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The Interpersonal Neuroscience of Social Learning

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Abstract

The study of the brain mechanisms underpinning social behavior is currently undergoing a paradigm shift, moving its focus from single individuals to the real-time interaction among groups of individuals. Although this development opens unprecedented opportunities to study how interpersonal brain activity shapes behaviors through learning, there have been few direct connections to the rich field of learning science. Our article examines how the rapidly developing field of interpersonal neuroscience is (and could be) contributing to our understanding of social learning. To this end, we first review recent research extracting indices of brain-to-brain coupling (BtBC) in the context of social behaviors and, in particular, social learning. We then discuss how studying communicative behaviors during learning can aid the interpretation of BtBC and how studying BtBC can inform our understanding of such behaviors. We then discuss how BtBC and communicative behaviors collectively can predict learning outcomes, and we suggest several causative and mechanistic models. Finally, we highlight key methodological and interpretational challenges as well as exciting opportunities for integrating research in interpersonal neuroscience with social learning, and we propose a multiperson framework for understanding how interpersonal transmission of information between individual brains shapes social learning.

Keywords

interpersonal neuroscience, social learning, brain-to-brain coupling, machine learning, causation, communication, synchronization, real-time interaction

Across the life span, much of human learning is shaped by observing and interacting with others, and such *social learning* (i.e., learning the value of stimuli, actions, or knowledge from others) is critical for a range of human activities, from basic survival behaviors to the mastering of complex cultural tasks (Apps et al., 2016; Bandura, 1977; Boyd et al., 2011; Debiec & Olsson, 2017; Olsson et al., 2020). For example, individuals commonly learn what is safe and dangerous by observing one another approaching rewards or avoiding threats (Lindström et al., 2019). Social learning often involves the exchange of complex information that must be swiftly and dynamically decoded by the human brain (e.g., Fan et al., 2016; Joiner et al., 2017; Lindström et al., 2018; Olsson et al., 2020). The aim of the present work is to integrate the growing knowledge about the neural bases of such social learning with new and exciting developments in the nascent field of interpersonal neuroscience—in particular, research using measures of brain-to-brain coupling (BtBC; i.e., neural processes in one brain that are temporally coupled to neural processes in another brain, Hasson et al., 2012; for more details, see the next section)—and to discuss how this integration can contribute to our understanding of social learning.

Despite the surge in interest in the neural mechanisms of social learning, important gaps in our understanding remain. First, although "social learning" involves, by definition, at least two agents (e.g., an

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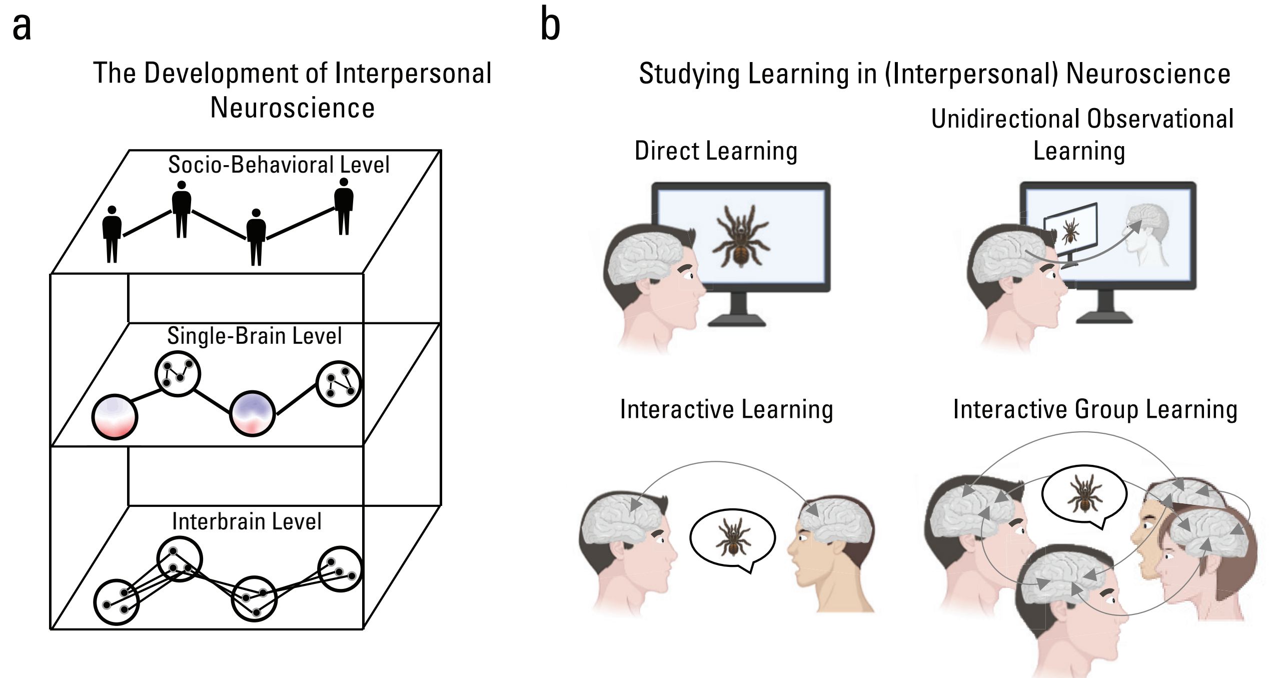

Fig. 1. Interpersonal neuroscience and its applications in social learning. (a) To study the neural processes of social behaviors and interactions (socio-behavioral level), conventional neuroimaging studies focus mostly on activation and/or functional connectivity of brains in isolation (single-brain level). The neurophysiological investigations of social behaviors have witnessed a transition from a single-brain focus to a brain-to-brain focus; the latter entails the examination of coupling between brain regions across individuals (interbrain level). (b) Experimental paradigms studying different types of learning are illustrated. Direct (Pavlovian) learning: A single brain is monitored while the learner is presented with a conditioned stimulus (e.g., a spider), previously paired with a painful unconditioned stimulus (e.g., an electric shock; see, e.g., Lindström et al., 2018). Unidirectional observational learning: The learner observes a demonstrator's defensive responses (anxiety, fear) to a conditioned stimulus (unidirectional dashed line represents potential sequential brain-to-brain coupling, indicating that brain activity of the observer/learner measured at a later time could be coupled with that of the demonstrator; see, e.g., Kostorz et al., 2020). Interactive learning: A learner acquires threat information by interacting with another individual (bidirectional solid line denotes concurrent coupling, indicating that simultaneously measured brain activity from two individuals couple with each other; see, e.g., J. Liu et al., 2019). Interactive group learning: A group of individuals learns about threat information through interaction (bidirectional lines constitute a complex coupling network, indicating that simultaneously measured brain activity from group members couple with each other; see, e.g., Dikker et al., 2017). Panel (b) created with BioRender.com.

observer and a demonstrator), conventional neuroscientific approaches to social learning have mostly focused on the activity of single brains (Lindström et al., 2019; Olsson et al., 2007), without exploring the dependencies among activities in two or more (interacting) brains (Cui et al., 2012; Montague, 2002). Second, most studies in the field of social learning have adopted ecologically deprived setups in which natural behavior is strongly constrained (Pan, Dikker, et al., 2020), requiring further validation in more naturalistic situations (D'Ausilio et al., 2015; Holleman et al., 2020).

Recent efforts to bridge these two major gaps in understanding have prompted a paradigm shift (Fig. 1a) in studying social behaviors from the use of single-person, ecologically deprived experiments to multiperson, ecologically valid tasks (Gvirts & Perlmutter, 2020; Shamay-Tsoory & Mendelsohn, 2019; Wass et al., 2020). This paradigm shift is seen as a development toward a *second-person neuroscience* (Redcay & Schilbach, 2019; Schilbach et al., 2013) or *interpersonal neuroscience* (hereafter). Although this development has opened unprecedented opportunities to study how interpersonal neural responses shape memories and behaviors through learning (Fig. 1b), there have been few direct links to the rich field of learning science, including that focusing on social learning. Strikingly, research on the neural mechanisms of social learning, which lends itself particularly well for such an integration, has largely progressed in parallel domains of research with little integration with the work in interpersonal neuroscience.

To fill this blank in the literature, we aim to provide a perspective on the research emerging in the nexus between the fields of interpersonal neuroscience and social learning. Our review (a) highlights important recent developments of interpersonal neuroscience and (b) offers a novel, synthesized framework for better understanding the transmission of information between individual brains during social learning and how such interactions shape memories and behavior.

BtBC and Social Learning

Social learning, defined as the process through which individuals learn from others instead of through direct, individual experience only, is crucial for survival in many species and plays an important role in evolution of human culture (Gariépy et al., 2014). Learning by capitalizing on others' experiences can guide decisions and facilitate the acquisition of new skills and values without paying the costs of individual trial-and-error learning. Social learning has been observed across many social species, including octopuses, birds, rodents, and humans (Debiec & Olsson, 2017; Fiorito & Scotto, 1992; Sherry & Galef, 1984; Thornton, 2008; van de Waal et al., 2013), and has been applied to multiple domains, ranging from decision-making and fear responses to problem-solving (Gruber et al., 2009; Lindström et al., 2019; Olsson & Phelps, 2007; Wisdom et al., 2013; L. Zhang & Gläscher, 2020). Here, we use "social learning" to refer to any form of learning acquired by observing or interacting with conspecifics.

A key prerequisite of social learning is the presence of at least two individuals—one learning from another. Accordingly, a recent methodological advance (i.e., hyperscanning—the measurement of brain activity from two or more individuals simultaneously; Babiloni & Astolfi, 2014; Cui et al., 2012; Montague et al., 2002) allows researchers to measure similar or synchronized neural responses, known as BtBC (see Hasson et al., 2012), across dyads and groups of individuals during social learning in an ecologically valid setting (Dikker et al., 2017; Holper et al., 2013).

BtBC during learning has been demonstrated across multiple brain regions, predominantly including temporoparietal junctions and prefrontal regions (Holper et al., 2013; Pan, Dikker, et al., 2020; Pan, Guyon, et al., 2020; Pan et al., 2018; Takeuchi et al., 2017; Zheng et al., 2018). According to some authors, these regions may contribute to mentalizing and interpreting the intentions of others (Behrens et al., 2009; Carter et al., 2012; Gvirts & Perlmutter, 2020; Knoch et al., 2006), which is of course relevant for any form of social learning. In addition, BtBC has been measured using various statistical approaches (for a review, see Fairhurst & Dumas, 2019) and imaging modalities (for a review, see Babiloni & Astolfi, 2014). For the sake of simplicity, here we refer to BtBC as a unitary phenomenon without making distinctions between underlying neural structures, imaging modalities, and measurement sources (for a detailed review of BtBC, see, e.g., Babiloni & Astolfi, 2014; Fairhurst & Dumas, 2019; Gvirts & Perlmutter, 2020; Wass et al., 2020). Our goal is to understand how BtBC in interpersonal neuroscience can contribute to our knowledge about social learning.

Whereas single-brain studies are useful in localizing and characterizing brain activity associated with social learning (Apps et al., 2016; Lindström et al., 2018; Olsson et al., 2020), BtBC can directly assess the dynamic interaction of two or more brains (Fig. 2; also see Cui et al., 2012). Thus, studying BtBC is key to a full understanding of social learning, which requires dynamic social engagement. Surprisingly few studies have directly examined the role of BtBC in social learning. To address this gap in the literature, we review four broad strains of research (Fig. 1b): direct (Pavlovian) learning, unidirectional observational learning, interactive learning, and interactive group learning (varied by different forms of learning).

First, research examining *direct (Pavlovian) learning* has mostly used a single-brain approach (serving as a contrast to the BtBC described below): activity in a single brain is measured while the learner passively observes a conditioned stimulus (e.g., a spider), which was previously paired with an unconditioned stimulus (e.g., an electric shock). For example, using fMRI, Lindström et al. (2018) found that direct fear learning activates a neural network that has been linked to the acquisition, storage, and expression of conditioned fear (LeDoux, 2012), as well as the aversive value of pain (Kober et al., 2019; López-Solà et al., 2019).

Second, recent advances examining *unidirectional observational learning* have attempted to measure sequential BtBC (Redcay & Schilbach, 2019): In these studies, a stimulus is first shown to a demonstrator whose responses are recorded and later presented to an observer; sequential BtBC is identified when brain activity of the observer (measured at a later time) is coupled with that of the demonstrator. For example, using fMRI, Kostorz et al., (2020) scanned the brains of a demonstrator and observers when the observers were learning an origami skill. Brain activity of the demonstrator during action production was coupled with that of the observer during later viewing of the demonstrator's videotaped actions. The results revealed a sequential demonstrator–observer brain coupling, which was reported to support action understanding, mentalizing, and visual simulation (Hesslow, 2002; Van Overwalle et al., 2015).

Third, research examining *interactive learning* in naturalistic situations has measured concurrent (simultaneous) BtBC: In these studies, a learner acquires information by interacting with another individual;

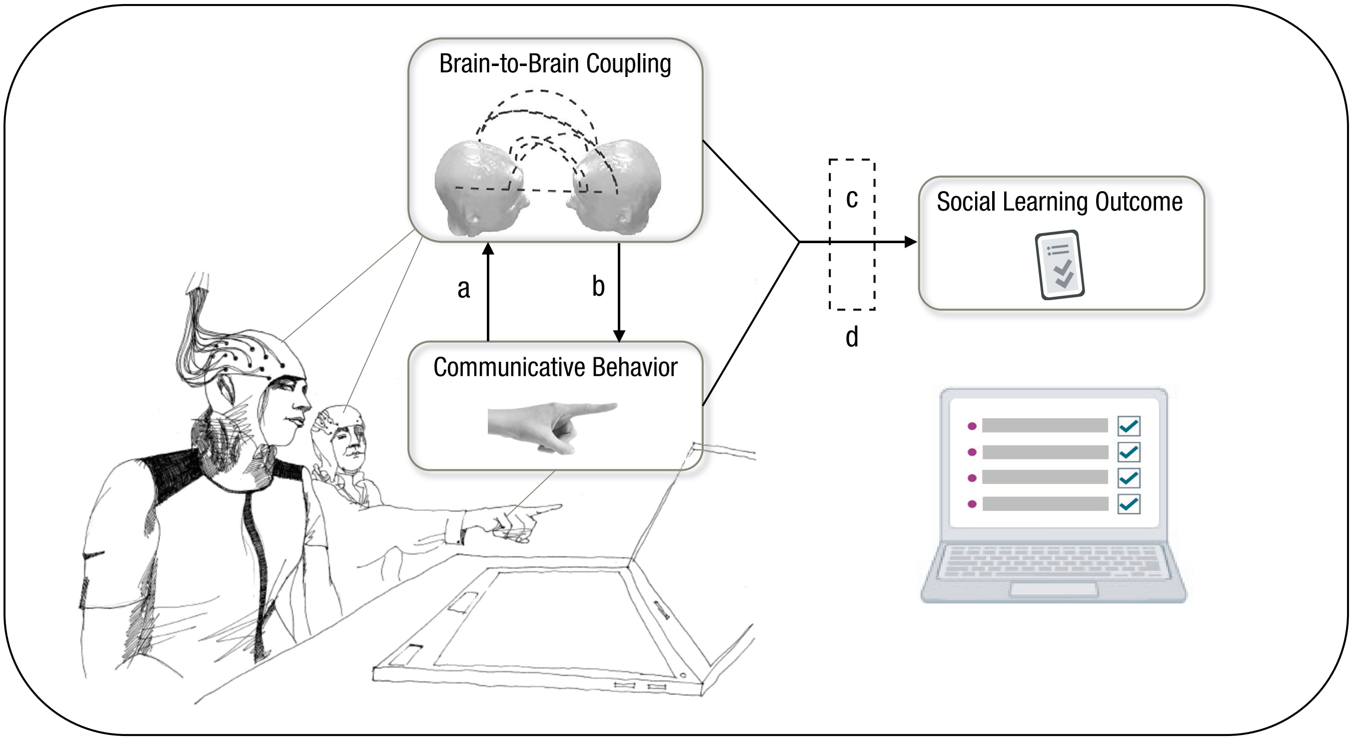

Fig. 2. Illustration of the relationship among brain-to-brain coupling (BtBC), communicative behavior, and social learning outcome. A demonstrator is transmitting knowledge to an observer, during which their brain activities are simultaneously recorded; BtBC emerges as a result of learning interactions within the dyad. Communicative behaviors (e.g., gestures) during learning (a) can help interpreting the significance of BtBC; conversely, BtBC can help in understanding those behaviors (b). BtBC and communicative behaviors (c) can collectively predict future learning outcome. BtBC and communicative behaviors (d) jointly cause social learning through various mechanisms. The laptop in the right bottom corner represents the collection of learning outcome. Adapted and reprinted by permission from Springer *Brain Topography* (Applications of functional near-infrared spectroscopy in fatigue, sleep deprivation, and social cognition, Pan, Y., Borragán, G., & Peigneux, P.), Copyright © 2019.

concurrent BtBC is identified when brain activity between two individuals is coupled simultaneously during interactions. For example, using functional near-infrared spectroscopy (fNIRS), Liu and colleagues showed that ongoing demonstrator–observer interaction elicited concurrent BtBC in the left prefrontal cortex (J. Liu et al., 2019). Such BtBC was dependent on the observer's knowledge state (with vs. without prior knowledge about learning materials) and communication mode (face-to-face communication vs. computer-mediated communication): Observers with prior knowledge and in a face-to-face communication elicited the strongest BtBC with demonstrators.

Fourth, BtBC was found to track *interactive group learning*, which can be seen as extending the work described above on BtBC between two individuals to BtBC across a group of individuals. For example, in a real-world classroom situation, Dikker et al. (2017) followed a group of high-school students and recorded their brain activity using EEG during regular class activities. Students' BtBC predicted how much they were engaged during class and how much they liked the teacher and other students.

Apart from the four broad strains of research reviewed above, many additional domains of social learning could be investigated in future multibrain studies (not shown in Fig. 1). These additional domains entail, for instance, a learner acquiring information about threat by observing a real person interacting with a real conditioned stimulus (e.g., a real spider) or observing artificial stimuli (e.g., a static picture of a spider) versus observing real stimuli (e.g., a real spider).

The studies reviewed so far illustrate how the growing research interest in BtBC can inform the study of interpersonal learning. For the research on BtBC to be maximally informative about social learning, we need a better understanding of the behavioral significance of BtBC (Hamilton, 2020). In the next sections, we first discuss how communicative behaviors during learning can help interpreting BtBC (Fig. 2a) and, conversely, how BtBC can help understanding those behaviors (Fig. 2b). Then, we discuss how BtBC and communicative behaviors collectively can predict learning outcomes (Fig. 2c). We discuss several important causative and mechanistic considerations for BtBC and learning (Fig. 2d).

Understanding BtBC via Communicative Behaviors

We discuss how to improve the interpretability of BtBC by examining communicative behaviors during interpersonal learning (Fig. 2a). In an endeavor to advance understanding of BtBC, researchers have used video-based behavioral tools to measure communicative behaviors ("behavioral coding") of two or more interacting agents to quantify the degree that specific communicative behaviors contribute to BtBC (Jiang et al., 2012, 2015; Leong & Schilbach, 2019; Pan et al., 2018; Pan, Dikker, et al., 2020; Piazza et al., 2020; Wass et al., 2018, 2020). In an interactive learning setting, examples of behavioral coding data are measures of exact start and end times of turn-taking behaviors (e.g., dialog, demonstration, and imitation) and body language (e.g., orofacial movements, facial expressions, body kinematics, and gestures), all of which might contribute to learning in different ways during social interaction (e.g., verbal interactions transmit abstract information, body language facilitating acquisition of behaviors).

The behavioral-coding approach has been successfully applied for tracking communicative behaviors across both humans (e.g., mutual gaze and smile; Bilek et al., 2015; Leong et al., 2017; Leong & Schilbach, 2019; Piazza et al., 2020; Wass et al., 2018) and nonhuman animals (e.g., grooming and sniffing; Kingsbury et al., 2019; W. Zhang & Yartsev, 2019), as well as across scientific fields, such as sociology (e.g., turn-taking and nod; Jiang et al., 2012), pedagogy (e.g., observation and imitation; Pan, Dikker, et al., 2020; Pan et al., 2018), and psychiatry (e.g., posture and gaze; Leong & Schilbach, 2019). For example, Jiang and colleagues showed that, compared with no interaction behaviors, interaction elicited stronger BtBC during face-to-face communication (Jiang et al., 2012). Pan and colleagues (2018) further categorized learning-relevant behaviors into vocal interactions and nonvocal interactions and found that BtBC during interpersonal learning was driven mainly by vocal interactions. In another study, infant language learning (phonemic discrimination) was found to improve in the presence of peers; such improved early learning was related to behaviorally coded infant vocalizations and eye gaze (Lytle et al., 2018).

How can the use of behavioral coding be optimized to examine social learning? A common practice based on recent applications entails the following three steps when collecting behavioral data (Jiang et al., 2012, 2015; Leong et al., 2017; Leong & Schilbach, 2019; Pan, Dikker, et al., 2020; Pan et al., 2018; Wass et al., 2018, 2020): (a) Specifying a coding scheme, which includes defining different types of communicative behaviors during learning (e.g., turn-taking behaviors and body language); (b) coding communicative behaviors either manually or semiautomatically on the basis of digital videos recorded during the whole learning procedure; and finally, (c) obtaining time-stamped behavioral markers. These behavioral indices can be further analyzed along with the brain data (Fig. 3).

What are the potential limitations of the behavioral coding approach? One limitation is the subjective nature of the rating procedure, raising concerns about reliability. It is therefore important to predetermine a detailed coding scheme and include multiple raters to allow for formal testing of the inter-rater reliability. Sufficient training in the relevant method and theory for raters is also needed to ensure valid and reliable interrater coding. A second limitation is that manual coding is time consuming. These constraints can, however, be mitigated by the use of automated algorithms to extract behavioral information from videos (Cao et al., 2021; Ramseyer & Tschacher, 2011). For example, a motion-energy-analysis algorithm can quantify the pixel changes from one frame to the next, providing a continuous measure of movement (Ramseyer & Tschacher, 2011); and a real-time multiperson system (i.e., OpenPose) allows for jointly detecting human body, hand, facial, and foot keypoints on images or videos and tracking their kinematics (Cao et al., 2021).

In sum, we contend that learning-relevant behavioral coding (i.e., the measurement of concurrent social behaviors of interacting individuals) is highly relevant for interpreting BtBC, parsing learning procedures, and quantifying brain–behavior relationships. The behavioral coding approach is advantageous for researchers to quantify the contribution of specific communicative behaviors to BtBC, thus enhancing our knowledge about the functional significance of BtBC.

Understanding Communicative Behaviors via BtBC

Apart from the role of communicative behaviors during interpersonal learning in improving our understanding of BtBC (Fig. 2a), BtBC can be used to decode behaviors during learning (Fig. 2b). In this section, we propose that the study of BtBC can add importantly to our ability to decode or classify behaviors in social learning tasks.

Decoding analyses have previously been used to better understand social-learning paradigms (Aquino et al., 2020; Haaker et al., 2017), but they have seldom been approached from an interpersonal-neuroscience perspective. Methods used to decode behaviors during learning (e.g., turn-taking behaviors and body language) based on BtBC during interpersonal learning

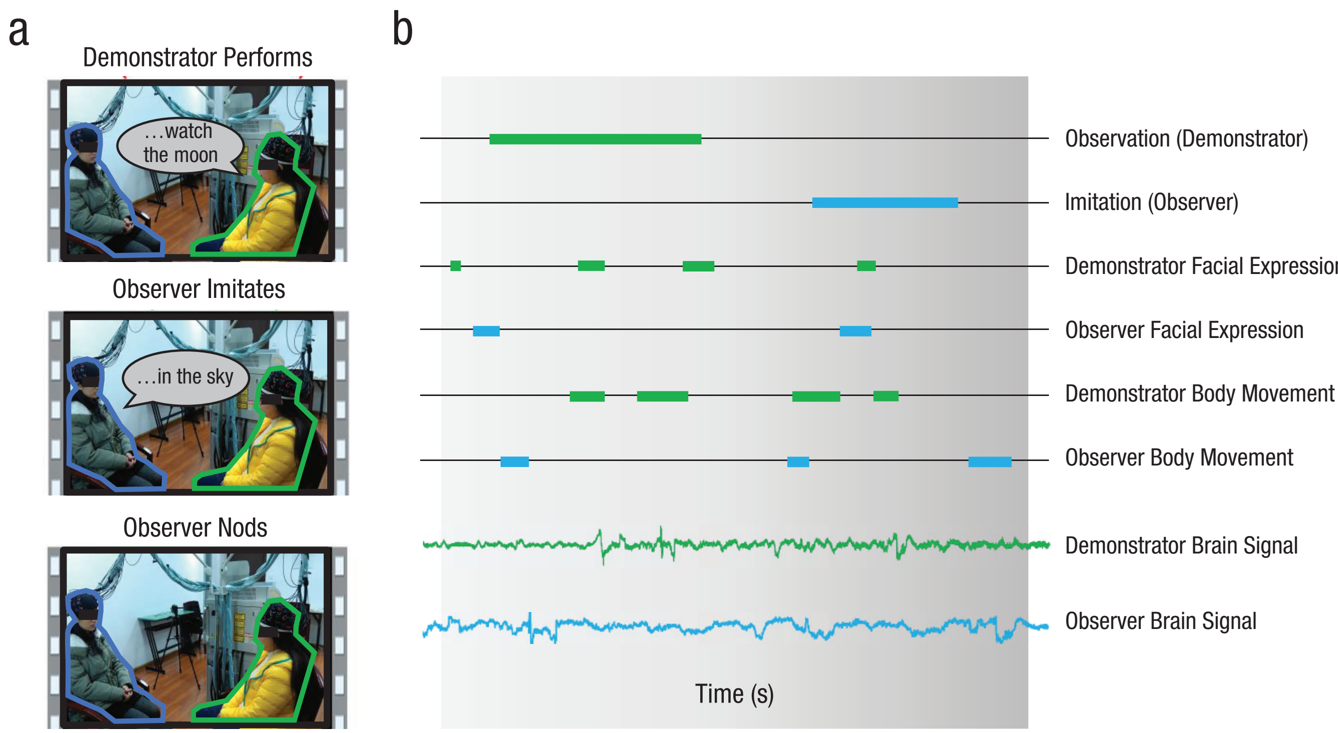

Fig. 3. A learning-relevant behavioral coding approach. Example behaviors are coded from video frames (a). The demonstrator and the observer are outlined in green and blue, respectively. Brain signals recorded from the demonstrator and the observer are analyzed (b) as a function of dyadic communicative behavior (including observation, imitation, facial expressions, and body movements) across time (in seconds). The demonstrator's and observer's behaviors (and brain signals) are marked in green and blue, respectively. Parts of (a) adapted from *NeuroImage*, Vol. 183, Pan, Y., Novembre, G., Song, B., Li, X., & Hu, Y., Interpersonal synchronization of inferior frontal cortices tracks social interactive learning of a song, pp. 280–290, Copyright © 2018, with permission from Elsevier.

have gained increasing attention lately. One such approach is the use of machine-learning-based decoding, which builds mathematical models from sample data (i.e., a training set) to classify behaviors automatically (Koza et al., 1996). This machine-learning-based decoding approach has several benefits: It allows us to (a) assess how accurately BtBC can classify learning behaviors (i.e., accuracy), (b) test whether data from various brain regions provide distinctive information for classification (i.e., spatial information), and (c) track the temporal evolution of the performance of the decoding algorithms (i.e., temporal information). In these ways, the decoding approach can provide valuable (accuracy, spatial, and temporal) information about whether learning states or learning-relevant communicative behaviors of an individual can be inferred solely on the basis of BtBC (Dai et al., 2018; Jiang et al., 2015).

To provide an intuition of how machine learning can be applied to BtBC, aiding our understanding of learning relevant behavior, we describe the generic steps of this procedure (Fig. 4; see also Dai et al., 2018; Hou et al., 2020; Jiang et al., 2012, 2015; Pan, Dikker, et al., 2020). First, BtBC is estimated for every time point and every participating dyad; communicative behaviors during learning are labeled via the video-based behavioral coding technique (see the previous section). Next, brain data and behavioral markers are combined. The whole data set is then split into training and testing sets. Finally, a classification algorithm on BtBC is trained to classify different types of communicative behaviors during learning (see Dai et al., 2018; Hou et al., 2020; Jiang et al., 2012, 2015; Pan, Dikker, et al., 2020).

Very few studies have combined machine learning and BtBC to examine social learning. In a pioneering study using EEG, Cohen and colleagues asked students to watch a series of educational videos, during which students' brain activity was recorded (Cohen et al., 2018). The researchers found that BtBC (indexed by the intersubject correlation of the video-evoked EEG) discriminated between attentive and inattentive video viewing of the students. In addition, students with higher BtBC retained more learning content. In another study, using the same approach, Zhu and colleagues further found that BtBC among students discriminates between different levels of learning desire toward online courses (Zhu et al., 2019). However, these combinations of machine learning and BtBC in educational settings did not involve real-time learning interactions

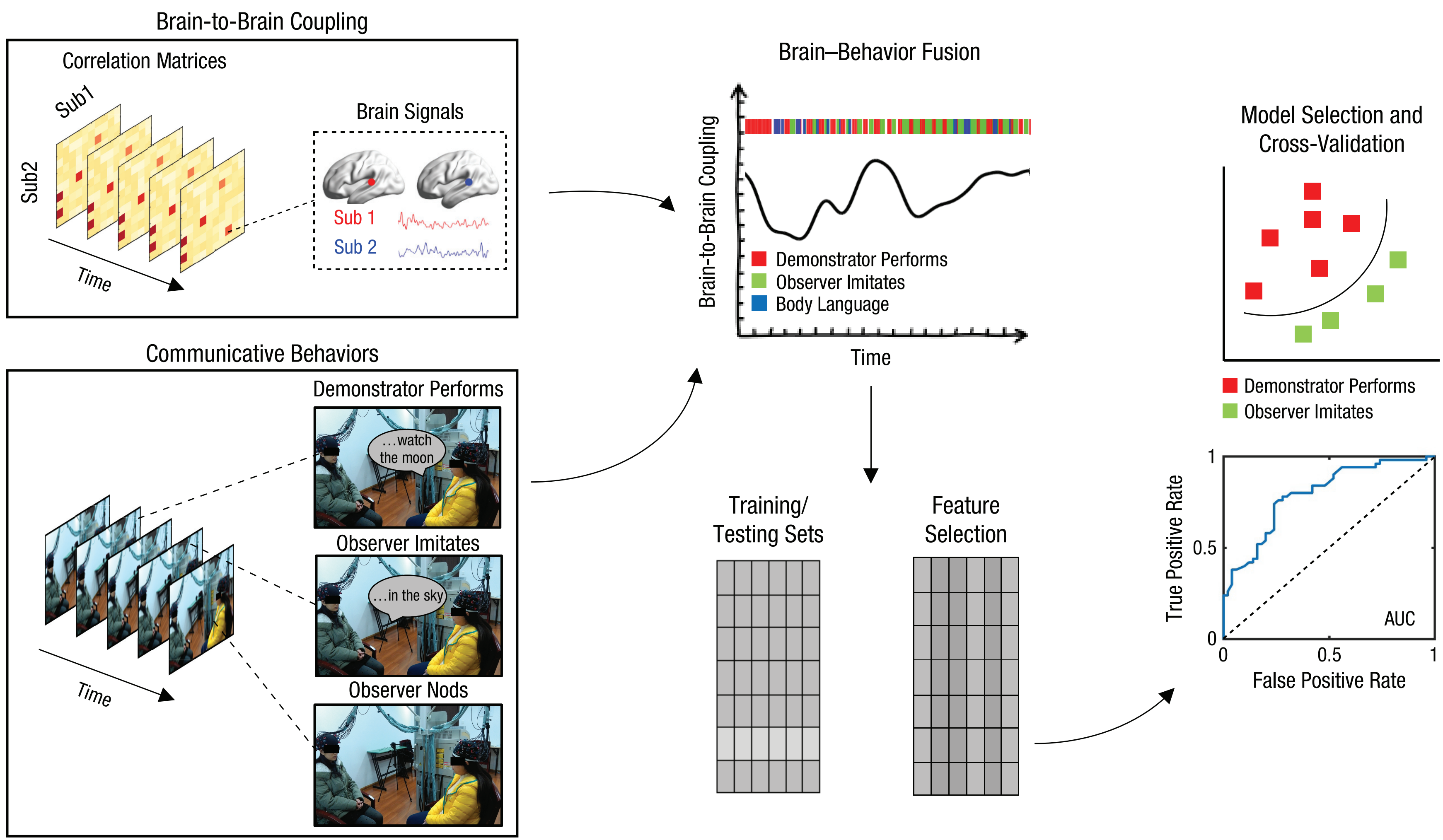

Fig. 4. Exemplified steps of analysis for decoding communicative behaviors from brain-to-brain coupling (BtBC). First, BtBC and communicative behaviors during learning are estimated for each time point. Brain data and behavioral labels are then combined. The whole data set is split into training and testing sets. Finally, a classification algorithm is implemented to differentiate different types of communicative behaviors (e.g., demonstrator performs vs. observer imitates) during learning. Classification performance is evaluated using, for example, accuracy or area under the receiver operating characteristic curve (AUC). Video frames are adapted from *NeuroImage*, Vol. 183, Pan, Y., Novembre, G., Song, B., Li, X., & Hu, Y., Interpersonal synchronization of inferior frontal cortices tracks social interactive learning of a song, pp. 280–290, Copyright © 2018, with permission from Elsevier.

between individuals. In other words, they did not entail an actual bidirectional interaction among individuals.

To address this gap in previous research, we recently combined machine learning and BtBC in a naturalistic learning task that allowed for real-time interactions (Pan, Dikker, et al., 2020). A demonstrator was asked to teach psychological concepts to an observer, during which the two participants' brain activity was recorded simultaneously. The demonstrator could use either a scaffolding strategy (e.g., asking guiding questions or providing hints) or an explanation strategy (e.g., providing definitions or clarifications) to transmit the knowledge. A logistic regression classifier based on demonstrator–observer brain coupling successfully distinguished demonstrators who used the scaffolding or explanation strategy with nearly perfect decoding performance. To evaluate the additional value of BtBC in decoding, we applied the same decoding analysis but based it on individual brain activation. Extending previous research, we found that machine-learning techniques were more successful when decoding behaviors during learning from BtBC data than when using a single-brain method: Whereas BtBC allowed us to discriminate between instructional strategies with a reasonable classification performance, the decoding analysis performed on the basis of the individual brain activation was insufficient to do so (possibly because BtBC data may be associated with a higher signal-to-noise ratio, as opposed to single-brain data; Parkinson et al., 2018; Simony et al., 2016). These findings echo previous studies showing that BtBC predicts memory retention (as a form of learning outcome) more accurately than individual brain measures (Davidesco et al., 2019).

In light of current evidence, we argue that BtBC serves as a good neural-classification feature that optimizes the decoding of social learning. Machine learning in combination with interpersonal neuroscience is promising yet nascent, and many outstanding questions remain unanswered. For example, how can sample size be optimized to reach a reliable decoding performance in interpersonal neuroscience? How can the dual brain-based machine-learning model (e.g., logistic regression) be developed?

BtBC Predicting Learning Outcome

Here, we have suggested that BtBC can aid better understanding of social behaviors *during* learning (Fig. 2a and 2b). In addition, we suggest that BtBC can predict *future* learning outcome (Fig. 2c). To the extent that BtBC has functional significance in social learning (i.e., contributing to successfully learned and adaptive behaviors), BtBC measured during learning should be positively correlated with behavioral-learning outcomes and memory retention.

Indeed, recent studies have shown that BtBC during learning is reliably linked to the success of social learning across different tasks (Holper et al., 2013; J. Liu et al., 2019; Pan, Dikker, et al., 2020; Pan et al., 2018; Zheng et al., 2018). For example, using fNIRS, Zheng et al. (2018) monitored and recorded the brain activity of a teacher and student simultaneously. Their results showed that stronger BtBC between the right temporoparietal junction of the teacher and anterior superior temporal cortex of the student (regions classically associated with high-level mentalizing and semantic representation; Carter et al., 2012; Pobric et al., 2016) predicted better learning outcomes; this was the case when the teacher's brain activity preceded that of the student (i.e., time-lagged BtBC—neural processes in one brain are coupled with those in another brain with a time delay), regardless of teaching style. BtBC can predict not only immediate learning performance but also long-term memory retention: For example, Davidesco et al. (2019) recorded EEG in a classroom from groups of four students and a teacher during a science course, showing that BtBC successfully predicted how much information students retained immediately, as well as after 1 week.

The link between coupled neurophysiological responses (i.e., synchronized neurophysiological signals) and learning outcomes was also found in an observational-learning task examining skin-conductance responses (as an index of threat learning) in observer–demonstrator dyads (Pärnamets et al., 2020): Observers successfully acquired threat responses by observing the fearful reactions of demonstrators who sat beside them. Note that greater synchronization of phasic skin conductance between demonstrator and observer during the learning phase predicted the observer's threat learning performance as measured later in the absence of the observer.

Some researchers have not observed the association between BtBC and learning outcome in an interactive learning task (Bevilacqua et al., 2019). This lack of relationship deserves further exploration, given that it may reflect a lack of sensitivity of learning paradigms, may depend on learning interaction modality (J. Liu et al., 2019) or instructional strategy (Pan, Dikker, et al., 2020), or may require a moment-to-moment variance analysis (Davidesco et al., 2019; Pan et al., 2018).

On the basis of recent advances showing that synchronicity between brains' signals predicts learning outcomes (J. Liu et al., 2019; Pan, Dikker, et al., 2020; Pan et al., 2018; Zheng et al., 2018), we propose that BtBC during social learning can be described as a means to a functional end—contributing to successfully learned and adaptive behavior (measured as expressed memories and behavioral performance). It is possible that the functional qualities of BtBC result from an improved real-time transfer of information. One of the ultimate goals of studying BtBC is to enable individualized predictions of learning outcomes that may eventually benefit pedagogical and clinical practices. Certainly, this will require massive future efforts to consolidate existing findings, and extend them to various real-world learning settings (e.g., classroom and field).

Causation Between BtBC and Social Learning

Despite the observation that BtBC measured during the learning procedure is strongly linked to learning outcomes, nearly all evidence in this area is purely correlational: Synchronicity between brains' signals is only measured and correlated with learning. Scarcely any studies examine whether BtBC is simply epiphenomenal to interpersonal learning—BtBC might emerge as a biproduct of intrinsic motoric and perceptual similarities between individuals during learning, or it might play a causative role in social-learning mechanisms. To provide causal insights into the functional role of BtBC in learning (Fig. 2d), it is imperative to control or manipulate BtBC and observe its effects on learning.

Recently, we addressed this open question (i.e., epiphenomenal vs. causative perspectives on BtBC) by taking a novel approach (Pan et al., 2021): We used a protocol involving multiperson transcranial alternating-current stimulation developed by Novembre et al. (2017) to exogenously synchronize two brains, thereby manipulating BtBC, and we measured the resulting behavioral effects on social learning (this is generally called *multibrain stimulation*; Novembre & Iannetti, 2021). We collected two distinct measures of behavior—learning outcome and interpersonal body movements. The second measure was meant to be exploratory; it was inspired by previous research indicating that interpersonal synchronous movement can promote prosocial behaviors (Hu et al., 2017; Reddish et al., 2016) and therefore possibly learning as well. In our study, a demonstrator was asked to teach a four-phrase musical song to an observer, without constraints on using natural movements or body language to facilitate learning. During this learning session, the demonstrator's and observer's inferior frontal cortices (regions associated with interactive learning of musical songs; Pan et al., 2018) were synchronized through multibrain alternating-current stimulation. The results showed that during multibrain stimulation, the dyad exhibited spontaneous body movements that were synchronized. This result is intriguing in that it reflects an action synchronization in a social setting that was not the result of explicit instruction (Yun et al., 2012), and so it possibly had communicative significance. Note that multibrain stimulation also enhanced final learning outcome. Further analysis disclosed that interpersonal-movement synchrony acted as a partial mediator of the effect of multibrain stimulation on learning performance; that is, movement synchrony possibly facilitated the effect of brain stimulation on learning. All together, we provided a causal demonstration that exogenous manipulation of BtBC enhanced interpersonal learning through communicative behavior.

Apart from multibrain stimulation, another experimental approach that has been discussed as relevant for addressing the potentially causal role of BtBC is cross-brain neurofeedback (Dikker et al., 2019; Duan et al., 2013). Cross-brain neurofeedback entails providing feedback of indices of brain activity to interacting people to allow those people to possibly regulate BtBC. This could allow researchers to tease apart experimental conditions associated with either higher or lower BtBC and measure the consequences on social behavior (as a dependent variable). A pioneering study in this area has shown that cross-brain neurofeedback is feasible (Duan et al., 2013), although its consequences on social behavior have not been explored yet. We note that this approach is not qualitatively different from hyperscanning (i.e., the measurement of two or more brains simultaneously, Babiloni & Astolfi, 2014; Montague et al., 2002), because here the experimenters are not exogenously manipulating BtBC, but they are creating an experimental situation favoring the emergence of BtBC. Yet, as Duan et al. (2013) put it, this approach could provide "more causal insights" (para. 2) than classical hyperscanning does. We believe this is a promising approach and should be exploited further.

In summary, we have highlighted a causative role of BtBC in facilitating social learning. Our view that BtBC can be causally efficacious in improving real-time information transfer between live pairs of individuals stands in contrast to the view of BtBC as purely an epiphenomenon of social learning (at least in some instances).

Mechanistic Models for BtBC and Learning

Several potential mechanistic models can be proposed to account for the suggested (causal) influence of BtBC in social learning (Fig. 5). Before such proposals are presented, however, a better understanding of how the field has explained social learning so far is needed. Current knowledge of social learning suggests that transmission of information during social learning can occur through a variety of mechanisms (Gariépy et al.,

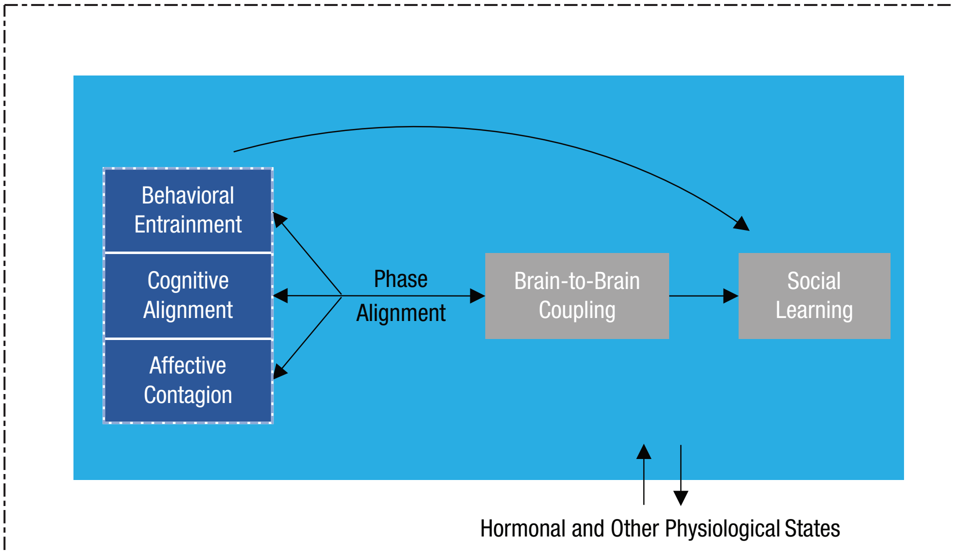

Fig. 5. A synthesized mechanistic framework for brain-to-brain coupling (BtBC) and social learning. BtBC may reflect phase alignment of neural processes across individuals, facilitating efficient information transfer between brains, and therefore social learning. BtBC might either cause, or be caused by, distinct kinds of social alignment (i.e., the coupling of behavioral, cognitive, or emotional states of multiple individuals; Shamay-Tsoory et al., 2019), such as behavioral entrainment (e.g., interpersonal movement synchrony), cognitive alignment (e.g., shared understanding and joint attention), and affective contagion (e.g., emotional contagion and empathy). The above mechanistic processes could further interact with hormonal and other physiological states. Note that the three distinct kinds of social alignment might affect learning, either directly or indirectly through other neural mechanisms, irrespectively of BtBC (top arrow); it is also possible that social learning might, in turn, affect BtBC.

2014), including enhancement of attention to others (van de Waal et al., 2010; Watson & Platt, 2012), recognition of others' reactions (e.g., facial expressions, approach or avoidance behaviors) to stimuli (Golkar et al., 2013; Olsson et al., 2007; Olsson & Phelps, 2007), motor simulation and imitation (Charpentier et al., 2020; Iacoboni & Mazziotta, 2007), and theory of mind (i.e., modeling the goals, intentions, and emotions of others; Burke et al., 2010; Joiner et al., 2017; Koster-Hale & Saxe, 2013). Though informative, existing models mostly focused on the mechanistic features within the boundary of observers (learners), leaving behavioral/cognitive/affective dependencies between observers and demonstrators less explored.

Beyond the single-person mechanisms for social learning reviewed above, interpersonal neuroscience along with measures of BtBC can offer novel insights. Below, we propose several mechanistic models for BtBC and social learning that are based on a multiperson perspective (Fig. 5).

First, temporally concurrent patterns of task-related shared experiences may lead to phase alignment of neural processes across individuals (Leong et al., 2017). Alignment of the phase of brain oscillations was proposed to facilitate efficient information transfer between multiple brain regions in a single brain (Buzsáki, 2009; Fell & Axmacher, 2011). Here, we extend the previous proposal by arguing that phase alignment also contributes to information transfer across brains. Such BtBC might affect real-time transfer of ongoing information and eventually learning (Pan et al., 2018; Wass et al., 2020). In addition, communicative behaviors (e.g., eye-to-eye contact; Hirsch et al., 2017; Noah et al., 2020) might help resetting the phase of neural oscillations between individuals: One plausible explanation might be that if the timing of behaviors during learning reflected the phase of the oscillations in one individual, then this timing information could be used to synchronize the phase of the neural oscillations of another individual (Hu et al., 2018; Leong et al., 2017).

Second, BtBC might either cause, or be caused by, behavioral entrainment (or interpersonal movement synchrony) between individuals (Pan et al., 2021). Behavioral entrainment (associated with BtBC) between individuals has been reported to lead to prosocial effects (Hu et al., 2017), which hypothetically affect learning outcomes (Bevilacqua et al., 2019). The effect of BtBC could also call for other high-order cognitive functions—for instance, joint attention (Dikker et al., 2017; Lachat et al., 2012; Tomasello, 1995) and shared understanding (Y. Liu et al., 2017; Stephens et al., 2010)—that affect learning. Specifically, joint attention has been reported to scaffold social cognition in various social contexts (Mundy & Newell, 2007) and real-life classroom learning (Dikker et al., 2017); shared narrative understanding was correlated with shared neural responses across individuals (Nguyen et al., 2019), both of which may lead to better memory retention and learning performance. Moreover, social affective or reward networks might also be recruited (Fairhurst et al., 2013) and facilitate empathy and emotional contagion that in turn can promote social learning (Pärnamets et al., 2020). Note that the potential causal mechanisms described here are not mutually exclusive and could be working interdependently and/or jointly to promote social learning.

The aforementioned mechanistic models for BtBC and learning are likely to also interact with hormonal and other physiological states (Gvirts & Perlmutter, 2020). Prior reports have demonstrated the roles of opioids and oxytocin in both social behaviors and learning. For instance, Haaker et al. (2017) reported that blockade of endogenous opioids enhanced observational threat learning and activity within the amygdala, midline thalamus, and periaqueductal gray in humans (Haaker et al., 2017). The administration of oxytocin enhanced coordination of behaviors (Arueti et al., 2013) and enhanced BtBC during social coordination (Mu et al., 2016). A large pool of evidence also suggests that oxytocin is crucial for forming social memories and regulating social behaviors in interactive settings. For example, exposure to a stressed (familiar) partner increased consolation behaviors and anterior cingulate activity of an unstressed partner in rodents, and an injection of an oxytocin-receptor antagonist in the anterior cingulate cortex abolished these consolation behaviors (Burkett et al., 2016).

Although these mechanistic models all have merit, the question of whether and how emerging multibrain techniques can carve nature at its joints, and tap into the real mechanisms, deserves further examination (Hamilton, 2020; Novembre & Iannetti, 2021).

Current Challenges and Future Opportunities

Currently, the major challenges that constrain the advancements of interpersonal neuroscience in social learning are methodological and interpretational. One significant challenge comes from the lack of a uniform and user-friendly data analysis workflow for interpersonal neuroscience. Compared with standard statistical approaches used in single-person neuroscience, analyzing pipelines for interpersonal neuroscience should consider not only ongoing activity in individuals but also mutual temporal dependencies between individuals and the potential nesting of participants in dyads and dependence of data points (e.g., when one demonstrator is paired with multiple observers; see, e.g., Davidesco et al., 2019). Along this line, pioneering research has attempted to set up standardized analyzing guidelines for interpersonal neuroscience (Ayrolles et al., 2020; Nastase et al., 2019). Another challenge is related to whether BtBC can be described as a mechanism in itself (Hasson et al., 2012) or is a measurable reflection or biproduct of psychological processes (e.g., joint attention; Dikker et al., 2017). In our view, BtBC mechanisms (e.g., how multiple brains are coupled together to allow for efficient interpersonal information transfer; Hasson et al., 2012) are distinguishable from "mechanisms" in conventional neuroscience (by which latent neural properties within a single brain biophysically underlie emergent psychological constructs; Cavanagh & Frank, 2014). The fact that BtBC plays functional roles in social behaviors suggests that it is not epiphenomenal (although the aforementioned evidence should not be taken as conclusive for all sorts of BtBC discussed in previous studies). Future investigations are needed to address causative issues by, for example, exclusively testing how BtBC can be augmented or perturbed following interventions (e.g., neurostimulation or distractor) and testing the resulting effects upon psychological constructs and behaviors in an endeavor to better understand the role of BtBC in learning.

We identify three other important avenues for future research, the first being to apply computational-modeling techniques to integrate interpersonal neuroscience and social learning. Computational approaches have been increasingly applied in social-learning tasks (Burke et al., 2010; Charpentier et al., 2020; Lindström et al., 2018, 2019; Selbing et al., 2014), but there have been limited attempts in interpersonal neuroscience (but see Bolis & Schilbach, 2017; Hampton et al., 2008; Heggli et al., 2019). Future efforts are needed to formulate a neurocomputational account for social learning in two- or multiperson experimental setups. A second important research avenue pertains to the diagnostic techniques and complementary interventions for learning deficits or maladaptive learning (Schilbach, 2016). Compared with social observation scales and instruments, which rely heavily on raters' subjective experience, interpersonal neuroscientific approaches might lead to earlier and more sensitive identification of atypical interpersonal/social-learning behaviors (Leong & Schilbach, 2019; Schilbach, 2016). Those state-of-the-art technologies—for example, multibrain stimulation (Novembre et al., 2017; Novembre & Iannetti, 2021; Pan et al., 2021) and cross-brain neurofeedback (Dikker et al., 2019; Duan et al., 2013)—could make a significant contribution by addressing methodological and translational barriers. Finally, when aiming for a better understanding of the significance of BtBC, it might be ideal for future research to adopt multimodal recordings, such as electroencephalography–functional MRI hyperscanning, to obtain complementary temporal and spatial information.

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