



The Dynamics of Belief Updating in Human Cooperation: Findings from inter-brain ERP hyperscanning



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ABSTRACT

Generally, successful cooperation can only be established when the interacting persons believe that they would not be betrayed; this belief can be updated by observing the other persons' actual choices. Thus, the process of belief updating plays an important role in conditional cooperation. Using the Prisoner's Dilemma Game (PDG) with event-related potential (ERP) hyperscanning, this study investigated the dynamics of belief updating in a dyad. During the task, participants were asked if they believed that their opponent would cooperate in the next trial, and their answers functioned as a self-reported index of reciprocal belief. The results suggested that this index shows strong associations with participants' behavioral choices (cooperate/betray). At the individual level, the amplitudes of the ERP components frontal P3a and parietal P3b elicited by the decision outcome were sensitive to belief updating. At the interpersonal level, the between-subject synchronization in P3b was higher than those in the other conditions when the paired participants confirmed each other's reciprocal beliefs. Since previous studies have linked the P3b with memory updating, we suggest that a cooperative relationship is built up when the memory systems (which support belief updating) of two interacting persons reach a high level of coordination. These findings may help explain how conditional cooperation develops between strangers.

1. Introduction

Unlike other species, humans are exceptional in their abilities to engage in large-scale cooperation that is well beyond the boundary of blood ties (Bowles and Gintis, 2011; Boyd and Richerson, 1988). This mystery of human evolution as “super-cooperators” (Nowak and Highfield, 2011) has sparked numerous studies to understand the biological, psychological, and institutional bases underlying human cooperation (for reviews, see Fehr, 2009; Rand and Nowak, 2013). While some of these studies have explored the dynamics of how people learn to interact with strangers to facilitate cooperation (e.g., Cui et al., 2012; Holper et al., 2013; Stolk et al., 2014; Stolk et al., 2013; Zheng et al., 2018), few have considered the importance of reciprocal belief updating in this learning process. In the current study, we utilized a cutting-edge neuroscience technique—hyperscanning—to record and analyze people's brain activities while two persons choose to cooperate with each other or not.

Specifically, we were interested in determining (1) whether brain synchronization can be detected while individuals intend to cooperate, and (2) how brain synchronization and the experience of successful cooperation may mutually reinforce each other, potentially through the updating of reciprocal beliefs.

1.1. The importance of reciprocal belief in human cooperation

To understand the prevalence of voluntary cooperation in human societies, researchers have proposed various theoretical accounts. For example, the act of cooperation might be inherently rewarding to people (e.g., Decety et al., 2004; Palfrey and Prisbrey, 1997; Tabibnia and Lieberman, 2007). Also, people may have an altruistic preference to benefit others (e.g., care for other people's well-being or social equality: Fehr and Fischbacher, 2003; Fehr and Schmidt, 1999). While these theories suggest important motivations for cooperation from the intrapersonal

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perspective, they do not address the interpersonal dynamics, i.e., a cooperative decision depends largely on the actions of other people. Most people are conditional cooperators; while they might have a desire to cooperate, it would be converted to action only if they believe others will cooperate as well (Gächter, 2006; Keser and van Winden, 2000). Cooperation can hardly be established when people believe that others will take advantage of their altruistic gesture (Pruitt and Kimmel, 1977; Yamagishi, 1986). Thus, the belief in another individual's benevolent motive is the key to conditional cooperation (Dufwenberg et al., 2011; Holmes, 2004; Simpson, 2007). In an iterated social dilemma, this belief may be modified by the opponents' actual choices, and people would adjust their response strategy based on these updated beliefs (D. Lee and Seo, 2016). Consequently, for conditional cooperators, their opponents' cooperation would reinforce their tendency to cooperate in return (e.g., Rilling et al., 2004b; Yi and Rachlin, 2004). This social mechanism may also have implications for the nature of trust because one definition of trust is the positive belief in other's socially interdependent behavior (Balliet and Van Lange, 2013). When multiple strangers interact, the mutual reinforcement of each other's reciprocal beliefs may generate a sense of mutual trust, which could function as the basis for long-term cooperation.

Efforts have been made to uncover the neural substrates of reciprocal belief during cooperation. Neuroimaging studies have revealed the involvement of a series of brain regions in social decision-making, including the medial prefrontal cortex (MPFC), rostral anterior cingulate cortex (rACC), superior temporal sulcus (STS), and temporo-parietal junction (TPJ), which are associated with belief updating and its relevant mental processes, such as social learning, mentalizing, theory of mind (ToM), and trust (Carter et al., 2012; e.g., Elliott et al., 2006; Emonds et al., 2012; Krach et al., 2008; Rilling et al., 2004a; Singer et al., 2004). Generally, these regions are more active when personal beliefs about another individual's behavior are violated (i.e., belief prediction error; see Suzuki et al., 2012; Zhu et al., 2012). Using a cooperation game, Yoshida et al. (2010) found that the rostral MPFC encoded the level of belief uncertainty about another person's strategy (see also Hampton et al., 2008). Huber et al. (2015) found that the activity of the parietal cortex indicated whether participants updated their beliefs according to social influence or personal knowledge. These findings, as well as many others, were acquired at the single-brain level (Bhatt et al., 2012; Collins and Frank, 2018; e.g., Kircher et al., 2009; Krach et al., 2009; Schippers et al., 2010; Stephens et al., 2010). However, belief updating during social decision-making is an interpersonal phenomenon since an individual whose belief is shaped by other people could also make decisions to shape other people's beliefs. Accordingly, we suggest that the dynamics of belief updating and its neural mechanisms could be fully revealed only by taking all the interacting persons into account.

1.2. Hyperscanning and its findings

Considering the concerns outlined above, this study employed the hyperscanning technique, which involves simultaneous recording of neural activity from two or more persons (Montague et al., 2002). Hyperscanning can unravel brain-to-brain synchronization among individuals, which could be measured by between-subject correlation of brain activation (Hasson et al., 2012). Neural synchronization can be enhanced through not only body-movement synchrony (e.g., gesture and action imitation), but also “mindset synchrony,” i.e., sharing similar opinions and beliefs with other people (Frith and Singer, 2008; Hasson et al., 2012). Accordingly, we expected that there would be a high level of inter-brain synchronization when all interacting persons believe that each of them would cooperate. Most importantly, the synchronization level should increase when reciprocal beliefs are confirmed by other people's actual cooperation (i.e., positive belief updating).

In a classic functional magnetic resonance imaging (fMRI) hyperscanning study, King-Casas et al. (2005) found that after many rounds of the Trust Game, the cross-brain correlation of the dorsal striatum

activation between the investor and the trustee became stronger before the revelation of the investor's decision, indicating that mutual trust was strengthened as a result of previous interactions (see also King-Casas et al., 2008; Tomlin et al., 2006). Electroencephalography (EEG) hyperscanning studies have discovered that inter-subject connectivity is much stronger for cooperation than for defection (Astolfi et al., 2011; De Vico Fallani et al., 2010) and that the activities of the MPFC (including the ACC) and orbitofrontal regions are different between participants' cooperative and defective attitudes (Astolfi et al., 2010; Babiloni et al., 2007). Recently, Jahng et al. (2017) used the Prisoner's Dilemma Game (PDG) and found that compared to the face-blocked condition, two participants who finished the task face-to-face showed greater inter-brain synchronies in the EEG alpha frequency, which was localized in the right TPJ and could predict whether participants would cooperate or defect in the upcoming round. In contrast to the face-blocked condition, Jahng et al. (2017) suggested that the face-to-face condition facilitated the updating of one's belief about the partner's intention. Similarly, Tang et al. (2016) found that players were more likely to trust each other in the face-to-face condition as compared to the face-blocked condition when playing the Ultimatum Game (UG); further, their functional near-infrared spectroscopy (fNIRS) results revealed that the right TPJ showed greater activation in the former condition. Meanwhile, in the PDG, Hu et al. (2018) reported that the theta/alpha-band inter-brain synchrony was enhanced in a high (compared to low) cooperative context and that this effect was mediated by perceived cooperativeness. In light of these studies, we suggest that the trial-by-trial fluctuation of neural synchronization associated with belief updating would be worth noting. That is, when two strangers interact, the confirmation of each other's reciprocal belief should immediately strengthen their tendency to cooperate, as well as their between-brain synchronization, on a single-trial basis. This hypothesis focuses on the crucial role of online (i.e., trial-by-trial) belief updating in cooperation.

1.3. The present study

We used the PDG as an experimental paradigm, which requires two players to independently choose between cooperating and defecting, and their payoffs are determined by the joint outcome. Although a cooperative player being defected by his/her partner receives the lowest possible payoff (Luce and Raiffa, 1957), a large body of research has revealed that human participants cooperate much more often than predicted by standard economic theory (Raihani and Bshary, 2011). To explain this phenomenon, researchers have pointed out that cooperative decisions in the PDG are often conditional, that is, a cooperative player holds the belief that his/her partner also intends to cooperate; when no information from the partner is available, people may even “deceive” themselves that the partner would not defect (Surbey and McNally, 1997). The importance of reciprocal belief to PDG performance has been evidenced in behavioral studies (Ellingsen et al., 2012). Also, neuroimaging studies show that the brain areas related to belief updating are consistently activated in the PDG (e.g., Elliott et al., 2006; Emonds et al., 2012; Krach et al., 2008; Rilling et al., 2004a; Singer et al., 2004).

Since investigations of inter-brain synchronization associated with belief updating require a timely measure of the neural processes reflecting transient information exchanges, this study relied on the event-related potentials (ERPs) derived from time-locked EEG signals (Balconi and Vanutelli, 2017; D. Zhang, 2018). The ERP is a powerful tool for probing the time dimension of social processes (Amodio et al., 2014). The temporal resolution of ERPs could even be superior to EEG oscillations since ERPs are instantaneous neural responses to events, while EEG spectral fluctuations reflect subsequent changes in neural connectivity within and between brain networks (Pfurtscheller & Lopes da Silva, 1999). Here, we assigned pairs of participants to finish the PDG, and in each trial they were asked if they believed that their partner would cooperate. To investigate belief updating, we focused on the time window of the decision outcome presentation (see the *Methods* section),

during which the participants' prior belief was confirmed or not. Regarding the ERPs elicited by the decision outcome, we mainly considered the feedback-related negativity (FRN) and P3 component according to the literature (Gehring and Willoughby, 2002; San Martín, 2012; Wu and Zhou, 2009). The FRN serves as a "prediction error signal" that indicates the deviation between prior expectation and actual outcome; therefore, it is larger for unexpected outcomes than for expected ones (Ferdinand et al., 2012; Sambrook and Goslin, 2014). The P3 can be divided into two subcomponents: a frontocentral localized P3a and a parietal localized P3b (Polich and Criado, 2006). In decision-making studies, the P3a is suggested to reflect the tendency to adjust decision strategies in response to a changing environment (Zhang et al., 2013a). Meanwhile, the P3b is frequently associated with memory updating and storage (Polich, 2007); thus, it is often observed in learning tasks (Brumaghin and Klorman, 1998; Schlaghecken et al., 2000). Both the FRN and P3 are sensitive to the comparison between cooperation and defection (Bell et al., 2016; Wang et al., 2013, 2017). In light of our recent studies (e.g., Gu et al., 2018; Zhang et al., 2017a), we also took the early ERP components (i.e., the P1 and N1) into consideration, which reflect the initial stage of selective attention (Parasuraman, 1980).

For data analysis, we broke the consecutive interactions between personal belief and decision-making into two stages. First, we expected that the decision outcome could update subsequent beliefs about the opponent at the behavioral level and that ERP components elicited by the outcome may predict the changes in beliefs. Second, we expected that the updated beliefs would modulate the tendency to cooperate (reflected by behavioral data) and the way of outcome processing (reflected by ERP data). Finally, we investigated if the ERP components of interest would not only be sensitive to experimental conditions at the individual level, but also exhibit enhanced inter-brain synchronization when reciprocal beliefs were confirmed by the decision outcome.

2. Methods

2.1. Participants

Seventy-four healthy college students (34 females) aged 20.4 ± 2.2 years (mean \pm standard deviation [SD], hereinafter the same) were recruited from Shenzhen University as paid participants. All participants were right-handed and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment. The experimental protocol was approved by the Ethics Committee of Shenzhen University.

2.2. Experimental design

In the classic PDG, two players choose between two options: "cooperate" and "defect," after which each of them receives a payoff that depends on their joint decisions. If both participants cooperate (CC), each of them receives a reward of R_{CC} units; if both participants defect (DD), each of them receives a reward of R_{DD} ; finally, if a participant cooperates but his/her opponent defects (CD), or the reverse is true (DC), then the defector receives a reward of R_{DC} , whereas the cooperator receives a reward of R_{CD} . According to the PDG literature, there are two payoff rules: (1) $R_{DC} > R_{CC} > R_{DD} > R_{CD}$ (accordingly, for each individual, the expected payoff of defecting [$R_{DC} + R_{DD}$] is higher than that of cooperating [$R_{CC} + R_{CD}$]), and (2) $2R_{CC} > R_{CD} + R_{DC}$ (accordingly, reciprocal cooperation maximizes the total sum of payoffs for the two participants; see Gradin et al., 2016; Rapoport and Chammah, 1965; Rilling et al., 2002; Wang et al., 2015).

The task design in this study followed the above rules, but we slightly modified two aspects of the traditional PDG. First, the three constants (R_{DC} , R_{CC} , and R_{DD}) in the payoff matrix were transferred as three variables with uniform distribution (range = mean \pm 0.4, step = 0.1), while their mean value was set to 3, 2, and 1, respectively. For example, the value of R_{DC} varied between 2.6 and 3.4 across trials. Meanwhile, the

value of R_{CD} was set to 0 constantly. The modified payoff matrix still conformed to the classic payoff rules (see above). This modification was performed to ensure that participants would focus on the task in each trial (since the expected payoff of each option fluctuates across trials), rather than making decisions without considerations.

Second, at the end of each trial, participants were required to disclose their beliefs about whether their opponents would cooperate or defect (see also the Introduction). Thus, we were able to examine the influence of the decision outcome on the subsequent belief (i.e., belief updating).

2.3. Procedure

Participants were randomly paired with a same-gender opponent. Prior to the experiment, the paired participants were questioned to make sure that they were strangers to one another, after which they were randomly labeled as player #1 and player #2. The roles of the participants and game rules were explained. The participants finished a practice session of 10 trials to ensure that they had fully comprehended the rules. They were also informed that their final payoff depended on individual task performance (i.e., the total score accumulated in the task).

During the experiment, the paired participants sat on opposite sides of a table, each facing a computer screen that displayed the same content. Neither verbal nor nonverbal communication was allowed. An opaque board was placed in the gap between the two screens in order to block any facial or body cues between participants (see the face-blocked condition in Jahng et al., 2017). This setting was applied because face-to-face contact exposes participants to irrelevant factors, such as physical attractiveness (Mobius and Rosenblat, 2006). According to the literature, denial of face-to-face contact should not affect belief updating (Hu et al., 2017). Still, to ensure that they were interacting with real people, pairs of participants were instructed to finish the task in the same room. Additionally, previous studies have revealed that spatial closeness promotes cooperation (e.g., Greiner et al., 2014; Hoffman et al., 1994).

The formal task, which lasted for approximately 30 min, consisted of four blocks (60 trials in each block) separated by self-paced rest periods. Each trial started with the presentation of a 2×2 decision matrix (printed in black on a white background: Fig. 1), which represented the potential payoffs in different conditions (CC/CD/DC/DD) and the ID of each participant (#1 and #2). Participants chose "cooperate" or "defect" by pressing two buttons on a keyboard with their right index and middle fingers. To facilitate the off-line classification of behavioral data, the button assignment was different between the two participants. Specifically, player #1 was asked to press D and F, and player #2 pressed J and K. The meanings (cooperate/defect) of these buttons were counter-balanced across different pairs of participants. There was no time limit for decision-making. As soon as one of the participants chose an option, his/her ID would be highlighted in red. After both participants made their choices, the corresponding cell in the payoff matrix would change from white to dark gray for 1500 ms, indicating the decision outcome of this trial. Next, participants were asked if they believed that their opponents would cooperate in the next trial (see also Macoveanu et al., 2016). Consistent with the decision stage, player #1 reported his/her belief by choosing between D and F, and player #2 used J and K. The inter-trial interval was 1 s.

After the experiment, participants were asked to rate their feelings and emotions in each condition of the PDG. Please refer to Supplementary Material (Part 1: Post-task rating) for details. Finally, each participant was paid 100–180 Chinese Yuan (approximately 15–30 US dollars) according to their total score amount.

2.4. Electroencephalography (EEG) recording and analysis

Brain electrical activity was recorded using two 32-channel wireless EEG amplifiers (NeuSen.W32, Neuracle, Changzhou, China) with a sampling frequency of 250 Hz. Data were recorded online referentially against the left mastoid and re-referenced off-line to average activities

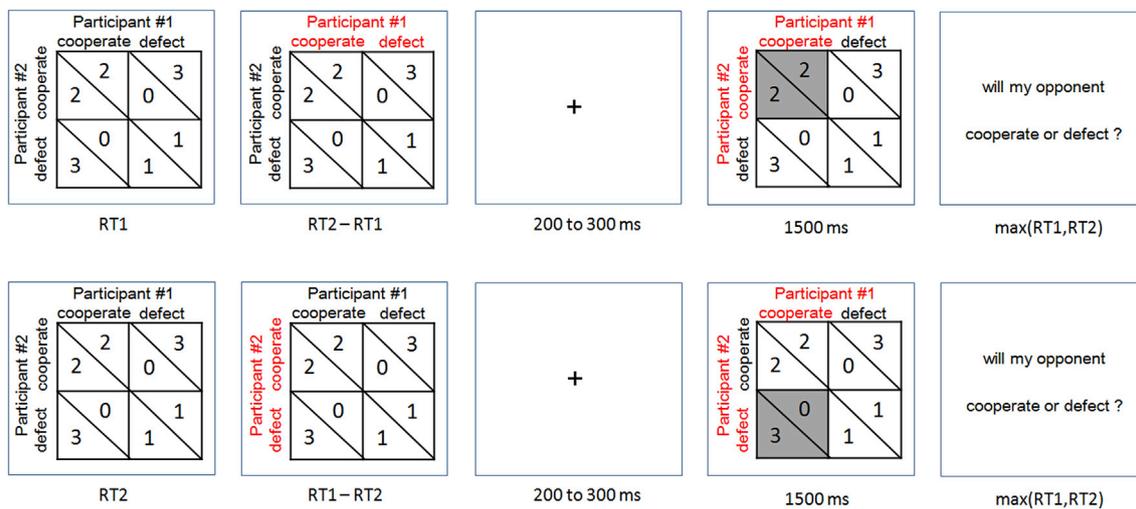


Fig. 1. Illustration of two exemplar trials. RT1: response time of player #1; RT2: response time of player #2. In the first trial (upper sequence), player #1 responded faster than player #2; thus, his/her ID was highlighted in red first. In the second exemplar trial (lower sequence), player #2 responded faster than player #1.

over the scalp. EEG data were collected with electrode impedances below 5 k Ω . Ocular artifacts were removed from the EEG using a regression procedure implemented in the commercial software Scan 4.3 (Compumedics Neuroscan, El Paso, TX, USA).

The recorded EEG data were filtered (0.01–30 Hz) and segmented beginning 200 ms prior to the onset of outcome and lasting for 1700 ms. All epochs were baseline-corrected and averaged according to the experimental conditions. The trial number in each condition is reported in Supplementary Material (Part 2: ERP trial numbers in different conditions). Epochs containing artifacts exceeding $\pm 150 \mu\text{V}$ were rejected. Two pairs of EEG data were excluded from data analysis due to technique problems. Consequently, the final sample size was 70 participants (i.e., 35 pairs).

We focused on four ERP components (occipital N1, FRN, frontal P3a, and parietal P3b). Visual detection on the grand-averaged waveform confirmed that these components were elicited by the decision outcome. The mean amplitude of N1 (time window: 140–180 ms) was calculated as the arithmetic average of electrodes at the left (O1 and P7) and right (O2 and P8) hemispheres. The mean amplitudes of the FRN and frontal P3a were calculated as the arithmetic average of electrodes Fz, FC1, FC2, and FCz (time windows: 260–330 ms for FRN and 400–800 ms for frontal P3a). Finally, the parietal P3b amplitude was calculated as the arithmetic average of the values for the electrodes Pz, P3, and P4 between 500 and 900 ms. Standardized low-resolution brain electromagnetic tomography (sLORETA; updated on 04/15/2015) was employed to explore the possible neural generators of each ERP component (Pascual-Marqui, 2002).

In addition to the traditional ERP analysis based on individual datasets, this study also investigated the inter-brain synchronization of ERP components, which was defined as the similarity in single-trial latency or amplitude between the ERP components of two brains. Both latency and amplitude were analyzed because the average ERP amplitude differences between experimental conditions could be attributable to variations in single-trial latency, amplitude, or both; however, this issue is obscured in traditional grand-averaged waveforms (Blankertz et al., 2011; Jung et al., 2001; Zhang et al., 2013b). In our opinion, latency similarity reflects in-phase bursting of corresponding neural networks in two brains, while amplitude similarity reflects the homogeneous strength of neural activation in two brains. In order to distinguish between these two phenomena, two measures were employed (i.e., *latency difference* and *amplitude difference*); a smaller absolute value of these measures indicates a higher level of synchronization of ERP components between brains. Specifically, we calculated the difference in peak amplitude as well as the

difference in peak latency between two simultaneously recorded single trials from the two interactive brains ($n = 35$ pairs) at the same electrode. Consistent with the traditional approach, the ERP waveforms for single-trial peak detection were averaged from the selected electrodes (see above). The Maximum Likelihood Estimation technique was employed to detect the occurrence of the ERP peak (Jaśkowski and Verleger, 1999).

2.5. Statistics

Descriptive data were presented as arithmetic mean \pm SD. The significance level was set at $p = 0.05$. Greenhouse-Geisser and Bonferroni corrections were used whenever appropriate. We also provided partial eta-squared (η_p^2) values to demonstrate effect size for significant results.

As mentioned in the Introduction, this study reported ERP results at both the individual brain level and inter-brain level. Regarding the individual level, we used traditional multivariate ANOVA to analyze ERP amplitudes across conditions. This study considered within-subject factors including *own choice* (cooperate/defect [C/D]), *opponent choice* (C/D), *upcoming belief* (belief that the opponent would cooperate or defect [BC/BD]), and *prior belief* (BC/BD). For the N1 component, an additional factor *laterality* (left/right) was added according to a suggestion from the literature (e.g., Bayard et al., 2004).

The analyses at the inter-brain level used two novel measures, *latency difference* and *amplitude difference*, to investigate ERP synchronization between two interacting brains. These analyses aimed to examine whether there were any ERP components containing inter-brain communication information that underlies conditional cooperation driven by reciprocal beliefs. For this purpose, a one-way ANOVA was performed across all conditions. Refer to Supplementary Material (Part 2) for a full list of conditions.

Previous studies have suggested that there are two potential causes of between-brain coherence of neural signals (Burgess, 2013). The first possible cause is “mindset synchrony,” i.e., a real inter-brain synchronization (see the Introduction). The second possible cause is “condition similarity,” i.e., two independent individuals perform the same task in the same environment; therefore, their brains activate in similar ways (Liu and Pelowski, 2014). To rule out condition similarity as an alternative explanation, we employed the permutation test examining the reliability of inter-brain synchronization. Specifically, individual ERP data (latency and amplitude) were first paired between two random participants from the whole sample who did not perform the task simultaneously. This procedure of participant permutation was repeated

500 times to generate a distribution of *latency difference* or *amplitude difference* under the null hypothesis (i.e., condition similarity). If the latency/amplitude difference between the paired participants in the real data fell out of the 95% confidence interval of this null-hypothesis distribution, we may conclude that their inter-brain synchronization was more likely due to real inter-brain communication.

3. Results

To compare the findings of previous studies, which focused on the ERPs elicited by decision outcome in social dilemma games (e.g., Bell et al., 2016; Wang et al., 2013), we briefly reported the effects of decision outcome without taking the self-reported beliefs into account. This information is outlined in subsection 3.1. To demonstrate that personal belief could be updated by decision outcomes, we focused on the impact of the opponent's decisions on one's beliefs in subsection 3.2. Finally, in subsection 3.3, we focused on the impact of prior beliefs on outcome processing, as well as subsequent decisions, which could denote the importance of belief updating in future cooperation.

3.1. General results

3.1.1. Cooperation rate

The average cooperation rate was $46.2\% \pm 10.5\%$ per individual. During the task (240 trials in total), the paired participants both cooperated (CC) in 60 ± 26 trials, one cooperated and the other defected (CD/DC) in 105 ± 18 trials, and both defected (DD) in 75 ± 24 trials.

3.1.2. ERPs

For brevity, only the major findings are presented here. Please refer to Supplementary Material (Part 3: Full ERP results regarding the effect of decision outcome) for a complete report.

Individual ERP data showed that the interaction between *own choice* and *opponent choice* was significant on the N1 ($F(1,69) = 14.9$, $p < 0.001$, $\eta_p^2 = 0.178$; Fig. 2A), FRN ($F(1,69) = 34.6$, $p < 0.001$, $\eta_p^2 = 0.334$; Fig. 2B) and P3b ($F(1,69) = 12.3$, $p = 0.001$, $\eta_p^2 = 0.151$; Fig. 2C). sLORETA showed that the neural sources of the N1, FRN, P3a, and P3b might be located in the precuneus, anterior cingulate, orbital gyrus, and posterior cingulate gyrus, respectively (Fig. 3).

Inter-brain ERP data showed that the FRN latency difference between two brains was significantly smaller in the CC condition (20.6 ± 18.3 ms) than in other conditions ($F(2,68) = 5.4$, $p = 0.008$, $\eta_p^2 = 0.136$; C + D = 39.2 ± 29.0 ms, $p = 0.009$; DD = 34.9 ± 26.3 ms, $p = 0.035$). However, a permutation test indicated that the decreased FRN latency difference was due to condition similarity rather than inter-brain communication.

3.2. Belief updating effect: the influence of outcome on subsequent beliefs

3.2.1. Cooperation rate

Two-way ANOVA was performed on *belief of cooperation rate* (measured by the number of trials in which participants believed their opponents would cooperate divided by the total number of trials) with *own choice* and *opponent choice* as two within-subject factors.

The main effect of *own choice* was significant ($F(1,69) = 40.3$, $p < 0.001$, $\eta_p^2 = 0.369$); participants believed that their opponents would cooperate more frequently after they themselves cooperated

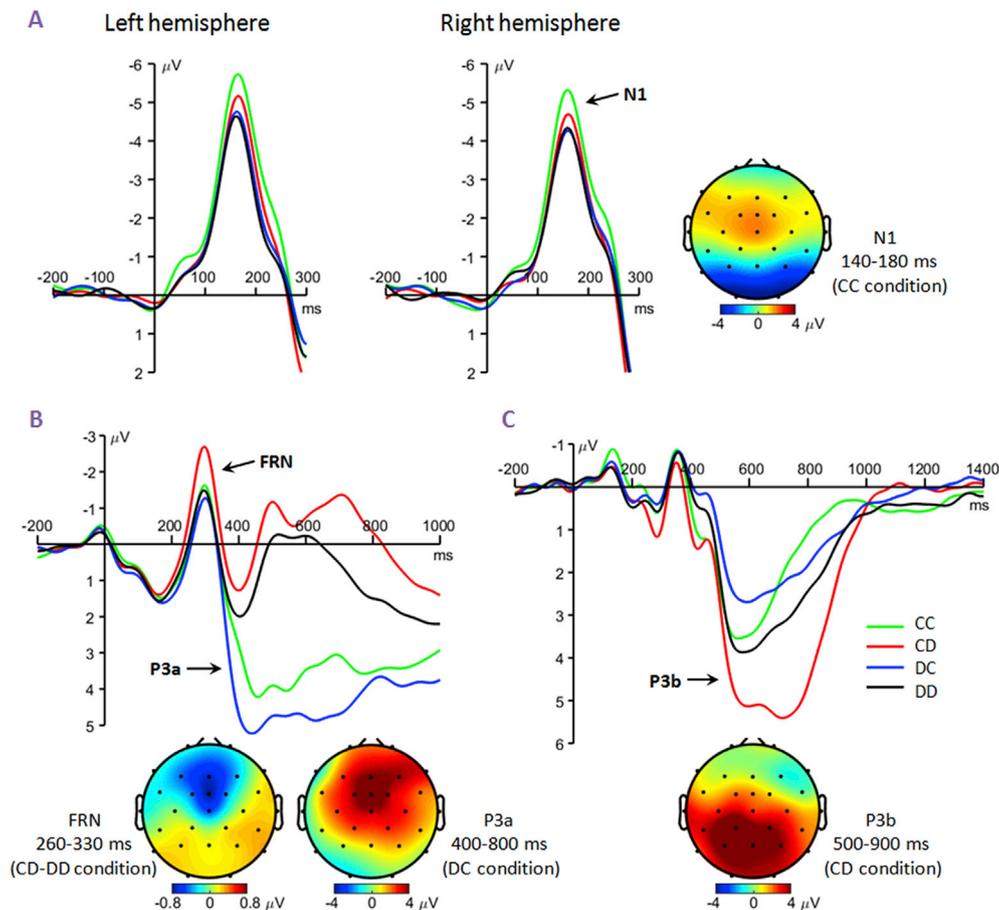


Fig. 2. (A) The effect of decision outcome on occipital N1. The data were averaged from O1 and P7 in the left hemisphere and O2 and P8 in the right hemisphere. (B) The effect of decision outcome on the FRN and frontal P3a. The data were averaged from Fz, FCz, FC1, and FC2. (C) The effect of decision outcome on parietal P3b. The data were averaged from Pz, P3, and P4.

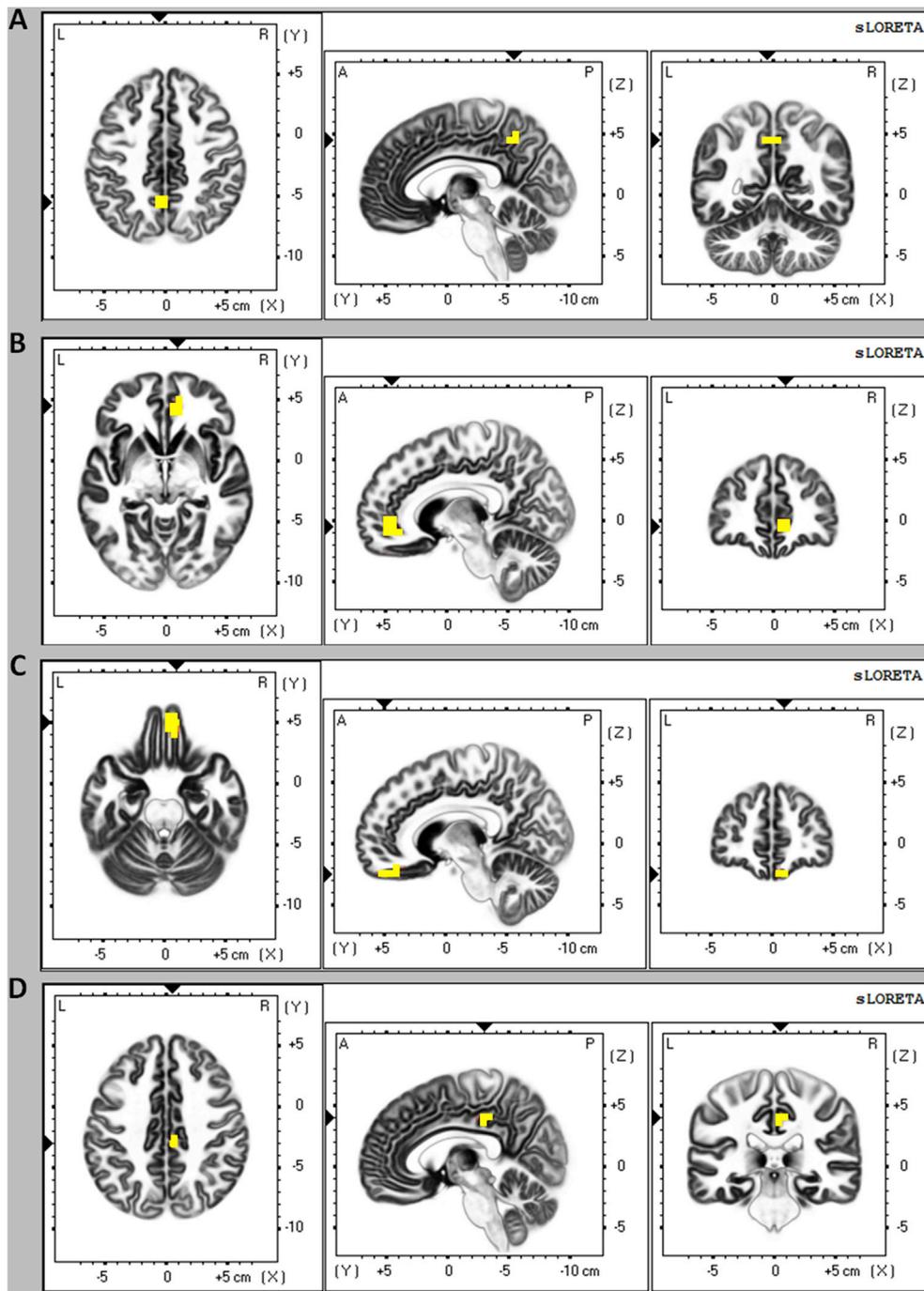


Fig. 3. The results of source analysis using sLORETA. (A) occipital N1, (B) FRN, (C) frontal P3a, and (D) parietal P3b.

(56.5% ± 23.0%) rather than defected (41.7% ± 20.1%) in the current trial. The main effect of *opponent choice* was also significant ($F(1,69) = 21.3$, $p < 0.001$, $\eta_p^2 = 0.236$); participants believed that their opponents would cooperate more frequently after the opponents cooperated (54.6% ± 22.4%) rather than defected (43.6% ± 21.9%) in the current trial. The interaction between *own choice* and *opponent choice* was also significant ($F(1,69) = 34.2$, $p < 0.001$, $\eta_p^2 = 0.331$); after participants cooperated in the current trial, they believed that their opponents would cooperate more frequently in the CC condition than the CD condition (66.6% ± 18.6% vs. 46.4% ± 22.7%; $F(1,69) = 43.6$, $p < 0.001$); in contrast, the difference between DC and DD was insignificant ($p > 0.1$).

3.2.2. ERPs: individual brain level

Although the decision outcome was determined by the decisions of both the participant and his/her opponent, this subsection only considered *opponent choice* (cooperate/defect [C/D]), seeing that *own choice* was not time-locked to outcome presentation; also, reducing the number of factors would allow for sufficient trials in each condition to produce reliable ERP waveforms (refer to Supplementary Material [Part 2]). Accordingly, ANOVAs were performed with *opponent choice* and *upcoming belief* as two within-subject factors. Below we focused on the effects associated with *upcoming belief*. Please refer to Supplementary Material (Part 3) for the main effect of *opponent choice*.

The results indicate no significant effect of *upcoming belief* on the N1,

FRN, or P3a. For the P3b, the main effect of *upcoming belief* ($F(1,69) = 3.08, p = 0.084$) was not significant. However, the interaction between *opponent choice* and *upcoming belief* ($F(1,69) = 6.30, p = 0.014, \eta_p^2 = 0.084$) was significant (Fig. 4A); when opponents defected in the current trial, the P3b was larger in the BC condition than in the BD condition ($3.9 \pm 2.1 \mu\text{V}$ vs. $3.3 \pm 1.8 \mu\text{V}$, respectively; $F(1,69) = 11.0, p = 0.001$); when opponents cooperated, no significant difference was detected between BC and BD conditions ($1.9 \pm 2.4 \mu\text{V}$ vs. $2.1 \pm 2.1 \mu\text{V}$, respectively; $p > 0.1$).

3.2.3. ERPs: inter-brain synchronization

Inter-brain synchronization was calculated using single-trial data, but no significant difference was found across conditions ($F(9,306) = 1.08, p = 0.374$; refer to Supplementary Material [Part 2] for all conditions).

3.3. Influence of updated beliefs on subsequent decision and outcome processing

3.3.1. Cooperation rate

Paired-sample *t*-test revealed that participants cooperated more frequently when they previously believed that their opponents would cooperate rather than defect ($56.5\% \pm 16.1\%$ vs. $33.9\% \pm 13.5\%$; $t(69) = 8.3, p < 0.001$).

3.3.2. ERPs: individual brain level

ANOVAs were performed with *prior belief* and *opponent choice* as two within-subject factors. Similar to subsection 3.2.2, here we focused on the effects associated with *prior belief*. The results indicated no significant effect of *prior belief* on the N1 and FRN.

Frontal P3a. The main effect of *prior belief* was significant ($F(1,69) = 6.44, p = 0.013, \eta_p^2 = 0.085$) and the P3a was larger in the BD condition than in the BC condition ($1.8 \pm 2.8 \mu\text{V}$ vs. $1.5 \pm 3.0 \mu\text{V}$, respectively). The interaction between *opponent choice* and *prior belief* was significant ($F(1,69) = 5.81, p = 0.019, \eta_p^2 = 0.078$; Fig. 4B); when

opponents defected in the current trial, the P3a was larger in the BD condition than in the BC condition ($0.4 \pm 2.5 \mu\text{V}$ vs. $-0.2 \pm 2.8 \mu\text{V}$, respectively; $F(1,69) = 10.9, p = 0.001$); when opponents cooperated in the current trial, there was no significant difference between BC and BD ($3.2 \pm 2.0 \mu\text{V}$ vs. $3.2 \pm 2.4 \mu\text{V}$, respectively; $p > 0.1$).

Parietal P3b. The main effect of *prior belief* was significant ($F(1,69) = 8.68, p = 0.004, \eta_p^2 = 0.112$); the P3b was larger in the BC condition than in the BD condition ($3.1 \pm 2.3 \mu\text{V}$ vs. $2.8 \pm 2.3 \mu\text{V}$, respectively). The interaction between *opponent choice* and *prior belief* was significant ($F(1,69) = 7.61, p = 0.007, \eta_p^2 = 0.099$; Fig. 4C); when opponents defected in the current trial, the P3b was larger in the BC condition than in the BD condition ($4.0 \pm 2.0 \mu\text{V}$ vs. $3.2 \pm 2.0 \mu\text{V}$, respectively; $F(1,69) = 31.2, p < 0.001$); when opponents cooperated in the current trial, there was no significant difference between BC and BD ($2.2 \pm 2.2 \mu\text{V}$ vs. $2.2 \pm 2.5 \mu\text{V}$, respectively; $p > 0.1$).

3.3.3. ERPs: inter-brain synchronization

A one-way ANOVA was performed on the *latency difference* and *amplitude difference* for the frontal P3a and parietal P3b. No significant effect was observed on the P3a ($p > 0.1$). Also, the P3b amplitude difference was not significantly different across conditions ($p = 0.242$).

The P3b latency difference between two brains was significantly smaller in the condition that both participants believed their opponents would cooperate and their opponents indeed cooperated (52.2 ± 34.5 ms; $F(9,306) = 2.6, p = 0.019, \eta_p^2 = 0.071$), compared to the other conditions (range of means = 74.3 – 96.2 ms; pairwise comparisons: $p \leq 0.073$; Fig. 5). To test the reliability of this result, a permutation test was performed to compute the 95% confidence interval for the null hypothesis of inter-brain P3b latency difference in the corresponding condition (95% confidence interval = 53.4 – 73.1 ms). Since the mean latency difference (52.2 ms) fell outside of the 95% confidence interval of the null-hypothesis distribution, we concluded that the decreased P3b latency difference only existed in simultaneously recorded P3b waveforms between two interactive brains at a significance level of $p < 0.05$.

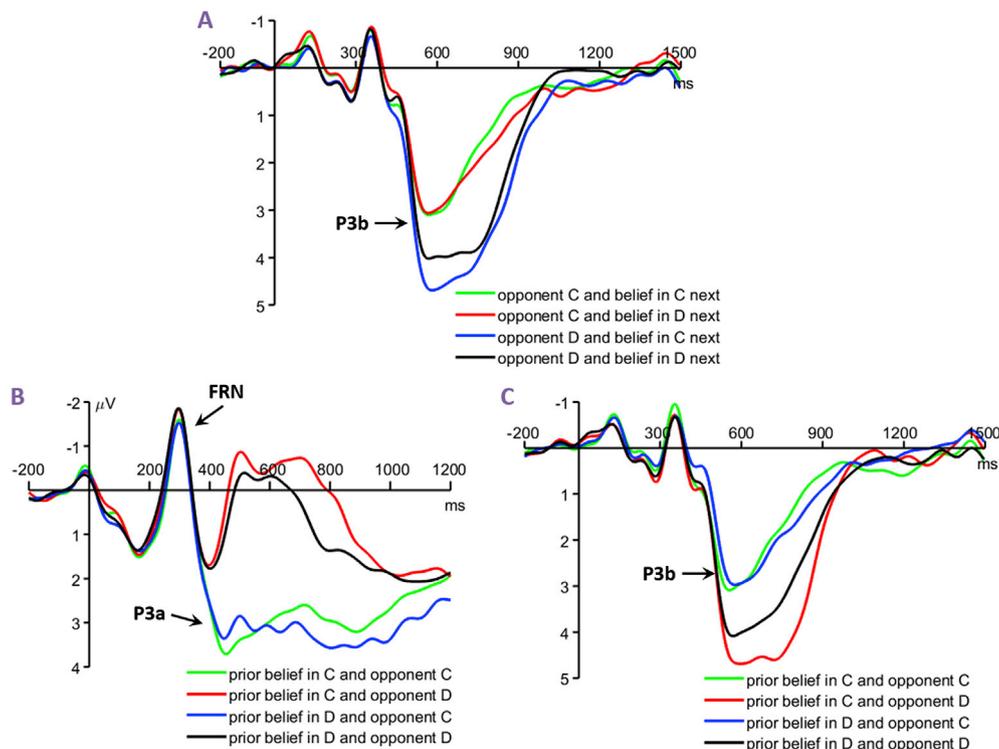


Fig. 4. (A) The influence of opponent choice on upcoming belief reflected by parietal P3b (averaged from Pz, P3, and P4). (B) The influence of prior belief on outcome processing reflected by the FRN, frontal P3a (both averaged from Fz, FCz, FC1, and FC2), and (C) parietal P3b (averaged from Pz, P3, and P4).

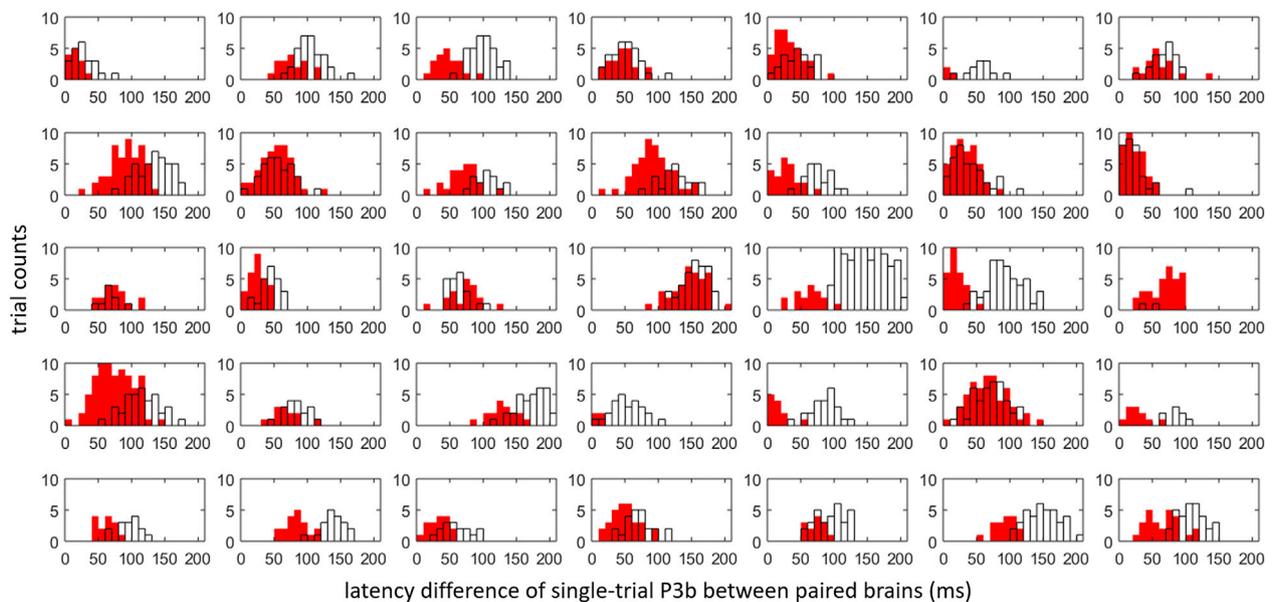


Fig. 5. The latency difference in single-trial P3b between brains of the 35 pairs of participants. For brevity, this figure focuses on two conditions: (1) participants mutually believed their opponents would cooperate followed by opponent cooperation (BC→C & BC→C; latency differences are shown in red bars), and (2) although both participants chose to cooperate, only one of them previously believed that his/her opponent would cooperate (BC→C & BD→C; latency differences are shown in white bars).

4. Discussion

4.1. General findings

In the PDG, both players make efforts to “read the other’s mind” and adjust decision strategies according to their beliefs (Jahng et al., 2017). This PDG study combined the self-reporting method with ERP recording to investigate the role of belief updating in mutual cooperation. At the individual level, we first explored whether reciprocal beliefs could be updated by the previous outcome. Indeed, behavioral results showed that after an opponent cooperated, participants were more likely to believe that he/she would continue to cooperate in the next trial, especially in the mutual cooperation condition (i.e., CC). ERP results showed that the amplitudes of the N1, FRN, P3a, and P3b elicited by outcome were sensitive to the opponent’s decision (cooperate > defect: N1, P3a; defect > cooperate: FRN, P3b). To examine whether any of these components were associated with the updating of reciprocal belief, we took the self-reported belief of the next trial into account and found that a larger P3b elicited by defection predicted that participants would be more likely to believe “my opponent will cooperate.”

We then explored whether the updated reciprocal belief would influence future decision and outcome processing. Again, behavioral results supported this hypothesis because participants generally followed the rule of conditional cooperation; their tendency to cooperate was stronger when they believed that the opponent would cooperate as well. Meanwhile, an opponent’s defection elicited a larger P3b (but a smaller P3a) when participants wrongly believed that their opponent would cooperate. In our opinion, the effect of belief updating in this condition should be the greatest (see also Rilling et al., 2004b). Collectively, we suggest that the P3b is a candidate ERP biomarker of changes in reciprocal belief.

After validating the interaction between belief updating and cooperative decision, we went on to explore whether confirming each other’s reciprocal belief would result in a mindset synchrony between two interacting brains and whether that synchrony could be captured by the ERPs (particularly the P3b) at the inter-brain level. Consistent with this idea, the results of ERP hyperscanning revealed that the P3b showed the strongest cross-brain synchronization when the paired participants found

that their beliefs in each other’s reciprocity were true. Specifically, the P3b latency difference of a dyad was the smallest (indicating similar P3b latency) in this condition, and the reliability of this finding has been proved by a permutation test. This finding, which indicates that the neural dynamics of belief updating manifested at not only the intrapersonal but also the interpersonal level, is the focus of the next subsection.

The FRN also showed a smaller latency difference when the paired participants chose to cooperate compared to other conditions. Nevertheless, this effect still existed after we disrupted the order of data by randomly pairing participants who had not undergone recordings simultaneously (i.e., permutation test). Therefore, we suggest that the FRN effect reflected a similarity in brain activity when two individuals behave in the same way simultaneously, rather than a real inter-brain synchronization (Burgess, 2013; Liu and Pelowski, 2014). Regarding that the FRN has been closely linked to expectancy deviation (Hajcak et al., 2007), the similarity in FRN latency may indicate that cooperating participants tended to compare the actual outcome with their prior expectation within the same time window (i.e., in an early stage of outcome processing).

4.2. The key finding: P3b synchronization

Considering the P3b as an index of belief updating is in line with a classic theory that the P3b reflects a memory process in which a mental representation is updated by new information; novel and unpredictable stimuli evoke a larger P3b than familiar and predictable ones do (Delplanque et al., 2005; Donchin and Coles, 1988). In this perspective, the increased synchronization of the P3b latency indicates that two interactive participants’ beliefs coordinated to a high degree; that is, they both believed that the opponent would show reciprocity in the next trial. The enhanced synchronization manifested in the form of decreased inter-brain latency differences rather than amplitude differences, suggesting concurrent neural firing in this condition. Critically, P3b synchronization was much weaker when the paired participants cooperated but did not share the belief that the opponent would make the same choice (i.e., when they disregarded the rule of conditional cooperation). Accordingly, we considered a high level of P3b synchronization as the neural manifestation of mutual reciprocal belief, at which a cooperative

relationship could be established. This synchronization effect might support the notion that conditional cooperators prefer to play with like-minded cooperators (Gächter, 2006).

To our knowledge, this is the first study using ERP hyperscanning. For our research aim, we developed two novel measures of inter-brain synchronization, i.e., “latency difference” and “amplitude difference” between simultaneously recorded single-trial ERP components in two brains. The Method section has explained the neural mechanisms of these inter-brain measures; however, their implications for social cooperation are less clear due to a lack of prior hyperscanning research on this interdisciplinary topic (see also Konvalinka and Roepstorff, 2012). Previous ERP studies investigating cooperation at the individual level may offer some suggestions. According to these studies, the latency of an ERP component reflects (in time domain) the emergence of the corresponding cognitive process involved in social cooperation, while the amplitude reflects the amount of cognitive resources allocated to that process (Apanovich et al., 2018; de Bruijn and von Rhein, 2012; Zeng et al., 2013). For example, based on the latency of the error-related negativity, Koban et al. (2010) suggested that the emergence of error detection was delayed when observing errors of cooperators compared to observing one's own errors. As illustrated in this example, understanding the psychological implications of latency and amplitude of an ERP component largely depends on the cognitive processes associated with that component. In this study, we propose that the P3b indicates the updating of reciprocal belief in memory. Therefore, a smaller P3b latency difference between two cooperating participants may be interpreted according to the role of memory processes in social cooperation (see also below). That is, when a cooperative relationship has been developed in a dyad, the coordinated partners may be more likely to rely on the memory about each other's reciprocal behaviors, rather than other cognitive processes (e.g., reasoning, calculation), to make future decisions. This behavioral synchrony leads to synchronization of the timing of memory system activity. To gain a better understanding of this complex and dynamic synchronization process, more hyperscanning studies on interpersonal cooperation are needed. Also, alternative measures are welcomed for a comprehensive description of ERP synchronization across interactive brains.

The role of memory systems in human cooperation has been acknowledged in the literature. People learn from their opponent's behavior and accordingly update their evaluation of that opponent in their memory (V. Lee and Harris, 2013). After participants had distinguished between cooperative and non-cooperative opponents based on past experience, their ventral striatum (associated with reward processing) showed greater activation when confronting cooperative opponents (Phan et al., 2010), while the dorsolateral prefrontal cortex (associated with top-down inhibition) showed greater activation when confronting non-cooperative opponents (Suzuki et al., 2011). In the iterated PDG, working memory capacity constrains cooperative performance because an individual needs to memorize his/her opponent's decision history during the task (Milinski and Wedekind, 1998). The current study takes a step further by revealing that the neural activity of two interacting persons' memory systems fired simultaneously when they both correctly predicted a mutual cooperation.

It should be noted that the P3 component has been related to emotional processing in social tasks (e.g., Campanella et al., 2013; Ibanez et al., 2012; Lust and Bartholow, 2009; Wu et al., 2012). For instance, a larger P3 is associated with the more familiar and emotionally laden faces compared to strangers' faces (Guerra et al., 2012). Many studies have demonstrated the sensitivity of P3 amplitude to the valence and intensity of emotional stimuli (Delplanque et al., 2006; Hajcak et al., 2010). Thus, it is possible that during the PDG, decision outcomes update memory templates by eliciting stronger emotional feelings. The P3b effect of memory updating might result from the emotional impact of the current outcome (e.g., the satisfaction towards a cooperative opponent or the anger of betrayal). In favor of this possibility, source analysis suggested that the P3b was generated from the posterior cingulate gyrus, which plays an important

role in memory retrieval especially for meaningful and emotionally salient events (Binder and Desai, 2011). More generally, the posterior cingulate cortex (PCC), where the posterior cingulate gyrus is located, mediates the interaction between emotion and memory (Nielsen et al., 2005). Considering the fact that the outcome expectancies and beliefs that navigate decision-making are largely based on memory retrieval of past experiences (particularly emotional memories) under similar situations (e.g., Sharot et al., 2007), it is understandable that the PCC contributes to decision-making in uncertain scenarios (Platt and Huettel, 2008). Our findings suggest that the PCC is important when one needs to consider his/her opponent's action to make interpersonal decisions because an individual may rely on the memory of outcome history to construct his/her belief about that opponent's future behavior.

One might expect that the level of neural synchronization associated with belief updating should increase not only for mutual cooperation, but also for mutual defection. However, no significant inter-brain coupling was observed in the latter condition. One possible explanation is that defections in the PDG are guided by the principle of expected value maximization rather than the belief that the opponent would defect (Balliet and Van Lange, 2013). Indeed, as the expected payoff of defection outweighs cooperation in the PDG (see the Methods section), a PDG player who chooses to defect may rationalize that he/she has made an optimal choice regardless of what his/her opponent would do, thus showing limited interest in tracking that opponent's actual decisions (Hargreaves-Heap and Varoufakis, 2004). Consistent with this possibility, brain areas associated with ToM and mentalizing show weaker activations during defection compared to cooperation (Elliott et al., 2006; Macoveanu et al., 2016). We encourage follow-up studies to use alternative paradigms to further explore the psychological mechanisms of defection.

4.3. Coda

While this study is most interested in inter-brain synchronization, the conventional ERP data at the single-brain level also added knowledge about the mental processes involved in the PDG. Most notably, the N1 amplitude was larger when an opponent cooperated rather than defected, and this effect was stronger when participants themselves also cooperated (i.e., mutual cooperation). The N1 finding indicates that people pay more attention to observe cooperative behaviors in order to make sure that an opponent is trustworthy. Additionally, source analysis located the N1 component to the precuneus (Brodmann area [BA] 7; see the Supplementary Material for details), which is in line with a number of previous studies focusing on visual attention (Proverbio et al., 2018; Stock et al., 2017). While the attentional N1 effect is a composite of temporally overlapping activations across a wide range of areas, the precuneus is considered one of the plausible contributors (e.g., Wynn et al., 2015). For instance, Natale et al. (2006) compared ERP and fMRI responses to visual stimulus and found that the N1 represents the activity of frontal (superior frontal sulcus) and parietal (superior precuneus) components of the attention network.

In summary, the brain-to-brain coupling (indexed by P3b synchronization) associated with mutual cooperation was enhanced when the paired participants believed that both of them held reciprocity ideas. In our opinion, this finding explains how reciprocal behaviors strengthen mutual cooperation through belief updating (see also Frith and Singer, 2008). Here, the P3b synchronization denotes that a “positive feedback cycle” has been developed in a dyad, which is beneficial for conditional cooperation. When two strangers make deals, social information (e.g., identification, life background, and personal reputation) might be unavailable. In this case, the build-up of trust depends on whether an individual's behavior deviates from his/her opponent's expectations (King-Casas et al., 2005). If one's memory system that tracks decision history indicates that his/her opponent consistently shows reciprocal gestures, he/she might be more likely to develop a trustworthy relationship with that opponent. In this sense, we suggest that the inter-brain P3b synchronization could even be used to measure the degree of mutual

trust for practical purposes. That is to say, we consider PDG performance as an indicator of trust level, which was in line with previous studies linking mutual trust with the PDG (Tedeschi et al., 1969; Tullock, 1967). One might suggest adding self-reported measures of interpersonal trust. However, trustworthy behavior in the PDG mainly concerns whether others are benevolent, which is different from interpersonal trust that focuses on whether others can be relied upon (for different kinds of trust, see Xu et al., 2016) and these two kinds of trust may be uncorrelated (MacDonald et al., 1972). Still, it could be intriguing to examine if the neural synchronization revealed by this study would show different patterns for interpersonal trust.

Finally, some potential directions for follow-up research are worth noting. First, we encourage future studies to examine individual differences, including gender (Cheng et al., 2015; Krach et al., 2009; Zhang et al., 2017b), e.g., by comparing pairs of same-gender with mixed-gender partners. Another issue is the impact of psychiatric conditions, many of which could modulate belief updating (e.g., depression, social anxiety). Researchers can investigate whether the inter-brain synchronization that results from successful belief updating would decline in patients and whether that effect could help explain their aberrant social behaviors. Moreover, while this study only considers interactions between strangers with similar social status, future studies may take different social roles into account. A series of studies conducted by Lu and his colleagues has revealed that the interpersonal neural synchronization shows unique neural features under the leader-follower or teacher-student relationship (Jiang et al., 2015; Zheng et al., 2018). Meanwhile, Pan et al. (2017) found that cooperation in lover dyads was associated with stronger neural synchronization than stranger dyads. It will be interesting to compare the importance of belief updating between different kinds of social relationships.

Author contributions

DZ, YL, and RG conceived the experiment. DZ and YL designed and performed the experiment. DZ analyzed the data. DZ, YJ, RG, and CF wrote the manuscript.

Declaration of ethics

All procedures performed in this study were in accordance with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Conflicts of interest

The authors have declared that there is no conflict of interest in relation to the subject of this study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2019.05.029>.

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