Verbally mediated cooperation is consistently associated with inter-brain synchrony in frontal and temporoparietal areas: A mini-review and meta analysis

Artur Czeszumski[1#]; Sophie Hsin-Yi Liang[2,3#]; Suzanne Dikker[4,5,6]; Peter König[1,7]; Chin-Pang Lee[2,8]; Brent Kelsen[9*]

[1] Institute of Cognitive Science, Universität Osnabrück, Osnabrück, Germany
[2] Section of Department of Child and Adolescent Psychiatry, Department of Psychiatry, Chang Gung Memorial Hospital at Taoyuan, Taiwan
[3] Chang Gung University College of Medicine, Linkou, Taiwan
[4] Max Planck - NYU Center for Language, Music and Emotion, New York, USA
[5] Department of Psychology, New York University, New York, USA
[6] Department of Clinical Psychology, Free University Amsterdam, Amsterdam, The Netherlands
[7] Institute of Neurophysiology and Pathophysiology, University Medical Center Hamburg-Eppendorf, Hamburg, Germany
[8] Department of Psychiatry, Chang Gung Memorial Hospital at Linkou, Taiwan
[9] Language Center, National Taipei University, New Taipei City, Taiwan

[#]Co-first authors
[*]Corresponding author

Abstract

Cooperation, often supported through verbal communication, is vital to the survival of our species. Recent research has suggested that cooperative behavior is associated with synchronized neural activity between dyads in the frontal and temporo-parietal regions, consistent with findings from single-brain laboratory studies. However, these studies use a variety of cooperation tasks, raising the question whether the reported results can be reliably linked to truly dynamic, verbally supported cooperation. To establish which of these regions, if any, consistently track naturalistic cooperative behavior, we conducted a brief review and meta-analysis of published functional near-infrared spectroscopy (fNIRS) hyperscanning studies examining the occurrence of inter-brain synchrony during cooperative interactions as participants engaged in verbal communication. Nine articles (n=737 participants) met selection criteria and provided evidence of inter-brain synchrony during spoken communication while cooperating, with significantly large overall effect sizes for the full set of experimental conditions in both frontal and temporoparietal areas, suggesting that inter-brain neural synchronization in these regions underlies cooperative behavior in humans. Together, our findings underscore the importance of meta-analyses as a tool to help discern patterns across studies, in this case shedding light on the neural basis of semi-naturalistic cooperative behavior.

Keywords: Inter-brain synchrony, interpersonal neural alignment, hyperscanning, oral communication, cooperation, fNIRS

Introduction

Complex social behavior requires the organization of conduct between individuals, often mediated by spoken language. The importance of cooperation stemming from coordinated communication has been underscored as a crucial aspect in group performance of a wide range of tasks, regularly exceeding what individuals could achieve alone (Kirschner et al., 2018; Reinero et al., 2021). Such social communication has been argued to engage, among other regions, the mirror neuron system as well as the mentalizing system. The former purportedly consists of the inferior frontal gyrus (IFG), inferior frontal lobule (IFL) and superior temporal gyrus (STG). The latter involves the temporoparietal junction (TPJ), precuneus and prefrontal cortex (PFC; Rizzolatti and Fabbri-Destro, 2008; van Overwalle and Baetens, 2009). Both systems are recruited during social interaction and evident in imitation of expressions and actions, understanding intentions, and identifying and interpreting emotions based on facial, gestural, and behavioral expressions (Frith and Frith, 2006). Moreover, research has highlighted the importance of both systems in theory of mind representations, language development and social processes (Saxe and Baron-Cohen, 2006, Frith and Frith, 2006, Perner and Aichhorn, 2008). However, while it is widely agreed upon that successful social collaboration and verbal communication require the alignment of actions and utterances at different levels of representation (Pickering and Garrod, 2013), most of the research has been conducted with single individuals in well-controlled laboratory tasks, largely ignoring the dynamic and interactive nature of cooperative behavior.

Thus, to fully understand the interactive aspects of human social behavior, researchers have argued in favor of more real-life experimental paradigms that increase the ecological validity of results (Matusz et al., 2019; Nastase et al., 2020), made possible in part by recent developments in brain imaging techniques that allow for measuring participants' brain activity during everyday social situations (Parada et al., 2020, Dikker et al., 2017). In addition, an increasing number of scientists have suggested that we need to study multiple participants concurrently to fully understand the underlying dynamics of social cognition. For example, "Second person neuroscience" holds the premise that the engagement arising from actual social interaction differs from observation of social interaction (Schilbach et al., 2013; Redcay and Schilbach, 2019), which is supported by evidence suggesting that certain neural signatures are only observable during 'true' social interaction (Tognoli et al., 2007). Dyadic interactions are of special interest as they are the most common in our social life (Peperkoorn et al., 2020). Therefore, the neural basis of cooperative behavior may only be fully elucidated if single-brain studies are paired with 'hyperscanning' studies, during which participants interact while their brains are simultaneously measured (Dumas et al., 2010, Czeszumski et al., 2020).

Hyperscanning can acquire neural activity through a variety of neural imaging procedures, including electroencephalography (EEG), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), and functional near-infrared spectroscopy (fNIRS) (respectively: Goldstein et al., 2018; Hirata et al., 2014; Koike et al., 2016; Scholkmann et al., 2013). Inter-brain relationships can be quantified as coupling and coherence between two brains (Yun et al., 2012, Cui et al., 2012) or represented as inter-brain networks with graph theory measures (Müller et al., 2013), and inter-brain synchrony has been proposed as a potential neural marker of various cognitive functions. Each apparatus and method has different advantages and disadvantages for hyperscanning (Czeszumski et al., 2020; Ayrolles et al., 2021). Hyperscanning research paradigms vary from studying coordinated finger movements (Tognoli et al., 2007), to real-life situations like playing guitar in a duet (Sanger et al., 2012) or studying multiple brains of high-school students inside the classroom (Dikker et al., 2017). These and many other studies have revealed that inter-brain synchrony plays a crucial role in joint attention, interpersonal communication and coordination, cooperation, and decision-making (reviews: Dumas et al., 2011; Hasson et al., 2012; Konvalinka and Roepstorff, 2012; Burgess, 2013, Koike et al., 2015, Wang et al., 2018, Czeszumski et al., 2020, Kelsen et al., 2020, Hamilton 2021; Dikker et al., 2021).

Many hyperscanning studies have used spoken language during interactions between participants (Kelsen et al., 2020; Pérez et al., 2017; Li et al., 2021), ranging from knowledge sharing, cooperation, turn-taking and naturalistic situations. Many of these studies have reported the emergence of inter-brain synchrony during interpersonal communication based on cooperative interaction in frontal and temporoparietal regions. For example, Holper et al., (2013) studied two interlocutors engaged in philosophical dialogues and found that frontal inter-brain synchrony in frontal areas was increased in dialogs focused on knowledge sharing. Similarly, inter-brain synchrony was found in frontal regions during the Tangram puzzle cooperative paradigm that required spatial and geometrical aptitude (Fishburn et al., 2018), while social communication enhanced inter-brain synchrony during a turn-taking game (Nozawa et al., 2016). Results of these studies suggest that inter-brain synchrony in frontal regions is associated with successful knowledge sharing and cooperative behavior with the use of spoken language. Studies have additionally reported higher inter-brain synchrony in temporoparietal regions present during teacher-student interactions (Zheng et al., 2018; Liu et al., 2019), cooperation (Xue et al., 2018; Lu et al., 2019b), and naturalistic discussion (Jiang et al., 2015).

While these hyperscanning studies largely appear to corroborate laboratory findings on social cooperation, the tasks vary dramatically across studies, ranging from open discussion to rigid games. Therefore, to better understand which regions consistently show inter-brain synchrony during naturalistic collaboration, we conducted a meta-analysis (Zlodowski et al., 2007) of hyperscanning studies that focused on cooperative tasks with oral communication. A recent review article (Kelsen et al., 2020) showed that hyperscanning studies of cooperation during spoken communication predominantly used fNIRS. To improve the comparability across studies, the present review therefore focused specifically on fNIRS studies. We performed a search and selected studies. Further, we calculated effect sizes and assessed the degree of heterogeneity in the selected studies. This study aims to review and assess consistency in findings of inter-brain synchrony in the frontal and temporoparietal areas.

Methods

Search strategy and inclusion criteria

MEDLINE and SCOPUS databases were searched for fNIRS hyperscanning studies of cooperation in accordance with preferred reporting items for systematic reviews and meta-analysis guidelines (PRISMA, Moher et al., 2009). Following consultation with a librarian, two authors independently conducted searches in December 2020 using keywords: ((hyperscanning

OR "social neuroscience" OR fnirs) AND (interbrain OR inter-brain OR interpersonal OR interneural OR inter-neural OR synchron* OR coupling OR alignment OR "functional connectivity") AND (cooperat* OR collaborat*)). Inclusion criteria included: fNIRS hyperscanning; cooperation/collaboration (where participants interacted to achieve a specific outcome such as solve a problem or puzzle or accomplish a particular result, thereby excluding turn-taking activities such as sequential counting and word games); spoken interaction used to share information/analysis/opinions; and healthy adult population. Discrepancies relating to inclusion were resolved through consensus.

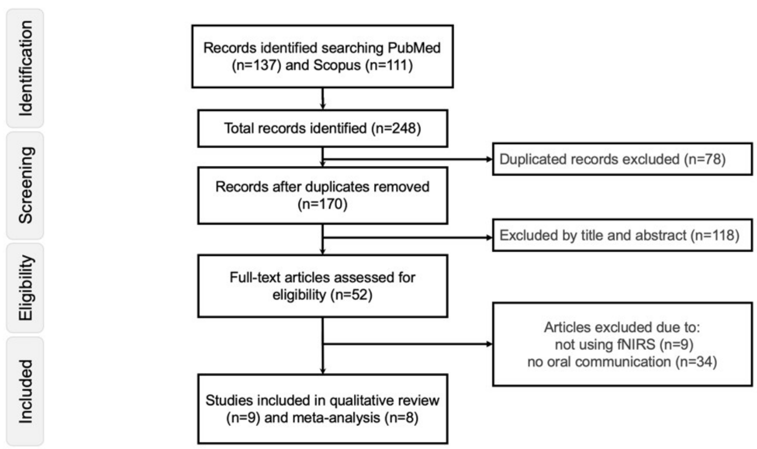


Figure 1. Flowchart of selection process.

Statistical analyses

Because functional equivalence was not expected to hold across the included studies, and a common effect size could not be assumed, we performed a random-effects meta-analysis (Borenstein et al., 2009). We set the threshold for type I errors (alpha) at 0.05 and used effect sizes provided in the selected articles (if reported). We used the Psychometrica website (Lenhard and Lenhard, 2016) to estimate Cohen's *d* from η^2 (if available in the article) or we estimated Cohen's *d* based on information provided in the article (statistical results)(Lipsey and Wilson, 2001). Further, we transformed effect sizes to Hedges' g, although similar to the classical Cohen's *d*, it controls for potential biases in studies with small sample sizes. The heterogeneity across studies was gauged by Cochrane's Q, I^2, τ^2 statistics, and forest plots. We used Cochrane's Q as a statistical test of the null-hypothesis of no heterogeneity, I^2 to quantitatively estimate the variance between studies, and forest plots to visualize all effect sizes. In addition, we used funnel plots to assess publication bias. Publication bias concerns the elevated probability of studies reporting positive results being published. The tendency of journals to give preference to research showing positive findings means negative results may remain unpublished, leading to bias and an increased likelihood of false-positive outcomes (Zlodowski et al., 2007). We tested funnel plots for symmetry with Egger's tests and adjusted effect sizes with trim and fill analysis when needed. Furthermore, we performed meta-regression analysis to test the influence of the variables Age, Gender and Language on overall effect sizes. All statistics were computed using the open-source JASP statistical computing environment (JASP Team, 2020).

Table 1. Selected studies

Study	Country Language	Sample size[#] Relationship	Age M	SD	Activity	Channels Phase analysis IBS regions	IBS comparison
Liu et al. (2016)	• USA • English	• 18 F-F=2 F-M=5 M-M=2 • strangers	21.1	1.7	Cooperation, parallel play, obstruction, dialog (control)	• 19 • WTC • MFG (BA 8 & 10) & dmPFC (BA9)	Cooperation > dialog Obstruction > dialog
Fishburn et al. (2018)	• USA • English	• 60 (57) F=37 • strangers	19.73	1.02	Triads solve tangram puzzle under active, passive, apart & movie conditions	• 18 spread over triad •Autoregressive model & robust correlation • PFC	Together active > movie Together active > apart Together active > together passive
Xue et al. (2018)	• China • Chinese	• 90 (60) F=43 • strangers	20	2.13	Solve RPP (creativity problem) in high-high, high-low & low-low creativity dyads	• 46 • WTC • rDLPFC & rTPJ	rDLPFC: low-low dyads > high-high & high-low dyads rTPJ: low-low dyads > high-low dyads
Lu & Hao (2019)	• China • Chinese	• 44 (42) F=40 • strangers	20.66	2.29	Compare cooperative interaction & similar task hypothesis in groups of real partners and with a confederate	• 22 • WTC • PFC & DLPFC	Real participant > confederate
Lu et al. (2019a)	• China • Chinese	• 118 F=102 • strangers	20.72	2.47	Triads (evaluator, target and non-target) brainstorm RPP under positive, negative & no feedback (control) conditions	• 22 • WTC • FPC & DLPFC	Positive & negative feedback > control
Lu et al. (2019b)	• China • Chinese	• 104(102) F=64 • strangers	21	1.52	Compare cooperation & competition on creativity (AUT) & control (OCT) task	• 46 • WTC • rDLPFC & rTPJ	AUT/cooperation > AUT/competition & OCT/cooperation
Mayseless et al. (2019)	• USA • English	• 56 F-F=8 F-M=8 M-M=9 • strangers	32.09	6.95	Creative cooperation task & cooperation without creativity (control)	• 8 • WTC • aPFC-pSTG, aPFC-TPJ & IFG-pSTG	Creative cooperation > control
Duan et al. (2020)	•China • Chinese	• 84 F-M dyads • lovers=20 strangers=22	20.3	0.84	Cooperate to solve realistic presented problem	• 19 • WTC, GCA • FPC, rTPJ	Lovers > strangers
Lu et al. (2020)	• China • Chinese	• 136(132) F-F=26 F-M=22 M-M=18 • strangers	21.23	2.91	Compare cooperation with creative (AUT) & memory (OCT) conditions	• 46 • WTC • rTPJ (=rPPC) for F-F dyads	F-F dyads > F-M & M-M dyads Creative (AUT) > memory (OCT)

[#] figures in parentheses=sample size after removing unused data. Relationship=participants either known or unknown to each other; F=female, M=male, MFG=middle frontal gyrus; BA=Brodman area; dmPFC=dorsomedial prefrontal cortex; FPC=frontopolar cortex, DLPFC=dorsolateral prefrontal cortex; TPJ=temporoparietal junction, PFC=prefrontal cortex, WTC=wavelet transform coherence, GCA=Granger causality analysis; RPP=realistic presented problem; AUT=alternative uses test; OCT=object characteristic task; rPPC=right posterior parietal cortex

Results

Selected studies

The search resulted in selecting nine studies over the period 2016 to 2020 with an initial total of 737 participants and 669 once unusable data was removed (see Table 1). Six studies were conducted in China, and three were performed in the USA. Therefore, the languages included were Chinese and English. HbO measures were used due to increased sensitivity to blood flow, with preprocessing including low-pass filtering and global detrending. All of the studies employed wavelet transform coherence (WTC; Grinsted et al., 2004) to convert the signal for inter-brain synchrony analysis. For the subsequent meta-analysis, the data from one study was exluded because the reported inter-brain synchrony was asymmetric between brain regions (Mayseless et al. 2019).

The conditions under which inter-brain synchrony occurred depended upon the experimental setup. Three studies examined communication by comparing cooperation with other conditions. One study included obstruction, parallel play, and dialog conditions while playing a Jenga game (Liu et al., 2016). Another required solving a tangram puzzle under active, passive, apart, and observation conditions (Fishburn et al., 2018). A further study compared cooperative performance in groups with real partners and a false collaborator (Lu and Hao, 2019). All reported inter-brain synchrony predominantly in frontal neural regions and recounted finding higher inter-brain synchrony in cooperative conditions as opposed to conditions without cooperation. For example, Fishburn et al. (2018) found that completing puzzles cooperatively resulted in heightened synchrony. Taken together, even though different paradigms were used in these studies, they all report higher inter-brain synchrony in frontal regions for cooperative conditions in comparison to other conditions.

Another group of studies investigated cooperation in spoken communication through the lens of creative activities. For example, Xue et al. (2018) paired participants according to their level of creativity and detected that low-low pairs showed higher inter-brain synchrony resulting from their improved cooperation behavior. Lu et al. (2019a & b) found in the first instance that solving a creative and realistically presented problem led to higher inter-brain synchrony with both positive and negative feedback compared to a control condition of no feedback, and in the second study that combined cooperation and creativity generated inter-brain synchrony greater than competition together with creativity and a control condition requiring memory and cooperation. In another study, Mayseless et al. (2019) reported asymmetric coupling between different neural regions while contrasting cooperative tasks with and without creativity. From a different perspective, Duan et al. (2020) applied a cooperative paradigm to solving problems among participants in a romantic heterosexual relationship or between strangers. Their discovery of higher inter-brain synchrony in lover dyads indicated the advantages of couples in interaction and cooperation while solving problems. Finally, in Lu et al.'s (2020) study, female-female dyads showed higher inter-brain synchrony while conducting cooperative tasks with creative and memory conditions in contrast to female-male and male-male pairs, suggesting females' enhanced ability to consider others' perspectives. These studies reported inter-brain synchrony in both frontal and temporoparietal regions.

Taken together, selected studies pointed in the direction that inter-brain synchrony in frontal and temporoparietal regions plays a crucial role in cooperation with oral communication. To test that, we performed a meta-analysis of the selected studies.

Meta-analysis

A random-effects model for all twenty five experimental conditions across the eight studies reported a significantly large overall effect size (g=0.92, 95% CI [0.78, 1.05], n=25, z=13.34, p<0.001). Cochran's Q-statistic (Q=288.75, p<0.001) showed significant variation around the weighted average effect for the studies included. The proportion of observed variance was significantly high at I^2=94.28 (> 75 representing large heterogeneity), and a scaled measure of dispersion between true effect sizes of the studies was τ^2=0.10 (Higgins and Thompson, 2002). These results suggest that the selected studies had an overall large effect size for comparison between cooperative and non-cooperative conditions. Furthermore, the variance between studies was high, suggesting that nearly all variance between studies was not due to chance.

Guided by the selected studies showing frontal and temporoparietal areas as neural regions of interest, we continued with subgroup analyses to directly evaluate inter-brain synchrony within these loci (Figure 2).

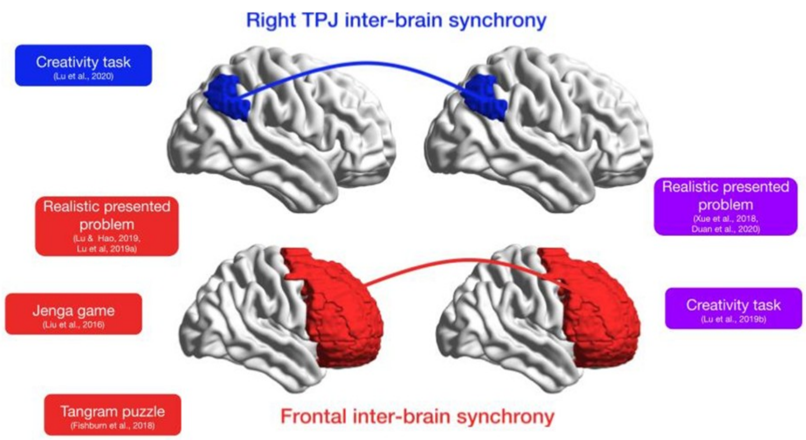
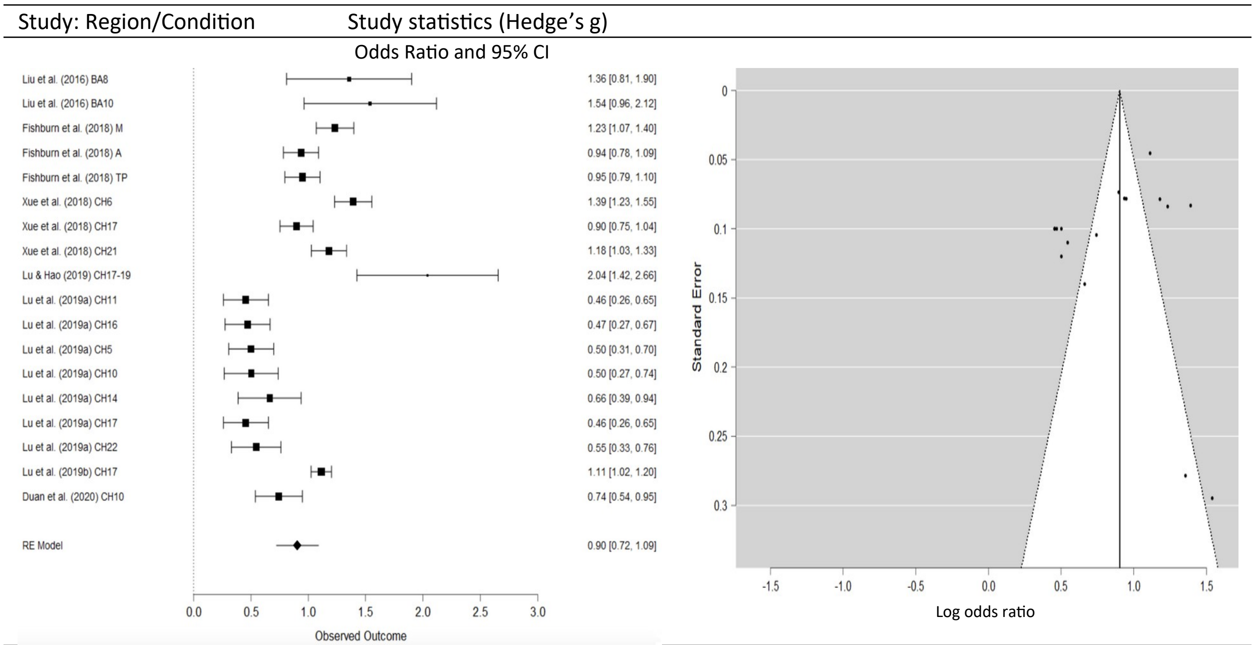


Figure 2. Inter-brain synchrony in frontal and temporoparietal regions (TPJ). Boxes represent tasks in selected studies. Inter-brain synchrony between participants in the temporoparietal region is shown in blue, and in frontal regions in red. Purple boxes represent tasks that showed inter-brain synchrony in both frontal and temporoparietal regions. The brain template and AAL 90 atlas was used to generate the figure (Xia 2013).

Frontal region analysis

A random-effects model of the selected studies (see Figure 3) reported a significantly large overall effect size (g=0.90, 95% CI [0.72, 1.09], n=18, z=9.72, p<0.001) for inter-brain synchrony in the frontal region of participants (n=481). The Cochran's Q-statistic (Q=205.62, p<0.001) showed significant variation for the studies included. The proportion of observed variance was significantly high at I^2=94.10, and a scaled measure of dispersion between true effect sizes of the studies was τ^2=0.14. Visual inspection of the funnel plot and Egger's test for the frontal region (t=2.22, p=0.027) indicated significant asymmetry (Egger et al., 1997). A follow-up trim and fill analysis resulted in a slightly smaller overall effect size and confidence interval (*g*=0.88, 95%CI [0.66, 1.09]). Taken together, the results suggest that across different studies and experimental paradigms there are differences in inter-brain synchrony between cooperative and non-cooperative conditions in frontal areas.



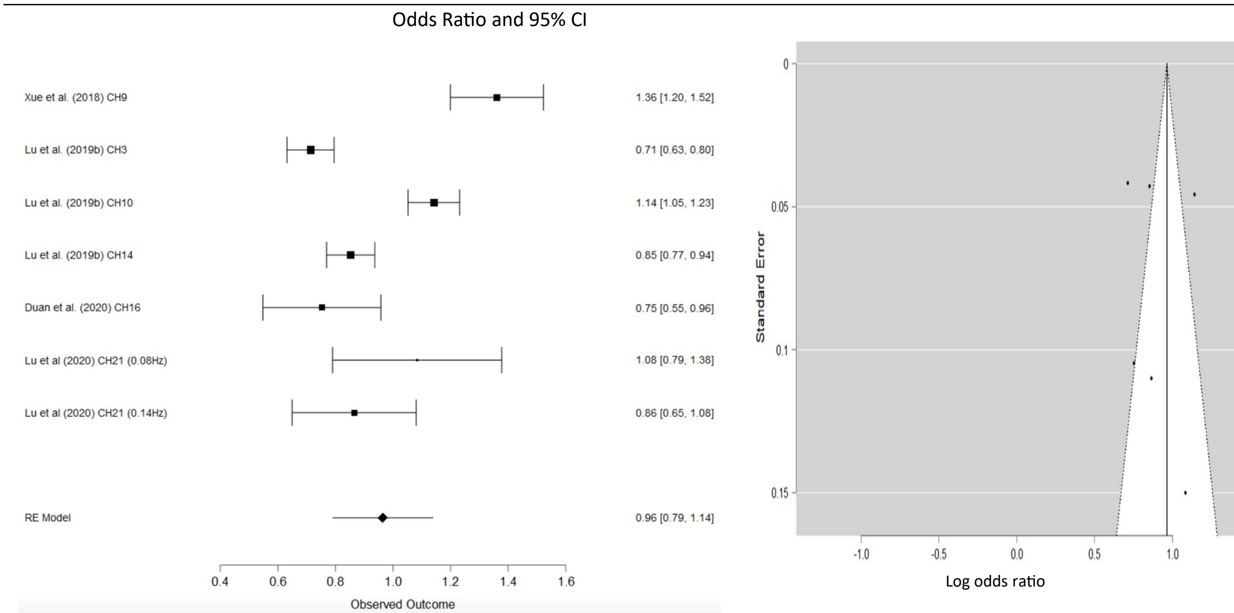
CI= confidence interval, BA=Brodman area, M=Movie (i.e., active vs. movie condition), A=Active (active vs. apart condition), TP=Together passive (active vs. together passive condition), CH=Channel, RE Model=overall random effects model

Figure 3. Forrest and funnel plots for frontal region inter-brain synchrony. On the left, boxes represent effect sizes, and whiskers confidence intervals. On the right, dots represent different studies.

TPJ analysis

A random-effects model for inter-brain synchrony in the TPJ region (see Figure 4) reported a significantly large overall effect size (*g*=0.96, 95%CI [0.79, 1.14], n=7, *z*=10.56, *p*<0.001) for participants (n=384). (It is important to note here that some studies tested both frontal and TPJ regions. That is why a number of participants reported for subgroup analysis is higher than the total number of participants.) We found that Cochran's Q-statistic (Q=83.13, *p*<0.001) for variation around the weighted average effect was significant. Furthermore, the proportion of observed variance (I^2=92.75) was high. Dispersion between true effect sizes of the studies (τ^2=0.05) was found as well. In addition, visual inspection of the funnel plot and an Egger's test indicated no significant lateral asymmetry for the TPJ region (*t*=0.33, *p*=0.74). Therefore, in the most part, these results are similar to what we found for the frontal region, suggesting that there are differences in inter-brain synchrony in the TPJ region between cooperative and non-cooperative conditions.

Study: Region/Condition Study statistics (Hedge's g)



CI= confidence interval, CH=Channel, Hz=hertz, RE Model=overall random effects model

Figure 4. Forrest and funnel plots for TPJ region inter-brain synchrony. On the left, boxes represent effect sizes, and whiskers confidence intervals. On the right, dots represent different studies.

Meta-regression

To test whether any of the independent variables (Age, Gender, Language) affected our analysis, we performed meta-regression examinations. Wald tests demonstrated no significant association between observed inter-brain synchrony and independent variables overall or for either of the subgroup regions. English was used as the reference language. For the full dataset, Age (*Beta*=-0.11, *S.E.*=0.14, *z*=-0.74, *p*=0.46), Gender (*Beta*=-0.90, *S.E.*=0.52, *z*=-1.73, *p*=0.084) and Language (*Beta*=0.11, *S.E.*=0.20, *z*=0.56, *p*=0.573) all displayed insignificant results. Regarding the frontal region, Age (*Beta*=-0.04, *S.E.*=0.20, *z*=-0.22, *p*=0.83), Gender (*Beta*=-1.18, *S.E.*=0.79, *z*=-1.50, *p*=0.133) and Language (*Beta*=0.10, *S.E.*=0.25, *z*=0.38, *p*=0.705) results similarly showed no significant associations. Additionally, results for the TPJ found no significance between variables Age (*Beta*=-0.09, *S.E.*=0.2, *z*=-0.46, *p*=0.64) and Gender (*Beta*=2.17, *S.E.*=1.41, *z*=1.54, *p*=0.124). The variable Language was not entered into the meta-regression equation for the TPJ region as all of the studies were conducted in Chinese. The results of meta-regression analysis suggest that Age, Gender, and Language differences did not modulate overall effect sizes for the studies overall or the frontal and temporoparietal subgroups.

Discussion

In this study, we reviewed and quantified overall effect sizes for inter-brain synchrony in hyperscanning studies of cooperation involving spoken interaction. We found that these studies reported significant overall effect sizes for inter-brain synchrony in both frontal and temporoparietal regions, in line with previous research showing that the FPC, PFC, DLPFC, and TPJ are commonly implicated in tasks requiring social interaction, coordination, and cooperation (Stallen and Sanfel, 2013). Furthermore, these areas have been associated with cooperation towards achieving common objectives and coordinated tasks such as finger tapping (Dumas et al., 2012) and educational interactions (Pan et al., 2018). The PFC has been identified for its role in working memory, and executive function processes (Heinonen et al., 2016), and the rTPJ is recognized for its function regarding attention, memory and social perspective taking (Liu et al., 2016; Xue et al., 2018, Dumas 2014).

Extending from this point, cooperation via spoken language connects with the theory of mind, which is known to be significant in pragmatic language processing and shared social interactions as interlocutors acknowledge different mental states, such as one's own and other's beliefs, aspirations and intentions. This cognitive ability is crucial for the information processing and behavioral regulation required to overcome the ambiguity of meaning necessary for efficient referential communication during reciprocal cooperative social exchanges (Liu et al., 2016; Paunov et al., 2019; Saxe and Kanwisher, 2003; Sidera et al., 2018). Therefore, results of our meta-analysis suggest that frontal and temporoparietal regions are not only involved in processing information during collaboration in separated brains, but actually synchronization between different brains in these regions plays a crucial role.

Thus, the results elucidate consistent patterns of inter-brain connectivity initiated while engaging in spoken communication during cooperation. Furthermore, the meta-analysis revealed a high variance between studies that cannot be explained by chance. This is most likely due to the large variety of conditions used in different studies. Despite these constraints, this meta-analysis is significant in that it represents the first attempt we are aware of to quantify inter-brain synchrony across a number of published studies where participants used spoken language to coordinate actions while completing a variety of tasks.

Further investigations into the emergence and mechanisms of inter-brain synchrony will advance our understanding of social communication and illuminate the role of neural processes and connectivity in fostering mutual understanding among cooperating interlocutors. Not only further investigations are required but also attempts to replicate mentioned results. The fNIRS community would highly benefit from a large scale replication project similar to the EEG community (Pavlov et al., 2021). Additionally, it is hoped that editorial teams remain open to publication of studies with variety in terms of language and experimental designs and the publication of research leading to insignificant and negative inter-brain synchrony outcomes, thereby reducing the likelihood of bias.

Conclusion

The results of this meta-analysis reveal that verbally mediated cooperation is consistently associated with inter-brain synchrony in frontal and temporoparietal areas, suggesting that inter-brain neural alignment in these regions underlies cooperative behavior in humans. These findings underscore the importance of meta-analyses in detecting patterns across studies and elucidating the neural basis of semi-naturalistic cooperative behavior. Finally, prospective study designs and analysis methods are recommended to further illuminate the mechanisms of verbally mediated social cooperation.

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SHYL, CPL and BAK conceived of the study; SHYL and BAK conducted the database search; AC and BAK prepared and analyzed the statistics; AC, SHYL, SD, PK and BAK wrote the initial manuscript; all authors revised and agreed upon the final version of the article.

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