the RTP region mediates the use of face-to-face cues to predict what others will do in either the Ultimatum (accept my proposed offer; determine honesty of proposer) or Prisoner's Dilemma (cooperate or defect) Games, particularly with respect to prosociality (Ultimatum Game: honesty, fairness; Prisoner's Dilemma Game: cooperation) versus self-interest.

At the same time, our findings also differ from those of the Tang et al. (2016) study, most notably (1) that RTP activity *increased* in the current study for the prosocial choices (' $C_S C_S$ ') but *decreased* in theirs (mutual positive predictions), and (2) the brain regions involved in the inter-brain synchronizations. For the synchronization results, given that the Tang et al. (2016) study only examined two brain regions (the rTPJ and dorsolateral prefrontal cortex), potential involvement of other regions is inconclusive. Nonetheless, they found synchronization between the two RTP regions of the participants, which we did not.

The discrepancy between the studies' findings might include methodological differences, but each study also used different tests of social processing: the Ultimatum Game (a modified version) versus the Prisoner's Dilemma Game. We consider two main differences between these games. First, their Ultimatum Game tested honesty and fairness of the proposer (and whether they would be punished by offer rejection) versus more of a direct focus on whether to cooperate in the Prisoner's Dilemma Game. One might speculate that increased activity in the RTP region with presumed dishonesty and unfairness reflects the fact that honesty and fairness are normally the expected,

default states (Sanfey, 2007), whereas the decision to cooperate or not may depend more on task demands, and thus may not necessarily be expected (Lee, 2008). Second, with respect to what each player must consider, in the Prisoner's Dilemma Game, both players must anticipate the other's intentions; whereas in the modified Ultimatum Game, although both players must anticipate the other's assessment, both assessments are based on the proposer's prior behavior (was he/she honest and fair). Thus, there may be significant periods of time when both individuals are thinking only about the proposer. Taken together, our findings provide evidence for how nonverbal social cues from face-to-face contact are used to determine what the other individual is thinking, especially with respect to whether they will engage in prosocial, cooperative behavior: i.e., their future intention to cooperate.

We also found four other cases of EEG activity related to the Prisoner's Dilemma Game strategies but were not affected by the face-to-face interaction (i.e., no difference between the face-to-face/face-blocked conditions): three of which were the left temporoparietal region (the other fronto-central cortex). Multiple regions may therefore underlie the decision to follow a cooperation strategy, but the temporoparietal region again appears to be a key area, with the right region appearing to use face-to-face nonverbal cues, while the left region may not.

Finally, our findings of significantly different spectra power and inter-brain phase synchronization in the alpha band depending on the degree of social interaction (i.e., face-to-face versus face-blocked conditions) contribute to a growing number of EEG studies, including hyperscanning studies, which point to the significance of alpha band activity for high-level cognitive processing. Alpha band activity appears to mediate visual and auditory working memory (Kawasaki et al., 2010), interactional synchrony between a model and an imitator of hand movements (Dumas et al., 2010), cooperation and defection during the Prisoner's Dilemma Game (Astolfi et al., 2011), emotional empathy during the observation of a musical group's own performance via video (Babiloni et al., 2012), and human-human communication coordination (Kawasaki et al., 2013). We now show that both spectra power and inter-brain phase synchronization in the alpha band underlie the use of face-to-face cues to predict a partner's intention to cooperate or defect in the Prisoner's Dilemma Game.

Conclusions

To the best of our knowledge, this is the first EEG hyperscanning study to investigate the effect of face-to-face contact on the brain mechanisms underlying the decision to cooperate or defect in the Prisoner's Dilemma Game. The presence of 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. Moreover, the EEG hyperscanning approach identified temporal dynamics and inter-brain synchronization across the cortex—most notably in the right temporal parietal region—providing evidence for involvement of these regions in the processing of face-to-face cues to read each other's intent to cooperate. The current study highlights the significance of power in the alpha band and inter-brain phase synchronizations in high-level socio-cognitive processing. It is also notable that the neural substrates uncovered here are deeply associated with brain regions of autism spectrum disorder (ASD) (Barnea-Goraly et al., 2004; Howlin et al., 2004; McAlonan et al., 2005; Pavlova et al., 2008; Tanabe et al., 2012; Waiter et al., 2004). The time-frequency activity and inter-brain synchronizations of the brain regions implicated in this study, particularly the right temporal-parietal cortical region, might therefore play an important role in the social interactions of ASD patients. Further hyperscanning studies on ASD patients and others who may be suffering from similar deficits in social processing should shed light on particular neural features underlying their deficits, proving potential insights for more targeted treatment strategies.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuroimage.2017.06.024.

References

- Adolphs, R., 2003. Cognitive neuroscience of human social behaviour. *Nat. Rev. Neurosci.* 4, 165–178.
- Adolphs, R., 2009. The social brain: neural basis of social knowledge. *Annu. Rev. Psychol.* 60, 693.
- Astolfi, L., Cincotti, F., Mattia, D., De Vico Fallani, F., Salinari, S., Marciani, M., Wilke, C., Doud, A., Yuan, H., He, B., 2009. Estimation of the cortical activity from simultaneous multi-subject recordings during the prisoner's dilemma. *Engineering in Medicine and Biology Society*, 2009. EMBC 2009. Annual International Conference of the IEEE. IEEE, pp. 1937–1939.
- Astolfi, L., Cincotti, F., Mattia, D., De Vico Fallani, F., Salinari, S., Vecchiato, G., Toppi, J., Wilke, C., Doud, A., Yuan, H., 2010. Simultaneous estimation of cortical activity during social interactions by using EEG hyperscannings. *Engineering in Medicine and Biology Society (EMBC), 2010 Annual International Conference of the IEEE*. IEEE, pp. 2814–2817.
- Astolfi, L., Toppi, J., Fallani, F.D.V., Vecchiato, G., Cincotti, F., Wilke, C.T., Yuan, H., Mattia, D., Salinari, S., He, B., 2011. Imaging the social brain by simultaneous hyperscanning during subject interaction. *IEEE Intell. Syst.* 26, 38.
- Babiloni, C., Buffo, P., Vecchio, F., Marzano, N., Del Percio, C., Spada, D., Rossi, S., Bruni, I., Rossini, P.M., Perani, D., 2012. Brains “in concert”: frontal oscillatory alpha rhythms and empathy in professional musicians. *Neuroimage* 60, 105–116.
- Babiloni, F., Astolfi, L., Cincotti, F., Mattia, D., Tocci, A., Tarantino, A., Marciani, M., Salinari, S., Gao, S., Colosimo, A., 2007a. Cortical activity and connectivity of human brain during the prisoner's dilemma: an EEG hyperscanning study. *Engineering in Medicine and Biology Society*, 2007. EMBS 2007. In: Proceedings of the 29th Annual International Conference of the IEEE. IEEE, pp. 4953–4956.
- Babiloni, F., Cincotti, F., Mattia, D., De Vico Fallani, F., Tocci, A., Bianchi, L., Salinari, S., Marciani, M., Colosimo, A., Astolfi, L., 2007b. High resolution EEG hyperscanning during a card game. *Engineering in Medicine and Biology Society*, 2007. EMBS 2007. In: Proceedings of the 29th Annual International Conference of the IEEE. IEEE, pp. 4957–4960.
- Barnea-Goraly, N., Kwon, H., Menon, V., Eliez, S., Lotspeich, L., Reiss, A.L., 2004. White matter structure in autism: preliminary evidence from diffusion tensor imaging. *Biol. Psychiatry* 55, 323–326.
- Chiu, P.H., Kayali, M.A., Kishida, K.T., Tomlin, D., Klinger, L.G., Klinger, M.R., Montague, P.R., 2008. Self responses along cingulate cortex reveal quantitative neural phenotype for high-functioning autism. *Neuron* 57, 463–473.
- Conty, L., Dezeache, G., Hugueville, L., Grèzes, J., 2012. Early binding of gaze, gesture, and emotion: neural time course and correlates. *J. Neurosci.* 32, 4531–4539.
- Conty, L., N'Diaye, K., Tijus, C., George, N., 2007. When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. *Neuropsychologia* 45, 3024–3037.
- Cromwell, H.C., Schultz, W., 2003. Effects of expectations for different reward magnitudes on neuronal activity in primate striatum. *J. Neurophysiol.* 89, 2823–2838.
- Cui, X., Bryant, D.M., Reiss, A.L., 2012. NIRS-based hyperscanning reveals increased interpersonal coherence in superior frontal cortex during cooperation. *Neuroimage* 59, 2430–2437.
- De Quervain, D.J., Fischbacher, U., Treyer, V., Schellhammer, M., 2004. The neural basis of altruistic punishment. *Science* 305, 1254.
- De Vico Fallani, F., Nicosia, V., Sinatra, R., Astolfi, L., Cincotti, F., Mattia, D., Wilke, C., Doud, A., Latora, V., He, B., 2010. Defecting or not defecting: how to “read” human behavior during cooperative games by EEG measurements. *PLoS One* 5, e14187.
- Decety, J., Jackson, P.L., Sommerville, J.A., Chaminade, T., Meltzoff, A.N., 2004. The neural bases of cooperation and competition: an fMRI investigation. *Neuroimage* 23, 744–751.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-round EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21.
- Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., Garnero, L., 2010. Inter-brain synchronization during social interaction. *PLoS One* 5, e12166.

- Emery, N., 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci. Biobehav. Rev.* 24, 581–604.
- Frank, R.H., Gilovich, T., Regan, D.T., 1993. Does studying economics inhibit cooperation? *J. Econ. Perspect.* 7, 159–171.
- Fukui, H., Murai, T., Shinozaki, J., Aso, T., Fukuyama, H., Hayashi, T., Hanakawa, T., 2006. The neural basis of social tactics: an fMRI study. *Neuroimage* 32, 913–920.
- Howlin, P., Goode, S., Hutton, J., Rutter, M., 2004. Adult outcome for children with autism. *J. Child Psychol. Psychiatry* 45, 212–229.
- Jasper, H.H., 1958. The ten twenty electrode system of the international federation. *Electroencephalogr. Clin. Neurophysiol.* 10, 371–375.
- Jiang, J., Dai, B., Peng, D., Zhu, C., Liu, L., Lu, C., 2012. Neural synchronization during face-to-face communication. *J. Neurosci.* 32, 16064–16069.
- Kawasaki, M., Kitajo, K., Yamaguchi, Y., 2010. Dynamic links between theta executive functions and alpha storage buffers in auditory and visual working memory. *Eur. J. Neurosci.* 31, 1683–1689.
- Kawasaki, M., Yamada, Y., Ushiku, Y., Miyauchi, E., Yamaguchi, Y., 2013. Inter-brain synchronization during coordination of speech rhythm in human-to-human social interaction. *Scientific reports* 3.
- King-Casas, B., Tomlin, D., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R., 2005. Getting to know you: reputation and trust in a two-person economic exchange. *Science* 308, 78–83.
- Knutson, B., Cooper, J.C., 2005. Functional magnetic resonance imaging of reward prediction. *Curr. Opin. Neurol.* 18, 411–417.
- Krach, S., Blumel, I., Marjoram, D., Lataster, T., Krabbendam, L., Weber, J., van Os, J., Kircher, T., 2009. Are women better mindreaders? Sex differences in neural correlates of mentalizing detected with functional MRI. *BMC Neurosci.* 10.
- Kuzmanovic, B., Georgescu, A.L., Eickhoff, S.B., Shah, N.J., Bente, G., Fink, G.R., Vogeley, K., 2009. Duration matters: dissociating neural correlates of detection and evaluation of social gaze. *Neuroimage* 46, 1154–1163.
- Lachaux, J.P., Rodriguez, E., Martinerie, J., Varela, F.J., 1999. Measuring phase synchrony in brain signals. *Hum. Brain Mapp.* 8, 194–208.
- Lee, D., 2008. Game theory and neural basis of social decision making. *Nat. Neurosci.* 11, 404–409.
- Logothetis, N.K., Wandell, B.A., 2004. Interpreting the BOLD signal. *Annu. Rev. Physiol.* 66, 735–769.
- Müller, V., Lindenberger, U., 2014. Hyper-Brain Networks Support Romantic Kissing in Humans.
- Müller, V., Sängler, J., Lindenberger, U., 2013. Intra- and inter-brain synchronization during musical improvisation on the guitar. *PLoS One* 8, e73852.
- McAlonan, G.M., Cheung, V., Cheung, C., Suckling, J., Lam, G.Y., Tai, K., Yip, L., Murphy, D.G., Chua, S.E., 2005. Mapping the brain in autism: A voxel-based MRI study of volumetric differences and intercorrelations in autism. *Brain* 128, 268–276.
- McCabe, K., Houser, D., Ryan, L., Smith, V., Trouard, T., 2001. A functional imaging study of cooperation in two-person reciprocal exchange. *Proc. Natl. Acad. Sci.* 98, 11832–11835.
- Mognon, A., Jovicich, J., Bruzzone, L., Buiatti, M., 2011. ADJUST: an automatic EEG artifact detector based on the joint use of spatial and temporal features. *Psychophysiology* 48, 229–240.
- Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., Grafman, J., 2006. Human fronto-mesolimbic networks guide decisions about charitable donation. *Proc. Natl. Acad. Sci.* 103, 15623–15628.
- Montague, P.R., Berns, G.S., Cohen, J.D., McClure, S.M., Pagnoni, G., Dhamala, M., Wiest, M.C., Karpov, I., King, R.D., Apple, N., 2002. Hyperscanning: simultaneous fMRI during linked social interactions. *Neuroimage* 16, 1159–1164.
- Naeem, M., McGinnity, T.M., Watson, D., Wong-Lin, K., Prasad, G., Kelso, J.S., 2012. Inter-brain mutual information in social interaction tasks. *Pattern Recognition in NeuroImaging (PRNI), 2012 International Workshop on. IEEE*, pp. 25–28.
- O'Doherty, J.P., 2004. Reward representations and reward-related learning in the human brain: insights from neuroimaging. *Curr. Opin. Neurobiol.* 14, 769–776.
- Ortmann, A., Tichy, L.K., 1999. Gender differences in the laboratory: evidence from prisoner's dilemma games. *J. Econ. Behav. Organ.* 39, 327–339.
- Pavlova, M., Birbaumer, N., Sokolov, A., 2006. Attentional modulation of cortical neuromagnetic gamma response to biological movement. *Cereb. Cortex* 16, 321–327.
- Pavlova, M., Sokolov, A.N., Birbaumer, N., Krägeloh-Mann, I., 2008. Perception and understanding of others' actions and brain connectivity. *J. Cogn. Neurosci.* 20, 494–504.
- Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 358, 435–445.
- Rapoport, A., Chammah, A.M., 1965. Sex differences in factors contributing to the level of cooperation in the Prisoner's Dilemma game. *J. Personal. Soc. Psychol.* 2, 831.
- Rilling, J.K., Goldsmith, D.R., Glenn, A.L., Jairam, M.R., Elfenbein, H.A., Dagenais, J.E., Murdock, C.D., Pagnoni, G., 2008. The neural correlates of the affective response to unreciprocated cooperation. *Neuropsychologia* 46, 1256–1266.
- Rilling, J.K., Gutman, D.A., Zeh, T.R., Pagnoni, G., Berns, G.S., Kilts, C.D., 2002. A neural basis for social cooperation. *Neuron* 35, 395–405.
- Rilling, J.K., Sanfey, A.G., 2011. The neuroscience of social decision-making. *Annu. Rev. Psychol.* 62, 23–48.
- Rilling, J.K., Sanfey, A.G., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2004. The neural correlates of theory of mind within interpersonal interactions. *Neuroimage* 22, 1694–1703.
- Sängler, J., Müller, V., Lindenberger, U., 2012. Intra- and interbrain synchronization and network properties when playing guitar in duets. *Front. Hum. Neurosci.* 6.
- Sängler, J., Müller, V., Lindenberger, U., 2013. Directionality in hyperbrain networks discriminates between leaders and followers in guitar duets. *Front. Human Neurosci.* 7.
- Sanfey, A.G., 2007. Social decision-making: insights from game theory and neuroscience. *Science* 318, 598–602.
- Saxe, R., 2006. Uniquely human social cognition. *Curr. Opin. Neurobiol.* 16, 235–239.
- Saxe, R., Kanwisher, N., 2003. People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. *Neuroimage* 19, 1835–1842.
- Senju, A., Johnson, M.H., 2009. The eye contact effect: mechanisms and development. *Trends Cogn. Sci.* 13, 127–134.
- Sharp, C., Monterosso, J., Montague, P.R., 2012. Neuroeconomics: a bridge for translational research. *Biol. Psychiatry* 72, 87–92.
- Siegal, M., Varley, R., 2002. Neural systems involved in ‘theory of mind’. *Nat. Rev. Neurosci.* 3, 463–471.
- Spitzer, M., Fischbacher, U., Herrnberger, B., Grön, G., Fehr, E., 2007. The neural signature of social norm compliance. *Neuron* 56, 185–196.
- Tanabe, H.C., Kosaka, H., Saito, D.N., Koike, T., Hayashi, M.J., Izuma, K., Komeda, H., Ishitobi, M., Omori, M., Munesue, T., 2012. Hard to “tune in”: neural mechanisms of live face-to-face interaction with high-functioning autistic spectrum disorder. *Front. Hum. Neurosci.* 6.
- Tang, H., Mai, X., Wang, S., Zhu, C., Krueger, F., Liu, C., 2016. Interpersonal brain synchronization in the right temporo-parietal junction during face-to-face economic exchange. *Soc. Cogn. Affect. Neurosci.* 11, 23–32.
- Tankersley, D., Stowe, C.J., Huettel, S.A., 2007. Altruism is associated with an increased neural response to agency. *Nat. Neurosci.* 10, 150–152.
- Teplan, M., 2002. Fundamentals of EEG measurement. *Meas. Sci. Rev.* 2, 1–11.
- Tognoli, E., Lagarde, J., DeGuzman, G.C., Kelso, J.S., 2007. The phi complex as a neuromarker of human social coordination. *Proc. Natl. Acad. Sci.* 104, 8190–8195.
- Tomlin, D., Kayali, M.A., King-Casas, B., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R., 2006. Agent-specific responses in the cingulate cortex during economic exchanges. *Science* 312, 1047–1050.
- Waiter, G.D., Williams, J.H., Murray, A.D., Gilchrist, A., Perrett, D.I., Whiten, A., 2004. A voxel-based investigation of brain structure in male adolescents with autistic spectrum disorder. *Neuroimage* 22, 619–625.
- Yun, K., Chung, D., Jeong, J., 2008. Emotional interactions in human decision making using EEG hyperscanning. *International Conference of Cognitive Science.*
- Yun, K., Watanabe, K., Shimojo, S., 2012. Interpersonal body and neural synchronization as a marker of implicit social interaction. *Sci. Rep.* 2.