OXFORD

Distinct neural couplings to shared goal and action coordination in joint action: evidence based on fNIRS hyperscanning

Xiaojun Cheng,[1] Bing Guo,[1] and Yinying Hu[2]

[1]School of Psychology, Shenzhen University, Shenzhen 518060, China
[2]Institute of Brain and Education Innovation, East China Normal University, Shanghai 200062, China
Correspondence should be addressed to Yinying Hu, Institute of Brain and Education Innovation, East China Normal University, No. 3663 Zhongshan North Road, Shanghai 200062, China. E-mail: huyy9088@gmail.com.

Abstract

Joint action is central to human nature, enabling individuals to coordinate in time and space to achieve a joint outcome. Such interaction typically involves two key elements: shared goal and action coordination. Yet, the substrates entrained to these two components in joint action remained unclear. In the current study, dyads performed two tasks involving both sharing goal and action coordination, i.e. complementary joint action and imitative joint action, a task only involving shared goal and a task only involving action coordination, while their brain activities were recorded by the functional near-infrared spectroscopy hyperscanning technique. The results showed that both complementary and imitative joint action (i.e. involving shared goal and action coordination) elicited better behavioral performance than the task only involving shared goal/action coordination. We observed that the interbrain synchronization (IBS) at the right inferior frontal cortex (IFC) entrained more to shared goal, while left-IFC IBS entrained more to action coordination. We also observed that the right-IFC IBS was greater during completing a complementary action than an imitative action. Our results suggest that IFC plays an important role in joint action, with distinct lateralization for the sub-components of joint action.

Key words: joint action; shared goal; action coordination; interbrain synchronization; fNIRS hyperscanning

Introduction

People coordinate their actions with others all the time, such as carrying tables together or playing piano duets. Such joint actions are aimed at accomplishing collective goals and require action coordination in time and space between individuals (Sebanz *et al.*, 2006). Specifically, collective goals, i.e. shared goals, are directed to the goal that is both in common between individuals and divided up into individual sub-goals. It relies on individuals to integrate self and others' movements and sub-goals in a single and coherent motor plan (Sacheli *et al.*, 2015). Action coordination, however, is based on the sensory-motor processes of each individual. It relies on internal models of one's own and the other's action sensory-motor processes. Individuals coordinate their actions during the execution phase to ensure the successful completion of joint action (Rizzolatti and Craighero, 2004). The functional differences between shared goal and action coordination hint at distinct neural mechanisms underlying these two processes.

In the cognitive psychology studies of joint action, both shared goal and action coordination have been considered as key processes in joint action (Knoblich *et al.*, 2011). When performing joint actions, individuals not only represent their own goals and tasks but also represent other aspects of each other's goals and tasks and even represent the relations between one's own and others' goals and tasks, and such representations can support joint action by eliminating the interference between individual tasks (Kourtis *et al.*, 2019; Schmitz *et al.*, 2017). People's propensity to form shared task representations allows them to start performing joint actions well prepared, but this is not sufficient to ensure successful coordination. The coordination mechanisms operating during performance have been investigated, including three aspects: (i) monitoring errors in one's own actions, in partner's actions and in joint outcomes, (ii) modulating or exaggerating certain parameters of an instrumental action to provide information to the partner and (iii) predicting partner's actions based on both of the representations of the prescribed joint action outcomes and the learned experience with partner's actions (Konvalinka *et al.*, 2010; Loehr *et al.*, 2013; Pezzulo *et al.*, 2013; Wolf *et al.*, 2018). The accounts of cognitive psychology suggest that joint action depends on complex neural mechanisms, that is, different neu-

ral substrates to different elements (i.e. shared goal and action coordination) that are required in joint action.

Previous neuroimaging studies have shown that there are specific neural substrates involved in joint action, in which the frontal and parietal regions are recruited (Newman-Norlund et al., 2007; Sacheli et al., 2015). Besides the single-brain framework, a growing number of neuroimaging studies have focused on the brain-to-brain couplings during joint action, as such social interaction like joint action can be seen as a feedback loop in a multibrain system (Kingsbury and Hong, 2020). Using the hyperscanning approach (i.e. simultaneously measuring two or more individuals' brain signals; Montague et al., 2002), recent studies provide evidence that there are brain-to-brain couplings (namely interbrain synchronization, IBS) across various types of joint action, such as key pressing (Funane et al., 2011), fingertip moving (Yun et al., 2012), finger tapping (Konvalinka et al., 2014), motor imitating (Dumas et al., 2010; Holper et al., 2012), playing guitar (Sanger et al., 2012; Muller et al., 2013), cooperative singing (Muller et al., 2019) and group drumming (Duan et al., 2015; Liu et al., 2021). The demonstrated IBS is mainly at the frontal and parietal areas (including frontopolar, inferior frontal cortex (IFC), premotor cortex and inferior parietal lobule), and it is correlated with behavioral coordination between persons (Cheng et al., 2015; Mu et al., 2016). However, to our knowledge, the specific IBS entrained to shared goal and action coordination in joint action remains unknown.

It has been reported that there is IBS to shared goal and action coordination during social interaction. For example, a higher IBS was observed at the right temporo-parietal junction when the dyad played an ultimatum game face-to-face compared to that with faces blocked. The IBS was found to be associated with the feeling of shared intentionality between interacting partners (Tang et al., 2016). A similar correlation between IBS and shared intentionality was also observed when dyads performed a coordinated tapping task (vs non-coordinated tapping task) (Hu et al., 2017) and between clients and counselors in a psychological counseling task (Zhang et al., 2018). A recent study further reported that the IBS represented the same internal representation of intentions and actions shared between the self and the other, and online imitative interaction enhanced the IBS that correlated with the similarity in facial movement kinematic profile (Miyata et al., 2021). Meanwhile, for action coordination, previous findings on interpersonal synchrony, which aimed at synchronous actions in time and space without shared goal, found the IBS at the left lateral prefrontal cortex when participant dyads underwent a rhythmic arm movement synchronously (Nozawa et al., 2019) and when a group of participants walked synchronously (Ikeda et al., 2017). Based on these findings, we assumed that distinct IBS entrained to shared goal and action coordination in joint action.

In the present study, we employed the functional near-infrared spectroscopy (fNIRS) based hyperscanning approach to investigate the specific IBS entrained to shared goal and action coordination in joint action. This optical imaging allows for the measurement of brain activity in more natural settings and is thought to be more robust against movement artifacts compared with functional magnetic resonance imaging (fMRI) and Electroencephalography (EEG) (Egetemeir et al., 2011). The bilateral IFC and right temporo-parietal junction (TPJ) were selected as the regions of interest here since the above-mentioned brain regions are in joint action, shared goal and action coordination. Pairs of participants co-drew shapes on the computer by using markers. They were randomly assigned as either the leader or the follower.

Since complementary (i.e. nonimitative or nonidentical; Sacheli et al., 2015) actions are favored over imitative responses in our real-life situations, we arranged a two-person nonidentical-shape joint action (Nonidentical) task in which the follower needed to perform complementary action (i.e. draw a nonidentical shape) when the leader drew the target shape. We also arranged a presumed human-computer (Hum-Com1) task in which the two participants were told to coordinate with the computer independently, but they actually coordinated with each other so that there was action coordination but without shared goal. Another turn-based human-computer (Hum-Com2) task was also arranged in which participants were told to draw together, and they took turns to draw the nonidentical shapes with the computer so that they did not experience the action coordination process, but they had shared goal. To confirm the repeatability of previous findings on the neural substrates of complementary joint action (Newman-Norlund et al., 2007; Sacheli et al., 2015), participants were also required to engage in an identical-shape joint action (Identical) task, where the follower had to imitate the leader's actions and then drew the same shapes with the leader. We hypothesized that there is greater IBS in Nonidentical or Identical tasks than the tasks of Hum-Com1 and Hum-Com2 but at different brain regions. We also hypothesized that the Nonidentical task induces higher frontal IBS compared to the Identical task since it has been reported that the frontal cortex was more active during complementary action compared with imitative action (Newman-Norlund et al., 2007).

Methods

Participants

Fifty-two students (age: 21.05 ± 2.47 years) were recruited via flyers spread throughout Shenzhen University, forming 26 same-gender dyads (9 male–male dyads and 17 female–female dyads). To control the potential effect of partner familiarity on joint action (Ames et al., 2006), the two participants in a dyad did not know each other before the experiment. All participants had a normal or corrected-to-normal vision and had no history of medical, psychiatric or neurological diagnoses. Written informed consent was obtained from every participant. Participants were compensated for their participation. The study was approved by the University Committee on Human Research Protection of Shenzhen University.

Experimental tasks and procedures

Upon arriving at the laboratory, two participants briefly met each other and confirmed that they had not been previously acquainted. Then, they were seated on the opposite sides of a table and separated by two computer monitors in a quiet room (Figure 1A). In our study, participants needed to perform four computerized continuous drawing tasks adapted from the children's drawing game 'Etch-a-Sketch' (Arueti et al., 2013; Gooijers et al., 2013; Cheng et al., 2019). Two participants in a dyad were randomly assigned as the roles of the leader and follower. Each of them had a pictorial space of 1380 × 540 and a marker with color (the leader's marker was red and the follower's was blue). They were required to draw several shapes in the pictorial space according to the instructions of the tasks. For each trial of the drawing task, a 2-s fixation ('+') first appeared at the center of the screen, then one participant drew the target shape (given by the experimenter) that was made up of line segments on the screen by pressing the specific keys (i.e. 'A'/'S' for horizontal movement and 'W'/'Z' for vertical movement) (Figure 1B). At the same time,
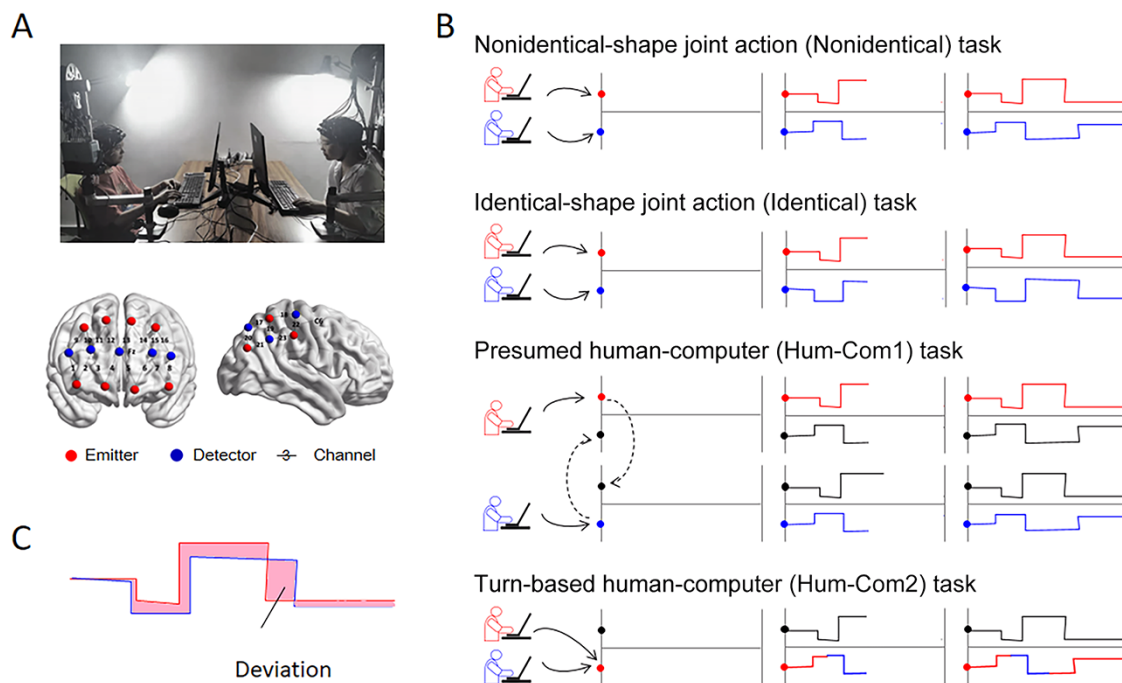
Fig. 1. Experimental design and task procedures. (A) Experimental setup and probe configuration. The integers on the cerebral cortex indicate the recording channels. (B) Events and time flow in a drawing trial of the tasks. The red color represents participant #1, the blue color represents participant #2 and the black color represents the computer. Specifically, in the Hum-Com1 task, two participants were instructed to interact with the computer. However, they dynamically coordinated with their partner. (C) The calculation for the behavioral performance. The given example was for the Identical task. The deviation scores were determined by the amounts of pixels that the follower's shape deviated from the leader's shape (the pink area). For the tasks involving complementary action (i.e. the Nonidentical, Hum-Com1 and Hum-Com2 tasks), we first performed a symmetric transformation on the follower's shape and then calculated the deviation.

the follower needed to draw the shape by pressing the specific keys (i.e. 'J'/'K' for horizontal movement and 'I'/'M' for vertical movement). The gain of each key pressing was set to 2 pixels. When the marker of the follower went to the endpoint (i.e. the x-coordinate = 1380), the drawing trial ended. During the process, participants were not allowed to communicate with each other verbally or nonverbally. They could adjust their actions according to the real-time tracing path displayed on the screen.

Participants completed four different drawing tasks. Prior to each task, instructions were presented to each participant. To establish the Nonidentical task, participants were told that they should co-draw the shapes with each other, and while the leader is drawing the target shape, the follower should draw a nonidentical (i.e. symmetrical) shape. Then, the two participants would draw shapes with complementary action, e.g. the leader pressed the key of 'up' movement, while the follower would press the key of 'down' movement. In the Identical task, participants were instructed to co-draw shapes with each other and the follower should draw the shape as same as the leader (e.g. 'up' moment for the leader, while 'up' moment for the follower). In the Hum-Com1 task, participants were informed that they were co-drawing with the computer, respectively, whereas they actually interacted with each other as same as the Nonidentical task. So, in this task, participants did not share the same representation about the task or the goal while they dynamically adapted to each other. In the Hum-Com2 task, the two participants were asked to co-draw shapes with each other, but they should draw nonidentical shapes following the computer, and they would act alternately. Each of them had 10 s to control the marker, and the current controller was indicated by the marker's color. Thus, in this task, two participants shared the representation of the goal but did not

dynamically adapt with each other. Each task had six drawing trials, and the order of the four tasks was counterbalanced.

Data acquisition

We used two of the same fNIRS systems (NirScan Inc., HuiChuang, Beijing) to record the brain signals of two participants in a dyad during the experiment. The changes of blood oxygenation at two wavelengths (760 and 850 nm) were measured with a 10-Hz sampling rate. For each participant, two sets of optode probes were placed covering the bilateral prefrontal cortex and right TPJ, with a total of 23 recording channels (CHs) (Figure 1A). The placements of the emitter and detector were according to the 10–20 system. The distance of emitters and detectors was about 3 cm. Specifically, the center of the prefrontal probe set is placed at the FPz position. The references of bilateral IFC were F7 (CH1) and F8 (CH8) (Koessler *et al.*, 2009). The references of the right TPJ were C6 (CH22), CP6 (CH19) and P6 (CH20) (Jurcak *et al.*, 2007). Our regions of interest were the left IFC (CH7–8, CH15–16), the right IFC (CH1–2, CH9–10) and the right TPJ (CH17–23). Thus, a total of 15 channels of interest were included in the current study.

Data analysis
Behavioral data

We recorded the coordinates of the marker's movements for two participants so that we could obtain dyads' tracing path by simple computation (Cheng *et al.*, 2019). For each trial, we first calculated the deviation index of participants' drawings. It was determined by the number of pixels that the traced shape created by the follower deviated from the target shape created by the leader (Figure 1C). For a given drawing block, the lower the deviation score indicated, the more accurate the precision by which the two

participants drew. The output deviation scores ranged between 0, representing a perfect score (flawless tracing), and tens of thousands, representing poor accuracy and a large deviation from the original shape.

fNIRS data

The oxy-Hemoglobin (HbO) and the deoxy-Hemoglobin (HbR) signals were extracted directly from the fNIRS devices. In the current study, we mainly focused on the HbO signal since it was sensitive to regional cerebral oxygenation changes and neural activity (Hoshi, 2003) and correlated with the fMRI signal (Strangman *et al.*, 2002; Kirilina *et al.*, 2012). During preprocessing, the raw HbO data were first passed through a 0.02–0.5-Hz bandpass filter to remove the longitudinal signal drift and the noise from the instrument. We then used the correlation-based signal improvement (CBSI) procedure to reduce motion artifacts caused by head movement. CBSI is a channel-by-channel approach based on the hypothesis that HbO and HbR signals should be negatively correlated during functional activation but become more positively correlated when a motion artifact occurs (Cui *et al.*, 2010). Specifically, the filtered HbO data were corrected by subtracting α times HbR values, where α was the ratio of the standard deviation of HbO and HbR values, and then divided by 2. Finally, a wavelet-based method was employed to remove the global physiological noise (Duan *et al.*, 2018), in which the wavelet transform coherence was used to identify and suppress the globally co-varying time-frequency points. In this method, the *k* threshold, a quantification definition of the globality of the global physiological noise, was set as 0.5 according to the default setting of the method.

After the preprocessing, all HbO data were entered into subsequent analysis. We adopted the Pearson's correlation to evaluate the interbrain synchronization (i.e. IBS) between two participants in a dyad. Specifically, for each channel of interest (i.e. CH1–2, CH7–8, CH9–10, CH15–16 and CH17–23), we calculated the *r* values between two participants' signals during the four tasks. Then the *r* values were Fisher-z transformed. To explore the IBS in a single condition, the Identical task was used as a baseline. In this way, the transformed *r* values of the Nonidentical, Hum-Com1 and Hum-Com2 tasks were subtracted from the transformed *r* values of the Identical task separately. The subtracted *r* values were subsequently entered into one-sample *t*-test. Finally, to compare the difference between conditions, the subtracted *r* values of the Nonidentical, Hum-Com1 and Hum-Com2 tasks were analyzed using repeated-measures analysis of variance (ANOVA). The false discovery rate (FDR) correction was applied for all 15 channels to control multiple comparisons, and the alpha level was set to $P < 0.05$.

Results
Behavioral performance
We conducted repeated-measures ANOVA on the deviations of the four drawing tasks. The results showed a significant main effect [$F = 14.03$, $P < 0.001$, $\eta^2 = 0.65$]. Further post hoc tests showed that the deviation in the Nonidentical task was significantly smaller than that in the Hum-Com1 task [$t\,(25) = 4.69$, $P < 0.001$, Cohen's $d = 0.92$], as well as in the Hum-Com2 task [$t\,(25) = 6.00$, $P < 0.001$, Cohen's $d = 1.18$]. Similarly, the deviation in the Identical task was significantly smaller than that in the Hum-Com1 task [$t\,(25) = 2.89$, $P < 0.01$, Cohen's $d = 0.57$], as well as in the Hum-Com2 task [$t\,(25) = 3.06$, $P < 0.01$, Cohen's $d = 0.60$]. No significant difference was found between the Hum-Com1 task and the
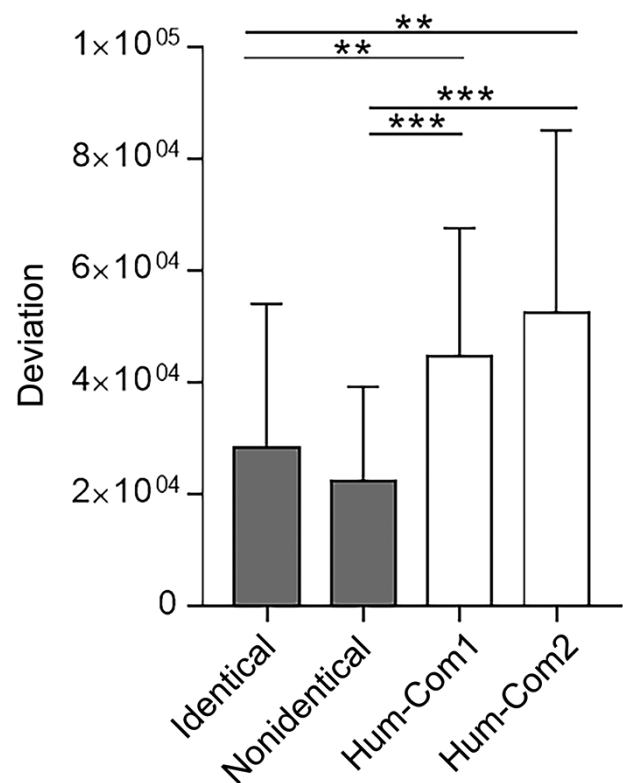
Fig. 2. Behavioral performance. The nonidentical-shape joint action (Nonidentical) and identical-shape joint action (Identical) tasks elicited better performance than the presumed human-computer (Hum-Com1) task and the turn-based human-computer (Hum-Com2) task. $^{**}P < 0.01$, $^{***}P < 0.001$. Error bars indicate the standard error.

Hum-Com2 task [$t\,(25) = 1.25$, $P > 0.05$] or between the Nonidentical task and the Nonidentical task [$t\,(25) = 1.29$, $P > 0.05$]. These results suggest that the tasks containing both shared goal and action coordination would elicit better performance (Figure 2).

Interbrain synchronization
A series of *t*-tests were used to explore the IBS in one single condition. The Nonidentical task, involving both shared goal and action coordination, elicited significantly higher IBS at CH1 [$t\,(25) = 3.46$, $P = 0.002$, Cohen's $d = 0.68$], CH2 [$t\,(25) = 3.24$, $P = 0.003$, Cohen's $d = 0.63$] and CH21 [$t\,(25) = 2.32$, $P = 0.029$, Cohen's $d = 0.46$] (Figure 3A). In particular, CH1 and CH2 survived after being FDR controlled. Both CH1 and CH2 were approximately located at the right IFC. The Hum-Com1 task (i.e. involving action coordination) induced significantly higher IBS at CH13 [$t\,(25) = -2.54$, $P = 0.018$, Cohen's $d = 0.50$], whereas the Hum-Com2 task (i.e. involving shared goal) induced significantly higher IBS at CH7 [$t\,(25) = -2.52$, $P = 0.019$, Cohen's $d = 0.49$]. However, neither CH7 nor CH13 was observed after FDR correction. These findings suggest that the IBS at the right IFC is more sensitive to the joint action that involves complementary action.

The repeated-measures ANOVA was conducted to compare the differences between conditions (i.e. the Nonidentical, Hum-Com1 and Hum-Com2 tasks). The results revealed that there was a significant main effect at CH1 [$F = 4.69$, $P = 0.014$, $\eta^2 = 0.16$], CH2 [$F = 7.02$, $P = 0.002$, $\eta^2 = 0.22$], CH7 [$F = 7.95$, $P = 0.001$, $\eta^2 = 0.24$] and CH21 [$F = 3.39$, $P = 0.047$, $\eta^2 = 0.12$]. After FDR correction, only CH2 and CH7 survived. Then, CH2 and CH7 were further entered into post hoc tests. The results showed a significantly
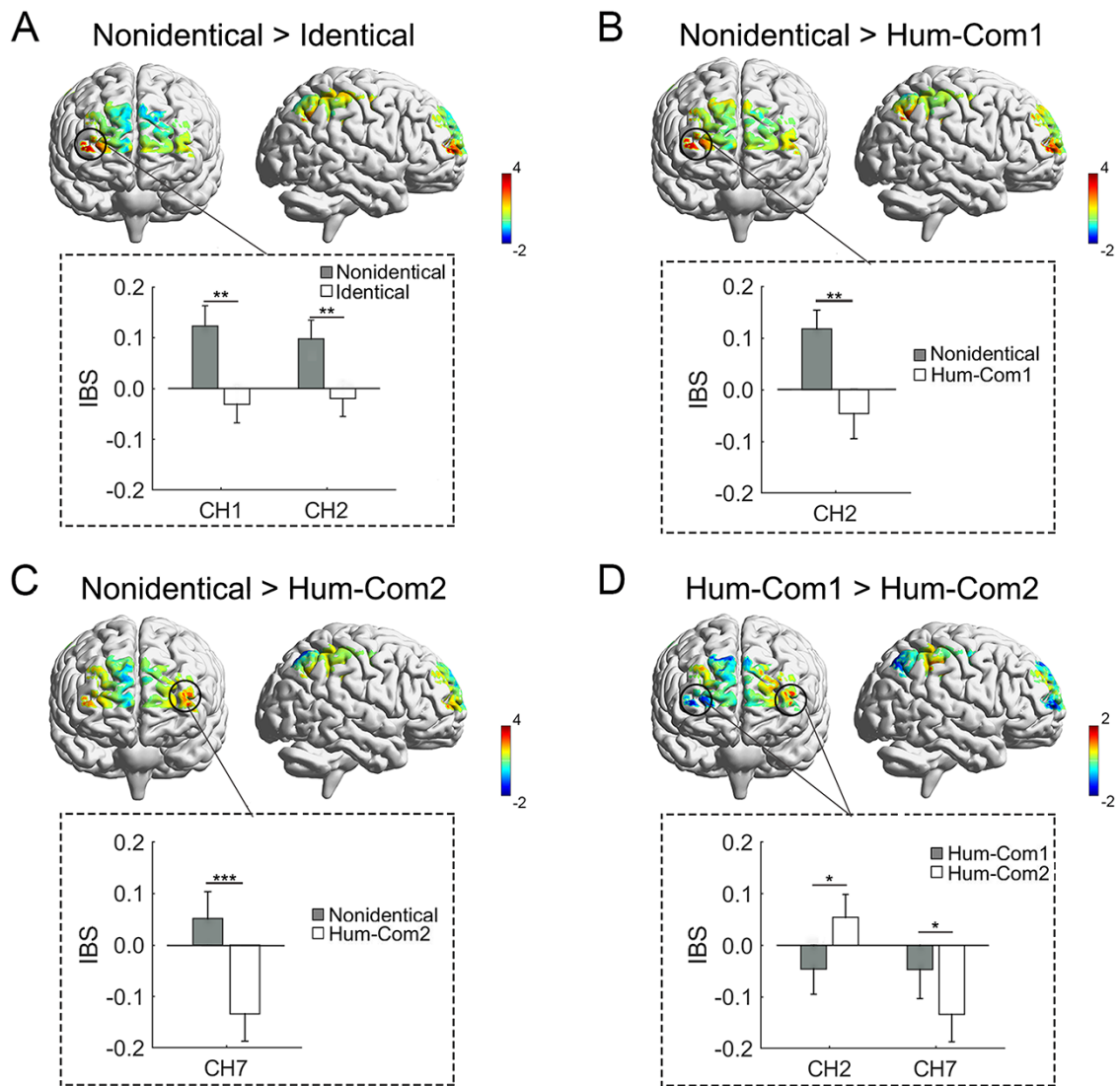
Fig. 3. Interbrain synchronization (IBS). (A) Comparison between the nonidentical-shape joint action (Nonidentical) task and the identical-shape joint action (Identical) task. A significantly higher IBS was found at CH1 and CH2 in the Nonidentical task. (B) Comparison between the Nonidentical task and the presumed human-computer (Hum-Com1) task. Significant higher IBS was found at CH2. (C) Comparison between the Nonidentical task and the turn-based human-computer (Hum-Com2) task. A significantly higher IBS was found at CH7. (D) Comparison between the Hum-Com1 task and the Hum-Com2 task. The Hum-Com1 task elicited higher IBS at CH7, while Hum-Com2 task elicited higher IBS at CH2. The brain image was visualized by BrainNet Viewer (Xia *et al.*, 2013). *$P < 0.01$, **$P < 0.01$, ***$P < 0.001$.

higher IBS at CH2 in the Nonidentical task compared to the Hum-Com1 task [$t(25) = 3.31$, $P = 0.003$, Cohen's $d = 0.65$] (Figure 3B). There was also a significantly higher IBS at CH7 in the Nonidentical task relative to the Hum-Com2 task [$t(25) = 4.10$, $P = 0.0004$, Cohen's $d = 0.80$] (Figure 3C). Moreover, compared to the Hum-Com2 task, the Hum-Com1 task elicited a decreased IBS at CH2 [$t(25) = -2.45$, $P = 0.021$, Cohen's $d = 0.48$], and an increased IBS at CH7 [$t(25) = 2.14$, $P = 0.043$, Cohen's $d = 0.42$] (Figure 3D). As mentioned above, CH2 was roughly located at the right IFC, while CH7 was roughly located at the left IFC. These findings suggest that the left IFC may be related to action coordination, while the right IFC may be associated with shared goal during joint action.

Discussion

In this study, we used the fNIRS hyperscanning approach to explore the neural couplings that entrain to shared goal and

action coordination in joint action. According to the accounts of cognitive psychology in joint action, the neural couplings that entrain to shared goal and action coordination should be different. Our results support this hypothesis as we found that the IBS in the right IFC entrains more to shared goal, while the IBS in the left IFC entrains more to action coordination.

We observed IBS during joint action, which echoes previous hyperscanning studies that joint action accompanies neural couplings between interacting individuals (Mu *et al.*, 2016; Muller *et al.*, 2019). The demonstrated IBS was located at the IFC, including both hemispheres. Such results are consistent with previous neuroimaging studies of joint action. It has been reported the brain activations at the bilateral IFC, while participants imagined doing a task together (Wriessnegger *et al.*, 2016). The activations of the bilateral IFC were also observed, while participants engaged in real-time gaze exchange in a joint attention task, although more prominently in the right hemisphere; moreover, there were

more prominent brain-to-brain correlations at the right IFC for paired participants than nonpaired participants (Saito *et al.*, 2010). In another case, compared to the face-to-wall condition, the right IFC showed an increased IBS when participants were singing or humming face-to-face with other people, while the left IFC showed an increase in IBS for a face-to-face humming (Osaka *et al.*, 2015). On the other hand, the IFC IBS has been found in various real-time social interactions, such as verbal communication between persons (Jiang *et al.*, 2012), unstructured game playing between persons (Li *et al.*, 2021), social learning between the instructor and learner (Pan *et al.*, 2018) and everyday joint activities between the parent and child (Azhari *et al.*, 2019).

We also revealed that there was IBS to shared goal and action coordination in joint action. These findings are in line with previous hyperscanning studies that, during social interaction, shared goal/action coordination is accompanied by the IBS (Tang *et al.*, 2016; Nozawa *et al.*, 2019). Specifically, the IBS at the right IFC entrained more to shared goal, but the IBS at the left IFC entrained more to action coordination. The former results are consistent with the previous findings that the right IFC is critical for the coding of intentions and goals during social cognition and interaction (Iacoboni *et al.*, 2005; Hamilton and Grafton, 2008; Canessa *et al.*, 2012). For example, increased activations in the right IFC were found when observing the action of others with extraordinary intentions compared to the ordinary action (de Lange *et al.*, 2008); interbrain correlations in the right IFC between normal persons during eye contact diminished between normal persons and people with autism (Tanabe *et al.*, 2012), who had deficits in understanding others' actions (Cattaneo *et al.*, 2007); interbrain correlations between the builder and competitor during a turn-based action were robust at the right IFC, implying that the competitor actively traced the builder's move to disturb the builder's goal (Liu *et al.*, 2015). For action coordination, our results are also in line with previous neuroimaging findings, in which the left IFC is involved in various aspects of motor processing, including the observation, imitation, imagery and learning of dynamic actions (Rizzolatti *et al.*, 1996; Gerardin *et al.*, 2000; Buccino *et al.*, 2001; Grezes and Decety, 2002). In a recent study, the bilateral IFC is more activated for both adults and children during action execution and interpersonal synchrony compared to action observation, while adults had greater cortical activation at left-hemispheric activation of IFC than right (Su *et al.*, 2020). Additionally, children with developmental coordination disorder, who have poor movement execution, showed decreased activation at the left IFC during performing hand movements compared to typically developing children (Zwicker *et al.*, 2010; Licari *et al.*, 2015). Together, our findings suggest that the IFC may play an important role in joint action, with distinct lateralization for sub-components of joint action.

The roles of the right and left IFC in this study are worth exploring further. As mentioned above, the IFC is believed to be a part of the human mirror neuron system, which is related to the processing of the actions and behaviors of others. However, previous research on the lateralization of mirror neuron system indicated that both the left and right IFC contributed to the processing of action observation and imitation although stronger in the hemisphere ipsilateral to the visual stimulus and response hand (Aziz-Zadeh *et al.*, 2006; Errante and Fogassi, 2021). It seems that the function of the IFC in the human mirror neuron system does not apply to explain our results of the lateralization of the IFC during joint action. In addition to the aforementioned function, the IFC is also linked with functions such as semantic and phonological processing, working memory, social empathy and movement

control (Liakakis *et al.*, 2011). In view of movement control, both the right and left IFC are related to response inhibition (Criaud and Boulinguez, 2013; Aron *et al.*, 2014). While the right IFC is generally associated with initiating stopping and interpreted as reprogramming action plans (Lenartowicz *et al.*, 2011), the left IFC is more specifically activated when controlled responses are required (Goghari and MacDonald, 2009), which applies to the present findings. For instance, a multimodal Magnetoencephalography/fMRI study, within 59 participants, reliably revealed that stopping response is initiated by the right IFC (Schaum *et al.*, 2021); an EEG study indicated the activation of the left IFC for successful response inhibition and switching (Serrien and Sovijärvi-Spapé, 2013). In addition, it has been proposed that the imagery of action together with others comprises the inhibiting of its real execution (Newman-Norlund *et al.*, 2007, 2008). Thus, it seems that the process of action planning, underlying shared goal of joint action, is vivid and accompanied by a stronger inhibition of its actual execution; action coordination may require the restraint of self's actions, i.e. successful implementation of inhibitory control over self's motor responses, to achieve the behavioral coordination with others.

Moreover, in line with previous findings, we observed the right IFC during complementary joint action compared to imitative joint action, with enhanced IBS at the right IFC in the former condition. Newman-Norlund *et al.* (2007) revealed significantly greater activation in the right IFC when preparing a complementary action than preparing an imitative action. Moreover, Newman-Norlund *et al.* (2008), in a continuous visuomotor balancing task, found that activation in the right IFC was associated with the extent to which participants were required to produce complementary responses. Here, we manipulated action congruency by asking participants to co-draw the same graphics or symmetrical graphics. Our results further confirm that the right IFC is sensitive to complementary joint action.

It seems surprising that we did not find a stabilizing role of the right TPJ in joint action in this study, given that the region is previously implicated in joint action (Newman-Norlund *et al.*, 2008; Humphreys and Bedford, 2011; Abe *et al.*, 2019; Chen *et al.*, 2020). Although it is difficult to interpret a null finding, it should be noted that participants in the current work were achieving an immediate goal (i.e. drawing together) in complementary action conditions. Neuroimaging studies suggest that inferring immediate goals (e.g. grasping a cookie) is related to the neural system for action understanding (e.g. the mirror neuron system), while the decoding of long-term intentions (e.g. grasping a cookie to eat it because she/he will skip dinner to complete a paper) is associated with the system subserving the attribution of mental states (e.g. the mentalizing system) (Canessa *et al.*, 2012; Arioli *et al.*, 2018). Future studies that compare different goals and intentions (i.e. immediate goals *vs* long-term intentions) could shed light on the functional roles of the right TPJ in joint action.

In this study, we designed four different drawing tasks to examine the neural couplings to shared goal and action coordination of joint action. For the Nonidentical and Identical tasks, there were both shared goal and action coordination; but the former referred to nonidentical (i.e. symmetrical) action, the latter concerned identical action. Thus, they corresponded to complementary and imitative joint action, respectively. Compared to the tasks above, the Hum-Com2 task did not involve action coordination, as participants were asked to in turn interact with the computer; whereas it had shared goal as participants had to complete the task together. For the Hum-Com1 task, there was no shared goal because participants were told that they had to

individually interact with the computer; but it involved action coordination since participants actually coordinated with each other as the displayed action feedback was from the partner. In this way, the two elements (i.e. shared goal and action coordination) of joint action were decomposed in this study. Notably, the Nonidentical, Hum-Com1 and Hum-Com2 tasks here were all associated with complementary action. Future studies could design the above tasks with imitative action to confirm the IBS to shared goal and action coordination in imitative joint action. In addition, frequency ratio can be included in future work by modulating the diagonal slopes of shapes since it was proved to be an important factor in our previous work (Cheng *et al.*, 2019).

One limitation of this work is that in our experimental task, participants could not see each other as they were blocked with the computer. However, face-to-face interactions are more ubiquitous in our real lives, with more social features (i.e. facial expressions, body language and social stance). Furthermore, previous hyperscanning studies have reported that there was increased IBS at the frontal cortex or right TPJ during face-to-face (*vs* non-face-to-face) interactions, including motor imitation (Miyata *et al.*, 2021), cooperative singing (Osaka *et al.*, 2015), verbal communication (Jiang *et al.*, 2012) and decision making (Tang *et al.*, 2016). It would be interesting to explore the neural couplings to shared goal and action coordination during face-to-face joint action in future studies.

In conclusion, we used an fNIRS hyperscanning approach to investigate neural couplings that entrain shared goal and action coordination in joint action. We observed that right-IFC IBS entrained more to shared goal, while left-IFC IBS entrained more to action coordination. We also observed that the IBS in the right IFC was greater during completing a complementary action than an imitative action joint action.

Acknowledgements

Funding

Conflict of interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

References

Abe, M.O., Koike, T., Okazaki, S., *et al.* (2019). Neural correlates of online cooperation during joint force production. *NeuroImage*, **191**, 150–61.

Ames, K., *et al.* (2006). Human friendship favours cooperation in the iterated prisoner's dilemma. *Behaviour.*, **143**(1), 1383–95.

Arioli, M., Perani, D., Cappa, S., *et al.* (2018). Affective and cooperative social interactions modulate effective connectivity within and between the mirror and mentalizing systems. *Human Brain Mapping*, **39**(3), 1412–27.

Aron, A.R., Robbins, T.W., Poldrack, R.A. (2014). Inhibition and the right inferior frontal cortex: one decade on. *Trends in Cognitive Sciences*, **18**(4), 177–85.

Arueti, M., Perach-Barzilay, N., Tsoory, M.M., Berger, B., Getter, N., Shamay-Tsoory, S.G. (2013). When two become one: the role of oxytocin in interpersonal coordination and cooperation. *Journal of Cognitive Neuroscience*, **25**(9), 1418–27.

Azhari, A., Leck, W.Q., Gabrieli, G., *et al.* (2019). Parenting stress undermines mother-child brain-to-brain synchrony: a hyperscanning study. *Scientific Reports*, **9**(1), 11407.

Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *Journal of Neuroscience*, **26**(11), 2964–70.

Buccino, G., Binkofski, F., Fink, G.R., *et al.* (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, **13**(2), 400–4.

Canessa, N., Alemanno, F., Riva, F., *et al.* (2012). The neural bases of social intention understanding: the role of interaction goals. *PLoS One*, **7**(7), e42347.

Cattaneo, L., Fabbri-Destro, M., Boria, S., *et al.* (2007). Impairment of actions chains in autism and its possible role in intention understanding. *Proceedings of the National Academy of Sciences*, **104**(45), 17825–30.

Chen, Y., Zhang, Q., Yuan, S., Zhao, B., Zhang, P., Bai, X. (2020). The influence of prior intention on joint action: an fNIRS-based hyperscanning study. *Social Cognitive and Affective Neuroscience*, **15**(12), 1351–60.

Cheng, X., Li, X., Hu, Y. (2015). Synchronous brain activity during cooperative exchange depends on gender of partner: a fNIRS-based hyperscanning study. *Human Brain Mapping*, **36**(6), 2039–48.

Cheng, X., Pan, Y., Hu, Y., Hu, Y. (2019). Coordination elicits synchronous brain activity between co-actors: frequency ratio matters. *Frontiers in Neuroscience*, **13**, 1071.

Criaud, M., Boulinguez, P. (2013). Have we been asking the right questions when assessing response inhibition in go/no-go tasks with fMRI? A meta-analysis and critical review. *Neuroscience and Biobehavioral Reviews*, **37**(1), 11–23.

Cui, X., Bray, S., Reiss, A.L. (2010). Functional near infrared spectroscopy (NIRS) signal improvement based on negative correlation between oxygenated and deoxygenated hemoglobin dynamics. *NeuroImage*, **49**(4), 3039–46.

de Lange, F.P., Spronk, M., Willems, R.M., Toni, I., Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current Biology*, **18**(6), 454–7.

Duan, L., Dai, R.N., Xiao, X., Sun, P.P., Li, Z., Zhu, C.Z. (2015). Cluster imaging of multi-brain networks (CIMBN): a general framework for hyperscanning and modeling a group of interacting brains. *Frontiers in Neuroscience*, **9**, 267.

Duan, L., Zhao, Z., Lin, Y., Wu, X., Luo, Y., Xu, P. (2018). Wavelet-based method for removing global physiological noise in functional near-infrared spectroscopy. *Biomedical Optics Express*, **9**(8), 3805–20.

Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., Garnero, L. (2010). Inter-brain synchronization during social interaction. *PLoS One*, **5**(8), e12166.

Egetemeir, J., Stenneken, P., Koehler, S., Fallgatter, A.J., Herrmann, M.J. (2011). Exploring the neural basis of real-life joint action: measuring brain activation during joint table setting with functional near-infrared spectroscopy. *Frontiers in Human Neuroscience*, **5**, 95.

Errante, A., Fogassi, L. (2021). Functional lateralization of the mirror neuron system in monkey and humans. *Symmetry*, **13**(1), 77.

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. *Journal of Biomedical Optics*, **16**(7), 077011.

Gerardin, E., Sirigu, A., Lehéricy, S., *et al.* (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex*, **10**(11), 1093–104.

Goghari, V.M., MacDonald, A.W., III (2009). The neural basis of cognitive control: response selection and inhibition. *Brain and Cognition*, **71**(2), 72–83.

Gooijers, J., Caeyenberghs, K., Sisti, H.M., *et al.* (2013). Diffusion tensor imaging metrics of the corpus callosum in relation to bimanual coordination: effect of task complexity and sensory feedback. *Human Brain Mapping*, **34**(1), 241–52.

Grezes, J., Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, **40**(2), 212–22.

Hamilton, A.F.D.C., Grafton, S.T. (2008). Action outcomes are represented in human inferior frontoparietal cortex. *Cerebral Cortex*, **18**(5), 1160–8.

Holper, L., Scholkmann, F., Wolf, M. (2012). Between-brain connectivity during imitation measured by fNIRS. *NeuroImage*, **63**(1), 212–22.

Hoshi, Y. (2003). Functional near-infrared optical imaging: utility and limitations in human brain mapping. *Psychophysiology*, **40**(4), 511–20.

Hu, Y., Hu, Y., Li, X., Pan, Y., Cheng, X. (2017). Brain-to-brain synchronization across two persons predicts mutual prosociality. *Social Cognitive and Affective Neuroscience*, **12**(12), 1835–44.

Humphreys, G.W., Bedford, J. (2011). The relations between joint action and theory of mind: a neuropsychological analysis. *Experimental Brain Research*, **211**(3-4), 357–69.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, **3**(3), e79.

Ikeda, S., Nozawa, T., Yokoyama, R., *et al.* (2017). Steady beat sound facilitates both coordinated group walking and inter-subject neural synchrony. *Frontiers in Human Neuroscience*, **11**, 147.

Jiang, J., Dai, B., Peng, D., Zhu, C., Liu, L., Lu, C. (2012). Neural synchronization during face-to-face communication. *Journal of Neuroscience*, **32**(45), 16064–9.

Jurcak, V., Tsuzuki, D., Dan, I. (2007). 10/20, 10/10, and 10/5 systems revisited: their validity as relative head-surface-based positioning systems. *NeuroImage*, **34**(4), 1600–11.

Kingsbury, L., Hong, W. (2020). A multi-brain framework for social interaction. *Trends in Neurosciences*, **43**(9), 651–66.

Kirilina, E., Jelzow, A., Heine, A., *et al.* (2012). The physiological origin of task-evoked systemic artefacts in functional near infrared spectroscopy. *NeuroImage*, **61**(1), 70–81.

Knoblich, G., Butterfill, S., Sebanz, N. (2011). Psychological research on joint action: theory and data. *Psychology of Learning and Motivation*, **54**, 59–101.

Koessler, L., Maillard, L., Benhadid, A., *et al.* (2009). Automated cortical projection of EEG sensors: anatomical correlation via the international 10–10 system. *NeuroImage*, **46**(1), 64–72.

Konvalinka, I., Vuust, P., Roepstorff, A., Frith, C.D. (2010). Follow you, follow me: continuous mutual prediction and adaptation in joint tapping. *Quarterly Journal of Experimental Psychology*, **63**(11), 2220–30.

Konvalinka, I., Bauer, M., Stahlhut, C., Hansen, L.K., Roepstorff, A., Frith, C.D. (2014). Frontal alpha oscillations distinguish leaders from followers: multivariate decoding of mutually interacting brains. *NeuroImage*, **94**, 79–88.

Kourtis, D., Woźniak, M., Sebanz, N., Knoblich, G. (2019). Evidence for we-representations during joint action planning. *Neuropsychologia*, **131**, 73–83.

Lenartowicz, A., Verbruggen, F., Logan, G.D., Poldrack, R.A. (2011). Inhibition-related activation in the right inferior frontal gyrus in the absence of inhibitory cues. *Journal of Cognitive Neuroscience*, **23**(11), 3388–99.

Li, Y., Chen, R., Turel, O., Feng, T., Zhu, C.-Z., He, Q. (2021). Dyad sex composition effect on inter-brain synchronization in face-to-face cooperation. *Brain Imaging and Behavior*, **15**, 1667–75.

Liakakis, G., Nickel, J., Seitz, R.J. (2011). Diversity of the inferior frontal gyrus—a meta-analysis of neuroimaging studies. *Behavioural Brain Research*, **225**(1), 341–7.

Licari, M.K., Billington, J., Reid, S.L., *et al.* (2015). Cortical functioning in children with developmental coordination disorder: a motor overflow study. *Experimental Brain Research*, **233**(6), 1703–10.

Liu, T., Saito, H., Oi, M. (2015). Role of the right inferior frontal gyrus in turn-based cooperation and competition: a near-infrared spectroscopy study. *Brain and Cognition*, **99**, 17–23.

Liu, T., Duan, L., Dai, R., Pelowski, M., Zhu, C. (2021). Team-work, Team-brain: exploring synchrony and team interdependence in a nine-person drumming task via multiparticipant hyperscanning and inter-brain network topology with fNIRS. *NeuroImage*, **237**, 118147.

Loehr, J.D., Kourtis, D., Vesper, C., Sebanz, N., Knoblich, G. (2013). Monitoring individual and joint action outcomes in duet music performance. *Journal of Cognitive Neuroscience*, **25**(7), 1049–61.

Miyata, K., Koike, T., Nakagawa, E., *et al.* (2021). Neural substrates for sharing intention in action during face-to-face imitation. *NeuroImage*, **233**, 117916.

Montague, P.R., Berns, G.S., Cohen, J.D., *et al.* (2002). Hyperscanning: simultaneous fMRI during linked social interactions. *NeuroImage*, **16**(4), 1159–64.

Mu, Y., Guo, C., Han, S. (2016). Oxytocin enhances inter-brain synchrony during social coordination in male adults. *Social Cognitive and Affective Neuroscience*, **11**(12), 1882–93.

Muller, V., Sanger, J., Lindenberger, U. (2013). Intra- and inter-brain synchronization during musical improvisation on the guitar. *PLoS One*, **8**(9), e73852.

Muller, V., Delius, J.A.M., Lindenberger, U. (2019). Hyper-frequency network topology changes during choral singing. *Frontiers in Physiology*, **10**, 207.

Newman-Norlund, R.D., van Schie, H.T., van Zuijlen, A.M., Bekkering, H. (2007). The mirror neuron system is more active during complementary compared with imitative action. *Nature Neuroscience*, **10**(7), 817–8.

Newman-Norlund, R.D., Bosga, J., Meulenbroek, R.G., Bekkering, H. (2008). Anatomical substrates of cooperative joint-action in a continuous motor task: virtual lifting and balancing. *NeuroImage*, **41**(1), 169–77.

Nozawa, T., Sakaki, K., Ikeda, S., *et al.* (2019). Prior physical synchrony enhances rapport and inter-brain synchronization during subsequent educational communication. *Scientific Reports*, **9**(1), 12747.

Osaka, N., Minamoto, T., Yaoi, K., Azuma, M., Shimada, Y.M., Osaka, M. (2015). How two brains make one synchronized mind in the inferior frontal cortex: fNIRS-based hyperscanning during cooperative singing. *Frontiers in Psychology*, **6**, 1811.

Pan, Y., Novembre, G., Song, B., Li, X., Hu, Y. (2018). Interpersonal synchronization of inferior frontal cortices tracks social interactive learning of a song. *NeuroImage*, **183**, 280–90.

Pezzulo, G., Iodice, P., Ferraina, S., Kessler, K. (2013). Shared action spaces: a basis function framework for social re-calibration of sensorimotor representations supporting joint action. *Frontiers in Human Neuroscience*, **7**, 800.

Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, **3**(2), 131–41.

Rizzolatti, G., Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, **27**, 169–92.

Sacheli, L.M., Candidi, M., Era, V., Aglioti, S.M. (2015). Causative role of left aIPS in coding shared goals during human-avatar complementary joint actions. *Nature Communications*, **6**, 7544.

Saito, D.N., Tanabe, H.C., Izuma, K., *et al.* (2010). "Stay tuned": interindividual neural synchronization during mutual gaze and joint attention. *Frontiers in Integrative Neuroscience*, **4**, 127.

Sanger, J., Muller, V., Lindenberger, U. (2012). Intra- and interbrain synchronization and network properties when playing guitar in duets. *Frontiers in Human Neuroscience*, **6**, 312.

Schaum, M., Pinzuti, E., Sebastian, A., *et al.* (2021). Right inferior frontal gyrus implements motor inhibitory control via beta-band oscillations in humans. *Elife*, **10**, e61679.

Schmitz, L., Vesper, C., Sebanz, N., Knoblich, G. (2017). Co-representation of others' task constraints in joint action. *Journal of Experimental Psychology. Human Perception and Performance*, **43**(8), 1480.

Sebanz, N., Bekkering, H., Knoblich, G. (2006). Joint action: bodies and minds moving together. *Trends in Cognitive Sciences*, **10**(2), 70–6.

Serrien, D.J., Sovijärvi-Spapé, M.M. (2013). Cognitive control of response inhibition and switching: hemispheric lateralization and hand preference. *Brain and Cognition*, **82**(3), 283–90.

Strangman, G., Boas, D.A., Sutton, J.P. (2002). Non-invasive neuroimaging using near-infrared light. *Biological Psychiatry*, **52**(7), 679–93.

Su, W.C., Culotta, M.L., Hoffman, M.D., *et al.* (2020). Developmental differences in cortical activation during action observation, action execution and interpersonal synchrony: an fNIRS study. *Frontiers in Human Neuroscience*, **14**, 57.

Tanabe, H.C., Kosaka, H., Saito, D.N., *et al.* (2012). Hard to "tune in": neural mechanisms of live face-to-face interaction with high-functioning autistic spectrum disorder. *Frontiers in Human Neuroscience*, **6**, 268.

Tang, H., Mai, X., Wang, S., Zhu, C., Krueger, F., Liu, C. (2016). Interpersonal brain synchronization in the right temporo-parietal junction during face-to-face economic exchange. *Social Cognitive and Affective Neuroscience*, **11**(1), 23–32.

Wolf, T., Sebanz, N., Knoblich, G. (2018). Joint action coordination in expert-novice pairs: can experts predict novices' suboptimal timing? *Cognition*, **178**, 103–8.

Wriessnegger, S.C., Steyrl, D., Koschutnig, K., Muller-Putz, G.R. (2016). Cooperation in mind: motor imagery of joint and single actions is represented in different brain areas. *Brain and Cognition*, **109**, 19–25.

Xia, M., Wang, J., Yong, H., Peter, C. (2013). Brainnet viewer: a network visualization tool for human brain connectomics. *PLos One*, **8**(7), e68910.

Yun, K., Watanabe, K., Shimojo, S. (2012). Interpersonal body and neural synchronization as a marker of implicit social interaction. *Scientific Reports*, **2**(1), 959.

Zhang, Y., Meng, T., Hou, Y., Pan, Y., Hu, Y. (2018). Interpersonal brain synchronization associated with working alliance during psychological counseling. *Psychiatry Research: NeuroImaging*, **282**, 103–9.

Zwicker, J.G., Missiuna, C., Harris, S.R., Boyd, L.A. (2010). Brain activation of children with developmental coordination disorder is different than peers. *Pediatrics*, **126**(3), e678–86.