Neural Correlates of Partnered Interaction as Revealed by Cross-Domain ALE Meta-Analysis

Kiah Prince and Steven Brown

Department of Psychology, Neuroscience and Behaviour, McMaster University

Objective: Partnered interactions are a key manifestation of the cooperative nature of the human species. Partnering can take on a diversity of formats, including cognitive activities like problem-oriented conversations and physical tasks like moving furniture together. The primary objective of the present study was to use quantitative meta-analysis techniques to explore the neural basis of partnered interaction in search of domain-general brain areas common across interaction modalities. ***Method:*** An activation likelihood estimation (ALE) meta-analysis of 18 functional neuroimaging studies was conducted that contrasted task performance with a partner and task performance in the absence of an interactive partner. Various interactive tasks were included that covered both cognitive and physical formats of partnering. ***Results:*** The results of the meta-analysis revealed a single significant ALE cluster with two subpeaks in the right temporoparietal junction (rTPJ), an area strongly associated with mentalizing, social prediction, and cooperation. ***Conclusions:*** The identification of the rTPJ as the principal cross-modal area for partnering highlights the role of implicit mentalizing in all forms of partnered interaction. The discovery of two distinct subpeaks may indicate unique differences in mentalizing function between the two areas.

Public Significance Statement
The neuroscience of real-time social interaction has garnered a great deal of attention among researchers in recent years. We conducted a meta-analysis of 18 neuroimaging studies of partnered interaction across both cognitive and physical tasks. The results indicate the importance of mentalizing and social prediction for the process of partnering across diverse modalities of interaction.

Humans are a highly cooperative species, and people readily engage in a multitude of collaborative behaviors that serve joint goals (Axelrod & Hamilton, 1981; McNeill, 1995; Pacherie, 2012; Trivers, 1971). Such behaviors include both cognitively oriented tasks (e.g., jointly consulting a map to determine the best route to a destination) and physical actions (e.g., moving furniture together, engaging in group dancing). Partnered interaction is predicated on the cooperative cognitive and motoric skills that emerged in early

human evolution and continue to shape cognition and culture in the modern era. The behavioral synchrony and interpersonal coordination found in human bonding rituals, such as music and dance, have been shown to promote the attribution and understanding of intentional states between interacting partners (Baimel et al., 2015, 2018), enhancing mutual cognitive alignment and cooperative engagement (Kokal et al., 2011; Reddish et al., 2013; Valdesolo et al., 2010).

Given the centrality of social interactions to human behavior, it is paradoxical that most social neuroscience research has been conducted using individual participants in isolation making social observations from the noninteractive "third-person" vantage point of an external spectator (Sameen et al., 2013; Schilbach et al., 2013). Redcay and Schilbach (2019) argued that research on the neural basis of social cognition needs to broach "second-person neuroscience" by examining real-time social interactions between people.

Partnering can be studied across a variety of tasks but is primarily defined as two or more individuals engaging in a cooperative interaction while adjusting their behaviors in response to one another's actions. Partnering depends on real-time feedback loops involving concurrent mutual adjustment and contingent cooperative coordination (Keller et al., 2014). This has been well studied at the sensorimotor level with regard to joint physical actions, such as the microadjustments in timing that two pianists make while performing a duet (Goebl & Palmer, 2009). Such phenomena have been analyzed in the literatures devoted to action coordination (Sebanz et al., 2007) and rhythmic synchronization (Keller et al., 2014). The tasks in these studies typically have high physical-effort requirements that rely on motor adaptivity and action simulation (Sebanz & Knoblich, 2009).

Partnering has also been studied in sociocognitive contexts that lack the precise motor synchrony requirements of joint physical actions. This includes tasks such as conversation (Rauchbauer et al., 2019), cooperative economic games (e.g., prisoner's dilemma game; Rilling et al., 2004), and collaborative problem-solving (Shpurov et al., 2020) that all require a high degree of mental effort and conceptual thinking. Although the various forms of partnered interactions rely on different effector systems and temporal dynamics, they all share a requirement for ongoing mutual adjustment to maintain the exchange. Despite recent advances in the neuro-imaging of social interactions (e.g., novel hyperscanning techniques; Czeszumski et al., 2020; Misaki et al., 2021), little work has attempted to identify domain-general mechanisms that are common to the various formats of partnering.

One such mechanism might be mentalizing, which is the process of inferring and predicting the mental states of another person, including their emotions, beliefs, and intentions (Frith & Frith, 2006; Nichols & Stich, 2003). The cognitive and neural bases of mentalizing have been well examined in experimental studies, but this has generally occurred outside of the context of partnering, typically employing fictional scenarios in which participants are tasked with making mental state inferences about characters from the perspective of a passive spectator (Koster-Hale & Saxe, 2013). Most of these studies have focused on the process of *explicit* mentalizing, whereby participants are directly asked to report on the mental states of others. The application of such studies to partnered interaction is limited by the fact that many forms of partnering are nonverbal (e.g., dancing), and even those that are verbal are far more likely to involve *implicit* mentalizing than explicit statements about a partner's emotions and beliefs. Key questions about the neural basis of partnering that need to be addressed include whether the brain system that mediates explicit mentalizing is also active during implicit mentalizing and whether the brain system that mediates mentalizing in a spectator context is also active during face-to-face social interactions (Alkire et al., 2018; Redcay et al., 2010).

The brain network that mediates mentalizing in spectator contexts is known as the mentalizing system and includes the temporoparietal junction (TPJ), posterior cingulate cortex (PCC), medial prefrontal cortex (mPFC), and anterior temporopolar cortex (ATPC; Frith & Frith, 2003, 2006; Spunt & Lieberman, 2013). Studies of physical partnering provide evidence that the mentalizing system can be activated by tasks that have no requirement for explicit mentalizing, such as when participants are instructed to jointly control a force transducer (Abe et al., 2019) or jointly balance a bar (Newman-Norlund et al., 2008) without verbal communication. This corroborates the results of cognitive studies showing that the mentalizing system is activated when people implicitly mentalize (i.e., in a passive manner)

during a social exchange (Naughtin et al., 2017; Van Overwalle & Vandekerckhove, 2013).

There is increasing evidence that the mentalizing system is active during face-to-face interactions (Redcay et al., 2010), suggesting a role for implicit mentalizing in partnering. In particular, the TPJ appears to be a promising candidate for a brain area that might mediate implicit mentalizing during collaborative actions. The TPJ is active during both joint actions and sociocognitive problem-solving spanning a wide variety of tasks (e.g., physical interaction, Chauvigné et al., 2018; joint attention, Koike et al., 2019; cooperative puzzle solving, Shpurov et al., 2020; cooperative word games, Salazar et al., 2021). The established role of the TPJ in intention processing and the attribution of mental states to others during passive spectator tasks (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005) may explain why this area is active during partnered tasks.

The principal objective of the present study was to conduct a meta-analysis of functional neuroimaging studies of partnered interaction with the aim of identifying domain-general brain areas that are active across the diverse formats of partnering. To the best of our knowledge, no previous studies have attempted to quantitatively address the overlap in brain areas reported across the functional magnetic resonance imaging (fMRI) literature on partnered interaction. We used activation likelihood estimation (ALE) meta-analysis to explore the neural correlates of partnered interaction in a cross-domain fashion, examining studies of both physical and sociocognitive interactions. The ALE meta-analysis was carried out on a set of 18 functional neuroimaging experiments that contained a contrast between a task performed with a partner and the same task performed individually without mutual adjustment requirements. This design was intended to reveal brain areas specific for partnering while controlling for the sensorimotor demands of task performance. The partnering tasks included in the meta-analysis covered the two broad categories of physical partnering (motor adaptivity, joint action) and cognitive partnering (sociocognitive problem-solving, conceptual thinking). The TPJ was predicted to be a major cross-domain brain area for partnering, as based on its presence in a number of studies of partnering across modalities (outlined above). Other mentalizing areas, such as the PCC and mPFC, were also expected to be concordant across studies. The cerebellum was predicted to be another concordant brain region due to its role in anticipatory adjustment and error correction (Van Overwalle et al., 2015). Finally, motor-planning areas such as the premotor cortex (PMC) and supplementary motor area were expected to be present due to the inclusion of tasks involving action observation and sensorimotor adaptivity.

Method

ALE is a coordinate-based statistical meta-analysis method that determines the convergence between activation foci reported in a set of neuroimaging experiments (Eickhoff et al., 2009; Turkeltaub et al., 2002). All foci are modeled as three-dimensional Gaussian probability distributions centered at the given stereotactic coordinates (x, y, z). The width of each distribution is based on empirical estimates of spatial uncertainty constrained by sample size such that an increase in participant number leads to increasing certainty in the activation profile (Eickhoff et al., 2009). The probability distributions are arranged into an activation map containing the probability of an activation being located at each individual voxel. The activation map is then tested for convergence against a null distribution of simulated, spatially independent gray matter activations using a random-effects analysis. The result provides an ALE score for each peak in a given significant distribution cluster based on the threshold permutations, cluster-level familywise error threshold (FWE), and a cluster-forming threshold determined a priori. An ALE score is analogous to an effect size reported in standard meta-analyses outside of the neuroimaging field (Eickhoff et al., 2012).

Inclusion Criteria

The neuroimaging studies included in the meta-analysis were obtained through searches of the PubMed database. To identify relevant studies, we used the search term "fMRI" followed by at least one of the following keywords: "partner," "mentalizing," "social," "interact," "cooperation," and "joint action." Further studies were obtained through an examination of the reference sections of the identified studies and any additionally identified studies also had their reference sections examined in the same manner,

thus extending the search beyond the PubMed database. Finally, the obtained articles were entered into the Google Scholar database to search for later articles that had cited them. A flow diagram of the article selection process is presented in Supplemental Figure 1 according to Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al., 2021). The articles covered two broad categories based on the nature of the task in the experiment (Figure 1). All joint action tasks were part of the "physical partnering" category. All interactive tasks without a joint action requirement were part of the "cognitive partnering" category. All studies were combined into a single meta-analysis, and the physical/cognitive distinction was only used for post hoc interpretation. The inclusion criteria for experiments in the meta-analysis were as follows:

1. Only neuroimaging studies using fMRI with healthy participants were included. All other forms of neuroimaging were excluded to maintain comparable spatial resolution for the ALE analysis.
2. The studies must have reported whole-brain activation analyses using standardized stereotaxic coordinates in either Talairach or Montreal Neurological Institute (MNI) space. Studies that used a masking procedure, reported only partial brain coverage, or reported only specific region-of-interest analyses were excluded.
3. The studies must have included participants concurrently performing a partnering task that required mutual adjustment, thereby excluding studies in which participants interacted over a considerable time delay or without reciprocity requirements.
4. The studies must have reported a contrast between a partnered task and a matched nonpartnered control task. The latter could take the form of either a solo task or a two-person task not requiring mutual adjustment.

For studies that reported two or more similar contrasts, only one of them was included in the analysis to avoid artificially increasing the concordance of the activated regions (Müller et al., 2018). The contrast that was selected was the one that best matched the contrasts in the other selected studies, without any consideration for the results. This restriction was applied to the following articles that met the inclusion criteria: Newman-Norlund et al. (2008), Chaminade et al. (2012), Decety et al. (2004), and Lee et al. (2018). Redcay et al. (2010) was the only publication to

Figure 1
List of Studies and Experiments Included in the Meta-Analysis

	Reference	Task	Selected Experiment
COGNITIVE	Alkire et al. (2018)	Mental state reasoning	Peer > Character
	Chaminade et al. (2012)	Rock/paper/scissors	Intentional agent > Random agent
	Decety et al. (2004)	Pattern making game	Cooperation > Independent
	Elliot et al. (2006)	Coin flip game	Cooperation > Playing alone
	Kircher et al. (2009)	Prisoner's dilemma game	Human > Computer
	Koike et al. (2020)	Joint attention	Joint attention > Control
	Lee et al. (2018)	Tetris-like game	Cooperation task > Individual task
	Redcay et al. (2010)	Joint attention	Joint attention > Solo attention
		Eye-gaze communication game	Live > Recorded
	Rice et al. (2016)	Mental state reasoning	Live > Recorded
	Salazar et al. (2021)	Word games	STST > LLG
	Schilbach et al. (2010)	Joint attention	Other > Self
	Schuwerk et al. (2017)	Posner spatial cueing paradigm	Social > Non-social
	Shpurov et al. (2020)	Grid puzzle	Group > Individual problem solving
	Xie et al. (2020)	Drawing	Collaborative > Independent
PHYSICAL	Abe et al. (2019)	Joint grip-force matching	Perform joint > Perform single
	Chauvigné et al. (2018)	Partnered hand dancing	Partnered > Non-partnered
	Newman-Norlund et al. (2008)	Joint grip-force bar balancing	Isomorphic > Solo

Note. LLG = last letter game; STST = "say the same thing" game.

run two separate participant groups in distinct experiments that both met the inclusion criteria. Data from both experiments of this article were included. The final meta-analysis included 18 experiments (273 foci, 431 participants) from 17 published studies. The study set (see Figure 1) comprised three physical partnering experiments (Abe et al., 2019; Chauvigné et al., 2018; Newman-Norlund et al., 2008) and 15 cognitive partnering experiments (Alkire et al., 2018; Chaminade et al., 2012; Decety et al., 2004; Elliott et al., 2006; Kircher et al., 2009; Koike et al., 2019; Lee et al., 2018; Redcay et al., 2010; Rice et al., 2016; Salazar et al., 2021; Schilbach et al., 2010; Schuwerk et al., 2017; Shpurov et al., 2020; Xie et al., 2020).

The meta-analysis was performed using Ginger-ALE 3.0.2 (www.brainmap.org/ale) according to standard methods (Eickhoff et al., 2009, 2012, 2016; Müller et al., 2018). We converted Talairach coordinates to MNI coordinates within GingerALE prior to the analysis because the majority of the included experiments reported coordinates in MNI space. The meta-analysis was performed with 5,000 threshold permutations and a cluster-level FWE threshold of $p < .05$ with a cluster-forming threshold of $p < .001$. The resulting ALE map was registered onto an MNI-normalized template brain using Mango 4.1 (ric.uthscsa.edu/mango).

Contribution Analysis

A descriptive "contribution analysis" (CA) was conducted to further investigate the brain areas involved in partnered interactions. The activated brain regions across all experiments were summarized to determine their prevalence across the sampled literature. This was done because of the stringent statistical constraints imposed by ALE meta-analysis, which require overlap at the voxel level. The CA was conducted at the coarser level of the anatomical region to serve as a qualitative parallel to the voxel-based approach of ALE. The activation coordinates reported in the included articles were classified with respect to two functional brain networks: (a) the mentalizing system, with four constituent anatomical regions (TPJ, PCC, precuneus [PCu], and mPFC) and (b) motor and premotor areas, with three constituent regions (lateral PMC, inferior frontal gyrus [IFG], and cerebellum). For each anatomical region, the percentage of experiments in the meta-analysis that reported a significant activation in that region was calculated.

Results

Figure 2 presents the results of the ALE meta-analysis registered onto a template brain. The MNI coordinates of the ALE peaks are listed in Table 1. The results revealed a single ALE cluster with two subpeaks differing in anteroposterior location. This cluster was located in the right TPJ (rTPJ; Figure 2), a core component of the mentalizing system. No additional clusters were found at lower cluster-forming thresholds (data not shown).

Figure 2
ALE Results Registered Onto an MNI-Normalized Template Brain
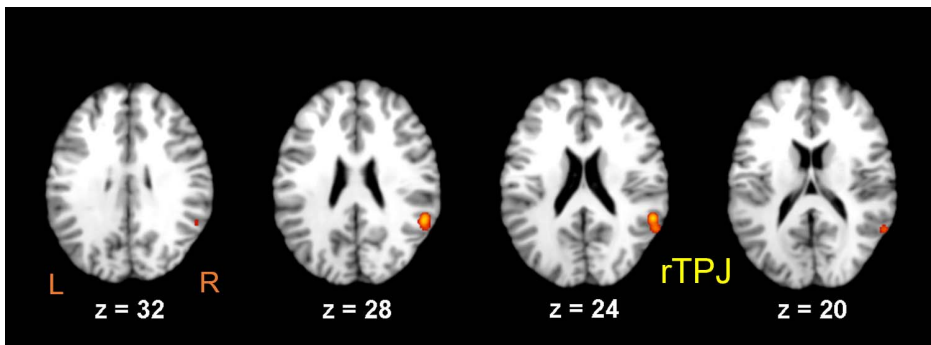
Note. The MNI z level is indicated below each slice. The left side of the slice (L) is the left side of the brain. ALE = activation likelihood estimation; MNI = Montreal Neurological Institute; rTPJ = right temporoparietal junction.

Table 1

Results of the ALE Meta-Analysis

Cluster/brain region	BA	MNI coordinates			ALE
		x	y	z	
rTPJ	39	58	−46	26	0.031
		60	−54	24	0.021

Note. Stereotaxic coordinates are presented in millimeters along the left–right (x), anterior–posterior (y), and superior–inferior (z) axes. The ALE column reports the ALE score for each cluster. ALE = activation likelihood estimation; MNI = Montreal Neurological Institute; BA = Broadman area; rTPJ = right temporoparietal junction.

The results of the CA are presented in Table 2. The rTPJ activation from the ALE analysis was reported in 50% (9/18) of the experiments. Additional functional areas that were found in the CA but were not sufficiently concordant to form significant ALE clusters included: (a) mentalizing areas: left TPJ (lTPJ; 44.4%), PCC (22.2%), PCu (38.9%), and mPFC (33.3%) and (b) motor/premotor areas: PMC (44.4%), IFG (44.4%), and cerebellum (44.4%). In total, 12 experiments (66.7%) reported activation in either the lTPJ or rTPJ and, of those experiments, five reported bilateral TPJ activations. The rTPJ appeared to be more prominent in the physical tasks than the cognitive tasks (100% vs. 40%, respectively). In addition, while the IFG and cerebellum were more prominent in the physical tasks than the cognitive tasks, the PMC was more similar across the task categories.

The observed ALE peaks were compared to rTPJ peaks reported in seven published ALE meta-analyses of theory-of-mind functioning (Bzdok et al., 2012; Decety & Lamm, 2007; Krall et al., 2015; Kubit & Jack, 2013; Molenberghs et al., 2016; Schurz et al., 2014; van Veluw & Chance, 2014) to validate that the rTPJ coordinates observed in the present ALE analysis could be reasonably associated with the process of mentalizing. Table 3 presents 13 rTPJ peaks from these analyses, all derived from standard spectator-based mentalizing tasks. All peaks are reported in MNI space. The accrued meta-analyses indicate an average mentalizing-related rTPJ coordinate of $x = 55$, $y = −53$, $z = 22$, marking the location of the angular gyrus in the inferior parietal lobule. The rTPJ subpeaks from the present meta-analysis—with coordinates $x = 58$, $y = −46$, $z = 26$ and $x = 60$, $y = −54$, $z = 24$—thus appear to be compatible with the peaks reported in the meta-analyses of theory-of-mind, with the posterior peak appearing to be especially similar.

Discussion

To investigate the neural basis of partnered interaction cross-modally, we conducted an ALE meta-analysis of 18 neuroimaging experiments, incorporating tasks of both physical and socio-cognitive partnering (Figure 1), all of which controlled for the sensorimotor features of partnered task performance using a matched noninteractive baseline condition. The rTPJ was found to be the most concordant area of activation across these studies. This result conforms with the prediction that the rTPJ would be a cross-modal brain area across domains of partnering, suggesting that implicit mentalizing may be a

Table 2

Contribution Analysis

Experiment category	Mentalizing system					Motor/premotor areas		
	rTPJ	lTPJ	PCC	PCu	mPFC	PMC	IFG	Cerebellum
Physical	3/3	2/3	0/3	3/3	1/3	1/3	2/3	2/3
	100%	66.7%	0%	100%	33.3%	33.3%	66.7%	66.7%
Cognitive	6/15	6/15	4/15	4/15	5/15	6/15	6/15	6/15
	40%	40%	26.7%	26.7%	33.3%	46.7%	40%	40%
Total	9/18	8/18	4/18	7/18	6/18	8/18	8/18	8/18
	50%	44.4%	22.2%	38.9%	33.3%	44.4%	44.4%	44.4%

Note. The table indicates the number (and percentage) of studies that report activations in eight anatomical regions across the three physical experiments, 15 cognitive experiments, and 18 experiments overall. rTPJ = right temporoparietal junction; lTPJ = left temporoparietal junction; PCC = posterior cingulate cortex; PCu = precuneus; mPFC = medial prefrontal cortex; PMC = premotor cortex; IFG = inferior frontal gyrus.

Table 3

Summary of rTPJ Peaks Reported in Seven Published Meta-Analyses of Theory-of-Mind Functioning

Authors	Meta-analysis	rTPJ peak (x, y, z)
Bzdok et al. (2012)	Theory-of-mind	56, −50, 18
	Empathy	52, −58, 22
	Conjunction	52, −58, 20
Decety and Lamm (2007)	Empathy	56, −56, 22
	Theory-of-mind	60, −52, 20
Krall et al. (2015)	False belief	54, −52, 26
Kubit and Jack (2013)	Attention reorienting	60, −46, 22
	Theory-of-mind	56, −55, 26
Molenberghs et al. (2016)	Theory-of-mind	52, −52, 22
		54, −54, 26
Schurz et al. (2014)	False belief	56, −47, 24
	Theory-of-mind	56, −56, 18
van Veluw and Chance (2014)	False belief	55, −53, 24
The present analysis	Partnered interaction	58, −46, 26
	(cross-modal)	60, −54, 24

Note. The studies are listed alphabetically. Coordinates are reported in MNI space. rTPJ = right temporoparietal junction; MNI = Montreal Neurological Institute.

critical mediating process for partnered interaction, regardless of the modality of the interaction. The association of this area with mentalizing was demonstrated by the overlap of its coordinates with rTPJ clusters found in meta-analyses of spectator-based mentalizing separate from partnered interaction (Table 3). Next, the CA looked beyond the ALE analysis to reveal the importance of other relevant brain areas that mediate both mentalizing (most notably the lTPJ and PCu) and motor planning (the PMC, IFG, and cerebellum), but whose overlap at the voxel level was too low to generate ALE clusters. The overall results suggest that partnering results from a combination of mentalizing and motoric processes related to joint action.

Mentalizing and Partnering

The observation of a significant ALE cluster in this meta-analysis was perhaps surprising given the diversity of the experimental tasks that were included. The finding that the rTPJ is a key area for partnered interaction across both motoric and sociocognitive forms of partnering is consistent with the results of Yuan et al. (2018), who showed that the TPJ and PCC were active during story-telling tasks regardless of whether the story was told using speech, pantomime, or drawing for production. While cognitive partnering tasks

often have a clear mentalizing component (if only implicitly), the role of mentalizing in motoric partnering is less intuitive. Research has shown that participants in motoric synchrony experiments show an increase in mental state attribution to their partners, but not to other nonrelevant individuals (Baimel et al., 2015, 2018), supporting an association between physical partnering and mentalizing. Enrici et al. (2019) suggested that the mentalizing system is an intention-processing network that functions as a core component of both gestural and verbal human communication. Mentalizing is an underappreciated component of physical partnering, where almost all of the attention in research studies is directed toward sensorimotor adaptivity, rather than psychological processes associated with inferring a partner's intentions and emotions.

The domain-generality of the TPJ in standard theory-of-mind studies is demonstrated by its responsiveness to both self and other processing and to both implicit and explicit mentalizing (Brown, 2020). The posterior rTPJ subpeak from the ALE analysis strongly overlapped with rTPJ peaks found in seven previous meta-analyses of standard theory-of-mind processing from a spectator perspective (Table 3), thereby strengthening the case for the engagement of implicit mentalizing during partnered interaction. Taken together, these results suggest that

partnered interaction may recruit the rTPJ regardless of the task requirements and effector system employed.

Implications for a "Second-Person Neuroscience"

The ALE results suggest that the mentalizing system active during second-person social interaction might be the same as that engaged during third-person social observation. While mentalizing is undoubtedly a key component of partnered interaction, it has no necessary association with partnering because it readily occurs during spectator-based observation in the absence of interaction. Therefore, unless there is compelling evidence that partner mentalizing functions in a different manner than spectator mentalizing at the level of perspective taking, it is best to consider the two as being the same third-person process. It is for this reason that we contend that the defining feature of partnered interaction is not mentalizing, but instead real-time behavioral adaptivity between the partners, as studied in a large literature devoted to joint action and joint agency (e.g., Accetto et al., 2018; Fairhurst et al., 2013; Izawa et al., 2008; Keller et al., 2014; Pacherie, 2012). This interpretation is based on the similarity of the posterior rTPJ subpeak and the peaks of the meta-analyses of standard theory-of-mind processing from a spectator perspective.

However, the anterior rTPJ subpeak did not appear to align closely with standard spectator mentalizing peaks and may be a possible candidate for an indication of a partner-specific mentalizing process. Abe et al. (2019) reported activation in both the posterior and anterior regions of the rTPJ, but only the anterior region was correlated with the level of cooperation in a joint action task. Chauvigné et al. (2018) and Redcay et al. (2010) also reported anterior rTPJ peaks, both of which involved partnered joint action between participants. We tentatively propose that the posterior region of the rTPJ may be associated with a more reactive aspect of mentalizing during partnering, while the anterior region may represent a more directive, action-oriented aspect of partner mentalizing.

Behavioral Adaptivity and Partnering

The present meta-analysis suggests that mentalizing may be a domain-general process that operates across various formats of partnering. If this interpretation is correct, then the mentalizing system needs to interface with modal systems that mediate partnering in a domain-specific fashion, for example, connecting with speech and language systems for conversational discourse, but with locomotor and limb systems for dancing. How the mentalizing system interacts with the motor system is not well understood, possibly because the historical focus of mentalizing studies has been on spectator-based tasks that are far removed from motor actions and mutual adaptivity.

The CA can shed light on possible anatomical connections between the mentalizing and motor systems that may mediate the diversity of partnering formats. In particular, the PMC, IFG, and cerebellum were reported in 44% of the included studies. It is most likely that these areas did not show up as ALE clusters due to the variation in the task demands across experiments. Despite this limitation, there are well-established anatomical pathways projecting from the inferior parietal lobule—where the TPJ is located in the angular gyrus—to the frontal lobe. Most notable among these are the system of tracts that constitute to the superior longitudinal fasciculus (SLF). The branch known as SLF II projects from the parietal lobe to the PMC in the middle frontal gyrus, whereas the branch known as SLF III projects from the parietal lobe to the IFG (Barbeau et al., 2020). SLF II and III may represent a route by which information derived from mentalizing in the inferior parietal lobule can connect with domain-specific motor-planning systems in the PMC and IFG that mediate behavioral adaptivity during partnered interaction.

Mars et al.'s (2012) connectivity analysis indicates that the anterior region of the rTPJ is more connected to the IFG, whereas the posterior region of the rTPJ is not. The posterior region is instead more connected to the established mentalizing system and default mode network. It may be that the anterior subpeak from the ALE analysis indicates a mediating connection between the mentalizing and domain-specific motor systems required for partnering, while the posterior subpeak is indicative of a more reactive mode of mentalizing during partnering. This interpretation would corroborate our earlier tentative suggestion that the anterior and posterior regions of the rTPJ might be differentiated with regard to mentalizing function.

Overall, partnered interaction requires at least two key components: (a) implicit mentalizing and (b) mutual adaptivity, both of which serve a predictive role during partnered interactions. Based on the ALE results, it is proposed that mentalizing is a domain-general process, while mutual adaptivity is a domain-specific process linked to particular effector systems. A key question about partnering is how these two types of processes interact at the neural level. While the present meta-analysis is not able to address this issue directly, it is telling that the sets of brain areas that appeared across both the meta-analysis and the CA were some combination of mentalizing areas (TPJ, PCC, mPFC) and motor-planning areas (IFG, PMC, cerebellum).

Limitations

An important limitation of the present study relates to the low number of physical partnering experiments that were included. This was driven by the small number of studies that have been carried out in this area, most likely due to the technical challenges associated with physical interaction in the magnetic resonance imaging (MRI) scanner. Some studies of physical interaction have used single participants in the scanner (e.g., Chauvigné et al., 2018), whereas others have used hyperscanning to simultaneously scan two people in different scanners (e.g., Abe et al., 2019), but recent meta-analyses of the hyperscanning literature indicate that there are very few experiments of motoric adaptivity using two-person interactions (Misaki et al., 2021; Nam et al., 2020). It will be important to see if future studies of physical interaction corroborate the role of the rTPJ in partnering.

The incorporation of a diverse selection of experimental tasks was both a strength and weakness of the meta-analysis. The approach allowed us to highlight the cross-modal nature of the results, albeit for a single ALE cluster, but prohibited us from identifying specific effects associated with different types of partnering, allowing for only a general interpretation of the results. In this regard, the CA served as an important (though nonstatistical) adjunct to the ALE analysis, permitting a more nuanced analysis of the anatomical regions associated with partnering because this analysis was not subject to the voxel-level statistical constraints of the ALE method.

Finally, although cognitive and physical forms of partnering were dichotomized in this analysis, many forms of partnered interaction involve a combination of the two. For instance, even two people moving a piece of furniture together are likely to verbalize about their actions while engaging in them. Hence, it will be important in future studies of social interaction to study tasks that combine cognitive and physical forms of partnering, compared to each on its own.

Conclusions

An ALE meta-analysis of 18 neuroimaging experiments of both joint action and sociocognitive interactions was conducted to shed light on the neural basis of partnered interaction cross-modally using a statistical quantitative methodology for the first time. A highly concordant area of activation across the set of experiments was identified in the rTPJ despite the diversity of tasks included in the analysis. Additional mentalizing and motor-planning areas were evident across the contributing studies, although they were not concordant enough at the voxel level to appear as clusters in the ALE analysis. These results highlight the critical interaction between mentalizing and behavioral adaptivity during partnered interactions, regardless of task modality. The two subpeaks of the concordant rTPJ cluster also suggest the possibility that the anterior and posterior regions of the rTPJ may correspond to differences in mentalizing function (e.g., directive and reactive mentalizing, respectively, during partnering). Future studies of partnering, whether of joint action or social cognition, need to account for the combined role of mentalizing and mutual adaptivity during real-time social interactions.

References

Abe, M. O., Koike, T., Okazaki, S., Sugawara, S. K., Takahashi, K., Watanabe, K., & Sadato, N. (2019). Neural correlates of online cooperation during joint force production. *NeuroImage*, *191*, 150–161. https://doi.org/10.1016/j.neuroimage.2019.02.003

Accetto, M., Treur, J., & Villa, V. (2018). An adaptive cognitive-social model for mirroring and social bonding during synchronous joint action. *Procedia Computer Science*, *145*, 3–12. https://doi.org/10.1016/j.procs.2018.11.002

Alkire, D., Levitas, D., Warnell, K. R., & Redcay, E. (2018). Social interaction recruits mentalizing and

reward systems in middle childhood. *Human Brain Mapping*, *39*(10), 3928–3942. https://doi.org/10.1002/hbm.24221

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*(4489), 1390–1396. https://doi.org/10.1126/science.7466396

Baimel, A., Birch, S. A. J., & Norenzayan, A. (2018). Coordinating bodies and minds: Behavioral synchrony fosters mentalizing. *Journal of Experimental Social Psychology*, *74*, 281–290. https://doi.org/10.1016/j.jesp.2017.10.008

Baimel, A., Severson, R. L., Baron, A. S., & Birch, S. A. J. (2015). Enhancing "theory of mind" through behavioral synchrony. *Frontiers in Psychology*, *6*, Article 870. https://doi.org/10.3389/fpsyg.2015.00870

Barbeau, E. B., Descoteaux, M., & Petrides, M. (2020). Dissociating the white matter tracts connecting the temporo-parietal cortical region with frontal cortex using diffusion tractography. *Scientific Reports*, *10*(1), Article 8186. https://doi.org/10.1038/s41598-020-64124-y

Brown, S. (2020). The "who" system of the human brain: A system for social cognition about the self and others. *Frontiers in Human Neuroscience*, *14*, Article 224. https://doi.org/10.3389/fnhum.2020.00224

Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A. R., Langner, R., & Eickhoff, S. B. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Structure and Function*, *217*, 783–796. https://doi.org/10.1007/s00429-012-0380-y

Chaminade, T., Rosset, D., Da Fonseca, D., Nazarian, B., Lutcher, E., Cheng, G., & Deruelle, C. (2012). How do we think machines think? An fMRI study of alleged competition with an artificial intelligence. *Frontiers in Human Neuroscience*, *6*, Article 103. https://doi.org/10.3389/fnhum.2012.00103

Chauvigné, L. A. S., Belyk, M., & Brown, S. (2018). Taking two to tango: fMRI analysis of improvised joint action with physical contact. *PLOS ONE*, *13*, Article e0191098. https://doi.org/10.1371/journal.pone.0191098

Czeszumski, A., Eustergerling, S., Lang, A., Menrath, D., Gerstenberger, M., Schuberth, S., Schreiber, F., Rendon, Z. Z., & König, P. (2020). Hyperscanning: A valid method to study neural inter-brain underpinnings of social interaction. *Frontiers in Human Neuroscience*, *14*, Article 39. https://doi.org/10.3389/fnhum.2020.00039

Decety, J., Jackson, P. L., Sommerville, J. A., Chaminade, T., & Meltzoff, A. N. (2004). The neural bases of cooperation and competition: An fMRI investigation. *NeuroImage*, *23*(2), 744–751. https://doi.org/10.1016/j.neuroimage.2004.05.025

Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: How low-level computational processes contribute to

meta-cognition. *The Neuroscientist*, *13*(6), 580–593. https://doi.org/10.1177/1073858407304654

Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood estimation meta-analysis revisited. *NeuroImage*, *59*(3), 2349–2361. https://doi.org/10.1016/j.neuroimage.2011.09.017

Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Human Brain Mapping*, *30*(9), 2907–2926. https://doi.org/10.1002/hbm.20718

Eickhoff, S. B., Nichols, T. E., Laird, A. R., Hoffstaedter, F., Amunts, K., Fox, P. T., Bzdok, D., & Eickhoff, C. R. (2016). Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. *NeuroImage*, *137*, 70–85. https://doi.org/10.1016/j.neuroimage.2016.04.072

Elliott, R., Völlm, B., Drury, A., McKie, S., Richardson, P., & Deakin, J. F. W. (2006). Co-operation with another player in a financially rewarded guessing game activates regions implicated in theory of mind. *Social Neuroscience*, *1*(3–4), 385–395. https://doi.org/10.1080/17470910601041358

Enrici, I., Bara, B. G., & Adenzato, M. (2019). Theory of mind, pragmatics and the brain: Converging evidence for the role of intention processing as a core feature of human communication. *Pragmatics and Cognition*, *26*(1), 5–38. https://doi.org/10.1075/pc.19010.enr

Fairhurst, M. T., Janata, P., & Keller, P. E. (2013). Being and feeling in sync with an adaptive virtual partner: Brain mechanisms underlying dynamic cooperativity. *Cerebral Cortex*, *23*(11), 2592–2600. https://doi.org/10.1093/cercor/bhs243

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, *50*(4), 531–534. https://doi.org/10.1016/j.neuron.2006.05.001

Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *358*(1431), 459–473. https://doi.org/10.1098/rstb.2002.1218

Goebl, W., & Palmer, C. (2009). Synchronization of timing and motion among performing musicians. *Music Perception*, *26*(5), 427–438. https://doi.org/10.1525/mp.2009.26.5.427

Izawa, J., Rane, T., Donchin, O., & Shadmehr, R. (2008). Motor adaptation as a process of reoptimization. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *28*(11), 2883–2891. https://doi.org/10.1523/JNEUROSCI.5359-07.2008

Keller, P. E., Novembre, G., & Hove, M. J. (2014). Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal

coordination. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *369*(1658), Article 20130394. https://doi.org/10.1098/rstb.2013.0394

Kircher, T., Blümel, I., Marjoram, D., Lataster, T., Krabbendam, L., Weber, J., van Os, J., & Krach, S. (2009). Online mentalising investigated with functional MRI. *Neuroscience Letters*, *454*(3), 176–181. https://doi.org/10.1016/j.neulet.2009.03.026

Koike, T., Tanabe, H. C., Adachi-Abe, S., Okazaki, S., Nakagawa, E., Sasaki, A. T., Shimada, K., Sugawara, S. K., Takahashi, H. K., Yoshihara, K., & Sadato, N. (2019). Role of the right anterior insular cortex in joint attention-related identification with a partner. *Social Cognitive and Affective Neuroscience*, *14*(10), 1131–1145. https://doi.org/10.1093/scan/nsz087

Kokal, I., Engel, A., Kirschner, S., & Keysers, C. (2011). Synchronized drumming enhances activity in the caudate and facilitates prosocial commitment—If the rhythm comes easily. *PLOS ONE*, *6*(11), Article e27272. https://doi.org/10.1371/journal.pone.0027272

Koster-Hale, J., & Saxe, R. (2013). Functional neuroimaging of theory of mind. In S. Baron-Cohen, H. Tager-Flusberg, & M. V. Lombardo (Eds.), *Understanding other minds: Perspectives from developmental social neuroscience* (pp. 132–163). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199692972.003.0009

Krall, S. C., Rottschy, C., Oberwelland, E., Bzdok, D., Fox, P. T., Eickhoff, S. B., Fink, G. R., & Konrad, K. (2015). The role of the right temporoparietal junction in attention and social interaction as revealed by ALE meta-analysis. *Brain Structure and Function*, *220*(2), 587–604. https://doi.org/10.1007/s00429-014-0803-z

Kubit, B., & Jack, A. I. (2013). Rethinking the role of the rTPJ in attention and social cognition in light of the opposing domains hypothesis: Findings from an ALE-based meta-analysis and resting-state functional connectivity. *Frontiers in Human Neuroscience*, *7*, Article 323. https://doi.org/10.3389/fnhum.2013.00323

Lee, M., Ahn, H. S., Kwon, S. K., & Kim, S. I. (2018). Cooperative and competitive contextual effects on social cognitive and empathic neural responses. *Frontiers in Human Neuroscience*, *12*, Article 218. https://doi.org/10.3389/fnhum.2018.00218

Mars, R. B., Sallet, J., Schüffelgen, U., Jbabdi, S., Toni, I., & Rushworth, M. F. S. (2012). Connectivity-based subdivisions of the human right "temporoparietal junction area": Evidence for different areas participating in different cortical networks. *Cerebral Cortex 22*(8), 1894–1903. https://doi.org/10.1093/cercor/bhr268

McNeill, W. H. (1995). *Keeping together in time: Dance and drill in human history*. Harvard University Press.

Misaki, M., Kerr, K. L., Ratliff, E. L., Cosgrove, K. T., Simmons, W. K., Morris, A. S., & Bodurka, J. (2021). Beyond synchrony: The capacity of fMRI hyperscanning for the study of human social interaction. *Social Cognitive and Affective Neuroscience*, *16*(1–2), 84–92. https://doi.org/10.1093/scan/nsaa143

Molenberghs, P., Johnson, H., Henry, J. D., & Mattingley, J. B. (2016). Understanding the minds of others: A neuroimaging meta-analysis. *Neuroscience and Biobehavioral Reviews*, *65*, 276–291. https://doi.org/10.1016/j.neubiorev.2016.03.020

Müller, V. I., Cieslik, E. C., Laird, A. R., Fox, P. T., Radua, J., Mataix-Cols, D., Tench, C. R., Yarkoni, T., Nichols, T. E., Turkeltaub, P. E., Wager, T. D., & Eickhoff, S. B. (2018). Ten simple rules for neuroimaging meta-analysis. *Neuroscience and Biobehavioral Reviews*, *84*, 151–161. https://doi.org/10.1016/j.neubiorev.2017.11.012

Nam, C. S., Choo, S., Huang, J., & Park, J. (2020). Brain-to-brain neural synchrony during social interactions: A systematic review on hyperscanning studies. *Applied Sciences*, *10*(19), Article 6669. https://doi.org/10.3390/app10196669

Naughtin, C. K., Horne, K., Schneider, D., Venini, D., York, A., & Dux, P. E. (2017). Do implicit and explicit belief processing share neural substrates? *Human Brain Mapping*, *38*(9), 4760–4772. https://doi.org/10.1002/hbm.23700

Newman-Norlund, R. D., Bosga, J., Meulenbroek, R. G. J., & Bekkering, H. (2008). Anatomical substrates of cooperative joint-action in a continuous motor task: Virtual lifting and balancing. *NeuroImage*, *41*(1), 169–177. https://doi.org/10.1016/j.neuroimage.2008.02.026

Nichols, S., & Stich, S. P. (2003). *Mindreading: An integrated account of pretence, self-awareness, and understanding other minds*. Oxford University Press. https://doi.org/10.1093/0198236107.001.0001

Pacherie, E. (2012). The phenomenology of joint action: Self-agency vs. joint-agency. In A. Seeman (Ed.), *Joint attention: New developments* (pp. 343–389). MIT Press.

Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L., Tetzlaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hróbjartsson, A., Lalu, M. M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., . . . Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *PLoS Medicine*, *18*(3), Article e1003583. https://doi.org/10.1371/journal.pmed.1003583

Rauchbauer, B., Nazarian, B., Bourhis, M., Ochs, M., Prévot, L., & Chaminade, T. (2019). Brain activity during reciprocal social interaction investigated using conversational robots as control condition. *Philosophical Transactions of the Royal Society B:*

Biological Sciences, *374*(1771), Article 20180033. https://doi.org/10.1098/rstb.2018.0033

Redcay, E., Dodell-Feder, D., Pearrow, M. J., Mavros, P. L., Kleiner, M., Gabrieli, J. D. E., & Saxe, R. (2010). Live face-to-face interaction during fMRI: A new tool for social cognitive neuroscience. *NeuroImage*, *50*(4), 1639–1647. https://doi.org/10.1016/j.neuroimage.2010.01.052

Redcay, E., & Schilbach, L. (2019). Using second-person neuroscience to elucidate the mechanisms of social interaction. *Nature Reviews Neuroscience*, *20*(8), 495–505. https://doi.org/10.1038/s41583-019-0179-4

Reddish, P., Fischer, R., & Bulbulia, J. (2013). Let's dance together: Synchrony, shared intentionality and cooperation. *PLOS ONE*, *8*(8), Article e71182. https://doi.org/10.1371/journal.pone.0071182

Rice, K., Moraczewski, D., & Redcay, E. (2016). Perceived live interaction modulates the developing social brain. *Social Cognitive and Affective Neuroscience*, *11*(9), 1354–1362. https://doi.org/10.1093/scan/nsw060

Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. *NeuroImage*, *22*(4), 1694–1703. https://doi.org/10.1016/j.neuroimage.2004.04.015

Salazar, M., Shaw, D. J., Gajdoš, M., Mareček, R., Czekóová, K., Mikl, M., & Brázdil, M. (2021). You took the words right out of my mouth: Dual-fMRI reveals intra- and inter-personal neural processes supporting verbal interaction. *NeuroImage*, *228*, Article 117697. https://doi.org/10.1016/j.neuroimage.2020.117697

Sameen, N., Thompson, J., & Carpendale, J. I. M. (2013). Further steps toward a second-person neuroscience. *Behavioral and Brain Sciences*, *36*(4), 437–437. https://doi.org/10.1017/S0140525X1200204X

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in "theory of mind." *NeuroImage*, *19*(4), 1835–1842. https://doi.org/10.1016/S1053-8119(03)00230-1

Saxe, R., & Wexler, A. (2005). Making sense of another mind: The role of the right temporo-parietal junction. *Neuropsychologia*, *43*(10), 1391–1399. https://doi.org/10.1016/j.neuropsychologia.2005.02.013

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Vogeley, K. (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences*, *36*(4), 393–414. https://doi.org/10.1017/S0140525X12000660

Schilbach, L., Wilms, M., Eickhoff, S. B., Romanzetti, S., Tepest, R., Bente, G., Shah, N. J., Fink, G. R., & Vogeley, K. (2010). Minds made for sharing: Initiating joint attention recruits reward-related neurocircuitry. *Journal of Cognitive Neuroscience*, *22*(12), 2702–2715. https://doi.org/10.1162/jocn.2009.21401

Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neuroscience and Biobehavioral Reviews*, *42*, 9–34. https://doi.org/10.1016/j.neubiorev.2014.01.009

Schuwerk, T., Schurz, M., Müller, F., Rupprecht, R., & Sommer, M. (2017). The rTPJ's overarching cognitive function in networks for attention and theory of mind. *Social Cognitive and Affective Neuroscience*, *12*(1), 157–168. https://doi.org/10.1093/scan/nsw163

Sebanz, N., & Knoblich, G. (2009). Prediction in joint action: What, when, and where. *Topics in Cognitive Science*, *1*(2), 353–367. https://doi.org/10.1111/j.1756-8765.2009.01024.x

Sebanz, N., Rebbechi, D., Knoblich, G., Prinz, W., & Frith, C. D. (2007). Is it really my turn? An event-related fMRI study of task sharing. *Social Neuroscience*, *2*(2), 81–95. https://doi.org/10.1080/17470910701237989

Shpurov, I. Y., Vlasova, R. M., Rumshiskaya, A. D., Rozovskaya, R. I., Mershina, E. A., Sinitsyn, V. E., & Pechenkova, E. V. (2020). Neural correlates of group versus individual problem solving revealed by fMRI. *Frontiers in Human Neuroscience*, *14*, Article 290. https://doi.org/10.3389/fnhum.2020.00290

Spunt, R. P., & Lieberman, M. D. (2013). The busy social brain: Evidence for automaticity and control in the neural systems supporting social cognition and action understanding. *Psychological Science*, *24*(1), 80–86. https://doi.org/10.1177/0956797612450884

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*(1), 35–57. https://doi.org/10.1086/406755

Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage*, *16*(3 I), 765–780. https://doi.org/10.1006/nimg.2002.1131

Valdesolo, P., Ouyang, J., & DeSteno, D. (2010). The rhythm of joint action: Synchrony promotes cooperative ability. *Journal of Experimental Social Psychology*, *46*(4), 693–695. https://doi.org/10.1016/j.jesp.2010.03.004

Van Overwalle, F., Baetens, K., Mariën, P., & Vandekerckhove, M. (2015). Social cognition and the cerebellum: A meta-analysis of over 350 fMRI studies. *Human Brain Mapping*, *36*(12), 5137–5154. https://doi.org/10.1002/hbm.23002

Van Overwalle, F., & Vandekerckhove, M. (2013). Implicit and explicit social mentalizing: Dual processes driven by a shared neural network. *Frontiers in Human Neuroscience*, *7*, Article 560. https://doi.org/10.3389/fnhum.2013.00560

van Veluw, S. J., & Chance, S. A. (2014). Differentiating between self and others: An ALE meta-analysis of fMRI studies of self-recognition and theory of mind. *Brain Imaging and Behavior*,

8(1), 24–38. https://doi.org/10.1007/s11682-013-9266-8

Xie, H., Karipidis, I. I., Howell, A., Schreier, M., Sheau, K. E., Manchanda, M. K., Ayub, R., Glover, G. H., Jung, M., Reiss, A. L., & Saggar, M. (2020). Finding the neural correlates of collaboration using a three-person fMRI hyperscanning paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(37), 23066–23072. https://doi.org/10.1073/pnas.1917407117

Yuan, Y., Major-Girardin, J., & Brown, S. (2018). Storytelling is intrinsically mentalistic: A functional magnetic resonance imaging study of narrative production across modalities. *Journal of Cognitive Neuroscience*, *30*(9), 1298–1314. https://doi.org/10.1162/jocn_a_01294