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# Neural mechanisms underlying interpersonal coordination: A review of hyperscanning research

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**Abstract**
The ability to coordinate our behaviors with those of others is crucial for our success as individuals and groups. There are many forms of interpersonal coordination where a group of individuals need to coordinate their attention, actions, minds, or speech to achieve a mutual goal. In the present paper, we review previous hyperscanning research on the neural mechanisms underlying a variety of interpersonal coordination. Then we highlight how social and cultural factors modulate the interbrain mechanisms of interpersonal coordination. Finally, we conclude with a discussion of exciting future directions that await investigation from a cultural neuroscience perspective.

## 1 | INTRODUCTION

From sharing attention to singing together in choir to synchronizing steps in marching, the ability of coordinating one's behaviors with other—namely interpersonal coordination—penetrates into every level of social engagement in daily life. There are two types of interpersonal coordination: matching/mimicry and interactional synchrony. Mimicry refers to the direct imitation of actors by perceivers, such as one person mimicking the facial expression of another (Chartrand & Bargh, 1999; Dimberg, 1982; LaFrance, 1982), while interactional synchrony refers to the coordination of rhythmic and timing elements (Bernieri, 1988; Condon & Sander, 1974). Some coordinative behaviors occur spontaneously and unconsciously (i.e., coordinated heart rate, synchronized footsteps between walking strangers, and mimicry in speech communication), while others happen intentionally and consciously (i.e., dancing together, collective singing, playing instruments, and collaboration between captain and first officer during flights). The importance of interpersonal coordination and its underlying mechanisms has been widely discussed by researchers from different disciplines, such as behavioral sciences (Ackerman & Bargh, 2010), social psychology (Finkel et al., 2006), political sciences (Scharpf, 1994), and child development (Duncan & Farley, 1990). From an evolutionary perspective, the cognitive mechanisms required for successful coordination among humans have been designed for mutually beneficial collaboration. For example, humans have evolved the ability to share resources after working together to retrieve food unlike chimpanzees engaging in the same activity (Melis, 2013). Therefore, it is highly possible that a unique and integrative brain system has evolved to support this social ability. Through the

  
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use of a frontier approach, namely hyperscanning, recent neuroscience studies have highlighted interbrain neural mechanisms (i.e., interbrain synchrony and interbrain connectivity) underlying different forms of interpersonal coordination, including joint attention (Lachat, Hugueville, Lemaréchal, Conty, & George, 2012; Saito et al., 2010), coordinated body movements (Dumas, Nadel, Soussignan, Martinerie, & Garnero, 2010; Yun, Watanabe, & Shimojo, 2012), mental coordination (Mu, Guo, & Han, 2016; Mu, Han, & Gelfand, 2017), coordinated activities during music performance (Lindenberger, Li, Gruber, & Müller, 2009; Osaka et al., 2015), and flights (Astolfi et al., 2011; Astolfi et al., 2012).

In the current paper, we review the growing literature of hyperscanning studies that investigate the interbrain mechanisms underlying the ability to coordinate with others' attention, body movements, mental states, and speech in various tasks and social contexts. First, the present piece begins with a brief discussion of interpersonal coordination and its influences on other behaviors. We then address how hyperscanning approaches provide a better understanding of social behaviors, particularly interpersonal coordination. Next, we focus on the underlying interbrain mechanisms involved in a variety of interpersonal coordination, including joint attention, coordinated body movements, mental and speech coordination, and coordinated activities in ecological contexts. We then highlight the effects of other factors, such as gender, leadership, and sociocultural contexts, in modulating the interbrain substrates of interpersonal coordination. Finally, we discuss the promise of a cultural neuroscience approach to interpersonal coordination and conclude with an agenda identifying intriguing opportunities for future research.

## 2 | INTERPERSONAL COORDINATION

*Interpersonal coordination* is the phenomenon when two or more individuals coordinate their attention, actions, feelings, and mental states with one another to engage in variety of social activities in unison (Ackerman & Bargh, 2010). There is a wide range of interpersonal coordination, such as synchronized steps during walking, coordinated activities at a party involving several people, and coordinating different strategies in a card game. However, in this paper, we are mainly focusing on the following types of interpersonal coordination (Box1): joint attention, body coordination, speech coordination, mental coordination, and coordination in music performance and flight simulation. Accumulating behavioral research has revealed the influences of interpersonal coordination on other behaviors. For instance, Kirschner and Tomasello (2010) investigated coordinated instrument playing in 4-year-old children and found an increase in subsequent helping behaviors in the children who engaged in coordinated instrument playing than in

**Box 1. Glossary**

- *Interpersonal coordination*: occurs when two or more individuals coordinate (i.e., synchronize) their attention, actions, feelings, and mental states with one another to engage in variety of social activities in unison. There are two main types of interpersonal coordination: matching/mimicry and interactional synchrony.
- *Joint attention*: refers to the capacity to coordinate one's attention with others' in order to share a mutual awareness of the objects or events.
- *Body coordination*: refers to the ability to coordinate one's actions with those of others to act as a single unit for a joint outcome.
- *Speech coordination*: refers to coordinated behaviors (i.e., coordination of speech rhythm) between speakers and listeners during verbal communication.
- *Mental coordination*: occurs when two or more individuals coordinate their inner and mental states (i.e., inner timing clock) for mutual goals.

those who did not engage in coordinated playing. Likewise, in another study, researchers had 14-month-old infants bounce to music either in synchrony or out of synchrony (Cirelli, Einarson, & Trainor, 2014). They found that the infants who bounced in synchrony were more likely to help the researcher pick up an item she had “accidentally” dropped. Interpersonal coordination can promote prosocial behavior (Kirschner & Tomasello, 2010), while it also leads to an increase in positive affect (Mogan, Fischer, & Bulbulia, 2017) and feelings of interpersonal rapport (Bernieri, 1988). Most importantly, coordination fosters group cooperation (Valdesolo, Ouyang, & DeSteno, 2010; Wiltermuth & Heath, 2009). For example, Wiltermuth and Heath (2009) had participants synchronize with others' walking, singing, and other movements and then tested whether they would cooperate more in a subsequent group economic game. They found acting in synchrony with others resulted in greater and more persistent contributions to the public account over time, showing that interpersonal coordination promotes greater cooperation among group members. Consistently, Valdesolo et al. (2010) revealed that rocking in synchrony could enhance individuals' perceptual sensitivity in identifying the movement of an object, which thereby increased their success in a subsequent cooperative joint-action task, further supporting the idea that coordination experiences facilitate subsequent cooperation. Taken together, interpersonal coordination not only benefits individuals but also leads to better cohesion in human groups, resulting in working together more effectively.

In terms of human evolution, interpersonal coordination plays an essential role in survival. For example, coordinating interpersonal behaviors such as mimicry allowed for better communication between individuals, which in turn gives rise to greater chances of group survival (Lakin, Jefferis, Cheng, & Chartrand, 2003). Another possible reason why interpersonal coordination has evolutionary roots is coordinative activities such as ritual group dances before hunting trips boost positive feelings among group members, which may lead to more successful hunting and group collaboration (Wiltermuth & Heath, 2009). By using an evolutionary game simulation modeling, it has been demonstrated that human groups that face a high degree of ecological threats (e.g., low resources and high natural disasters) are more likely to evolve more coordinated behaviors than those that face a low degree of threats (e.g., high resources and low natural disasters), which supports the necessity of social coordination for group survival (Roos, Gelfand, Nau, & Lun, 2015). Given the evolutionary needs for this ability, it is highly possible that the brain has evolved unique and specialized neural mechanisms in support for coordination that binds human groups to fight against threats effectively.

## 3 | ADVANTAGES OF HYPERSCANNING APPROACH

With the use of neuroimaging techniques, the understanding of interpersonal coordination has been constantly moving forward. Neuroimaging literature has mapped distributed brain networks that are engaged in interpersonal coordination, including the activation of the primary sensorimotor cortex in the hand, coordinative hand tapping (Jäncke et al., 2000); the activation of the contralateral sensorimotor and caudal supplementary motor cortices as well as the (primarily ipsilateral) cerebellum in the rhythmic coordination task (Mayville, Jantzen, Fuchs, Steinberg, & Kelso, 2002); and the involvement of the supplementary motor area, the cingulate motor cortex, the premotor cortex, the primary sensorimotor cortex, and the cerebellum in the coordination of limb movements (Debaere et al., 2001). Most of the brain regions are derived from two systems: mirror neurons and mentalizing systems. The mirror system serves as a role in the preparation of one's own actions and simulating other's actions, while the mentalizing system involves the anticipation of other's intention (Sperduti, Guionnet, Fossati, & Nadel, 2014).

However, one of the limitations of these studies is that it examines neural activity in single isolated brains and does not provide assessment of the interbrain neural co-activations of multiple subjects' brains simultaneously during social interaction. Hyperscanning techniques, which simultaneously measure the brain activity from two or more people, can resolve this issue and assess the interbrain neural patterns between interactive individuals (Babiloni & Astolfi, 2014; Dumas, Lachat, Martinerie, Nadel, & George, 2011; Konvalinka & Roepstorff, 2012; Montague, 2002; Box 2). Specifically, the hyperscanning electroencephalography (EEG) is widely used because it guarantees millisecond-range

**Box 2. Hyperscanning technique and metrics**

• *Hyperscanning*: refers to the neuroimaging techniques that simultaneously measure the brain activity from two or more individuals to elucidate how co-variations in their neural activity (i.e., interbrain synchrony) are influenced by their social interactions. There are various types of hyperscanning techniques based on brain recording devices, such as hyperscanning functional magnetic resonance imaging (fMRI), hyperscanning electroencephalograph (EEG), hyperscanning functional near-infrared spectroscopy (fNIRS), and hyperscanning magnetoencephalography (MEG).

• *Hyperscanning functional magnetic resonance imaging (fMRI)*: refers to the hyperscanning technique that uses two or more scanners to simultaneously measure changes of brain activity associated with blood flow from multiple subjects while they are interacting with each other. This method allows simultaneous view in a high spatial resolution of the functional neuroanatomy of two or more subjects' brains engaged in a social interaction.

• *Hyperscanning electroencephalograph (EEG)*: refers to the hyperscanning technique that employs two or more EEG devices to record electrical activity of the two or more subjects' brains while they are interacting with each other. This method is widely used because of its high temporal resolution and naturalistic experimental settings.

• *Hyperscanning functional near-infrared spectroscopy (fNIRS)*: refers to the hyperscanning technique that uses simultaneous fNIRS to record hemodynamic activity of two or more subjects involved in a social interaction. This optical imaging allows for the measurement of brain activity in more natural real-life situation (i.e., face-to-face oral communication) and is thought to be more robust against movement artifacts than are EEG and fMRI.

• *Hyperscanning magnetoencephalography (MEG)*: refers to the hyperscanning technique that uses simultaneous MEG to measure brain activity of two or more subjects involve in a social interaction. This method provides high resolution of spatiotemporal characteristics of neuromagnetic fields of brain signal.

• *Interbrain activity*: refers to the interbrain neural pattern (i.e., interbrain synchrony and interbrain connectivity) between two or more subjects while they are interacting with each other.

• *Interbrain synchrony*: refers to a measure assessing phase synchronization between distant brain signals of interacting individuals in a social interaction.

• *Interbrain connectivity*: refers to a measure assessing brain connectivity (i.e., functional or effective connectivity) between distant brain regions of interacting individuals in a social interaction.

temporal resolution and also provides a naturalistic social environment (Burgess, 2013). However, EEG has very limited spatial resolution (around 1–2 cm), which hardly localizes the epicenter of brain activation and record deep brain structures (Niedermeyer & da Silva, 2005; Srinivasan, 1999). Thus, researchers need to take cautious when they try to use EEG for precisely determining the spatial pattern of the interbrain networks involved in social interactions. Another hyperscanning approach is simultaneous functional magnetic resonance imaging (fMRI) with its advantages in precisely localizing the regions involved in interbrain effects. However, due to the limitations of temporal resolution, this method has restrained power in assessing temporal characteristics of the interbrain network. Another main challenge of using fMRI is that lying in a scanner compromises the realism of the social interaction (Konvalinka & Roepstorff, 2012). The hyperscanning functional near-infrared spectroscopy (fNIRS), as an emerging technique, offers a relatively non-invasive, safe, ecological way of measuring the changes in oxy- and deoxyhemoglobin concentration at different regions of two brains simultaneously, but it cannot measure the subcortical regions (Scholkmann, Holper, Wolf, & Wolf, 2013). Recently, researchers suggest using the combination of different approaches, namely hyperscanning EEG–fMRI, as a means of precisely assessing both temporal and spatial characteristics of interbrain effects, which allows to analyze neural effects via a unified method (Koike et al., 2015). By employing different techniques, accumulating neuroscientists have begun to gradually determine interbrain characteristics (i.e., temporal, oscillatory, and spatial) underlying interpersonal coordination in distinct ways.

## 4 | NEURAL MECHANISMS OF INTERPERSONAL COORDINATION

How can two individuals follow each other's eye gaze to a target object? How can people naturally coordinate their walking pace? How can we adjust our internal time clocks with others? How are we able to easily engage in turn-taking communication? How can people play instruments together to create a beautiful melody? In this section, we will review previous hyperscanning research on different forms of interpersonal coordination. Table 1 summarizes the studies that are reviewed in this paper. As for the search strategy of these papers, we used the PubMed, PsycINFO (EBSCO), and ISI databases. First, we performed a search using the terms "hyperscanning," "multiple scanning," "dual EEG/fMRI/fNIRS," and "simultaneous EEG/fMRI/fNIRS." Then we reviewed the contents of all of the searched papers and chose the ones that investigated interpersonal coordination, including joint attention, coordinated movement, speech coordination, mental coordination, and coordinated activities in social and ecological contexts (i.e., music performance and flight simulation).

### 4.1 | Joint attention

Joint attention refers to the ability to coordinate attention between individuals in order to share a mutual awareness of the objects or events (Mundy, Sigman, Ungerer, & Sherman, 1986). It plays a critical role in social communication and is viewed as an evolutionary element that facilitates coordination and cooperation in a nonverbal way (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998). Such ability starts as early as 6 months old, where a baby will begin to switch their gaze back and forth between an object and their caregiver (Bakeman & Adamson, 1984). This skill allows us to readily detect others' focus of attention and correspondingly orient our own attention to the same location. It also allows us to draw cognitive inferences regarding their goals, intentions, and actions. It further plays an essential role for other types of social interactions. Recently, great progress in understanding the neural mechanisms of joint attention has been achieved by a series of hyperscanning studies. For example, Lachat et al. (2012) used EEG technique to record the neural activities of dyads of participants while they were orienting their attention toward either the same (i.e., joint attention periods) or different LED lights (i.e., non-joint attention periods). They found decreased alpha activity (around 8~13 Hz), namely alpha suppression, at the posterior regions in the joint attention compared with the non-joint attention periods. The authors speculated that decreased alpha activity was related to the mirror neuron system (i.e., a group of specialized neurons that "mirrors" the actions and behavior of others) and served as the function of processing socially relevant stimuli to promote gaze following and attention mirroring in joint attention (Lachat et al., 2012). However, this study failed to provide information on the interbrain mechanism of joint attention. A follow-up hyperscanning EEG study examined the modulations of interbrain synchrony,i.e., an index of phase synchronization between two distinct brain signals (Box 2), of participants while they were asked to indicate the number of targets present in a display individually or cooperatively (i.e., with a partner) in an enumeration visual searching task (Szymanski et al., 2017). The results showed increased delta and alpha interbrain synchrony of dyads of participants in the cooperative condition (i.e., completing the tasks as a team) compared with the control condition (i.e., completing the tasks individually). In addition, interbrain synchronization was associated with higher team performance (i.e., more efficiently and faster when working as a team), suggesting the functional role of interbrain synchronization in a general heightening of attention in social facilitation (Szymanski et al., 2017).

Furthermore, evidence from hyperscanning fMRI studies revealed that the paired participants who shared eye contact during a joint attention task, relative to the non-paired participants who had no eye contact, recruited more interbrain synchrony in the right inferior frontal gyrus (i.e., a brain region that has been found to be related to shared

**TABLE 1** List of the selected hyperscanning studies

| Authors | Year | Technical | Category | Paradigm | Neural findings |
|---|---|---|---|---|---|
| Ahn et al. | 2018 | EEG/MEG | Speech coordination | Turn-taking verbal interaction | Increased interbrain synchrony in alpha as well as gamma bands was observed during a verbal interacting task compared with a non-interactive task. |
| Astolfi et al. | 2011 | EEG | Coordination in flight simulation | Flight simulation | More alpha interbrain connectivity between the two brains was shown in the takeoff and landing phases, when the cooperation between them is maximal, in contrast with phases during which the activity of the two pilots was independent, when no or quite few links were shown. |
| Astolfi et al. | 2012 | EEG | Coordination in flight simulation | Flight simulation | More alpha interbrain connectivity between the captain and the first officer was shown in the high cooperation conditions (i.e., the takeoff and landing phases) than the low cooperation conditions (i.e., brain computer interface [BCI] rest). |
| Babiloni et al. | 2007 | EEG | Social interaction | A card game | Greater neural activity in the prefrontal and anterior cingulated cortex in multiple frequency bands for the player who start the game when compared with the other players. |
| Baker et al. | 2016 | fNIRS | Cooperation | Cooperation game | Female–female dyad exhibited greater interbrain synchrony in the right temporal cortex, while male–male dyads showed increased interbrain synchrony in the right inferior prefrontal cortex, which highlight the impact of gender on concurrent neural and behavioral signatures of cooperation. |
| Bilek et al. | 2015 | fMRI | Joint attention | Joint attention on target location | Neural coupling of the sender's right temporoparietal junction (rTPJ) and the receiver's rTPJ was only observed in the pairs who were interacting with each other but not in the pairs who didn't actually interact. |
| Cheng et al. | 2015 | fNIRS | Cooperation | Cooperation game | Interbrain synchrony in the prefrontal cortex was increased during the cooperation task for the mix-gender dyads (i.e., female–male dyads) but not for the same -gender dyads (i.e., female–female and male–male dyads), and this neural index was correlated with behavioral cooperation performance. |
| Duan et al. | 2015 | fNIRS | Coordination in musical performance | Drumming | Using graph theory method, this work provides preliminary findings of multi-brain network from nine persons engaged in a drumming interaction. |
| Dumas et al. | 2010 | EEG | Body coordination | Imitation hand movement | Increased interbrain synchrony in the alpha, beta, and gamma bands observed in the synchronized but not the non-synchronized hand movement periods. |
| Funane et al. | 2011 | fNIRS | Mental coordination | Real-time counting task | Enhanced brain covariance was found between the prefrontal regions of two interacting humans. |
| Jiang et al. | 2012 | fNIRS | Speech coordination | Face-to-face dialog | Increased interbrain synchrony between the inferior frontal regions of two individuals' brain was selectively induced during the face-to-face dialog but not the non-face-to-face conditions. |
| Jiang et al. | 2015 | fNIRS | Speech coordination | Face-to-face discussion | Interbrain synchrony of the leader–follower pairs was stronger than that of the follower–follower pairs, providing the first piece of interbrain neural evidence on leader emergence in verbal communication. |

(Continues)

**TABLE 1** (Continued)

| Authors | Year | Technical | Category | Paradigm | Neural findings |
|---|---|---|---|---|---|
| Kawasaki et al. | 2013 | EEG | Speech coordination | Alternating speech task | Theta/alpha interbrain synchrony was linked with behavioral speech synchronization and was enhanced as the speech coordination developed. |
| Konvalinka et al. | 2014 | EEG | Body coordination | Finger tapping Task | Alpha suppression in the right frontal region was observed when subjects were in a cooperative human condition (e.g., receiving feedback of the other person's tapping) compared with a computer control condition. |
| Lachat et al. | 2012 | EEG | Joint attention | Live joint attention paradigm | Decreased alpha activity was shown in the joint attention compared with non-joint attention periods. |
| Lindenberger et al. | 2009 | EEG | Coordination in musical performance | Playing guitar | Interbrain synchrony was increased during the periods of preparatory metronome tempo setting and coordinated play onset. |
| Montague et al. | 2002 | fMRI | Social interaction | A revised "dandy-dandy" game | A cluster of activity is identified in the region of the supplementary motor area, but this is stronger in the sender than in the receiver. |
| Mu et al. | 2016 | EEG | Mental coordination | Cooperative counting task | Enhanced alpha interbrain synchrony was observed in the coordination (i.e., coordinating with a human partner) compared with the control (i.e., coordinating with a computer partner) conditions. What's more, alpha interbrain synchrony was higher in female compared with male dyads. Intranasal OT vs. placebo administration specifically enhanced alpha interbrain synchrony of coordinating with human partner vs. computer. |
| Mu et al. | 2017 | EEG | Mental coordination | Cooperative counting task | Interbrain synchrony of gamma band oscillations that are highly related to threat processing is enhanced when people are under high societal threats. This gamma interbrain synchrony is associated with higher behavioral coordination performances. This work opens up interesting questions regarding the cultural factors that modulate interbrain patterns when humans coordinate with each other. |
| Naeem et al. | 2012 | EEG | Body coordination | Finger movement task | Alpha activity varied as a function of coordination context, showing more decreased alpha activity in the coordination condition (e.g., coordinating with their partner's finger movement in the in-phase and anti-phase conditions) compared with the control conditions (e.g., maintaining their own and ignoring partner's finger movement). |
| Osaka et al. | 2015 | fNIRS | Coordination in musical performance | Cooperative singing/humming | Increased synchronization of the left inferior frontal cortex was observed in the cooperative singing/humming relative to control conditions (i.e., singing/humming alone).<br>Increased interbrain synchronization in the left inferior frontal cortex in the face-to-face condition compared with the face-to-wall humming condition. |
| Szymanski et al. | 2017 | EEG | Joint attention | Visual searching task | Increased interbrain synchronization was higher in the cooperative condition (i.e., completing the tasks as a team) compared with the control condition (i.e., completing the tasks individually). |

(Continues)

**TABLE 1** (Continued)

| Authors | Year | Technical | Category | Paradigm | Neural findings |
|---|---|---|---|---|---|
| Saito et al. | 2010 | fMRI | Joint attention | Eye contact task | More interbrain synchronization in the right inferior frontal gyrus for partners who shared eye contact in joint attention task than in partners who did not share eye contact. |
| Tognoli et al. | 2007 | EEG | Body coordination | Finger movement task | Alpha activity (i.e., phi1 and phi2) in the right centro-parietal cortex could differentiate between synchronized and unsynchronized coordination sessions. |
| Toppi et al. | 2016 | EEG | Coordination in flight simulation | Flight simulation | Interbrain connectivity in the theta and alpha bands was higher during the parts of flight that required high coordination (i.e., takeoff and landing) than during the parts of flight that required low coordination (i.e., cruise).<br>Higher interbrain connectivity was only shown in the real pilots who were interacting with each other but not the randomly paired pilots. |
| Spiegelhalder et al. | 2014 | fMRI | Speech coordination | Live verbal communication | Interbrain analysis showed the time course of neural activity in areas associated with speech production was coupled with the time course of neural activity in the interlocutor's auditory cortex. |
| Sänger et al. | 2012 | EEG | Coordination in musical performance | Playing guitar | Results showed that theta and delta band synchronization within and between players was enhanced during preparatory tempo setting and at coordinated play onsets when there is high demand of coordination.<br>The synchronization patterns varied as a function of role assignment (i.e., leader vs. follower). |
| Sänger et al. | 2013 | EEG | Coordination in musical performance | Playing guitar | Results found evidence suggesting that the musical roles of leader and follower are associated with different interbrain patterns. |
| Yun et al. | 2012 | EEG | Body coordination | Fingertip coordination task | Increased theta and beta interbrain synchrony was observed between two subjects, which was found in the post-training session relative to the pre-training session. |
| Zhou et al. | 2016 | MEG | Body coordination | Imitation hand movement | Higher beta modulation index was shown in the occipital region in the following sessions (i.e., follower) compared with leading sessions (i.e., leader). |

representation of others' actions and intentions), suggesting brain coupling between the neural activation associated with sharing intention in support for joint attention (Saito et al., 2010). Likewise, Bilek et al. (2015) used hyperscanning fMRI to assess the interbrain neural couplings (i.e., cross-correlations of the time course of a pair of regions) involved in a joint attention task where information on a target location was only given to one participant (i.e., sender) only and the sender needed to transfer this information to another participant (i.e., receiver) to ensure both participants knew the location. The authors identified that the neural coupling of the right temporoparietal junction (i.e., a brain region that is linked with mentalizing others' minds) between the senders and the receivers was only observed in the pairs who were interacting with each other but not the pairs who didn't actually interact with each other, suggesting an integration of mentalizing areas in support for integrating social information and forming social behavior in joint attention (Bilek et al., 2015). Taken together, these results suggest that joint attention requires neural couplings of the brain regions related to sharing other's actions and mentalizing others' mental states.

## 4.2 | Body coordination

The ability to coordinate one's actions with those of others to act as a single unit is crucial for the success of both individuals and groups. For example, infants will stick out their tongue after viewing an adult performing the action (Meltzoff & Moore, 1997). Accumulating evidence from hyperscanning EEG has shown that coordinating actions is linked with alpha activity. For example, Tognoli, Lagarde, DeGuzman, and Kelso (2007) used a real-time finger movement task in which pairs of participants moved their fingers with and without vision of each other's actions to identify the neural signatures of real-time finger coordination. Their results demonstrated that a pair of neural components of alpha activity in the range between 9.2 and 11.5 Hz localized in the right centro-parietal cortex could differentiate between synchronized and unsynchronized coordination sessions, suggesting the role of alpha activity in support for body coordination (Tognoli et al., 2007). In a similar vein, Naeem, Prasad, Watson, and Kelso (2012) found that decreased alpha activity was observed in the coordination condition (e.g., coordinating with their partner's finger movement in the in-phase and anti-phase conditions) compared with the control conditions (e.g., maintaining their own and ignoring partner's finger movement), suggesting the notion that alpha activity is involved in integrating the mutual information (i.e., intention of action) of movement among individuals to ensure social interactions occur smoothly (Naeem et al., 2012). Moreover, another EEG study revealed that decreased alpha activity in the right frontal region was observed in a finger tapping task, especially when participants were in a cooperative human condition (e.g., receiving feedback of the other person's tapping) compared with a computer control condition (e.g., receiving feedback from a non-responsive computer; Konvalinka et al., 2014). Body coordination is also correlated with other frequency bands, such as theta (around 4–7 Hz), beta (around 12–30 Hz), and gamma band (usually above 28 Hz) activities. Yun et al. (2012) employed a fingertip coordination task to evaluate unconscious body synchrony changes as an index of implicit interpersonal interaction between the participants and its underlying neural mechanisms. Uniquely, this study compared pairs of participants' coordination in a pre-training session with the coordination in a post-training session. Increased theta and beta interbrain synchrony occurred between two participants in the post-training session relative to the pre-training session, suggesting that training could increase interbrain synchronization, which in turn facilitated coordinated finger movements (Yun et al., 2012). By adopting a coordinative hand movement task in which two participants were asked to imitate each other whenever they wanted, Dumas et al. (2010) found increased interbrain synchrony in multiple bands, including alpha, beta, and gamma bands, which were associated with the synchronized hand movements but not the non-synchronized hand movement periods (Dumas et al., 2010). The involvement of beta band in hand coordination has been replicated by another hyperscanning magnetoencephalography (MEG) study. Zhou, Bourguignon, Parkkonen, and Hari (2016) simultaneously measured MEG signals from pairs of participants who were performing coordinative hand movements as leaders or followers in successive runs. The authors reported a higher beta modulation index (i.e., a cross-frequency coupling measure, which is used to quantify the coupling between the phase of the acceleration signal and the amplitude of MEG signals) in the occipital region in the following sessions compared with leading sessions. They speculated that the modulation of beta activity may reflect different strategies that leaders and followers applied in integrating visual information, controlling body movements, and adapting others' actions to achieve coordination (Zhou et al., 2016). Taken together, EEG and MEG hyperscanning research uncovers the oscillatory traits of brain activity involved in body movement coordination, with coupled alpha activity as well as other frequency bands of interactive participants in support for mirroring and coordinating others' actions.

### 4.3 | Mental coordination

In most cases, to achieve successful motor coordination (i.e., dancing together and marching in same rhythm), individuals need to adjust their internal time clocks in order to jointly act in a precise manner. Using a combination of hyperscanning EEG setup and a novel real-time counting coordination game, Mu et al. (2016) investigated interbrain synchronization involved in mental coordination of dyads of participants while they were cooperatively counting time (i.e., 6 s) in their mind in order to make a button press at the same time. The coordination task was compared with a control task, which required counting to synchronize with a computer clock. The authors reported enhanced interbrain alpha synchrony between the central and posterior regions when participants were coordinating with a human partner compared with when they were coordinating with a computer. Furthermore, this alpha interbrain synchrony predicted synchronous behavioral performances, indicating an interbrain neural marker of supporting mental coordination without the need of face-to-face communication (Mu et al., 2016). Consistently, Funane et al. (2011) used fNIRS to measure coinstantaneous brain-activation signals while pairs of participants counted 10 s in their mind after an auditory cue. Their results illustrated such mental coordination of internal counting, which was supported by enhanced covariance between the prefrontal regions of the two interacting subjects (Funane et al., 2011). Mental coordination in the cooperative counting condition (i.e., coordinating with a partner), relative to the control condition (i.e., coordinating with a computer), requires the process of mentalizing other people's intentions. It has been proven that frontal regions, such as medial prefrontal cortex, are activated when people are inferring the thinking or future activities of others (Amodio & Frith, 2006). Likewise, alpha activity is demonstrated to be related to understanding of others' mental states, emotion, and behavior (Muthukumaraswamy & Johnson, 2004; Oberman et al., 2005). Thus, it is highly possible that the enhanced alpha interbrain synchrony and higher covariance of the frontal regions between individuals during mental coordination may reflect enhanced neural couplings of the brain activity associated with sharing/understanding others' mental states so as to coordinate with others mentally.

### 4.4 | Speech coordination

Human communication relies on speech coordination that requires the nervous system to control orofacial muscles and the brain mechanisms to regulate the semantics, syntax, and phonology of speech (Smith & Zelaznik, 2004). Face-to-face communication is grounded in the collective process of a mutual understanding of each other (Clark & Brennan, 1991) and involves turn taking between two individuals (Wilson & Wilson, 2005). Consistent evidence supports the notion that interbrain synchronization becomes enhanced when speech rhythms are synchronized between two subjects in verbal communication. One hyperscanning EEG study investigated the interbrain neural mechanisms involved in a turn-taking speech task in which subjects were instructed to alternately pronounce letters of the alphabet with either a human or a machine (Kawasaki, Yamada, Ushiku, Miyauchi, & Yamaguchi, 2013). The authors showed that theta and alpha interbrain synchrony between two participants was enhanced as their speech rhythms synchronization developed after training (i.e., coordinating with a machine's rhythm), suggesting that an interbrain function facilitates speech rhythm synchronization between individuals during communication (Kawasaki et al., 2013). Similarly, increased interbrain synchrony in alpha as well as gamma band interbrain synchrony was observed during a verbal interacting task (i.e., subjects engaged in turn-taking number counting) compared with a non-interactive task (i.e., subject counted numbers individually; Ahn et al., 2018). The authors suggest that alpha synchronization, which was induced during rapid turn-taking interaction, may reflect an increased load of short-term memory, while gamma activated in the temporal and frontal regions may play a role in promoting speech perception and controlling speech motor during turn-taking verbal interactions (Ahn et al., 2018). Evidence of fNIRS research uncovered that increased interbrain synchrony between the inferior frontal regions (i.e., a brain region involved in action-perception system) of two individuals' brain selectively induced during the face-to-face dialog but not the non-face-to-face conditions (i.e., face-to-face monologue and back-to-back dialog and back-to-back monologue), suggesting that a system in association with the action–perception function was serving as a bridge for face-to-face communication (Jiang et al., 2012). However, this study does not provide detailed information on to what extent neural activity associated with encoding of information by the speaker is mirrored in the activity associated with the decoding of information by the listener. To fill this gap, a simultaneous fMRI study estimated neural coupling of pairs of participants while they were talking about (i.e., one speaking and the other listening) or imaging autobiographical life events. The authors revealed that the time course of neural activity in areas associated with speech production of the speaker's brain (i.e., the primary motor, the premotor, the supplementary motor regions, and the cerebellar regions) was coupled with the time course of neural activity in the listener's auditory cortex (Spiegelhalder et al., 2014). Their results compliment previous EEG findings by providing elaborative spatial information on the interbrain foundations of the two coordinated participants during conversation.

## 4.5 | Social coordination in ecological context

Multiple levels of social coordination, such as church choir singing, bands and orchestras performing together, and friends singing together to the radio, make everyday life more harmonious, eventful, and successful. It is ideal to test social coordination in ecological contexts (i.e., group musical performances), because it could perfectly balance ecological validity and experimental control (D'Ausilio, Novembre, Fadiga, & Keller, 2015). There are an increasing number of hyperscanning studies that aim to test social coordination in a variety of music collaboration contexts, including drumming (Duan et al., 2015), guitar playing (Lindenberger et al., 2009; Sänger, Müller, & Lindenberger, 2012), singing, and humming (Osaka et al., 2015). For example, Lindenberger et al. (2009) simultaneously recorded EEG signals from pairs of guitarists who were playing the same melody together to assess interbrain synchrony during music production. They found that increased interbrain synchrony of lower frequency bands, namely the theta and delta bands, was observed when the musicians listened to the metronome to set their tempo and when they started playing a short melody together, suggesting interbrain synchronization plays a causal role in initiating and maintaining interpersonal coordinated actions during music performance (Lindenberger et al., 2009). In a follow-up EEG study, researchers had pairs of guitarists repeatedly play a duet in two voices and found enhanced interbrain synchrony of lower frequency bands (i.e., delta and theta) at the frontal and central electrodes during the periods when the needs of coordination is particularly high, such as periods of preparatory tempo setting and musical coordination (Sänger et al., 2012). The involvement of interbrain connections of lower frequency bands may represent coordinated firing of neuronal assemblies located in motor and somatosensory cortex in support for joint action in music production (Sänger et al., 2012).

While music making is a great way to measure social coordination, pilots and copilots working together to maneuver an aircraft is a high-stakes task that also requires a great deal of coordination. For this reason, neuroscientists have utilized flight simulations as a naturalistic way to measure social coordination. For example, Toppi et al. (2016) investigated interbrain connectivity, namely effective connectivity, which estimates directed influences of brain regions on each other, between pilots in different phases of flight simulation, including takeoff, cruise, and landing. They found more interbrain connectivity in the theta and alpha bands during the parts of flight that required high coordination (i.e., takeoff and landing) than in the parts of flight that required low coordination (i.e., cruise). In addition, this interbrain connectivity was only shown in the real pilots who were interacting with each other but not the randomly paired pilots (Toppi et al., 2016). Using the similar flight simulation, other EEG studies also validated that alpha interbrain connectivity of the two pilots was higher during the high coordination conditions (i.e., takeoff and landing) relative to the low coordination conditions (i.e., performing task individually; Astolfi et al., 2011, 2012).

The evidence above highlighted the role of interbrain mechanisms, especially the coupled neural oscillations of the lower frequency bands, in support for complex and multilevel coordination in various ecological and social contexts.

## 5 | SOCIAL AND CULTURAL FACTORS INFLUENCE INTERPERSONAL COORDINATION

In this section, we will discuss how other factors influence interpersonal coordination through modulating its interbrain mechanism. We will mainly focus on the social and cultural influences, such as leadership, gender, social contact, and sociocultural contexts.

### 5.1 | Leadership

Leader–follower relationship during social interaction has been discussed in previous hyperscanning research. Human leaders play an important role in coordination and cooperation. For instance, they not only initiate group action but also motivate, direct, organize, and monitor others to achieve group action. How do they make it? How does the brain change as a function of leadership during social interactions? To address these questions, previous hyperscanning research explicitly assigns participants a leader or follower role to see whether and how different roles will influence the interbrain mechanisms during various types of interpersonal coordination. In particular, in one half of the sessions, one subject is instructed to play a certain role (i.e., leader) and his/her partner is assigned the other role (i.e., follower), and in the other half of the sessions, they will switch roles (Zhou et al., 2016). By comparing the neural activity of being a leader with that of being a follower, Zhou et al. (2016) found that a role-specific beta activity in the occipital region was higher in the follower sessions than in the leader sessions, which offered an explanation for different strategies of followers (i.e., needs of accurately integrating the visual information about the leader's actions to plan their own actions) and leaders (i.e., performing actions without relying on visual information), which were utilized during coordinating hand movements. The influences of leadership on interbrain activity are further demonstrated during verbal communication. Jiang et al. (2015) investigated how leadership emergence would affect interbrain synchronization during speech communication and determined that the interbrain synchronization of the leader–follower pairs was stronger than that of the follower–follower pairs. The mean causality from the leaders to the followers was higher than that from the followers to the leaders, providing the first piece of interbrain neural evidence on leader emergence in verbal communication (Jiang et al., 2015). In addition, the impacts of the leader and follower roles on interbrain networks exist when guitarists are coordinating with each other to play music together, indicating that leader and follower differ in the directionality of the interbrain couplings involved in musical coordination (Sänger, Müller, & Lindenberger, 2013). Given the fact that leadership is a complex construct that is related to multiple psychological elements, such as attention, motivation, empowerment, and personality, it would be interesting to test the role of the different leadership subcomponents in modulating interbrain networks.

### 5.2 | Gender

Gender differences in cooperation have been widely discussed but are still unfolded (Balliet, Li, Macfarlan, & Van Vugt, 2011). There are increasing interests on how gender differences modulate the interbrain mechanisms underlying interpersonal coordination. For example, using a mental coordination task, Mu et al. (2016) found that relative to male–male dyads, female–female dyads exhibited more behavioral coordination and greater alpha interbrain synchronization when they were coordinating with each other compared with when they were coordinating with a computer partner. This study examined female–female and male–male dyads during interpersonal coordination and proposed an open question about mix-gender coordination and its neural mechanism. Two fNIRS studies further filled this gap by comparing the neural activity of the same-gender dyads and that of the mix-gender dyads. In one fNIRS study, Cheng, Li, and Hu (2015) tested whether the interbrain synchrony would be modulated by the gender of the partner (i.e., opposite or same to the participant) in a cooperation task (vs. competition and non-cooperation conditions) and revealed that interbrain synchrony in the prefrontal cortex was increased during the cooperation task for the mix-gender dyads (i.e., female–male dyads) but not for the same-gender dyads (i.e., female–female and male–male dyads), and this neural index was correlated with behavioral cooperation performance (Cheng et al., 2015). Using a similar cooperative task, another fNIRS study demonstrated that same-gender dyads, relative to the mix-gender dyads, induced greater interbrain synchrony in general, with the effect shown in the right temporal cortex for the female–female dyads and in the right inferior prefrontal cortex for the male–male dyads (Baker et al., 2016). From the evidence above, the role of gender in modulating interbrain activity of interpersonal coordination is still unsolved. Due to the method and techniques that previous work used, it is difficult to compare and evaluate between studies. Future studies need to consider the potential underlying factors, such as brain structure, evolution, genetics, self-construal, and social roles, that account for gender differences. This may help to clarify the gender effects on modulating interbrain signatures during social interactions.

### 5.3 | Social contact

Face-to-face interaction as one of the most common types of social contact has been validated to play a critical role in facilitating group coordination through modulating its underlying interbrain networks. For example, Jiang et al. (2012) reported that face-to-face communication, relative to other types of communication (i.e., back-to-back dialog), induced increased interbrain synchronization in the left inferior frontal cortex. Their results suggest that face-to-face communication is associated with unique neural substrates that differ from other types of communication. In a recent fNIRS study, the authors provided an additional justification for the modulations of the face-to-face interaction on interbrain networks during collective singing, showing an increased interbrain synchronization in the left inferior frontal cortex in the face-to-face humming condition compared with the face-to-wall humming condition (Osaka et al., 2015). It is not surprising that social contact, namely face-to-face interaction, activates the neural mechanisms that are related to processing social information and mentalizing others (i.e., the inferior frontal cortex), because it provides social information about others (i.e., facial expression or body movements) and also allows people to share their attention, emotions, and mental states. Future studies are needed to further separate the effects of specific social information embedded in face-to-face interaction (i.e., emotional or mental states) on changing the interbrain systems of interpersonal coordination.

### 5.4 | Sociocultural context

Human minds and different aspects of brain function are shaped by social and cultural environment. Yet surprisingly, the understanding of the modulations of social and cultural contexts on interbrain mechanism is still in its infancy. A recent EEG study combined a societal threat manipulation (i.e., reading an article reporting that their own country was facing external threats from is neighbor) and a coordination game (i.e., a mental coordination task, see Mu et al., 2016) to examine whether interbrain synchrony would help humans coordinate under societal threats (Mu et al., 2017). Their results suggest that an interbrain synchrony of gamma band oscillations that are highly related to threat processing is enhanced when people are under high societal threats. This gamma interbrain synchrony is associated with higher behavioral coordination performances. This work opens up interesting questions regarding the cultural factors that modulate interbrain patterns when humans coordinate with each other.

## 6 | CONCLUSION AND FUTURE DIRECTIONS

We are all born with an innate desire and ability to coordinate our behaviors with others', which is essential for group living. People with impaired motor coordination at an age appropriate level are usually diagnosed as developmental coordination disorder (American Psychiatric Association, 2013). It has been noted that such impairment is neurologically based, such as dysfunction in the brain activity (Brown-Lum & Zwicker, 2015). Obviously, behavioral studies have limitations on uncovering the behind neurobiological foundations that support coordination. The neuroimaging research on mirror neurons provides a possible behind mechanism that facilitates gesture imitation and behavioral synchrony during social interaction (Peters, Maathuis, & Hadders-Algra, 2013). However, due to the limitations of investigating single isolated brain functions, these studies hardly address whether or how the mirror neurons co-activate and connect across brains during social interaction.

Social interaction is a dynamic and interactive process. To achieve synchronized behaviors or successful coordination, individuals usually need to adapt their behaviors according to others' and, as a result, their cognitive and neural patterns are shaped by this interplay. Thus, there is an urge for neuroscience research on various aspects of interpersonal coordination to shift from one brain to multi-brain approach, which provides both methodological and theoretical understandings toward human coordination. Hyperscanning—which measures the behavioral and neural activity of multiple individuals' brains simultaneously—makes it possible to examine the coupling brain mechanisms. Specifically, hyperscanning approach has multiple advantages. First, converging evidence reveals that relative to intrabrain index (i.e., intrabrain spectral power), interbrain markers (i.e., interbrain synchronization) are more powerful in predicting coordination performances (Mu et al., 2016, 2017). Second, hyperscanning approach allows researchers to collect diverse data (i.e., intrabrain/interbrain neural signals and behavioral measurements) and assess a variety of neural traits (i.e., brain synchrony, functional connectivity, Granger-based causality, and small world), which provides substantial information of interactive brains during social interactions (Dumas et al., 2011). Third, this advanced method, relative to traditional neuroimaging approaches (i.e., EEG and fMRI), offers us a way to understand group processes, such as the functional connectivity among three-person group discussion (Jiang et al., 2015), four subjects in a card game (Babiloni et al., 2007), and the multi-brain networks among nine people during drumming (Duan et al., 2015). Finally, hyperscanning approaches are well suited for illuminating neural co-activation among interactive individuals in the social contexts. For instance, it has been demonstrated that coordination relies on neural couplings of multiple interactive individuals during natural communication,i.e., the coupling between the speaker's and listener's brain responses (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Jiang et al., 2012).

Taking advantage of this technique, the hyperscanning studies reviewed above have consistently highlighted domain-general interbrain oscillatory and spatial characteristics are served as certain fundamental function required in a wide range of coordination. Alpha oscillatory activity, for example, plays a crucial role in interpersonal coordination across paradigms and domains, including facilitating joint attention (Lachat et al., 2012; Szymanski et al., 2017), differentiating synchronized vs. unsynchronized actions (Konvalinka et al., 2014; Tognoli et al., 2007), synchronizing internal time clock in support for mental coordination (Mu et al., 2016), and contributing to coordination between speakers and listeners during verbal communication (Ahn et al., 2018; Kawasaki et al., 2013) and between two pilots during flights (Astolfi et al., 2011, 2012). Another consistent neural signature of interpersonal coordination is the brain couplings between frontal regions, such as higher interbrain synchrony of the right inferior frontal gyrus in support for joint attention (Saito et al., 2010), enhanced covariance of the frontal regions during mental coordination (Funane et al., 2011), and increased interbrain synchrony of the inferior frontal regions during face-to-face communication (Jiang et al., 2012). On the other hand, inconsistent results and domain-specific neural components (i.e., gender effect) inspire us to revisit the methodology (i.e., design, sample, data analysis, and confoundings) and rethink the behind cognitive and neural mechanisms. Given that little attention has been drawn on differentiating between the domain-general and domain-specific neural substrates underlying interpersonal coordination, future research is encouraged to address this clearly.

Culture, which is a collection of shared attitudes, expectations, rules, customs, and beliefs, guides individuals' behaviors within a cultural group and influences group actions, such as coordination and cooperation. Nevertheless, cultural influences on the neural mechanisms related to group coordination have remained largely unexplored. From a cultural neuroscience perspective, human minds and their brains are shaped by different sociocultural contexts (Ambady & Bharucha, 2009; Han et al., 2013; Kitayama & Uskul, 2011). It has been noted that cultures vary with respect to strength of social norms and degree of sanctioning (Gelfand et al., 2011; Pelto, 1968). Societies with a high degree of historical and ecological threats (i.e., more natural disasters, higher disease prevalence, fewer natural resources, and more territorial invasions) tend to develop stronger norms and sanctions to coordinate to survive such threats. By contrast, those that are subject to serious ecological and man-made threats usually have less need for social coordination (Gelfand et al., 2011). Given the influences of cultural variations on strength of social norms on human coordination behaviors, it would be interesting to see how these cultural contexts may influence the interbrain network associated with interpersonal coordination. For example, do people from tight cultures compared with those from loose cultures exhibit greater interbrain activity that in turn facilitates more effective coordination? How would such interbrain neural differences affect other group activities, such as team creativity and group cooperation? There is also a limited understanding of how people from different cultures interact with each other. For instance, an intriguing question for future researchers will be to identify whether people interact with a partner from their own culture, relative to a partner from a different culture, activate greater interbrain synchrony. Another critical question in this field needs to address is how culture interacts with various genetic factors to affect the brain. One hyperscanning study suggests the potential role of genetic factors in social coordination, showing that oxytocin, as a neuropeptide related to human social behaviors (i.e., empathy and trust), enhances interbrain synchrony in male subjects to facilitate social coordination (Mu et al., 2016). Following this line, future researchers are encouraged to examine whether cultural contexts selectively influence interbrain mechanisms of certain genotype carriers but not the others.

In conclusion, the hyperscanning approach has fostered our understanding of the neural mechanisms underlying coordinating attention, actions, speech, and mental states. Future cross-cultural neuroscience research will hopefully provide us with a more integrative neural model with culture, behavior, and the brain. Last but not the least, we provide a list of suggestions that may help future research (see Box 3).

**Box 3. Suggestions for future hyperscanning research**

- Selecting appropriate controls as baseline (i.e., using the human–computer interaction as the control for the human–human interaction).
- Using comparable stimuli across conditions to minimize confoundings at the perceptual/psychological levels.
- Balancing between experimentally-controlled and ecological/naturalistic settings.
- Using interactive (vs. isolated) tasks where multiple participants share an environment that they can interact with each other.
- Ensuring the synchronization of different acquisition devices (i.e., using same sample rate and attaching to the same trigger).
- Selecting suitable hyperscanning approaches based on the characteristics of each technique and the research goal (i.e., hyperscanning EEG for detecting temporal dynamics and oscillatory patterns and hyperscanning fMRI for localizing the neural circuits and pathways).
- Selecting appropriate analysis (i.e., interbrain correlational analysis and causality connectivity analysis).
- Increasing statistical power (i.e., a larger sample size and correction for multiple comparisons).
- Validating research results (i.e., conducting replication study).

*(To be noted, these above are not listed in order of priority or importance.)*

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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