

doi: 10.1093/scan/nsy060

Advance Access Publication Date: 6 August 2018 Original article

Putting our heads together: interpersonal neural synchronization as a biological mechanism for shared intentionality

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Abstract

Shared intentionality, or collaborative interactions in which individuals have a shared goal and must coordinate their efforts, is a core component of human interaction. However, the biological bases of shared intentionality and, specifically, the processes by which the brain adjusts to the sharing of common goals, remain largely unknown. Using functional near infrared spectroscopy (fNIRS), coordination of cerebral hemodynamic activation was found in subject pairs when completing a puzzle together in contrast to a condition in which subjects completed identical but individual puzzles (same intention without shared intentionality). Interpersonal neural coordination was also greater when completing a puzzle together compared to two control conditions including the observation of another pair completing the same puzzle task or watching a movie with a partner (shared experience). Further, permutation testing revealed that the time course of neural activation of one subject predicted that of their partner, but not that of others completing the identical puzzle in different partner sets. Results indicate unique brain-to-brain coupling specific to shared intentionality beyond what has been previously found by investigating the fundamentals of social exchange.

Key words: functional near infrared spectroscopy (fNIRS); interagency; intention; pre-frontal cortex; hyperscanning

Introduction

Human beings possess an extraordinary ability to coordinate their actions with those of others. This ability, termed 'shared intentionality' refers to collaborative interactions in which individuals have a mutual goal and coordinated action roles for its pursuit (Searle, 1983). During shared intentionality, two or more individuals synchronize their actions in space and time

to instigate change in their environment, a complex skill that depends on the abilities to share representations, predict actions and integrate predicted actions of others (Sebanz et al., 2006). Bratman (1992) notes that shared intentionality requires three common features, which are mutual responsiveness, commitment to the joint activity and mutual support for the role of each partner. Others propose that the additional sense of 'interagency' allows for a feeling of cohesive accomplishment (Searle,

Received: 2 May 2018; Revised: 11 July 2018; Accepted: 16 July 2018

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1980; Crivelli & Balconi, 2010; Obhi & Hall, 2011). While some aspects of collaborative social interaction are found in primates [e.g. basic intention understanding (Call et al., 2004), rudimentary theory of mind (Hare et al., 2000), cooperative group hunting (Boesch, 1994)], a synthesis of the literature concludes that humans are motivated to higher degrees than other species to share emotions, experiences and activities with others of their own kind (Tomasello et al., 2005).

The foundations of shared intentionality develop early, incrementally maturing in complexity to reach the multi-faceted nature of intricate adult social interactions. This protracted developmental trajectory points to the integral nature of this construct among humans. The fundamentals of shared intentionality are apparent during the first months of life when human infants demonstrate mutual and synchronous responsiveness during face-to-face interaction with caregivers (Trevarthen, 1979). Between 9-12 months this skill develops more features of shared intentionality as both parties of the interaction are able to direct their attention and actions towards a third person or object (Ross & Lollis, 1987), with active engagement led by the infant reaching maturational peak before 15 months of age (Bakeman & Adamson, 1984). Findings from the adult social interaction literature note that humans have a natural tendency to unintentionally coordinate their motor behavior with others with whom they are working on a task and that this synchronization facilitates the smoothness of interaction, liking and rapport between interaction partners (Chartrand & Bargh, 1999). Studies designed to experimentally facilitate or hinder behavioral synchronization have found that increased synchronization correlates with more positive feelings about the interaction, a sense of connectedness with an interaction partner and increased perception of unity by thirdparty individuals (Marsh et al., 2009). Further support for the role that synchronization plays in general human society comes from studies finding that individuals who coordinate actions with their partners tend to be more empathic and pro-social and that this synchronization enhances altruistic behavior and cooperation during shared intentionality (Chartrand & Bargh, 1999).

Although attention has been paid to the behavioral aspects of shared intentionality (Marsh et al., 2009), as well as its hypothesized role in shaping of human societal institutions (Tomasello et al., 2005), the mechanism in which an individual brain might adjust to goal-sharing beyond the already demanding neural processes involved in the pursuit of a complex objective is a question under ongoing investigation (Sebanz et al., 2006). Previous research has investigated the brain bases of the relevant building blocks of shared intentionality, such as biological motion perception (Bonda et al., 1996), eye contact (Pelphrey et al., 2004), and theory of mind/mentalizing (Saxe & Kanwisher, 2003), localizing a portion of its circuitry to the medial and lateral pre-frontal cortex (PFC) and temporal regions (Van Overwalle, 2009). One study by Pfeiffer et al., (2014) incorporated those basic building blocks into a controlled interaction in which participants perceived an avatar to either be controlled by a person or a computer program. The perception of social interaction with a human partner produced activation in reward-related circuitry including the striatum and portions of the PFC. However, despite these studies demonstrating the central role of social interaction in shaping cognition, most have focused on the neural underpinnings of the isolated individual rather than on the synchronization of neural activation between partners during interaction. Some studies have noted inter-individual coupling of activation patterns during storytelling (Stephens et al., 2010; Liu et al., 2017), gesture (Schippers et al., 2010), facial expression (Anders et al., 2011), and film viewing (Hasson et al., 2004); however, brain activation data were collected individually while simulating social interaction in an experimental context (e.g. viewing videos of the social partner).

This focus on the individual brain while probing the underlying neural systems involved in inherently social processes has led to a recent call for a field shift away from 'isolation paradigms' (Becchio et al., 2010) and towards 'second-person neuroscience' in which the cerebral underpinnings of social cognition are fundamentally different when a person is involved in, vs merely observing and social interaction (Schilbach et al., 2013). Since hyperscanning (i.e. measuring the activation of interacting brains simultaneously) was first introduced (Montague et al., 2002), a variety of paradigms has been employed to assess interpersonal brain synchrony using fMRI (functional magnetic resonance imaging), EEG (electroencephalography) and fNIRS (functional near-infrared spectroscopy). These paradigms have included directed imitation of hand gestures (Dumas et al., 2010), directed eye gaze in a joint attention task (Saito et al., 2010), coordination of response time (Cui et al., 2012; Hu et al., 2017), cooperative singing (Osaka et al., 2015) and playing Jenga (Liu et al., 2016). Findings from these studies have routinely implicated multiple regions of the PFC in interpersonal neural synchronization during social interaction. Other studies have produced similar findings when social discourse is unrestrained (Jiang et al., 2012, 2015) or even outside of the typical laboratory context (Lindenberger et al., 2009; Dikker et al., 2017;). While the previously cited studies have provided ground breaking evidence of inter-brain synchronization during multiple levels of general social interaction and experimenterdirected simple cooperation, it remains unclear how the brains of multiple individuals might coordinate during more complex and unconstrained problem-solving.

Our goal in the current study was to conduct a wellcontrolled investigation of interpersonal PFC synchrony during shared intentionality, using a simple yet challenging problemsolving task. We monitored the lateral PFC of trios of subjects simultaneously, during an interactive task with three control conditions designed to simulate similar audiovisual conditions without shared intentionality. While the medial PFC and temporoparietal junction (TPJ) have also been implicated in social cognition, we chose to image only the lateral PFC as there were only a limited number of channels to be divided among the three subjects, and the lateral PFC is known to yield high-quality fNIRS data. We hypothesized that inter-individual synchronization would be greater during shared intentionality than while individuals either worked on identical tasks but did not share intention or observed others completing a similar task.

Materials and methods

Subjects

Twenty triads of adult subjects (n = 60 individuals) were included in the experiment. Subjects were asked to participate in the experiment with two companions of their choice, provided that none of the group of three was in a romantic or family relationship (e.g. friends, colleagues). We chose to limit the groups to non-family or romantic relationships in order to limit the range of intimacy of the sample as much as possible. Subjects selfidentified as 63% Caucasian, 7% African-American, 28% Asian, and 2% Biracial (mean age = 19.73, s.d. = 1.02, range 18-22 years). All were currently enrolled in college. Thirty-seven females and 23 males participated. Eleven triads consisted of all females,

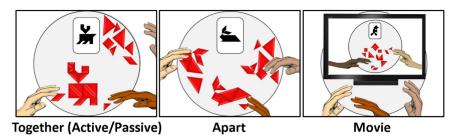


Fig. 1. Visual representation of the Tangram puzzle task. Subjects were asked to complete a single puzzle working as a dyad in the 'together active' condition but were asked to complete the same puzzle while working individually in the 'apart' condition. In order to control for equal sensory input across subjects and conditions, subjects observed an unknown pair completing a puzzle as a dyad on a video screen in the 'movie' condition or observed their remaining two companions complete the puzzle in the 'together passive' condition.

5 triads consisted of all males and 4 triads contained both males and females. Subjects reported no use of psychotropic medications. Data were collected, but not analyzed, for a single triad due to equipment error, leaving a final sample of 19 triads (57 individuals).

Task procedure

Throughout the testing session, subjects completed Tangrams, which are dissection puzzles consisting of flat geometric shapes put together to form larger shapes (an object or animal), presented on a card. The objective of the task was to quickly form the larger shape, given only its silhouette, in a 2 min period. Tangrams are quite challenging and require advanced spatial and geometric skills. Before testing, subjects were familiarized with the concept and history of Tangrams and given time to practice a single puzzle both alone and with a partner.

All three subjects were seated at a round table. Our goal was to create one experimental condition in which subjects completed a task that encouraged shared intentionality and a second experimental condition in which the subjects completed the same task but were discouraged from the sharing of intention. We operationalized shared intentionality as joint attention to the stimulus with a mutual goal of problem-solving through interaction. Thus, subjects were asked to complete Tangram puzzles in cooperation with a partner during the 'together active' condition and individually during the 'apart' condition. All conditions contained a single puzzle card and 21 geometric shapes in the viewing area of all subjects; Seven pieces are assigned to each subject (Figure 1). In the 'together active' condition, two subjects were allowed to freely interact in order to complete the puzzle using their combined 14 pieces. Although they were not prevented from eye contact or gesture, this was rare given that subjects were seated directly next to each other in order to view the puzzle from the same perspective. Instead, participants mostly focused on the puzzle and communicated verbally while moving pieces. The third member of the triad silently watched the interaction without participation ('together passive' condition, see below). His/her seven puzzle pieces remained on the table but sat untouched.

In the 'apart' condition, all three subjects were given the exact same puzzle to work on at the exact same time but were told to complete the Tangram without interacting with their companions, each using his/her own 7 puzzle pieces. It was stressed that they were not in competition with each other. This allowed for conditions in which intentionality was equal, but shared intentionality (joint attention, mutual problem-solving and social interaction) differed. Puzzles used in the 'apart' condition required the standard seven geometric shapes (two

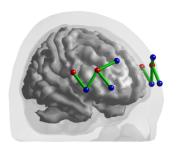
large right triangles, one medium-sized right triangle, two small right triangles, one small square and one parallelogram). Puzzles used in the 'together active' and 'together passive' conditions required two sets of Tangrams (14 geometric shapes), making these puzzles approximately twice as difficult as the 'apart' puzzles. We designed this task to be quite difficult to ensure that subjects spent as much of the full 2 min as possible engaged on the task rather than terminating joint/individual attention once a puzzle was completed. Subjects were given two backup cards and were told to flip the next card over and move on to the next puzzle in the event that they completed the Tangram before the 2 min period ended.

Two additional conditions were designed to control for the possibility that observed synchronous hemodynamic activation was due to shared sensory input rather than shared intentionality. In the 'movie' condition, the card and puzzle pieces were removed from the table. Subjects were directed to a movie screen sitting directly in front of the table in which they watched an unknown pair complete a 14-piece puzzle (equivalent to the 'together active/passive' conditions). Subjects were able to view the hands and hear the voices of the unknown pair to mimic the manner in which they would see and hear their own hands and voices during the 'together active' condition. The pair in the video contained one male and one female, one light-skinned and one dark-skinned, in order for the subjects to be able to distinguish the voices and hands of the pair. The pair in the video did not complete a single puzzle but worked on it for the duration of each movie. In the 'together passive' condition, interpersonal neural synchronization was measured between the passive participant and each of the two active participants in the 'together active' condition.

All task blocks lasted for 2 min in duration with 45 s between each period to get situated (clear puzzles, prepare for next trial, etc.). Subjects completed three task blocks for each of the four conditions (movie, apart and together), for a total of 32 min and 15 s of data collection. The sequence of conditions was counterbalanced across triads. For the 'together' conditions, the experimenter assigned which two subjects would participate while the other watched, rotating between all three possibilities. Twenty-seven percent of total puzzles were completed (15% for 'together active' trials and 23% for 'apart' trials). No individual subjects or pairs of subjects were able to complete both the original and all backup puzzles during the 2 min period.

fNIRS Data Collection

Non-invasive optical imaging was performed using a continuouswave CW6 fNIRS system (TechEn Inc, Milford, MA). Light was emitted at 690 nm and 830 nm from a total of 12 sources



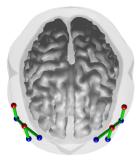


Fig. 2. Probe rendering on 3D brain. Renderings of the fNIRS probe superimposed on the right hemisphere (left) and dorsal (right) views of the Colin27 brain template. The red points represent sources, the blue points are detectors and the green lines are measurement channels.

and measured from 18 detectors, which were divided evenly between the subjects in each triad. Sensors were mounted onto a neoprene head cap, with a source-detector distance of 2.9-3.1 cm. The probe extended over the inferior frontal gyrus and middle frontal gyrus of each hemisphere of the PFC (Figure 2). The optical data were collected at 20 Hz.

Preprocessing

Raw fNIRS intensity signals were first converted to changes in optical density. The data were then corrected for motion artifacts by calculating the temporal derivative and iteratively reweighting the values using Tukey's bisquare function until the observation weights stabilized. This effectively reduces the magnitude of large fluctuations (i.e. motion) in the signal, while leaving small fluctuations (i.e. hemodynamics) intact. A manuscript detailing this method is currently under review. Signals were then resampled to 4 Hz and converted to oxygenated hemoglobin concentration using the modified Beer-Lambert relationship with a differential pathlength factor of six and a partial volume correction of 60 for both the 690 nm and 830 nm wavelengths.

Quantification of interpersonal neural synchronization

Data from the 19 triads of participants were divided pairwise into three dyads each (n = 57) for analysis of interpersonal synchronization. In other words, a triad containing subjects A, B and C, was split into dyadic synchrony calculations for A-B, B-C and C-A. This was necessary given that 'together' blocks were 'active' for two subjects and 'passive' for the other, prohibiting a common condition label for the entire triad.

Previous research from our group has shown that serial correlations in time series data can artificially inflate estimates of functional connectivity resulting from either Pearson correlation or wavelet transform coherence (Santosa et al., 2017). However, the false discovery rate can be controlled by calculating the robust correlation coefficient of the temporally whitened signals. Specifically, this was accomplished by fitting an autoregressive model to each signal, with the model order selected using the Bayesian Information Criterion. In Santosa et al., (2017), a maximum model order of 10–20 was found to be necessary to properly whiten fNIRS signals. We chose a conservative maximal model order of 32 to be certain that the signals were whitened. The new information introduced to the autoregressive model at each time point, also known as the innovations, were taken as the temporally whitened version of the signal for connectivity analysis.

The robust correlation coefficients were calculated between each pair of channels between participants using the robust regression approach, in which the geometric mean is taken of the robust regression coefficients obtained from regressing channel X onto channel Y and vice versa, e.g. $r = \sqrt{\hat{\beta}_{X \to Y} \hat{\beta}_{Y \to X}}$. Synchronization was then quantified using the Fisher z-transformation of the absolute value of the robust correlation coefficient.

Owing to the balanced nature of the design (e.g. each participant performed all conditions/roles), the position of each subject within the connectivity model was arbitrary. Therefore, any asymmetries in connectivity would not be interpretable (e.g. the presence of connectivity between the channel X of subject A to channel Y of subject B but not vice versa has no clear meaning). For this reason, symmetry was imposed such that the correlation between channel X of subject A and channel Y of subject B was made equal to the correlation between channel Y of subject A and channel X of subject B. This was done by taking the mean of the z-value, e.g. $Z_{XY} = \frac{1}{2} (Z_{X_AY_B} + Z_{X_BY_A})$. Symmetrized z-transformed connectivity matrices for each task block were then averaged to produce the mean connectivity for each condition within each dyad.

For visualization of data quality, we have provided a sample 1 min time series of the 'together active' and 'apart' conditions, taken from the same channel-pair and dyad (Figure 3). To aid in visualization, these time series were band-pass filtered with cutoffs at 0.01 Hz and 1.5 Hz and were not whitened. The shaded region represents the differences between the pairs of time series. In this figure, more synchrony can be seen in the 'together active' condition than in the 'apart' condition.

Statistical analysis

Group-level effects were analyzed for each channel-pair by submitting the connectivity values to a linear mixed effects model with condition ('Together Active', 'Together Passive', 'Apart' and 'Movie') as a fixed effect and subject dyad as a random effect. The 'Fixation' condition was not analyzed as it was deemed to serve more as a preparatory period than natural rest. The effect of each condition and each of the pairwise contrasts was assessed by applying the corresponding t-contrasts.

To determine the appropriate null hypotheses for the contrasts of interest, a parametric permutation test was used to estimate a null distribution for each contrast at each channelpair. This was done by performing the entire first- and secondlevel analysis 10 000 times on random non-concurrent sets of dyads (i.e. subjects from different scanning sessions). For each channel-pair and contrast, the null hypothesis was calculated as the contrast beta averaged across all 10 000 random permutations. The null hypothesis beta values were then supplied during the calculation of the t-contrasts on the observed data, e.g. $t = \frac{C^T(\widehat{\beta} - \beta_0)}{\sqrt{}}$ $\sqrt{\text{var}(C^T \hat{\beta})}$

Correction for multiple comparisons was performed by calculating the Benjamini-Hochberg false discovery rate (FDR)corrected p-value (Benjamini & Hochberg, 1995) (denoted throughout as 'q-value') across all unique channel-pairs and contrasts within each hypothesis family.

Results

Differences in inter-subject connectivity during shared intentionality

The estimated coefficients of the inter-subject connectivity networks for the 'together active', 'together passive', 'apart'

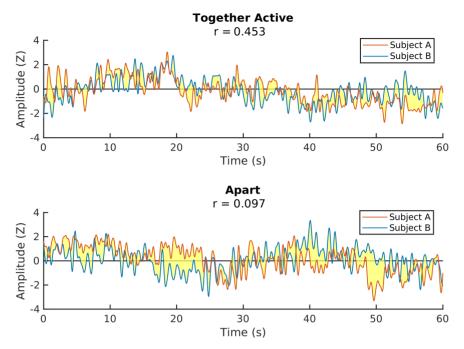


Fig. 3. Sample fNIRS signals. Normalized signals recorded from two subjects are shown, taken from the 'together active' (top) and 'apart' (bottom) conditions. Differences between each pair of signals are shaded. Synchronization is observed only in the 'together active' condition.

and 'movie' conditions relative to the null distribution derived from permutation testing are shown in Figure 4. Comparisons between 'together active' and each of the other conditions are shown in Figure 5. The 'together active' condition was found to have greater interpersonal neural synchronization than the 'movie' [peak connection: t(224) = 4.72, q < 0.001], 'apart' [peak connection: t(224) = 3.58, q < 0.05] and 'together passive' [peak connection: t(224) = 3.63, q < 0.05] conditions. We note that none of the control conditions ('movie, 'apart', 'together passive') had significant differences in interpersonal neural synchronization when compared to each other.

In Figure 6, we present the results of our permutation analyses for the peak connection for visualizations purposes, including the probability density function for the null distribution in reference to the observed values for each condition. Since the null distribution was computed independently for each condition, the results were transformed into the standard normal distribution for comparison. This was accomplished by subtracting the null mean and dividing by the null standard deviation $(Z = \frac{\beta - \mu_0}{\sigma_0})$, within each condition. Once the observed and null values were standardized, the null distribution was pooled across conditions for visualization. The range of values that are beyond the tail of the null distribution at q < 0.05 is shown as the shaded regions.

For posterity, a post hoc power analysis was conducted on the mean synchrony values for the 'Together Active' condition. In order for a two-tailed one-sample t-test against the permutation-derived null distribution to have a power of 0.90 with a significance level of p < 0.05, a sample size of N = 13 dyads is required.

Discussion

The current study examined the neural mechanistic features of shared intentionality. Our results uncovered a significant increase in interpersonal neural synchronization between the PFCs of individuals when the pair was engaged in action towards a mutually held goal. In contrast, when individuals were separated and engaged in identical, but individualistic, goaldirected action, or observing others complete that action, both by video and in person, significant changes in interpersonal neural synchronization were absent. Further, using a null distribution derived from non-interacting subjects, we demonstrate that these differences must be attributed to joint performance of the task, rather than some property of the task condition itself. This highlights the unique coupling in the neural processes between individual brains that has been hypothesized to occur via the transmission of signals through the environment (Hasson et al., 2004).

Our findings may indicate that there is a brain-to-brain coupling specific to shared intentionality during physical goal-directed behavior above and beyond what has been found by investigating the fundamentals of social exchange. Stephens et al., (2010) recorded the time course of BOLD signal change in fMRI while a speaker told a personal story. Correlations between fluctuations in that time course and the neural time course of others, while listening to the recording during a separate fMRI testing session, were found in the dorsolateral PFC among other regions. Similar results have been found in studies of gestural communication (Schippers et al., 2010). Specifically using fNIRS as a measurement technique, Jiang et al., (2012) found significantly increased interpersonal neural synchronization in the PFC when the speaker and listener were face-to-face compared to when they were back-to-back, which also correlated with increased multi-modal (i.e. speech, gestural) turn-taking behavior. Specific to joint action, pairs of guitarists playing a short melody together show increased between-brain oscillatory coupling, measured through EEG (Lindenberger et al., 2009), with recent similar findings emerging in the domain of classroom learning (Dikker et al., 2017). The current study, however, is the first to probe interpersonal neural synchronization as a mechanism for shared intentionality

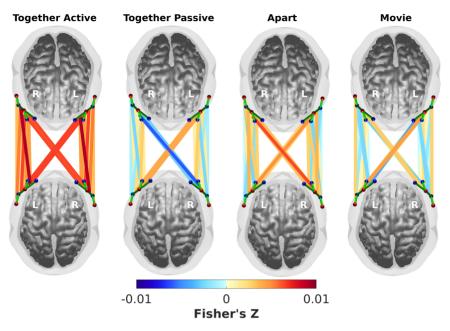


Fig. 4. Mean inter-subject synchronization for each condition. The inter-subject synchronization in the 'together active', 'together passive', 'apart' and 'movie' conditions relative to the null distribution derived from permutation testing. Relative Fisher's Z-values are shown for all possible connections. Warm colors indicate connections stronger than the null mean, while cool colors indicate those weaker.

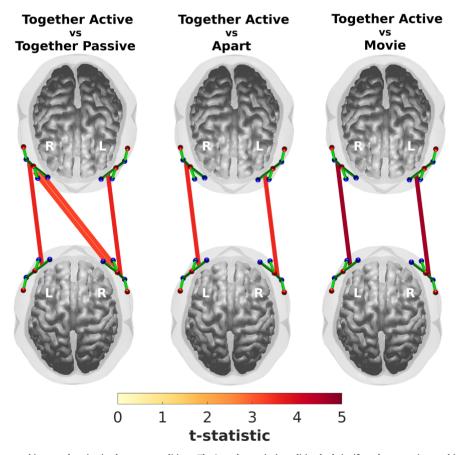


Fig. 5. Comparisons of inter-subject synchronization between conditions. The 'together active' condition had significantly greater inter-subject synchronization than the 'together passive', 'movie' and 'apart' conditions at an FDR-corrected threshold of q < 0.05. The 'together active' condition had no connections that were significantly less than any other condition.

by investigating the real-time, naturalistic interaction of two individuals during collaborative problem-solving, including all of Bratman's (1992) criteria (mutual responsiveness between partners, commitment to the joint activity and mutual support

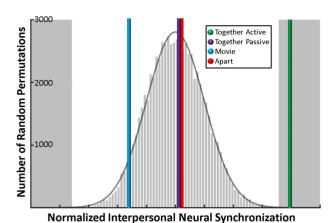


Fig. 6. Results from the permutation test visualized for a single channelpair. Grey bars represent the histogram of the standardized null distribution generated from non-concurrent participant pairs. The grey line represents the fit of a normal distribution to the null data. The shaded regions represent the

tails of the distribution significant at an FDR-corrected threshold of a < 0.05. The observed inter-subject synchronization for the 'together active' condition was significantly greater than the null distribution, while that of the 'together passive', 'apart' and 'movie' conditions was not.

of the role of each partner). Here, we demonstrate increased interpersonal neural synchronization in the PFC above and beyond that, which would be expected when two subjects simultaneously experience a rich auditory and visual stimulus such as a movie (Hasson et al., 2004). Thus, our findings are critical to advancing scientific knowledge of the biological demands of the integral social construct of shared intentionality.

Though speculative in the current context, some of the mechanistic 'building blocks' of shared intentionality may have been driving the findings of our study. In the 'together active' condition, participants were explicitly required to consider not only their own strategy and intentions for solving the puzzle but also that of their partner, with whom they were working concurrently. It is, therefore, likely that this condition required activation of action-perception system, which is hypothesized as the neural network underlying theory of mind and includes multiple regions of the PFC (Carrington & Bailey, 2009). It has been previously hypothesized that interpersonal neural synchronization, specifically, is facilitated as a function of the action-perception system (Jiang et al., 2012) which theorizes that each person influences his/her environment (including the actions of social partners), which, in turn, modifies the brain of the actor (Hari & Kujala, 2009). Thus, our study is among the first to demonstrate that the PFC is not only active when engaged in a collaborative task in which coordination and anticipation of a partner's action is necessary but that this activation is uniquely coordinated with that of the other to support active and successful shared intentionality.

Our findings also fall in line with a second mechanistic; 'building block' of shared intentionality called 'interagency' or a situation in which one member of the dyad may perceive the other's movement towards the mutual goal as his/her own agency when working collaboratively (Searle, 1980; Crivelli & Balconi, 2010;). Evidence for the existence of interagency comes from studying a phenomenon known as 'intentional binding', in which temporal judgment of the time between action and effect is judged by the operator to be shorter when the action is intentional rather than involuntary (Haggard et al., 2002). Intentional binding has been localized to the PFC through studies in which a sense of agency is blocked when PFC activation is interrupted through transcranial direct current stimulation (Khalighinejad et al., 2016). Obhi & Hall, 2011 and Strother et al., 2010 have noted that this implicit measure of agency appears independent of social role and can occur equally strongly for both the initiator and responder during shared intentionality. For example, in a study in which one member of a dyad was instructed to press a button, with the other joining in immediately after, only the initiator reported a subjective experience of agency but both demonstrated significant and indistinguishable intentional binding (Obhi & Hall, 2011). In the context of our own study, this interagency may manifest in heightened interpersonal neural synchronization within the PFC when, for example, one partner moved a puzzle piece towards the solution while the second partner only observed that movement, perceiving that action as partly his/her own. Indeed, interpersonal neural synchronization may represent what Searle (1980) described as 'we intentions' occurring through low-level processes to coordinate actions in a joint effort.

Although our study is limited in that it focused only upon the PFC rather than the whole of the social perception circuit (e.g. superior temporal sulcus (STS), amygdala), our results indicate a neural mechanism inherent in accomplishing a mutual goal. Future research on shared intentionality would be useful to investigate connectivity in the whole of the circuit during similar social-interactive paradigms that include tactile manipulation like the current study. A second limitation of this study is that not all behaviors may have been equalized between conditions. It is possible that the 'Together Active' condition had greater synchrony of movements due to turn-taking than other conditions. While we have employed motion correction, and while we note that not every pair necessarily took turns, it is impossible to say whether some residual effect remains in the data. Another limitation of our study that is ripe for future study was that it was designed to equalize some behaviors relevant to shared intentionality, like task completion and the relationship between partners. Further, it was not video recorded to examine inherent variability in variables relating to individual differences in shared intentionality (e.g. conversational turns, eye contact or gesture), making it difficult to assign specificity to cognitive processes in this context. We suggest that future studies encourage and examine more extensive variability in behavior and the nature of the relationship as variables of interests. For example, increased task length and difficulty might illuminate differences in skill or personality, potentially leading to leader/follower roles that could be studied systematically. In addition, the methodology of our current study has future implications for better characterizing the nature of social relationships. While we did not explicitly quantify the level of intimacy between partners, future studies could explicitly examine this as a variable, as well as experimentally manipulate the social relationship (e.g. friends vs strangers, parents and children) to better characterize change in interpersonal neural synchronization as a function of social support.

One additional future direction opens the door for more extensive application of our paradigm. Our findings shed light on the biological underpinnings of general human shared intentionality but also lend themselves to the possibility of mechanistic understanding of mental disorders in which shared intentionality is compromised in future work. Along these lines, developmental deficits in reciprocal social interaction (e.g. interactive speech) are considered primary diagnostic criteria of autism spectrum disorder (ASD) (American Psychiatric Association, 2013), although several other disorders show

deficits in general social interaction (Mueser et al., 1991; Segrin, 2000; Uekermann et al., 2010). Studies focusing on behavioral synchrony in ASD have found that coordination between children with ASD and their parents is correlated positively with language skills and negatively with stereotyped motor behaviors (Hudry et al., 2013). Marsh et al., (2013) found that children with ASD do not spontaneously rock in synchrony with their parent while sitting in rocking chairs, as do typically developing children. Landa et al., (2011) have found early evidence for social, language and cognitive gains in toddlers with ASD by targeting parent-child interpersonal synchrony during early intervention; however, brain-based mechanistic explanations for deficits in interpersonal synchrony have not been tested nor have their applications to therapeutic treatment. Thus, our findings are poised to contribute to our understanding of global psychological processes of human interaction, in addition to deficits of social dysfunction specific to psychiatric disorders, which highlights the broad clinical utility of our approach. Future work will address deficits in interpersonal neural synchronization in ASD and other disorders in which patients suffer from challenges related to shared intentionality.

Author Contributions

S.B.P., V.P.M. and T.J.H. developed the study concept. C.M., C.O.H., L.M.B., and M.E.M. performed data collection. T.J.H. and F.A.F. performed statistical analysis. F.A.F., S.B.P. and T.J.H. drafted the manuscript. All authors approved the final version of the manuscript for submission.

Funding

This work was supported by National Institutes of Health (K01 MH094467 to S.P., R21 MH100189 to S.P. and R01 MH107540 to S.P.) and the Brain and Behavior Research Foundation (NARSAD Young Investigator Award to S.P.) C.M.G. was supported by a NASA Pennsylvania Space Grant Consortium Research Scholarship.

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