Finding the neural correlates of collaboration using a three-person fMRI hyperscanning paradigm

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Humans have an extraordinary ability to interact and cooperate with others. Despite the social and evolutionary significance of collaboration, research on finding its neural correlates has been limited partly due to restrictions on the simultaneous neuroimaging of more than one participant (also known as hyperscanning). Several studies have used dyadic fMRI hyperscanning to examine the interaction between two participants. However, to our knowledge, no study to date has aimed at revealing the neural correlates of social interactions using a three-person (or triadic) fMRI hyperscanning paradigm. Here, we simultaneously measured the blood-oxygenation level-dependent signal from 12 triads ($n = 36$ participants), while they engaged in a collaborative drawing task based on the social game of *Pictionary*. General linear model analysis revealed increased activation in the brain regions previously linked with the theory of mind during the collaborative phase compared to the independent phase of the task. Furthermore, using intersubject correlation analysis, we revealed increased synchronization of the right temporo-parietal junction (R TPJ) during the collaborative phase. The increased synchrony in the R TPJ was observed to be positively associated with the overall team performance on the task. In sum, our paradigm revealed a vital role of the R TPJ among other theory-of-mind regions during a triadic collaborative drawing task.

three-person hyperscanning | intersubject brain synchronization | collaborative drawing | theory-of-mind network | right temporo-parietal junction

"Teamwork makes the dream work," a phrase coined originally by John Maxwell (1), emphasizes the importance of teamwork and collaboration as opposed to working independently or competing with others to achieve shared goals. Collaboration or joint action is a complex form of social interaction involving two or more individuals to coordinate their actions to achieve common goals (2). Collaboration is one of the defining qualities of being human and understanding the neural substrates of collaboration and social cognition has become a focus of study in recent years.

Single-person neuroimaging studies with prerecorded stimuli, such as pictures and videos, have significantly enriched our knowledge of neurobiological mechanisms underlying human social cognition (3, 4). Two neural subsystems, namely the theory-of-mind (ToM) network and the mirror neuron system (MNS), have been identified (5). The ToM network, often also referred to as the mentalizing network (6), has core regions consisting of the bilateral temporo-parietal junction (TPJ) and medial prefrontal cortex (mPFC). The ToM network is thought to help with understanding others' beliefs and intentions by integrating information from self and others (7–9). Several brain regions, such as the inferior frontal gyrus (IFG), posterior cingulate gyrus (PCC), precuneus (PreC), and medial temporal lobes (MTL) are also found to be part of the ToM network (10, 11). On the other hand, the MNS, a fronto-parietal sensorimotor network, is recruited during observation of an action, considered essential to understanding others' overt actions from low-level behavioral inputs (12).

Single-person studies, however, are inherently limited in examining the full essence of coordination as bidirectional interactions, and the aspect of continuous adaptation as evident in everyday collaborations is entirely absent (13, 14). Therefore, there has been a recent paradigm shift toward a second-person experimental design (i.e., using an interactor's view) to study the dynamics of bidirectional interactions beyond just passive observation (15). Pioneering social neuroscientists have coupled scanning instruments at the dyadic level, and simultaneously recorded brain activities from two individuals during relatively unconstrained real-time social interactions. It is commonly hypothesized that synchronized brain oscillations (i.e., interbrain synchronization) underlie coordinated cognition and behavior and successful communication (16). Of note, the main regions showing interbrain synchronization during such interactions are part of the MNS and ToM networks. For example, the right (R) IFG was synchronized in dyads during mutual gaze (17), whereas the R TPJ was more synchronized during a joint creative task (18). Moreover, higher interbrain synchronization during positive coordinated interpersonal behavior has been linked to greater shared understanding and intentionality (19).

Despite the increased popularity of hyperscanning, two issues remain. The first issue is that a large portion of previous hyperscanning studies (and all previous fMRI-based hyperscanning studies) have focused on the interaction between a pair of participants,

Significance

It is well-known that the presence of others drastically changes how we behave, yet a majority of social neuroscience studies are limited to single-person neuroimaging experiments. Using simultaneous imaging of multiple interacting brains (also known as hyperscanning), recent studies have started to examine the brain basis underlying social cognition beyond passive observation. Here we performed a three-person functional MRI hyperscanning study to investigate the brain-to-brain coupling using a social game of *Pictionary*. Our results highlight the importance of the theory-of-mind network, especially a brain region in the right temporo-parietal junction for improved triadic collaboration. Our work lays the foundation for studying the brain basis of complex and truly social group interactions.

or a dyad. Dyadic interactions, albeit useful, are limited in studying more complex group interactions, such as social rejection (i.e., being deliberately excluded from social interaction) or mediation (i.e., resolving conflicts via a neutral third party). Transitioning from a dyad to a triad fundamentally changes the way individuals think and interact empirically and theoretically (20, 21). Social interaction is also a core deficit in some neurodevelopmental disorders, such as autism spectrum disorder (ASD). Hyperscanning beyond dyads could boost our understanding of the neural correlates of atypical triadic social interactions, for example by studying atypical peer interaction patterns in children with ASD (22). The second issue pertains to the ecological validity of experiments. As with most neuroimaging studies, well-controlled laboratory experiments provide invaluable information about specific brain circuits, but recently more naturalistic experiments (e.g., games and movies) with high ecological (or real-life) validity are gaining favor (13). Hyperscanning based on paradigms like social games could facilitate increased ecological validity when studying collaboration.

To fill some of these gaps, herein we conducted a three-person fMRI hyperscanning experiment where participants played a version of the word-guessing improvisation game of *Pictionary* (23). In *Pictionary*, one player draws a target word so that others can guess the word based on drawing alone. In our multiplayer version, three players took turns to collaborate and draw a given set of action words (verbs) to enable word-guessing by another party, while no actual guessing was included in the paradigm. We have previously used this social improvisation game to study neural correlates of individuals' spontaneous improvisation and enhancement in creativity capacity (24, 25). Here, we modified the previous paradigm to include three phases: 1) An independent phase, where participants worked on their own to draw each given word; 2) an evaluation phase, where they could see and evaluate other team members' drawings from the independent phase; and 3) a collaboration phase, where participants worked jointly on a shared screen and took turns to redraw the word in a collaborative manner (Fig. 1).

Importantly, in the collaboration phase, participants could see each other's drawings in real time, thereby allowing us to examine brain-to-brain coupling. We also included control words (e.g., draw a spiral) in the independent phase to contrast for basic visuospatial activity. After the experiment, participants rated other team members (including themselves) on performance. Furthermore, to estimate task performance, the drawings generated by participants during the collaborative phase were rated on the ease of guessing (usefulness) and originality by an independent panel of judges (R.A. and H.X.).

We first performed a general linear model (GLM) analysis to identify the brain networks associated with collaborative drawing as compared to independent drawing. We then conducted an intersubject correlation (ISC) analysis to reveal brain regions that show increased correlation/synchronization during the collaboration phase. We posit that during the collaboration phase, drawers materialize their internal understanding through sketching, while the observers employ their MNS as the sketch unfolds and recruit their ToM network to make predictions regarding future moves. Thus, by incorporating both the MNS and ToM subsystems, the players adjust their plans dynamically to reach a joint solution. We hypothesized that social collaboration would recruit regions in the two networks and elicit higher ISC among teammates with better team performance.

Results

Here we conducted a three-person fMRI hyperscanning experiment where participants played a multiplayer version of the word-guessing improvisation game of *Pictionary* and took turns to collaborate and draw a given set of verbs. Participants first worked independently to draw each given word, followed by evaluating other players' drawings, and finally took turns to redraw the word

in a collaborative manner (Fig. 1). Importantly, in the collaboration phase, participants could see each other's drawings in real time. In this section, we first provide results from a GLM analysis to identify the brain regions associated with collaborative drawing as compared to independent drawing. We then report results from the ISC analysis, which revealed brain regions showing increased ISC during the collaboration phase.

Behavioral Data. Thirty-six right-handed adults (20 male, 16 female; age = 27.44 ± 4.98 y) were recruited for our study and written informed consent was obtained from all participants. The drawings generated during the collaborative drawing phase were evaluated by two raters on the scales of originality (uniqueness across all drawings) and usefulness (i.e., level of ease for another person to guess the word represented by the drawing). Furthermore, a composite team performance score was created by multiplying the two scores of originality and usefulness for each triad. See *Materials and Methods* and *SI Appendix*, Table S1 for detailed information on performance assessment.

Examining Neural Correlates of Collaboration Using GLM Analysis. We first set out to identify regions associated with collaboration while drawing. To control for basic visuospatial processing, we first contrasted independent and collaboration drawing with control drawing (i.e., drawing spiral shapes). Two group-level cluster-thresholded z-statistic maps ($z > 3.1$ and $P < 0.05$) were created using FEAT (fMRI Expert Analysis Tool) (26): Independent contrast (i.e., independent − control drawing) and collaborative contrast (i.e., collaborative − control drawing). We then examined the difference between these two main contrasts of interest using GLM.

As shown in Fig. 2*A* and Table 1, collaborative > independent contrast revealed increased activity in eight clusters, including the PCC/PreC, R angular gyrus (AG), bilateral ventral striatum (VS), R superior temporal gyrus/middle temporal gyrus (R STG/MTG), bilateral anterior insula/frontal opercular cortex (AI/FO), left anterior cingulate cortex (L ACC), R superior frontal gyrus (SFG), and R calcarine sulcus. For the reverse contrast (i.e., independent > collaborative) increased activity in the pre-supplementary motor area (pre-SMA) was revealed. We conducted an additional GLM analysis to directly compare collaborative with independent drawing (i.e., without using control drawing) and similar results were observed.

We also performed additional GLM analyses to explore the effects associated with the different components within collaborative drawing (detailed coding can be found in *SI Appendix*, Fig. S1). We first contrasted the active and passive observation (i.e., the observation phase before and after one's turn to draw, respectively) during the collaboration phase. Active observation induced higher activity in the L supramarginal gyrus (SMG) and anterior lobe of the cerebellum as compared with passive observation (Fig. 2*B*). We also found increased activation in the intracalcarine cortex and fusiform gyrus (FG) during the later phase of the collaborative drawing (i.e., second or third collaborative drawing block) (Fig. 2*C*). Moreover, we contrasted the first block of collaborative drawing with independent drawing to control for visual stimulation as both conditions started with a blank screen, and this analysis resulted in a highly similar contrast pattern (*SI Appendix*, Fig. S2) as compared with our main GLM result.

Examining Neural Correlates of Collaboration Using ISC Analysis. To further investigate the neural coupling among teammates, we applied ISC analysis to identify regions that were synchronized across teammates during the collaborative phase. After parcellating the brain into 241 regions-of-interest (ROIs) using the Shen atlas (27), the mean region-wise timeseries were z-scored after regressing out the signals driven by the common task
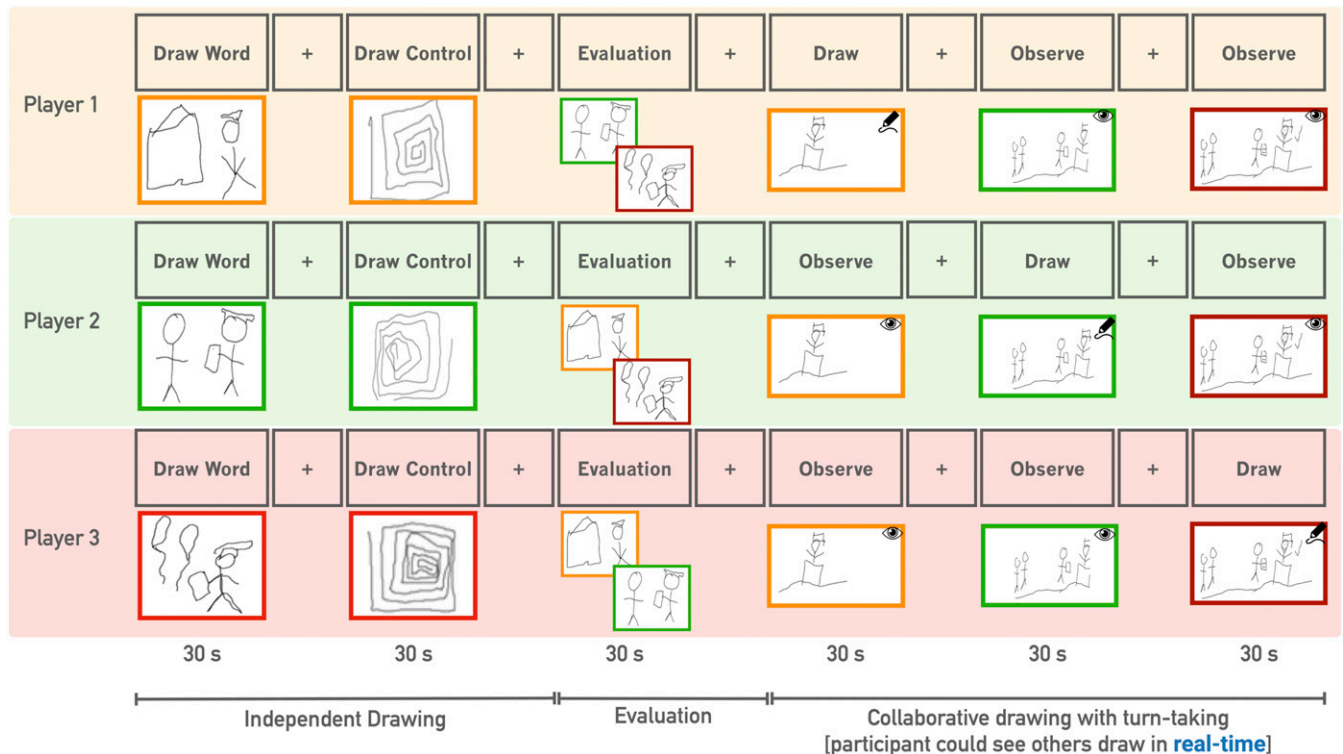
Fig. 1. An illustration of the multiplayer joint improvisation paradigm for the verb graduate. Participants used an MR-safe tablet and stylus to complete the drawing (24). A total of nine verbs were drawn in three runs. For each verb, there were three phases: Independent drawing, evaluation, and collaborative drawing. In the collaboration phase, participants took turns to draw (order was counterbalanced), while everyone could see each other's drawings in real time.

structure. ISC was estimated using the pairwise Pearson's correlation coefficients from the residual timeseries. To determine the brain regions that were significantly more synchronized across participants within each triad, we performed permutation testing to estimate the difference between ISC estimated from true triads with those estimated from fake triads. Fake triads were created by randomly shuffling team labels. Positive false-discovery rate (FDR) correction was performed to correct for multiple hypothesis testing (28), and ROIs with an FDR-corrected Q-value smaller than 0.05 are shown in Fig. 3. Significantly increased synchronization was found in a set of ROIs spanning across visual (e.g., cuneus and lingual gyrus), motor (frontal eye field [FEF] and superior parietal lobule [SPL]), visual association (lateral occipital cortex, LOC), and somatosensory association cortex (specifically the supramarginal gyrus; SMG). L IFG, R TPJ, R AG, and R planum temporale were also among the ROIs with increased ISC.

To ensure that the observed within-triad ISC was not spuriously driven by the remaining task structure shared within triads, we also performed ISC analysis on the timeseries derived from the independent phase. No significant results were obtained for any brain region during the independent phase. Additional blockwise ISC analysis was conducted to test if there is a significant difference across the collaborative phase (i.e., first vs. third block). A Wilcoxon signed-rank test revealed significantly more synchronized activity in the SPL and FEF, as well as in visual association areas, such as the LOC and face FG (*SI Appendix*, Fig. S3).

Additionally, we performed an exploratory three-way synchronization analysis to explore triadic interactions. We characterized the triadic interaction using multivariate mutual information (MMI) (29, 30), which quantifies the statistical interdependency among multiple variables, in this case, participants. Triadic MMI analysis revealed an elevated interdependency in multiple visual areas (*SI Appendix*, Fig. S4).

Examining the Relation between Increased ISC and Team Performance. To examine the brain–behavior relationship, we calculated the correlation between the team performance and the degree of observed ISC across participants within each triad. We hypothesized that the teams with higher ISC during the collaboration phase would perform better in the task. For task performance, we collected two metrics. The team performance was measured as the product of usefulness and originality scores of each triad's final drawing from the collaboration phase. These sketches were rated by two judges on the scales of usefulness and originality as per the previous work by Saggar et al. (24), with an interrater reliability >0.9 [using an intraclass correlation coefficient, ICC (2, 1)]. The second metric was pairwise rating from a postscan questionnaire, where each participant rated the performance of their team members during the entire paradigm.

We computed the team-averaged ISC and correlated each team's mean ISC with team-level composite score averaged across all verbs (Table 2). Fig. 4 shows averaged ISC within two ROIs of the R posterior TPJ extending to the inferior division of AG with significant correlation with team performance, more specifically, R AG ($\rho = 0.75$, $P = 0.007$, uncorrected) and R TPJ ($\rho = 0.63$, $P = 0.039$, uncorrected). We also explored using minimum or maximum within-triad ISC for the correlation with team performance, which yielded the same significant relationship. Additionally, we observed a statistically nonsignificant relation between ISC of the R TPJ and pairwise performance rating ($\rho = 0.30$, $P = 0.092$), as shown in *SI Appendix*, Fig. S5. Finally, *SI Appendix*, Fig. S6 provides scatterplots between teams' team-averaged ISC with team-level subscores of originality and usefulness.

Discussion

It is a well-known phenomenon that the presence of others drastically changes how we behave. Yet, the majority of social
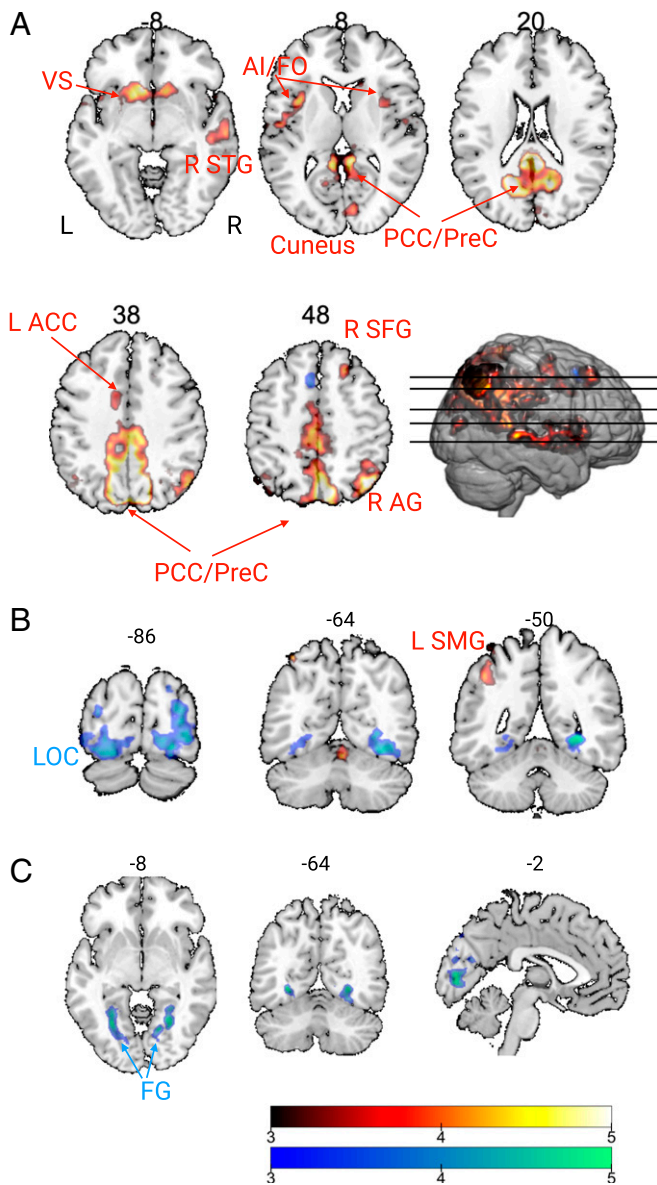
Fig. 2. The main GLM contrast (independent vs. collaborative drawing) and exploratory GLM contrasts comparing different components within the collaborative drawing. The results were cluster-thresholded at $P < 0.05$. (*A*) Collaborative versus independent drawing. The red-yellow scale depicts the *z*-values for the contrast of collaborative > independent drawing, while the blue-green scale represents the reverse contrast. (*B*) Red: Active collaborative observation > passive collaborative observation. Blue: Active collaborative observation < passive collaborative observation. (*C*) Blue: Following collaborative drawing > leading collaborative drawing. No significant activation was found in the reverse direction.

neuroscience is limited to single-person neuroimaging experiments, which in turn prevents us from studying more realistic complex social phenomena (31). Here, we conducted a three-person fMRI hyperscanning experiment to study the neural correlates of collaboration in the form of joint picture drawing using a social game of *Pictionary*. Our results highlighted the importance of the ToM network, especially a region containing the R posterior TPJ extending to the inferior division of the AG during the three-person social interaction.

Using single-subject neuroimaging experiments, neuroscientists have traditionally focused on studying our ability to understand the mental states of others as an observer. What is lesser

known is how brains dynamically adapt when we actively engage in social interactions. This lack of understanding about inter-brain interaction has also been referred to as the "dark matter" of social neuroscience (15). The recent development of hyperscanning tries to address the issue by simultaneously scanning multiple participants during real-time social interactions. To quantify between-subject brain coupling, ISC is typically used (32, 33). As a model-free approach, ISC does not require a priori experimental design and is well suited to study natural and open-ended social interactions (34). Here, using ISC in a three-person hyperscanning paradigm, we examined the neural correlates of collaboration while participants were engaged in a social improvisation paradigm of *Pictionary*.

The ToM network has been known to play a central role in social cognition. Two core regions in the ToM network include the mPFC and bilateral TPJ, while the PreC, IFG, and STG are also considered part of the ToM network (9). Despite being part of the same network, the two core regions (mPFC and TPJ) have been thought to assume distinct social cognitive functions (12, 35). It has been hypothesized that while the TPJ is linked with assessing transient mental inferences about other people's goals/beliefs, the mPFC is responsible for assessing trait judgments of others and self (instead of immediate actions/goals) (36). Furthermore, among the bilateral TPJs, the R TPJ has been specifically shown to play a critical role in establishing a social context and is of particular interest given its robust activation across a broad range of social cognitive tasks (9).

Our GLM results confirmed the role of the ToM network during the collaboration phase, as we saw increased activations in the PCC/PreC and R posterior STG/MTG as compared to the independent phase. We also observed increased activations in the regions of the AI/FO, L ACC, and VS. It should be noted that the AI/FO, ACC, and the amygdala are considered to be part of the emotional salience network, suggesting the involvement of subjective emotion, such as happiness, empathy, and uncertainty (37). Moreover, stronger activation in the VS was previously found during live interaction between participants and experimenters (38). To our surprise, we did not observe increased activation in the bilateral mPFC or TPJ during collaboration. The absence of the mPFC seemed to coincide with an earlier study by Schippers et al. (39), who also reported no evidence of involvement of the mPFC during a gestural communication task. This is likely because the mPFC is involved in inferences of enduring characteristics (personality traits) rather than transient information (actions/goals), as suggested by Van Overwalle (36). Despite the absence of increased activation in the TPJ, we did observe increased synchronization of the posterior part of the R TPJ during collaboration. Furthermore, the increased R TPJ/AG synchronization among teammates was also observed to be positively associated with team performance.

Our ISC analysis revealed a distinct set of brain regions being involved during collaboration as compared to activation patterns observed using GLM analysis. Besides the putative stimulus-locked ISC of the primary visual cortex, visual, and somatosensory association cortex, the dorsal attention network (e.g., SPL and FEF) was also observed to be more synchronized during collaboration. Increased ISC in the dorsal attention network potentially indicates a top-down control of visual attention. It is worth noting that ROIs of the FEF and L IFG with increased ISC partially overlapped with the dorsal and ventral premotor cortex, which is considered to be a core region of the MNS (5). Higher synchronization of the R TPJ/AG and L IFG was also observed, which are part of the ToM network. The degree of synchronization in the R TPJ/AG was positively related to the overall performance of each team (Fig. 4). The observed relationship between the brain-to-brain coupling of the R TPJ among teammates and their performance suggests that the R TPJ may be related to better coordination within a team. This postulation is also supported by recent studies (18, 40, 41). Tang et al. (40) showed that higher synchronization in the R TPJ is

Table 1. A summary of the contrast pattern of collaborative versus independent drawing (cluster-thresholded z > 3.1 and P < 0.05)

	Brain region	z-MAX	x (mm)	y (mm)	z (mm)	Cluster size (no. of voxels)
Collaborative > Independent						
1	PCC/PreC	6.39	13.5	−60.5	27.5	10,630
2	R AG	5.79	45.5	−66.5	49.5	1,096
3	VS	5.17	−8.5	21.5	−6.5	1,045
4	R STG/MTG	4.62	67.5	−34.5	−2.5	789
5	L AI/FO	4.63	−34.5	11.5	9.5	576
6	L LOC/AG	4.11	−48.5	−72.5	41.5	205
7	R SFG	4.31	23.5	27.5	51.5	143
8	R Calcarine sulcus	4.18	11.5	−82.5	9.5	115
Independent > Collaborative						
1	Pre-SMA	4.4	−4.5	15.5	53.5	107

The Montreal Neurological Institute coordinates with peak z-statistic and number of voxels within each cluster are reported.

linked to greater shared intentionality between individuals, while Lu et al. (18) found higher synchronization in the R TPJ/AG during a collaborative divergent thinking task and for better group creative performance. A recent study showed within-group ISC in the R TPJ to be related to intergroup hostility using a group-competition paradigm (41).

In addition to its role in the ToM network, the R TPJ is also postulated to be associated with humans' ability to reorient attention to unexpected stimuli (42). Recent neuromodulation studies have concluded that the R TPJ plays an overarching role in both domains of attention and social cognition (43). Thus, higher ISC in the R TPJ/AG during collaboration could be partially attributed to the emergence of an unexpected/salient idea put forth by other teammates. To delineate the attentional confounds, we conducted a block-wise ISC analysis and tested the difference in ISCs during different collaborative drawing blocks (i.e., the first block vs. the third block). It is likely that participants might be less attentive during the third block, leading to lower ISC as compared to the first. Regions responsible for top-down attentional control, such as the SPL and FEF, showed significantly higher ISC during the first collaborative block (*SI Appendix*, Fig. S3). Coinciding with our observation, Nummenmaa et al. (44) found that compared with passive clip viewing, active viewing (i.e., simulating a character's feelings in the clip) led to enhanced ISC in the FEF, SPL, and LOC. This suggested that our participants might be more attentive during the first collaborative block than during the third one. Importantly, the ISC pattern associated with active engagement did not include the R TPJ/AG, thus attentional confound did not explain the increased ISC in R TPJ/AG.

Intriguingly, little spatial overlap was found while comparing the GLM activation pattern with ISC cofluctuation pattern. However, such lack of overlap was partially intentional, as we removed task-related signals before conducting ISC analysis, otherwise, the ISC pattern would mainly reflect activation patterns driven by the shared task structure (45). Such procedures have been previously adopted for the ISC pattern to reflect additional information beyond merely task-related activation patterns (17).

Limitations and Future Directions. Increasing ecological validity and testing relatively unconstrained interactions between participants come with a cost. First, even though turn-taking is a common phenomenon in our daily interactions, such as conversation, it poses some difficulties in the behavioral and neuroimaging data analysis, especially in our design, which involved three individuals without fixed roles, such as drawer and observer. For example, within-condition differences may exist during the collaboration phase for both ISC and GLM analysis. In our main analysis, we combined data from all three collaborative blocks to compute the ISC without separating observation and drawing, mainly due to the limited sample size (Fig. 3). In the exploratory ISC analysis, we

quantified the ISC driven by joint observation by removing data corresponding to collaborative drawing blocks. We compared it with the original ISC computed from both observation and drawing blocks. No regions survived multiple comparisons correction, which is in line with the finding that the shared understanding of observers could be potentially driving higher ISC (19).

Moreover, individuals' attention/engagement levels could depend on the drawing order, as indicated by the results from block-wise ISC analysis (*SI Appendix*, Fig. S3). Moreover, as shown in Fig. 2B, active observation (observation before one's turn to draw) recruits brain regions responsible for novel idea generation, such as the L SMG (46), and motor preparation, such as the cerebellum (47). GLM analysis also revealed higher activation in visual areas, which might be evoked as a result of heavier visual load during later stages of collaborative drawing (Fig. 2C). Increased activation in the FG has been linked with the development of a more elaborate visual representation (48) and the process of integration of parts of an object into a whole or larger object (49). Attention/engagement difference may also impact our GLM results when contrasting collaborative drawing with independent drawing to study the neural correlates of collaboration. It has been shown that even minimal social interaction can elicit higher levels of arousal and capture attention. For example, the mere presence of an observer or the
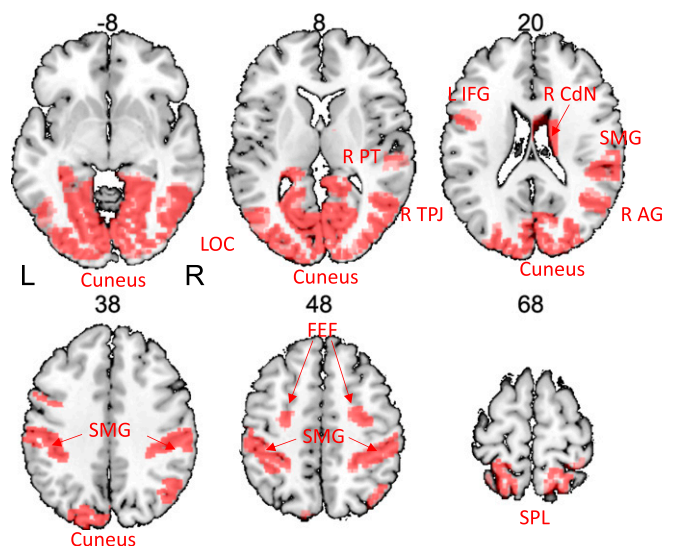

Fig. 3. A binary mask of regions with significantly higher within-triads ISC during the collaboration phase (Q < 0.05) are shown in red. Significant ROIs included lingual gyrus, occipital pole, cuneus, face FG (FFG), LOC, R planum temporale (R PT), posterior division of the R TPJ, R caudate nucleus (R CdN), L IFG, SMG, R AG, FEF, and SPL.

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Table 2. Summary of correlation analysis between team-averaged ISC and composite performance scores

ROI	COG x (mm)	COG y (mm)	COG z (mm)	P value
R AG	50.33	−60.06	36.14	0.007
R TPJ	51.54	−56.59	15.78	0.039

The Montreal Neurological Institute coordinates of the center of gravity (COG) for each ROI and associated P value are reported.

belief of being watched is sufficient to change an individual's behavior (audience effect) (50). As a result, higher engagement and arousal levels during the collaborative drawing could partially drive the contrast pattern observed in the collaborative drawing vs. independent drawing contrast.

Another limitation pertains to the sample size of this study, and even with 36 participants we only have 12 triads. The lack of power due to the relatively small number of triads could result in a less robust brain–behavior correlation analysis. Thus, care should be taken when interpreting the putative relation between increased ISC in the R TPJ and overall team performance of the triads given the limited sample size. Moreover, the team performance was estimated after the experiment by comparing drawings from different teams instead of guessing the verb in real time (as usually done in the social game of *Pictionary*). Alternative approaches, such as guessing the verb directly, could potentially be a better proxy of team performance, which can be added in future investigation. However, we believe our work constitutes an important first step to facilitate future hyperscanning work of second-person neuroscience in the lesser-studied area of triadic interactions.

The ISC, as measured here using Pearson's correlation, quantifies the bivariate relationship and does not take full advantage of triadic interactions. In order to characterize the team interaction beyond pairwise correlations, we performed higher-order multivariate analysis (i.e., MMI) (29). We were able to largely confirm our earlier ISC findings within visual areas (*SI Appendix*, Fig. S4), yet it remains to be clarified whether triadic effects are limited to these brain regions, or we simply did not have the power to detect higher-order interaction using MMI analysis. Future studies are warranted to further delineate the triadic interaction from a simple additive effect of dyadic interactions. We also extended our ISC analysis to different triadic arrangements by including minimum (or maximum) of the three bivariate ISCs to measure the triadic effect. The minimum ISC approach is akin to the mathematical approach of finding triangular interaction (also known as two-simplex) using persistent homology (51), which yielded a similarly significant relationship between triadic ISC and team performance.

We also acknowledge that individual differences (e.g., personality, drawing skills, and creativity level) could play an important role in team performance and neuroimaging analysis. Taking creativity as an example, Taggar (52) showed that groups made up of more creative members were found to be more creative on the team level, whereas Harvey (53) argued that team creative performance also depends on the effective integration of team members. While our analysis focused on the second perspective using team performance as a proxy of team integration/collaboration, it is likely that individual differences also affected the overall team performance (e.g., more creative or open participants might contribute more than in the collaborative phase). It would be interesting to study the influence of team composition and the size of the team in future studies. Additionally, it should also be noted that due to a technical error, some acquisition parameters differed across sites. We attempted to account for multisite variability by modeling sites as a fixed effect in the higher-level GLM analysis. ISC analysis should be less susceptible to such differences due to the averaging of voxel-wise timeseries within ROIs. Nonetheless, one-way ANOVA analysis revealed no significant group differences in ISC across sites.

Finally, given the nature of the task (drawing), despite our best effort of keeping participants from moving, the head motion could have influenced the results. We adopted a rigorous approach for removing head movement artifacts by first using ICA-AROMA (automatic removal of motion artifacts) (54) and then censoring high-motion frames (frame displacement > 0.5 mm), as well as dropping high-motion subjects (more than 30% frames discarded) from the analysis.

Conclusions

In this study, we performed a three-person fMRI hyperscanning experiment to study the neural underpinning of social collaboration using a *Pictionary*-like collaborative drawing paradigm. We found collaboration-related activation in ToM regions, including the PCC, PreC, and R posterior STG/MTG. We also highlighted the importance of the R TPJ and its putative relationship with positive interpersonal collaboration outcomes in the form of better team performance ratings. In sum, triadic hyperscanning joined by open-ended task paradigm offers a unique avenue for neuroscientists to disentangle complex everyday group interactions.

Materials and Methods

Participants. Thirty-six healthy adults were recruited in our study (age: 27.44 ± 4.98 y, 16 female), who were randomly assigned to 12 triads. Participants were considered eligible if they were 18 to 45 y old, right-handed, with no history of neurologic or psychiatric illness. The participants were not trained in any form of visual arts. The study was approved by Stanford University's Institutional Review Board (Human Subjects Division). All subjects provided written consent.

Multiplayer *Pictionary* Paradigm. The collaborative verb-drawing fMRI task is a multiplayer version of the *Pictionary* game developed based on a previous study by Saggar et al. (24). The goal of the task is to draw a verb independently and collectively for others to guess. Nine verbs were drawn over three runs (three verbs per run): That is, run 1: snore, graduate, accelerate; run 2: whisper, salute, vote; run 3: redial, boil, pinpoint. The drawing of each verb can be split into three phases: Independent phase (two blocks), evaluation phase (one block), and collaboration phase (three blocks), as shown in Fig. 1. Each block lasted for 30 s and was separated by a fixation period jittering around 7 to 8 s. Details are presented in *SI Appendix*.
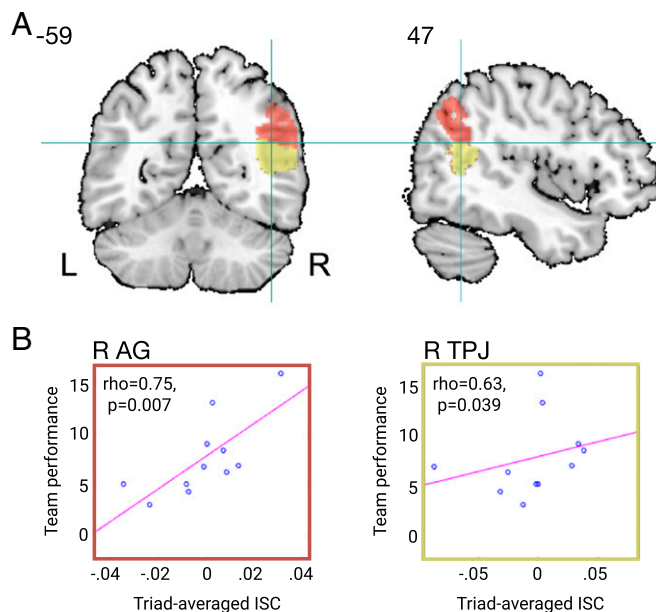

Fig. 4. Team performance and team-averaged ISC. (*A*) Regions with significant brain–behavior relationships between team-averaged ISC and team performance: That is, R AG (red) and R TPJ (yellow). (*B*) Scatterplots of team performance vs. ISC in R AG (ρ = 0.75, P = 0.007, uncorrected) and R TPJ (ρ = 0.63, P = 0.039, uncorrected).

Pairwise/Triadic Behavioral Metrics. The pairwise performance rating between the participants was collected in a postscan questionnaire, in which we asked them to rate all participants' performance on a five-point scale (1–5), with 1 being very strongly dissatisfied and 5 being strongly satisfied. As for the triadic performance, two raters evaluated the final drawings from the collaborative phase and generated two additional behavioral ratings: Originality (the number of the unique elements in the drawing) and usefulness (the level of ease for another person to guess the word represented by the drawing). The drawings were rated on a five-point scale, where 1 means not original/useful and 5 means very original/useful.

Data Preprocessing and Analysis. Details regarding each step are provided in *SI Appendix*. Briefly, we used fMRIPrep v1.1.4 (https://fmriprep.org/en/stable/index.html) (55), a preprocessing toolbox built on a combination of existing neuroimaging software, to preprocess our MRI data. For the general linear modeling, we used FEAT (v6.00) to identify the brain activations associated with each condition. For ISC analysis, we parcellated the functional data using the Shen atlas (27) to generate ROI timeseries. Here, ISC was quantified as the Pearson's correlation coefficients between time series of a given ROI between two subjects, which captures the time-locked neural cofluctuation across subjects. ISC was computed between all subject pairs, including ISC between subject pairs from the same triad (within-triad ISC), as well as

ISC between subject pairs from different triads (between-triad ISC) and the ISC difference between the two based on the true triad labels (ISC_{true}). We then randomly permutated the triad labels and recomputed the ISC difference ($ISC_{shuffled}$), and determined the statistical significance by comparing ISC_{true} and $ISC_{shuffled}$. Finally, MMI was used to explore the neural correlates of triadic interaction (30).

Data and Code Availability. The group-level maps for GLM as well as ISC analysis have been uploaded on the NeuroVault website: https://neurovault.org/collections/8401/. The code for setting up the web-server and running hyperscanning experiment is provided at https://github.com/braindynamicslab/fmri-hyperscan-3.

1. J. C. Maxwell, John C. Maxwell Quotes. BrainyQuote.com. Accessed 23 June 2019.
2. N. Sebanz, H. Bekkering, G. Knoblich, Joint action: Bodies and minds moving together. *Trends Cogn. Sci.* **10**, 70–76 (2006).
3. J. Rilling *et al.*, A neural basis for social cooperation. *Neuron* **35**, 395–405 (2002).
4. H. Walter *et al.*, Understanding intentions in social interaction: The role of the anterior paracingulate cortex. *J. Cogn. Neurosci.* **16**, 1854–1863 (2004).
5. F. Van Overwalle, K. Baetens, Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. *Neuroimage* **48**, 564–584 (2009).
6. L. Schilbach *et al.*, Differential patterns of dysconnectivity in mirror neuron and mentalizing networks in Schizophrenia. *Schizophr. Bull.* **42**, 1135–1148 (2016).
7. M. Arioli *et al.*, Affective and cooperative social interactions modulate effective connectivity within and between the mirror and mentalizing systems. *Hum. Brain Mapp.* **39**, 1412–1427 (2018).
8. D. M. Amodio, C. D. Frith, Meeting of minds: The medial frontal cortex and social cognition. *Nat. Rev. Neurosci.* **7**, 268–277 (2006).
9. M. Schurz, J. Radua, M. Aichhorn, F. Richlan, J. Perner, Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neurosci. Biobehav. Rev.* **42**, 9–34 (2014).
10. R. A. Mar, The neural bases of social cognition and story comprehension. *Annu. Rev. Psychol.* **62**, 103–134 (2011).
11. S. G. Shamay-Tsoory, The neural bases for empathy. *Neuroscientist* **17**, 18–24 (2011).
12. F. Babiloni, L. Astolfi, Social neuroscience and hyperscanning techniques: Past, present and future. *Neurosci. Biobehav. Rev.* **44**, 76–93 (2014).
13. R. Hari, M. V. Kujala, Brain basis of human social interaction: From concepts to brain imaging. *Physiol. Rev.* **89**, 453–479 (2009).
14. C. Camerer, D. Mobbs, Differences in behavior and brain activity during hypothetical and real choices. *Trends Cogn. Sci.* **21**, 46–56 (2017).
15. L. Schilbach *et al.*, Toward a second-person neuroscience. *Behav. Brain Sci.* **36**, 393–414 (2013).
16. G. J. Stephens, L. J. Silbert, U. Hasson, Speaker-listener neural coupling underlies successful communication. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 14425–14430 (2010).
17. D. N. Saito *et al.*, "Stay tuned": Inter-individual neural synchronization during mutual gaze and joint attention. *Front. Integr. Nuerosci.* **4**, 127 (2010).
18. K. Lu, H. Xue, T. Nozawa, N. Hao, Cooperation makes a group be more creative. *Cereb. Cortex* **29**, 3457–3470 (2019).
19. M. Nguyen, T. Vanderwal, U. Hasson, Shared understanding of narratives is correlated with shared neural responses. *Neuroimage* **184**, 161–170 (2019).
20. G. Simmel, *Soziologie: Untersuchungen über die formen der vergesellschaftung*, (Duncker & Humblot, 1908).
21. M. Zhang, C. Beetle, J. A. S. Kelso, E. Tognoli, Connecting empirical phenomena and theoretical models of biological coordination across scales. *J. R. Soc. Interface* **16**, 20190360 (2019).
22. N. Humphrey, W. Symes, Peer interaction patterns among adolescents with autistic spectrum disorders (ASDs) in mainstream school settings. *Autism* **15**, 397–419 (2011).
23. R. Angel, G. Everson, *Pictionary*, (Angel Games, Inc., 1985).
24. M. Saggar *et al.*, Pictionary-based fMRI paradigm to study the neural correlates of spontaneous improvisation and figural creativity. *Sci. Rep.* **5**, 10894 (2015).
25. M. Saggar *et al.*, Changes in brain activation associated with spontaneous improvization and figural creativity after design-thinking-based training: A longitudinal fMRI study. *Cereb. Cortex* **27**, 3542–3552 (2017).
26. S. M. Smith *et al.*, Advances in functional and structural MR image analysis and implementation as FSL. *Neuroimage* **23** (suppl. 1), S208–S219 (2004).
27. X. Shen, F. Tokoglu, X. Papademetris, R. T. Constable, Groupwise whole-brain parcellation from resting-state fMRI data for network node identification. *Neuroimage* **82**, 403–415 (2013).
28. J. D. Storey, A direct approach to false discovery rates. *J. R. Stat. Soc. Series B Stat. Methodol.* **64**, 479–498 (2002).
29. B. Chai, D. Walther, D. Beck, F.-f. Li, "Exploring functional connectivity of the human brain using multivariate information analysis" in Advance Neural Information Process. System 22–Proceedings of 2009 Conference (Curran Associates, Inc., 2009), pp. 270–278.
30. A. Kraskov, H. Stögbauer, P. Grassberger, Estimating mutual information. *Phys. Rev. E Stat. Nonlin. Soft Matter Phys.* **69**, 066138 (2004).
31. A. Todorov, L. T. Harris, S. T. Fiske, Toward socially inspired social neuroscience. *Brain Res.* **1079**, 76–85 (2006).
32. E. S. Finn, P. R. Corlett, G. Chen, P. A. Bandettini, R. T. Constable, Trait paranoia shapes inter-subject synchrony in brain activity during an ambiguous social narrative. *Nat. Commun.* **9**, 2043 (2018).
33. U. Hasson, A. A. Ghazanfar, B. Galantucci, S. Garrod, C. Keysers, Brain-to-brain coupling: A mechanism for creating and sharing a social world. *Trends Cogn. Sci.* **16**, 114–121 (2012).
34. L. Nummenmaa, J. M. Lahnakoski, E. Glerean, Sharing the social world via intersubject neural synchronisation. *Curr. Opin. Psychol.* **24**, 7–14 (2018).
35. L. Zheng *et al.*, Enhancement of teaching outcome through neural prediction of the students' knowledge state. *Hum. Brain Mapp.* **39**, 3046–3057 (2018).
36. F. Van Overwalle, Social cognition and the brain: A meta-analysis. *Hum. Brain Mapp.* **30**, 829–858 (2009).
37. A. D. B. Craig, How do you feel—Now? The anterior insula and human awareness. *Nat. Rev. Neurosci.* **10**, 59–70 (2009).
38. E. Redcay *et al.*, Live face-to-face interaction during fMRI: A new tool for social cognitive neuroscience. *Neuroimage* **50**, 1639–1647 (2010).
39. M. B. Schippers, V. Gazzola, R. Goebel, C. Keysers, Playing charades in the fMRI: Are mirror and/or mentalizing areas involved in gestural communication? *PLoS One* **4**, e6801 (2009).
40. H. Tang *et al.*, Interpersonal brain synchronization in the right temporo-parietal junction during face-to-face economic exchange. *Soc. Cogn. Affect. Neurosci.* **11**, 23–32 (2016).
41. J. Yang, H. Zhang, J. Ni, C. K. W. De Dreu, Y. Ma, Within-group synchronization in the prefrontal cortex associates with intergroup conflict. *Nat. Neurosci.* **23**, 754–760 (2020).
42. M. Corbetta, G. Patel, G. L. Shulman, The reorienting system of the human brain: From environment to theory of mind. *Neuron* **58**, 306–324 (2008).
43. S. C. Krall *et al.*, The right temporoparietal junction in attention and social interaction: A transcranial magnetic stimulation study. *Hum. Brain Mapp.* **37**, 796–807 (2016).
44. L. Nummenmaa *et al.*, Mental action simulation synchronizes action-observation circuits across individuals. *J. Neurosci.* **34**, 748–757 (2014).
45. J. Pajula, J. P. Kauppi, J. Tohka, Inter-subject correlation in fMRI: Method validation against stimulus-model based analysis. *PLoS One* **7**, e41196 (2012).
46. M. Benedek *et al.*, To create or to recall? Neural mechanisms underlying the generation of creative new ideas. *Neuroimage* **88**, 125–133 (2014).
47. C. J. Stoodley, J. D. Schmahmann, Evidence for topographic organization in the cerebellum of motor control versus cognitive and affective processing. *Cortex* **46**, 831–844 (2010).
48. H. Op de Beeck, E. Béatse, J. Wagemans, S. Sunaert, P. Van Hecke, The representation of shape in the context of visual object categorization tasks. *Neuroimage* **12**, 28–40 (2000).
49. R. Starrfelt, C. Gerlach, The visual what for area: Words and pictures in the left fusiform gyrus. *Neuroimage* **35**, 334–342 (2007).
50. N. Triplett, The dynamogenic factors in pacemaking and competition. *Am. J. Psychol.* **9**, 507–533 (1898).
51. J.-B. Bardin, G. Spreemann, K. Hess, Topological exploration of artificial neuronal network dynamics. *Netw. Neurosci.* **3**, 725–743 (2019).
52. S. Taggar, Group composition, creative synergy, and group performance. *J. Creat. Behav.* **35**, 261–286 (2001).
53. S. Harvey, Creative synthesis: Exploring the process of extraordinary group creativity. *Acad. Manage. Rev.* **39**, 324–343 (2014).
54. R. H. R. Pruim *et al.*, ICA-AROMA: A robust ICA-based strategy for removing motion artifacts from fMRI data. *NeuroImage* **112**, 267–277 (2015).
55. O. Esteban *et al.*, fMRIPrep: A robust preprocessing pipeline for functional MRI. *Nat. Methods* **16**, 111–116 (2019).