

Synchronous Brain Activity during Cooperative Exchange Depends on Gender of Partner: A fNIRS-based Hyperscanning Study

Xiaojun Cheng, Xianchun Li,* and Yi Hu

Key Laboratory of Brain Functional Genomics, Ministry of Education, Shanghai Key Laboratory of Brain Functional Genomics, School of Psychology and Cognitive science, East China Normal University, Shanghai, People's Republic of China

Abstract: Previous studies have shown that brain activity between partners is synchronized during cooperative exchange. Whether this neural synchronization depends on the gender of partner (i.e., opposite or same to the participant) is open to be explored. In current study, we used functional near-infrared spectroscopy (fNIRS) based hyperscanning to study cooperation in a two-person game (female–female, female–male, and male–male) while assaying brain-to-brain interactions. Cooperation was greater in male–male pairs than in female–female pairs, with intermediate cooperation levels for female–male pairs. More importantly, in dyads with partners with opposite gender (female–male pairs), we found significant task-related cross-brain coherence in frontal regions (i.e., frontopolar cortex, orbitofrontal cortex, and left dorsolateral prefrontal cortex) whereas the cooperation in same gender dyads (female–female pairs and male–male pairs) was not associated with such synchronization. Moreover, the changes of such interbrain coherence across task blocks were significantly correlated with change in degree of cooperation only in mixed-sex dyads. These findings suggested that different neural processes underlie cooperation between mixed-sex and same-sex dyadic interactions. *Hum Brain Mapp* 36:2039–2048, 2015. © 2015 Wiley Periodicals, Inc.

Key words: mixed-sex cooperation; interbrain coherence; functional near-infrared spectroscopy; hyperscanning; frontal cortex

INTRODUCTION

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: National Natural Science Foundation of China; Contract grant number: 31371052 (Y.H.)

*Correspondence to: Xianchun Li; School of Psychology and Cognitive science, East China Normal University, Shanghai, People's Republic of China. E-mail: Xianchun Li: xcli@psy.ecnu.edu.cn or Yi Hu; School of Psychology and Cognitive science, East China Normal University, Shanghai, People's Republic of China. E-mail: yhu@psy.ecnu.edu.cn

Received for publication 23 November 2014; Revised 14 January 2015; Accepted 20 January 2015.

DOI: 10.1002/hbm.22754

Published online 17 February 2015 in Wiley Online Library (wileyonlinelibrary.com).

Cooperation, defined as interactions with others that increase shared performance, is one of the most important human social behaviors [Fehr and Fischbacher, 2003]. Previous studies have identified brain regions in individual participants where activity increases coincident with cooperative behaviors, including prefrontal regions, orbitofrontal cortex, left parietal operculum, anterior cingulate cortex, nucleus accumbens, caudate nucleus, and right dorsolateral prefrontal cortex [Chaminade et al., 2012; Decety et al., 2004; McCabe et al., 2001; Rilling et al., 2002; Suzuki et al., 2011]. More interestingly, recent studies have revealed synchronous brain activity between two persons in cooperative states, including synchronized increased activity in right superior frontal cortices and medial

prefrontal region across people [Cui et al., 2012; Dommer et al., 2012; Funane et al., 2011]. Such increased prefrontal interbrain coherence has also been found in other social interactions, including imitation [Holper et al., 2012], teaching-learning interactions [Holper et al., 2013], face-to-face communication [Jiang et al., 2012], and mother-child interactions [Hirata et al., 2014]

Some studies have shown that individual differences in preferences for cooperation are reflected in difference in brain activation and structure. For example, higher preference for cooperation in females relative to males was linked with differential activation of medial prefrontal cortex [Garbarini et al., 2014], and larger gray matter volumes in bilateral posterior inferior frontal and left anterior medial prefrontal cortices [Yamasue et al., 2008]. With these findings, it is worth determining whether cooperation, as simultaneously measured brain activity in dyads, is different across groups with different physiological or social characteristics. In the current study, we tested for such differences across dyads in which the partners were of opposite gender (mixed-sex cooperation) compared with same gender dyads (same-sex cooperation).

Cooperative behaviors were studied in three dyadic categories: female–female, male–male, and female–male cooperation. Based on social-cultural theory, female–female cooperation may differ given their special social roles in society [Eagly and Wood, 1999]. Historically, women are expected to undertake predominantly domestic role and thus were more communal (e.g., caring, friendly, and emotionally expressive). By contrast, the roles of high status and power in men made them more agentic (e.g., independent, assertive, ambitious, and dominant) [Eagly, 2009]. The basis of male–male cooperation, based on the evolutionary theory, could derive from having evolved coalitional strategies critical for strategic interactions such as hunting [Geary et al., 2003; Thayer, 2004]. For mixed-sex interaction, evolution theory posits that both sexes evolved strategies to signal desirable traits to potential opposite sex partners [Buss and Schmitt, 1993]. Differences in performance across female–female, male–male, and female–male dyads during cooperation have been identified in previous behavioral studies. A comprehensive meta-analytic study on 203 research articles revealed that male–male groups are overall more cooperative than are female–female groups [Balliet et al., 2011]. For the comparison of mixed-sex cooperation and same-sex cooperation, some studies have reported that women and men perform better while interacting with opposite-sex partners than with same-sex partners [Deaux and Major, 1987; Hirnstein et al., 2014].

We tested for differences in synchronized brain activity during cooperative behavioral based on genders in dyadic interactions. We adopted the hyperscanning technique to access correlated neural activity across two brains [Montague et al., 2002]. Hyperscanning has mainly been used with fMRI or EEG recording to studying multiagent games and social interactions [Babiloni and Astolfi, 2014;

Duan et al., 2013; Dumas et al., 2010; Fliessbach et al., 2007; King-Casas et al., 2005; Koike et al., 2015; Scholkmann et al., 2013b]. It should be noted that fMRI or EEG studies using hyperscanning technique require calibration to account for different sensitivities of the devices. In current study, we used near-infrared spectroscopy (NIRS), which allows a single device to be used to measure two or more participants simultaneously. This offers the advantage of obviating the need for the calibration process. Our priori region of interest was frontal cortex, where synchronous activity across brains increased was identified in previous NIRS-based studies [Cui et al., 2012; Dommer et al., 2012; Funane et al., 2011].

METHOD

Participants

A total of 90 (46 female) graduate and undergraduate students (age: 21.96 ± 2.15 yrs) participated in the study. All participants were right handed, with normal or corrected-to-normal vision. They were randomly assigned as pairs; members of pairs were not acquainted with each other before experiment. Forty-five pairs would then be created, including 15 female–female (F-F) pairs, 14 male–male (M-M) pairs, and 16 female–male (F-M) pairs. Informed consent was obtained from each participant. Participants would be paid based on their task performance (ranging from 30 to 50 yuan). The study procedures were approved by the Institutional Review Board of East China Normal University.

Tasks and Procedures

Each pair of participants sat side-by-side in front of a computer screen. The participant on the left side was denoted as participant #1 and the right one as participant #2. They were asked to complete four computer-based tasks that were the same as used in a previous study [Cui et al., 2012]. The tasks included a cooperation task and three control tasks (competition task and two single tasks) (see Fig. 1).

Cooperation task

Each trial began with a hollow gray circle at the center of the screen that stayed visible for a random interval between 0.6 and 1.5 s. Subsequently, a green cue signaled participants were to press keys simultaneously using the index or middle finger of the right hands. Participant #1 was instructed to press the “1” key and participant #2 was asked to press the “0” key. If the difference between their response times was smaller than a threshold, both participants were rewarded with one point; otherwise, both participants lost one point. The threshold (T) was defined by the following formula: $T = (RT1 + RT2)/8$ [Cui et al., 2012], where $RT1$ and $RT2$ were the response times of two

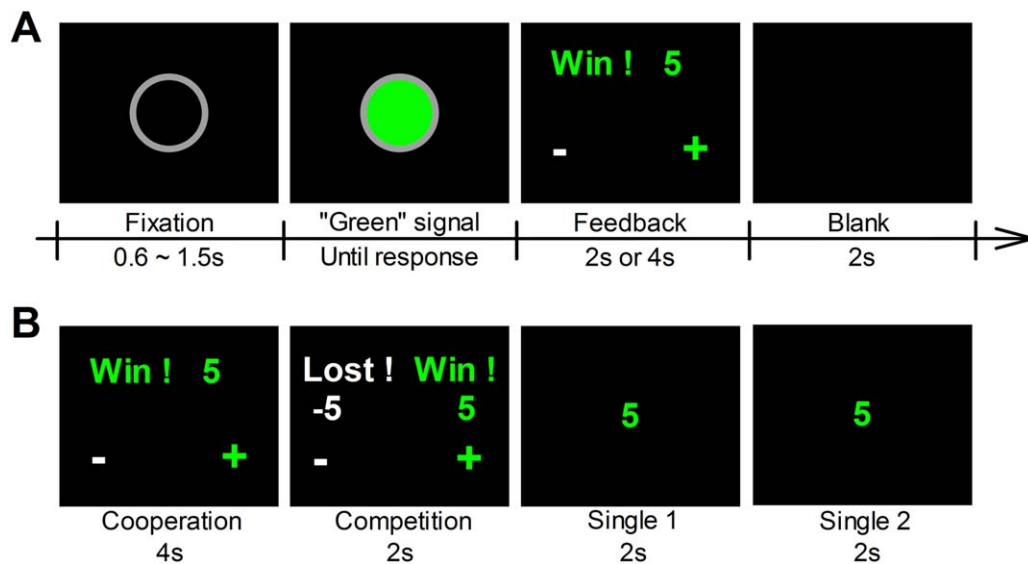


Figure 1.

Procedures for the four experimental tasks. (A) Sequence of events for one trial. The four tasks shared the same basic trial procedures. (B) Feedback was comparable in all of the four tasks.

participants, respectively. The parameter 1/8 was chosen to keep task a moderate level of difficulty (the average correct response rates were around 50–70%). The average T values were 118.12 ± 40.65 ms, 81.57 ± 5.99 ms, and 100.78 ± 13.14 ms in F-F cooperation, F-M cooperation, and M-M cooperation task, respectively. There were no significant differences among T values across groups, $F(2, 42) = 0.562$, $P > 0.05$, $\eta_{\text{partial}}^2 = 0.03$. During task performance, the two participants were not allowed to communicate with each other verbally or physically. After responding, a 4-s feedback screen was present. It was showing the result of the current trial (“Win!” or “Lost!”) and the cumulative points earned in the task through the current trial (see Fig. 1B). The feedback screen also indicated which participant responded the soonest by showing a green “+” on his/her side. The slower participant was shown a white “-” on the other side of the monitor. This feedback allowed participants to adjust their response times between trials. After the feedback, the trial ended (see below for intertrial interval and block lengths).

Control tasks

The other three tasks were used as controls. Specifically, the tasks were designed to eliminate the possibility that the action of pressing the key synchronously (competition) or the closeness of two participants (single 1 and single 2) could account for synchronous brain activity across participants. The competition task was similar to the cooperation task, except that participants were rewarded for responding faster than his/her partner. In the task, the participant who responded faster received a one-point reward and the

slower response incurred a one-point loss. In this way, competition instead of cooperation developed between two participants while key pressing remained almost synchronous, as in the main task. After responses were made, a 2-s feedback screen was presented, followed by a display showing the trial winner (“Win!”), trial loser (“Lost!”), and total points earned (see Fig. 1B). Unlike the cooperation and competition tasks, the two final control tasks involved only one participant (participant #1 in the single 1 task and participant #2 in the single 2 task). He/she was instructed to press the key as quickly as possible when the “green” signal showed and received a one-point reward for each key press. The cumulative points were shown on the feedback screen (see Fig. 1B). During the single participant tasks, the other participant passively observed the screen.

Each task included two blocks of 20 trials each. There were 2-s intervals between trials and a 30-s rest period between blocks. The order of the four tasks was counter-balanced across pairs of participants in each group. All points earned during the four tasks were summed and was used to determine final payment. This gave the participants an incentive to earn as many points as possible, motivating them to be actively engaged in the experiment.

Subjective Measurements

We collected participants’ subjective ratings of participants’ attitudes towards their partners and task performance. When the participant pairs arrived, they were first asked about the preference for the gender of partner when they needed to cooperate each other in daily life (1–7,

from the same-sex partner to the opposite-sex partner), and about favorability for the partner who would perform a two-person game subsequently in the experiment according to first impressions (1–7, from “not very much” to “very much”). Participants were not allowed to discuss their ratings during experiment. After finishing the tasks, participants were asked to rate the favorability of their partners again. Three additional evaluations were completed by the participants, including rating of the quality of their own performance, their cooperativeness, and how pleasant they found cooperating on the task. All ratings were made on 7-point Likert scales from negative “not very much” to positive “very much”.

Data Collection

Continuous measures of concentrations of oxygenated hemoglobin (Hbo) and deoxygenated hemoglobin (Hbr) were measured during task performance using a NIRS system (ETG-4000, Hitachi Medical Corporation, Japan). Two 3×5 probe patches (3 cm distance between emitter probes and detector probes), each including 22 recording channels, were put over the foreheads of two participants separately. The sampling rate was 10 Hz. The placement of the patch followed the International 10–20 system. The lowest probe row of patch was aligned with the horizontal reference curve, with the middle optode placed on the frontal pole midline point (Fpz). Meanwhile, the middle probe column of patches was aligned exactly along the sagittal reference curve (see Fig. 2). The correspondence between the NIRS channels and the measurement points on the cerebral cortex was determined using the virtual registration method [Lancaster et al., 2000; Singh et al., 2005; Tsuzuki et al., 2007; Tzourio-Mazoyer et al., 2002], and has been validated by a multisubject study of anatomical craniocerebral correlation [Okamoto et al., 2004].

Data Analysis

The cooperation rate of individual dyads was defined as the percentage of winning trials in each block of cooperation task. We also calculated the cooperation rate change across time, given by the changes in the percentage of the win trials between two blocks (i.e., [block 2 cooperation rate]–[block 1 cooperation rate]).

Two signals, namely the Hbo and Hbr time series, were collected from the NIRS channels. As the Hbo signal is more sensitive to the changes in cerebral blood flow than the Hbr signal [Hoshi, 2003; Lindenberger et al., 2009], only Hbo time series were analyzed in current study. We did not perform any preprocessing (i.e., high- or low-pass filtering) on the signals.

For each NIRS channel, the wavelet coherence indicating the synchronous activity between two brains was computed [Grinsted et al., 2004; Murphy et al., 2009]. We used the wavelet coherence MatLab package to examine rela-

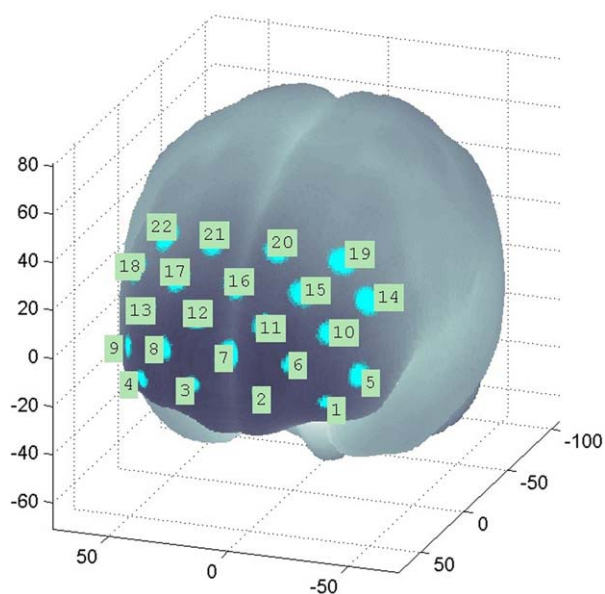


Figure 2.

Cap configuration. The patch covers the frontal area of each participant. The locations of NIRS channels are probabilistically estimated and anatomically labeled in standard brain space. The numbers indicate measurement channels.

tionships in time frequency space between the time series generated by two participants. The crosswavelet and wavelet coherence software were from A. Grinsted et al., [2004] (<http://noc.ac.uk/using-science/crosswavelet-wavelet-coherence>). Our analyses focused on the frequencies ranging from 0.08 Hz (period 12.8 s) and 0.31 Hz (period 3.2 s), which corresponds to the duration of a trial in our tasks.

We calculated the average interbrain coherence in our frequency band of interest (i.e. 0.08–0.31 Hz) during two task-blocks and the rest period. Task-related coherence was defined as increased coherence in a task (task – rest). Also, the coherence change was defined as the difference in coherence between two task blocks (block 2–block 1). The values of task-related coherence and coherence change were converted to Fisher z-statistics before statistical tests were performed [Chang and Glover, 2010; Cui et al., 2012].

RESULTS

Cooperation Performance

A two-way ANOVA was conducted on the cooperation rates with the between-subject variable of group (F-F, F-M, and M-M) and the within-dyad variable of block (block 1 and block 2). The results showed significant differences for the main effect of block, $F(1, 42) = 38.61$, $P < 0.001$, $\eta^2_{\text{partial}} = 0.48$, with the better cooperation performance in block 2 (0.667, SE = 0.02) compared to block 1 (0.55,

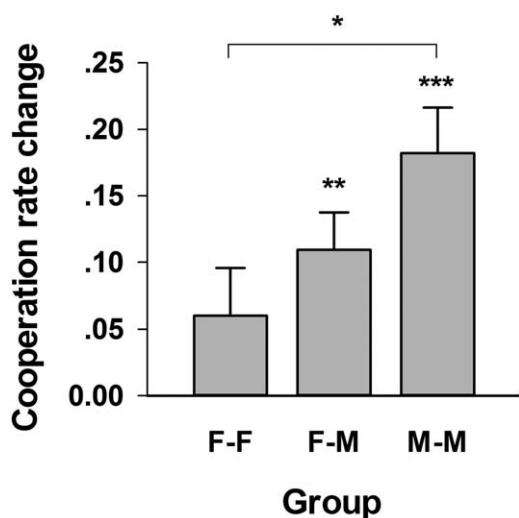


Figure 3.

The cooperation rate changes (block 2 – block 1) of three groups. The changes are significant in the female–male (F-M) and male–male (M-M) groups. The change is larger in male–male group than female–female group. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Error bars indicate the standard error of the mean.

SE = 0.02). Although no significant difference was found for the main effect of group, $F(2, 42) = 0.29$, $P > 0.05$, $\eta^2_{\text{partial}} = 0.01$, the interaction of group by time was significant, $F(2, 42) = 3.42$, $P < 0.05$, $\eta^2_{\text{partial}} = 0.14$. These findings indicated that the genders of participants in a dyad influenced the rate of successful cooperation across time.

We next tested how the change in performance between block 1 and block 2 differed across the three groups. Pairwise tests revealed significant improvements in rates of cooperation in the F-M groups, $t(15) = 3.88$, $P = 0.001$, and in M-M groups, $t(13) = 5.33$, $P < 0.001$, but not in F-F group, $t(14) = 1.69$, $P = 0.11$. Post hoc tests showed that the cooperation rate change was larger in M-M group than in F-F group (see Fig. 3).

Subjective Measurements

A one-way ANOVA on the preference for gender of partner while cooperating in daily life revealed that there was no group effect, $F(2, 87) = 0.59$, $P > 0.05$, $\eta^2_{\text{partial}} = 0.01$. Moreover, the three groups did not demonstrate differences in evaluations about their own performance, cooperativeness, or pleasantness ratings of the cooperation task (all $ps > 0.05$). Concerning partner favorability, a two-way ANOVA with the between-subject variable of group (F-F, F-M, and M-M) and the within-subject variable of time (before and after performing the tasks) showed that there was a main effect of time, $F(1, 87) = 31.28$, $P < 0.001$, $\eta^2_{\text{partial}} = 0.26$, indicating that participants formed more favorable impression of their counterparts over the course of performing the tasks. However, neither the main effect of group nor the

interaction between group and time were significant in this analysis. These results implied that the three groups had similar attitudes derived from cooperation in the study.

The Task-Related Coherence in Cooperation Task

Measured coherence of interbrain activity reflects synchronous brain activity in cooperation task. To identify such coherence, we first conducted a series of one-sample t -tests on task-related coherence (task - rest) for the cooperation task. For all participants, channel 2 and channel 17 demonstrated significant increases in task-related coherence relative to rest [channel 2: $t(44) = 2.30$; channel 17: $t(44) = 2.10$, $ps < 0.05$] (see Fig. 4A). Moreover, the coherence change from block 1 to block 2 in channel 17 was significantly correlated with the cooperation rate change ($r = 0.38$; see Fig. 4A). However, after FDR correction, no channels showed a significant change in task-related coherence among dyads.

Next, we examined the task-related coherence for three groups separately. In the F-M group, Channels 2, 3, 4, and 14 showed significant differences in task-related coherence [channel 2: $t(15) = 3.30$, $P < 0.05$; channel 3: $t(15) = 3.08$, $P < 0.05$; channel 4: $t(15) = 4.02$, $P < 0.05$; channel 14: $t(15) = 3.48$, $P < 0.05$, FDR corrected] (see Fig. 4B). However, the same analyses in F-F group and M-M group revealed no significance difference at any channel ($ts < 2.02$, $ps > 0.05$, FDR corrected; see Fig. 4B). A series of one-way ANOVAs further showed that there were significant group effects at channels 3, 4, and 14. Post hoc tests (Bonferroni corrected) revealed significantly higher task-related coherence in F-M group than in F-F group ($ps < 0.05$). These results imply that the task-related coherence estimated in current study was selective for opposite-sex dyads, with so no significant cross-brain synchronization among same-sex dyads.

To observe whether the significant task-related coherence in the F-M group was related to behavior performance, we performed a number of correlation analyses. The results showed positive correlations between coherence change (block 2 – block 1) and cooperation rate change (block 2 – block 1) at channel 3 ($r = 0.55$, $P < 0.05$), channel 4 ($r = 0.64$, $P < 0.01$), and channel 14 ($r = 0.55$, $P < 0.05$) (see Fig. 4B). Some surrounding channels also showed significant correlations (channel 1: $r = 0.71$, $P < 0.01$; channel 15: $r = 0.57$, $P < 0.05$). However, the equivalent correlations were not found in female–female or male–male groups at these channels (channels 3, 4, 14, $ps > 0.05$). These results indicated that the correlation between brain synchronization and performance on the cooperation task was specific to interactions in opposite-sex dyads.

The Task-Related Coherence in Control Tasks

We conducted parallel analyses to those reported above for activity measured during the competition task and the single-participant control tasks. No significance changes in

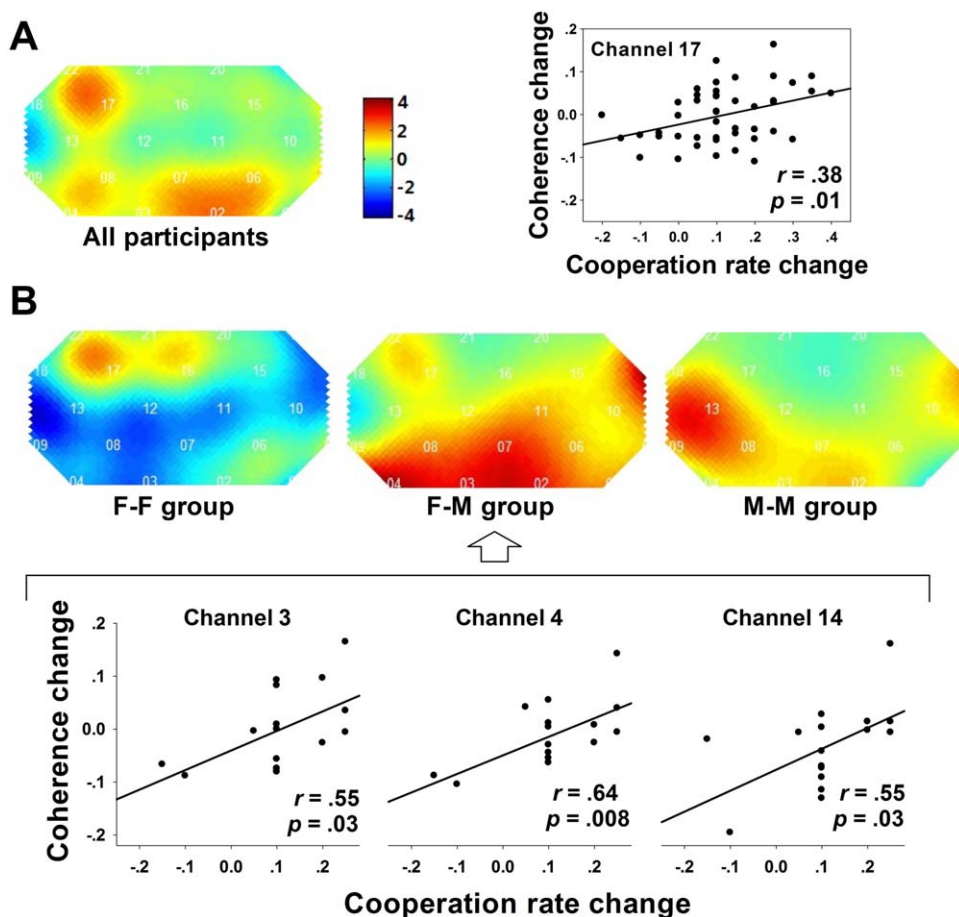


Figure 4.

Task-related coherence on cooperation task. (A) Across all participants: the *t*-test map for task-related coherence (significances at channel 2 and channel 17, FDR uncorrected); significant correlation between coherence change and cooperation rate change (channel 17). (B) Three groups: the *t*-test maps

for task-related coherence (only significances at channels 2, 3, 4, and 14 in female–male interaction, FDR controlled); significant correlation between coherence change and cooperation rate change (channel 3, 4, and 14 in female–male interaction).

task-related coherence were found at any of 22 channels in three groups ($t_s < 3.65$, $p_s > 0.05$, FDR controlled). These results showed that brain activity was not synchronized across participants in the control tasks.

that task-related coherence in brain activity was evident in regions of frontal cortex (i.e., channels 2, 3, 4, and 14) specifically during cooperation among opposite-sex partners. Measured interbrain coherence (i.e., channels 3, 4, and 14) was significantly correlated cooperative performance. In contrast, no significant task-related coherence was found in cooperation including the same-sex partners. To our knowledge, this is the first hyperscanning study attempting to elucidate neural processes related to differences in mixed-sex/same-sex cooperation.

DISCUSSION

Our experiment was motivated by the hypotheses that the gender of partners in a two-person task would influence the degree of synchronous brain activity evident during bouts of cooperative behavior. We found that both male–male and female–male dyads were capable of cooperating, with increased cooperation performance across time. male–male dyads further showed larger increase in performance during the task than did female–female dyads. More importantly, our fNIRS-based study revealed

Cooperation among opposite-sex partners was associated with the significant task-related coherence in frontopolar cortex (FPC, area 10, channel 3 and 4), orbitofrontal area (OFC, area 11, channel 4), and dorsolateral prefrontal cortex (Area 46, channel 14) [Lancaster et al., 2000]. Those areas have been linked to social cognition [Amodio and Frith, 2006; Contreras et al., 2012; Kringelbach and Rolls,

2004], such as thinking about the psychological attributes of self or another person [Amodio and Frith, 2006], judgments of social categories, and the attributes of men and women and their concepts of gender [Milne and Grafman, 2001]. Conversely, some studies found that FPC and OFC are also important for monitoring of outcomes and hence prefrontal activity scales with reward value [Kringelbach and Rolls, 2004; Ramnani and Owen, 2004; Rushworth et al., 2011]. The most anterior region of FPC has been suggested to be important for maintaining meta-cognitive representations that enable us to reflect on the values linked to outcomes and actions—that is, thinking about thinking [Amodio and Frith, 2006]. Whether these social, reward, and meta-cognitive processes have a combined effect or how they differ for mixed-sex interactions are fruitful avenues for further investigation.

With respect to cooperation among same-sex partners, it is intriguing that task-related coherence was absent in current study. Previous studies have suggested that during peer interactions, participants might be sensitive to peer norms or peer pressure, which may be reflected specifically in amygdala activity [Grosbras et al., 2007; Guyer et al., 2008]. Additionally, brain areas other than frontal cortex might be involved in producing cooperative behavior, including the left inferior parietal lobule (IPL), the medial and superior temporal gyrus, and the occipital cortex [Egetemeir et al., 2011]. Moreover, the level of cooperation could modify the magnitude of activation in IPL area [Egetemeir et al., 2011], left parietal operculum, and anterior cingulate cortex [Astolfi et al., 2010; Chaminade et al., 2012]. However, these areas were not measured in the current study. Therefore, we cannot rule out the possibility that the significantly task-related coherence for same-sex cooperation might be found in brain regions outside of frontal cortex.

The findings in current study were partly confirming of those reported in previous studies [Cui et al., 2012; Dommer et al., 2012; Funane et al., 2011]. The previous studies of cooperation identified increased coherence at the right superior frontal cortex [Cui et al., 2012] and medial prefrontal region [Funane et al., 2011]. In our study, the mixed-sex group demonstrated increased coherence in the medial prefrontal region but not in right superior frontal cortex (channel 17 or the channels nearby). However, when we considered all participants ($N = 45$ pairs), there was a strong trend in right superior prefrontal cortex, with the degree of correlation seeming to relate to cooperation performance (see Fig. 4A). It is worth noting that there were some differences in the experimental procedure in our study relative to previous experiments. Specifically, we intentionally controlled for familiarity among participants in each dyad (i.e. they were all strangers). We also queried and controlled for subjective attitudes about each participant's partner. The findings in previous studies were based on the average of both mixed-sex and same-sex dyads, whereas our specific intention was to identify differences across these subgroups

(i.e., mixed versus same-sex groups). Our finding that there were differences in task-related coherence between mixed-sex and same-sex dyads suggests that cooperation ought to be investigated at the subgroup level in the future studies.

In current study, the participants in each dyad did not know each other before experiment. All subjective measurements did not show any significant differences between mixed-sex and same-sex cooperation. These results could exclude the possible role of subjective feelings in task-related interbrain coherence. However, previous studies have shown that cooperation is greater with familiar social partners than with unknown partners in both humans [Majolo et al., 2006] and animals [Raihani et al., 2012]. It is reasonable to hypothesize that familiar partners (including friends, couples, and so on) would induce higher level of cooperation performance and stronger interbrain coherence, which needs to be tested in the future.

Several other factors could affect interbrain coherence. First, subtle motion resulting from pressing keys might produce synchronous artifacts that could impact our results. The participants in current study also performed a competition task, in which the level of motion should be the same to that generated in the cooperation task. We calculated the percentage of win trials in competition task by following the same formula for cooperation rate, and did not find any significant difference between two tasks (cooperation: 0.61 vs. competition: 0.65). However, the increased interbrain coherence in the cooperation task was absent in the competition task. Moreover, task related interbrain coherence was significantly correlated with performance in the cooperation task (see Fig. 4) but not in the competition task (channel 3: $r = -0.07$, $P > 0.05$; channel 4: $r = -0.14$, $P > 0.05$; channel 14: $r = -0.18$, $P > 0.05$). Therefore, we propose that the synchronous of motion (pressing the key) had little explanatory power for understanding our identified task-related interbrain coherence. Second, previous studies have shown that peripheral physiological effects could influence functional NIRS signals. For example, the larger interbrain coherence that derived from both heart rate-related frequency band ranging 0.7–4 Hz (corresponding to period length of 0.25–1.5 s) and low-frequency bands ranging from 0.06 to 0.2 Hz (corresponding to period length of 5–16 s) was obtained during performance of a n-back task in paired players as compared to single players [Dommer et al., 2012]. Further evidence indicates that blood flow in the skin was closely correlated with task-related NIRS responses when subjects performed a verbal fluency task [Cui et al., 2012]. The frequency band from 0.7 to 4 Hz (corresponding to period length of 0.25–1.5 s) is sensitive to heart rate, while bands lower than 0.2 Hz in frontal cortex are considered to be cognition-related NIRS activity [Cui et al., 2012; Dommer et al., 2012; Duan et al., 2013; Jiang et al., 2012]. The increased interbrain coherence in present study was observed at the low-frequency band (see Supporting information Fig. S1), which suggests that heart rate should not

be the primary determinant of our results, although we cannot completely rule out effects of synchronous cardiac cycles.

This study has some limitations. Participants shared a keyboard in the study, so that they could see the other person's hand and action. Therefore, the observed significant coherence might derive in part from participant's reaction to the other's motor activities. We were also limited by the relative poor spatial resolution of NIRS. If we wish to more specifically identify which areas of frontal cortex are important for cooperation, it will be important to use MRI [Emonds et al., 2014; Fett et al., 2014], high-density optical probes [Yamamoto et al., 2002], or diffuse optical tomography [Zeff et al., 2007]. A previous study showed that end-tidal CO₂ (P_{ET}CO₂) levels in prefrontal cortex change a lot as subjects perform different speech tasks [Scholkmann et al., 2013a]. This finding indicates that CO₂ intensity can be monitored during neuroimaging recordings, including the fNIRS and fMRI, to improve interpretations of changes in hemodynamics and blood oxygenation measures. Therefore, it would be beneficial to collect CO₂ measurements during our cooperation task to rule out or identify effects of CO₂ on the task-related inter-brain coherence in future study. Previous work has shown that there was a highly significant sex-related difference in CO₂-induced cerebral vasomotor reactivity [Kastrup et al., 1997], and cerebral autoregulation [Wang et al., 2005]. Such gender-related difference should not be critical factors affecting task-related interbrain coherence in our current study. Instead, these factors should have equal impact on fNIRS responses during the cooperation and competition tasks. These effects can therefore not explain the fact that we found increased interbrain interaction only in the cooperation task.

To conclude, the current study revealed coherent brain activity across dyads related with the cooperation specifically with opposite-sex partners. This synchronization occurred roughly in frontopolar, orbitofrontal, and left dorsolateral prefrontal cortex. Task-related coherence can therefore be used to differentiate the neural processes that underlie mixed-sex cooperation compared to same-sex cooperation. This study also provides some insight into the using of hyperscanning technique to understand social interactions in humans. Future studies could focus on neural correlates related to same-sex cooperation and their differences from those of mixed-sex cooperation, to determine how social context moderates performance among participants.

ACKNOWLEDGMENTS

The authors would like to thank Lili Zheng, Yue Cheng, and Shan Li for assisting data acquiring. The authors also thank a lot to Dr. McClure from the Department of Psychology at Stanford University for very good comments and correction for our manuscript. The authors have no conflict of interest to declare.

REFERENCES

- Amodio DM, Frith CD (2006): Meeting of minds: The medial frontal cortex and social cognition. *Nat Rev Neurosci* 7:268–277.
- Astolfi L, Toppi J, Fallani FD, Vecchiato G, Salinari S, Mattia D, Cincotti F, Babiloni F (2010): Neuroelectrical hyperscanning measures simultaneous brain activity in humans. *Brain Topogr* 23:243–256.
- Babiloni F, Astolfi L (2014): Social neuroscience and hyperscanning techniques: Past, present and future. *Neurosci Biobehav Rev* 44:76–93.
- Balliet D, Li NP, Macfarlan SJ, Van Vugt M (2011): Sex differences in cooperation: A meta-analytic review of social dilemmas. *Psychol Bull* 137:881–909.
- Buss DM, Schmitt DP (1993): Sexual strategies theory—An evolutionary perspective on human mating. *Psychol Rev* 100:204–232.
- Chaminade T, Marchant JL, Kilner J, Frith CD (2012): An fMRI study of joint action-varying levels of cooperation correlates with activity in control networks. *Front Hum Neurosci* 6:179.
- Chang C, Glover GH (2010): Time-frequency dynamics of resting-state brain connectivity measured with fMRI. *Neuroimage* 50: 81–98.
- Contreras JM, Banaji MR, Mitchell JP (2012): Dissociable neural correlates of stereotypes and other forms of semantic knowledge. *Soc Cogn Affect Neurosci* 7:764–770.
- Cui X, Bryant DM, Reiss AL (2012): NIRS-based hyperscanning reveals increased interpersonal coherence in superior frontal cortex during cooperation. *NeuroImage* 59:2430–2437.
- Deaux K, Major B (1987): Putting gender into context—An interactive model of gender-related behavior. *Psychol Rev* 94:369–389.
- Decety J, Jackson PL, Sommerville JA, Chaminade T, Meltzoff AN (2004): The neural bases of cooperation and competition: An fMRI investigation. *Neuroimage* 23:744–751.
- Dommer L, Jaeger N, Scholkmann F, Wolf M, Holper L (2012): Between-brain coherence during joint n-back task performance: A two-person functional near-infrared spectroscopy study. *Behav Brain Res* 234:212–222.
- Duan L, Liu WJ, Dai RN, Li R, Lu CM, Huang YX, Zhu CZ (2013): Cross-brain neurofeedback: Scientific concept and experimental platform. *Plos One* 8:e64590.
- Dumas G, Nadel J, Soussignan R, Martinerie J, Garnero L (2010): Inter-brain synchronization during social interaction. *Plos One* 5:e12166.
- Eagly AH (2009): The his and hers of prosocial behavior: An examination of the social psychology of gender. *Am Psychol* 64:644–658.
- Eagly AH, Wood W (1999): The origins of sex differences in human behavior - Evolved dispositions versus social roles. *Am Psychol* 54:408–423.
- Egetemeir J, Stenneken P, Koehler S, Fallgatter AJ, Herrmann MJ (2011): Exploring the neural basis of real-life joint action: Measuring brain activation during joint table setting with functional near-infrared spectroscopy. *Front Hum Neurosci* 5:95.
- Emonds G, Declerck CH, Boone C, Seurinck R, Achten R (2014): Establishing cooperation in a mixed-motive social dilemma. An fMRI study investigating the role of social value orientation and dispositional trust. *Soc Neurosci* 9:10–22.
- Fehr E, Fischbacher U (2003): The nature of human altruism. *Nature* 425:785–791.
- Fett A-KJ, Gromann PM, Giampietro V, Shergill SS, Krabbendam L (2014): Default distrust? An fMRI investigation of the neural

- development of trust and cooperation. *Soc Cogn Affect Neurosci* 9:395–402.
- Fliessbach K, Weber B, Trautner P, Dohmen T, Sunde U, Elger CE, Falk A (2007): Social comparison affects reward-related brain activity in the human ventral striatum. *Science* 318:1305–1308.
- Funane T, Kiguchi M, Atsumori H, Sato H, Kubota K, Koizumi H (2011): Synchronous activity of two people's prefrontal cortices during a cooperative task measured by simultaneous near-infrared spectroscopy. *J Biomed Opt* 16:077011.
- Garbarini F, Boero R, D'Agata F, Bravo G, Mosso C, Cauda F, Duca S, Geminiani G, Sacco K (2014): Neural correlates of gender differences in reputation building. *Plos One* 9:e106285.
- Geary DC, Byrd-Craven J, Hoard MK, Vigil J, Numtee C (2003): Evolution and development of boys' social behavior. *Dev Rev* 23:444–470.
- Grinsted A, Moore JC, Jevrejeva S (2004): Application of the cross wavelet transform and wavelet coherence to geophysical time series. *Nonlinear Processes Geophys* 11:561–566.
- Grosbras M-H, Jansen M, Leonard G, McIntosh A, Osswald K, Poulsen C, Steinberg L, Toro R, Paus T (2007): Neural mechanisms of resistance to peer influence in early adolescence. *J Neurosci* 27:8040–8045.
- Guyer AE, Lau JYF, McClure-Tone EB, Parrish J, Shiffrin ND, Reynolds RC, Chen G, Blair RJR, Leibenluft E, Fox NA and others (2008): Amygdala and ventrolateral prefrontal cortex function during anticipated peer evaluation in pediatric social anxiety. *Arch Gen Psychiat* 65:1303–1312.
- Hirata M, Ikeda T, Kikuchi M, Kimura T, Hiraishi H, Yoshimura Y, Asada M (2014): Hyperscanning MEG for understanding mother-child cerebral interactions. *Front Hum Neurosci* 8:118.
- Hirnstein M, Coloma Andrews L, Hausmann M (2014): Gender-stereotyping and cognitive sex differences in mixed- and same-sex groups. *Arch Sex Behav* 43:1663–1673.
- Holper L, Goldin A, Shalom D, Battroc A, Wolf M, Sigman M (2013): The teaching and the learning brain: A cortical hemodynamic marker of teacher–student interactions in the Socratic dialog. *Int J Educ Res* 59:1–10.
- Holper L, Scholkmann F, Wolf M (2012): Between-brain connectivity during imitation measured by fNIRS. *Neuroimage* 63:212–222.
- Hoshi Y (2003): Functional near-infrared optical imaging: Utility and limitations in human brain mapping. *Psychophysiology* 40:511–520.
- 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.
- Kastrup A, Thomas C, Hartmann C, Schabet M (1997): Sex dependency of cerebrovascular CO₂ reactivity in normal subjects. *Stroke* 28:2353–2356.
- King-Casas B, Tomlin D, Anen C, Camerer CF, Quartz SR, Montague PR (2005): Getting to know you: Reputation and trust in a two-person economic exchange. *Science* 308:78–83.
- Koike T, Tanabe HC, Sadato N (2015): Hyperscanning neuroimaging technique to reveal the “two-in-one” system in social interactions. *Neurosci Res* 90:25–32.
- Kringelbach ML, Rolls ET (2004): The functional neuroanatomy of the human orbitofrontal cortex: Evidence from neuroimaging and neuropsychology. *Prog Neurobiol* 72:341–372.
- Lancaster JL, Woldorff MG, Parsons LM, Liotti M, Freitas ES, Rainey L, Kochunov PV, Nickerson D, Mikiten SA, Fox PT (2000): Automated Talairach Atlas labels for functional brain mapping. *Hum Brain Mapp* 10:120–131.
- Lindenberger U, Li S-C, Gruber W, Mueller V (2009): Brains swinging in concert: Cortical phase synchronization while playing guitar. *BMC Neurosci* 10:22.
- Majolo B, Ames K, Brumpton R, Garratt R, Hall K, Wilson N (2006): Human friendship favours cooperation in the iterated prisoner's dilemma. *Behaviour* 143:1383–1395.
- 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 USA* 98:11832–11835.
- Milne E, Grafman J (2001): Ventromedial prefrontal cortex lesions in humans eliminate implicit gender stereotyping. *J Neurosci* 21:RC150.
- Montague PR, Berns GS, Cohen JD, McClure SM, Pagnoni G, Dhamala M, Wiest MC, Karpov I, King RD, Apple N and others (2002): Hyperscanning: Simultaneous fMRI during linked social interactions. *Neuroimage* 16:1159–1164.
- Murphy K, Birn RM, Handwerker DA, Jones TB, Bandettini PA (2009): The impact of global signal regression on resting state correlations: Are anti-correlated networks introduced? *Neuroimage* 44:893–905.
- Okamoto M, Dan H, Sakamoto K, Takeo K, Shimizu K, Kohno S, Oda I, Isobe S, Suzuki T, Kohyama K and others (2004): Three-dimensional probabilistic anatomical cranio-cerebral correlation via the international 10–20 system oriented for transcranial functional brain mapping. *Neuroimage* 21:99–111.
- Raihani NJ, Grutter AS, Bshary R (2012): Female cleaner fish cooperate more with unfamiliar males. *Proc Biol Sci R Soc* 279:2479–2486.
- Rammani N, Owen AM (2004): Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nat Rev Neurosci* 5:184–194.
- Rilling JK, Gutman DA, Zeh TR, Pagnoni G, Berns GS, Kilts CD (2002): A neural basis for social cooperation. *Neuron* 35:395–405.
- Rushworth MFS, Noonan MP, Boorman ED, Walton ME, Behrens TE (2011): Frontal cortex and reward-guided learning and decision-making. *Neuron* 70:1054–1069.
- Scholkmann F, Gerber U, Wolf M, Wolf U (2013a): End-tidal CO₂: An important parameter for a correct interpretation in functional brain studies using speech tasks. *Neuroimage* 66:71–9.
- Scholkmann F, Holper L, Wolf U, Wolf M (2013b): A new methodical approach in neuroscience: Assessing inter-personal brain coupling using functional near-infrared imaging (fNIRI) hyperscanning. *Front Hum Neurosci* 7:813.
- Singh AK, Okamoto M, Dan H, Jurcak V, Dan I (2005): Spatial registration of multichannel multi-subject fNIRS data to MNI space without MRI. *Neuroimage* 27:842–851.
- Suzuki S, Niki K, Fujisaki S, Akiyama E (2011): Neural basis of conditional cooperation. *Soc Cogn Affect Neurosci* 6:338–347.
- Thayer BA, editor (2004): Darwin and international relations: On the evolutionary origins of war and ethnic conflict. Lexington, KY: University Press of Kentucky.
- Tsuzuki D, Jurcak V, Singh AK, Okamoto M, Watanabe E, Dan I (2007): Virtual spatial registration of stand-alone MRS data to MNI space. *Neuroimage* 34:1506–1518.
- Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M (2002): Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 15:273–289.

- Wang X, Krishnamurthy S, Evans J, Bhakta D, Justice L, Bruce E, Patwardhan A (2005): Transfer function analysis of gender-related differences in cerebral autoregulation. *Biomed Sci Instrum* 41:48–53.
- Yamamoto T, Maki A, Kadoya T, Tanikawa Y, Yamada Y, Okada E, Koizumi H (2002): Arranging optical fibres for the spatial resolution improvement of topographical images. *Phys Med Biol* 47:3429–3440.
- Yamasue H, Abe O, Suga M, Yamada H, Rogers MA, Aoki S, Kato N, Kasai K (2008): Sex-linked neuroanatomical basis of human altruistic cooperativeness. *Cereb Cortex* 18:2331–2340.
- Zeff BW, White BR, Dehghani H, Schlaggar BL, Culver JP (2007): Retinotopic mapping of adult human visual cortex with high-density diffuse optical tomography. *Proc Natl Acad Sci USA* 104:12169–12174.