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Synchrony Across Brains

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Abstract

Second-person neuroscience focuses on studying the behavioral and neuronal mechanisms of real-time social interactions within single and across interacting brains. In this review article, we describe the developments that have been undertaken to study socially interactive phenomena and the behavioral and neurobiological processes that extend across interaction partners. More specifically, we focus on the role that synchrony across brains plays in enabling and facilitating social interaction and communication and in shaping social coordination and learning, and we consider how reduced synchrony across brains may constitute a core feature of psychopathology.

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INTRODUCTION

The field of social neuroscience started out with the idea of studying the biological basis of "interacting minds" (Frith & Frith 1999). In early years this was typically done by studying one brain at a time. Moreover, the experimental tasks typically used did not involve study participants in reciprocal social interaction but rather engaged them in social observation, such that a study participant was asked to observe a face stimulus rather than interact with another person. The advent and growing availability of functional magnetic resonance imaging (fMRI) as a powerful, noninvasive technique accelerated the study of the neural correlates of social perception and cognition in subsequent years. Already in 2002, however, it was demonstrated that fMRI could be extended to studying the brains of two interaction partners, which was described as hyperscanning (Montague et al. 2002). To this end, two MRI machines were linked up technically in such a way that two study participants could simultaneously undergo neuroimaging while interacting by means of a computerized task. In its initial implementation, data analysis of these hyperscans was conducted similarly to the analysis of single brains, which raised the questions of whether hyperscanning could provide specific scientific advantages other than helping to collect neuroimaging data more quickly and of when measuring two brains was really necessary to learn something new about social interactions (Konvalinka & Roepstorff 2012). Answers to this question have been given in different ways and using different methodologies, some of which are presented in greater detail in this article and focus on studying the neurobiology of social cognition and behavior across the brains of interaction partners during live, real-time encounters or in cases where the experimental manipulation recreated an interaction sequence or tested whether participants' brains responded similarly to social stimuli.

Hyperscanning: the process of collecting neuroimaging data from at least two individuals while they are engaging in mutual interaction

It is important to note that these developments and growing numbers of studies have been scaffolded by conceptual advances that tried to pinpoint why two-brain neuroscience was needed: Based on the idea that being in an ongoing, reciprocal social exchange with another person might be fundamentally different in terms of subjective experience, behavioral coordination, and the underlying neurobiological mechanisms as compared to merely observing another person, the development of a "second-person neuroscience" has been suggested (Schilbach et al. 2013). By drawing upon embodied, enactive accounts of social cognition, this approach has led to a stronger focus on studying socially interactive phenomena while investigating one person's brain, but it also meant obtaining neuroimaging recordings from both interaction partners (Redcay & Schilbach 2019).

In order to study the neurobiology underlying social interactions, it is necessary to use experimental paradigms that involve participants in structured or—ideally—ecologically valid, dynamically unfolding social interactions. The interactions can be real or perceived; however, they should always take place in real time and be reciprocal, such that one partner's actions directly affect the other and vice versa. These important developments have yielded completely new insights into the workings of the so-called social brain. For instance, it has been shown that regions of the so-called mentalizing network [or default mode network (DMN)], typically activated by explicitly asking study participants to think about the mental states of another person, also respond similarly during social interaction with or without explicit task demands to engage in mental-state reasoning (e.g., Redcay et al. 2010, Schilbach et al. 2010, Rice & Redcay 2016, Rice et al. 2016, Alkire et al. 2018). In addition, second-person neuroscience studies have questioned the distinction between the mentalizing and action observation networks by showing integration between both networks during real-time social interaction (Schippers et al. 2010, Ciaramidaro et al. 2014, Sperduti et al. 2014). This raises the question of why these networks might act in concert during social interaction but not during observation. Studies investigating the inhibition of spontaneous mimicry give some insight by suggesting that mentalizing regions (particularly the medial prefrontal cortex) may act to control the automatic shared representations between social partners (Wang et al. 2011). Indeed, second-person neuroscience studies point toward greater resonance, or shared representations, during social interaction and have suggested the exploration of these phenomena within interacting brains.

In other words, second-person neuroscience findings have challenged the traditional stimulus-response view of how the brain infers and reasons about others' mental states, including their goals, intentions, and beliefs. Furthermore, it has opened up new avenues for research that focus on collecting and analyzing data from the brains of all interaction partners. In fact, simultaneous dual-brain approaches are the only method potentially able to examine the emergent dynamics between two interactors in real time. Such emergent dynamics rely on the contribution of (at least) two autonomous agents and can only be described by using interpersonal measures that capture, for instance, how the gaze behavior of person A changes contingent upon the gaze behavior of person B (Leong & Schilbach 2019). Furthermore, it has been shown that people behave differently during real-life social interaction (Becchio et al. 2010) and that interactions with trained confederates during lab-based experiments may not capture natural behavior (Kuhlen & Brennan 2013). Initial simultaneous dual-brain studies as introduced above, however, were limited in that they often used highly constrained tasks originating from game theory (such as economic bargaining games), which did not allow for freely forming, face-to-face interactions but rather relied on a sequential exchange of symbols. In recent years, paradigms involving more ecologically valid social situations, including gaze-based and verbal communication tasks (Hirsch et al. 2017, Kinreich et al. 2017), have been developed and have been put to more frequent use. With simultaneous dual-brain approaches, researchers can, thus, identify interindividual synchrony at the behavioral and neural

Social brain: a group of brain networks and regions that are associated with social processing, including the default mode network and networks associated with affect and reward processing, social salience, social perception, and action understanding

Mentalizing network: network overlapping with the default mode network but referring to regions that respond more when making judgements about another person's mental state

Default mode network (DMN): network including bilateral anterior and posterior midline regions, temporoparietal junction, and anterior temporal lobes at its core, which is reliably engaged during tasks involving social processing

Action observation network: social brain network that is engaged both when performing actions and when observing others perform actions, suggesting an important role in self-other representation and imitation level when two (or more) participants are engaged in a reciprocal and freely forming interaction. In other words, research has shifted toward the investigation of how real-time social interactions lead to synchrony across bodies and brains, and it is to the discussion of this topic that we now turn.

Simultaneous dual-brain approaches: approaches in which neuroimaging data are acquired from two individuals concurrently while in an interaction (synonymous with hyperscanning)

MAKING MINDS MORE SIMILAR: MEASURES OF INTERPERSONAL BEHAVIORAL AND NEURAL SYNCHRONY

Behavioral Synchrony

Interpersonal coordination, that is, coordinating one's behavior with that of conspecifics, is recognized as an important human ability across different fields of research. It has been suggested that the act of keeping together in time with others may foster our social bonds (Wheatley et al. 2012, Vicaria & Dickens 2016). Furthermore, synchronized and coordinated behavior across individuals may help groups of individuals to act as a single or social unit, which allows them to achieve goals jointly that would otherwise not be attainable (e.g., Kourtis et al. 2019; for a review, see Sebanz & Knoblich 2021).

Behavioral synchrony can be created in multiple ways, including synchronizing the same basic actions—for example, walking together or imitating a partner's actions or coordinating different actions with another person. In the category of synchronizing basic actions is the phenomenon of behavioral mimicry, which refers to the unconscious or automatic imitation of speech and movements, gestures, facial expressions, and eye gaze (Chartrand & van Baaren 2009). Here, social psychology has demonstrated that producing the same behavior as someone else increases sympathy and rapport with others, unless one realizes that such mimicry is done intentionally and not spontaneously, and it can help to induce more complex forms of interpersonal coordination (e.g., Lakin 2013, Dumas et al. 2014, Duffy & Chartrand 2015). Apart from mimicry in terms of observable behaviors, there is also evidence for mimicry on other levels, such as similarity of heart rates and synchrony of pupil dilation (Palumbo et al. 2017, Wohltjen & Wheatley 2021). Furthermore, such instances of behavioral mimicry appear to be closely connected to what is called emotional contagion, that is, the human ability to be affected and share affective states with others (Hatfield et al. 1993). According to the perception-action model of empathy (Preston & de Waal 2002), emotional contagion and our ability to automatically track and integrate the bodily and affective states of another person can be described as a basic form of empathy, which may allow us to intuitively grasp what goes on in another person. Indeed, a large body of literature in social neuroscience demonstrates that observing others' actions and emotions activates brain regions that are involved in generating these same behaviors or emotions in oneself, which has been described as a simulation or mirror mechanism (Rizzolatti & Sinigaglia 2010, 2016).

Apart from studies that focus on the temporal link and coupling of simple and similar movements or actions, other studies have also studied task-directed complementary or joint action tasks, which address the notion of behavioral or interactional synchrony. Interactional synchrony refers to situations in which people coordinate their movements, which may or may not be similar, to coincide with those of others. Here, one needs to produce actions but also anticipate those of others in order to coordinate with them to produce joint actions (Knoblich et al. 2011). In a study by Richardson et al. (2015), dyads of participants performed a targeting task in which they both moved computer stimuli without colliding with one another. The results demonstrated that participants were able to establish an asymmetric pattern of synchronous movement, which was essential to task success. In other words, patterns of complementary, interpersonal action synchronization can sustain more complex joint actions. Interestingly, recent evidence in adults suggests that behavioral coordination across people also affects their cognitive systems, in particular those that are involved in reasoning about others' mental states. A study by Baimel et al. (2018), for instance, demonstrated that physically moving together with others increased mental state attribution and feelings of social connection specifically to those with whom participants had behaviorally synchronized. In other words, aspects of interpersonal coordination appear to go deeper than the skin and influence both emotional and cognitive processes of those involved by making them—in some cases—more similar and more susceptible to reading each other's minds.

This brings us to the question of whether we can also observe synchrony across persons at the neural level, and what such measures could help to explain. Below we discuss two forms of neural synchrony: neural similarity and interactive neural synchrony (INS). Neural similarity is an offline measure of how similar two brains are, while INS is an online measure that captures alignment between brains in real time.

Neural similarity: how similarly individuals' brains respond to the same stimulus and can be measured through sequential data acquisition (synonymous with non-interactive synchrony)

Interactive neural synchrony (INS): a measure of real-time neural synchrony thought to reflect a process of coming into alignment with an interactive social partner (though it can be influenced by neural similarity between partners)

Intersubject correlations: a dominant method used to measure neural similarity in which similarity in which brain response (or time series) between individuals are correlated

Neural Similarity

Seminal work by Hasson and colleagues has repeatedly demonstrated that in early sensory areas, shared neural patterns across individuals, so-called intersubject correlations (a type of neural similarity), are coupled to the low-level properties of the stimulus, while in high-order brain areas, shared neural patterns are coupled to high-level aspects of the stimulus, such as meaning (e.g., Silbert et al. 2014, Chang et al. 2022). Nummenmaa et al. (2012) used fMRI to investigate brain activity while participants were individually watching movies depicting unpleasant, neutral, and pleasant emotions. The results demonstrate that during movie viewing, participants' brain activity was, indeed, synchronized both in lower- and higher-order sensory areas, but that valence ratings obtained after the movie watching also showed increased intersubject correlation, which suggests that emotions play a particularly important role for binding people together, because they strongly contribute to similarity in neural responses across individuals—that is, to stronger synchrony across brains—which might facilitate social interaction and communication. In another set of groundbreaking studies, Parkinson et al. (2018) investigated whether familiarity, social network proximity, and friendship with other persons is related to interpersonal similarity of neural responses obtained during movie watching. The results, indeed, demonstrate that neural responses are exceptionally similar among friends and that the similarity in neural responses, in fact, decreases with increasing distance of the participants in real-world social networks. An additional study demonstrated that the extent to which neural responses are synchronized across persons when viewing naturalistic stimuli is closely related to their personality profile and may further reflect related similarities in the interpretation of the seen stimuli (Matz et al. 2022). An open question is whether neural similarity leads to more social interactions (and ultimately friendships) or greater social interaction leads to greater neural similarity. Recent work suggests the latter, as neural similarity during movie viewing was greater following conversation between strangers (Sievers et al. 2024). Additionally, neural synchrony during movie coviewing was increased following conversation between partners that was unrelated to the movie (De Felice et al. 2024). As these examples demonstrate, completely new insights into the working of the social brain and its functional relevance for real-life social interactions and social relationships have been made possible by focusing on measures of synchrony across brains without synchronously measuring two interacting brains (**Figure 1**).

Interactive Neural Synchrony

INS or hyperscanning studies as described above, however, are able to synchronously measure two interactive brains by examining coherence in neural activity and behavior in two (or more) persons in the context of a live, reciprocal social interaction. Crucially, this approach helps to investigate how behavioral and neural processes in one person affect those that are present and/or developing

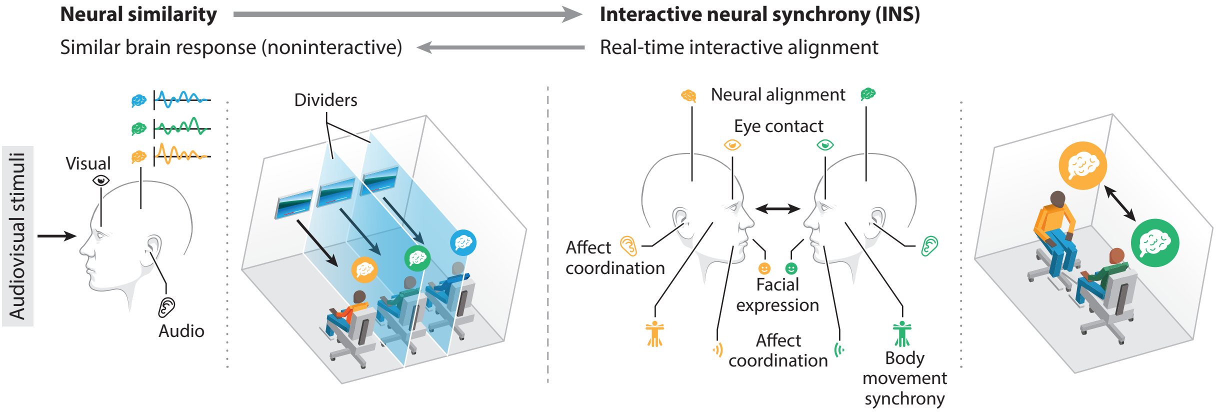

Figure 1

Interactive versus noninteractive neural synchrony. Neural similarity refers to how similarly a pair or group of individuals process the same audiovisual stimuli. Because individuals are not in a real-time interaction, this reflects similarities in existing brain function and organization rather than a real-time alignment between partners. Interactive neural synchrony (INS) refers to synchrony calculated during a real-time interaction using a variety of methodological approaches. INS can reflect existing neural similarity as well as conceptual alignment and behavioral coordination between partners that emerge over the course of the interaction. Unlike neural similarity, INS is also influenced by the social partner's behavior in real time. Social partners who begin their interaction with higher neural similarity will also show higher INS during the interaction. Further, repeated interactions with high INS with the same social partner have the potential to create more neural similarity between partners.

in the interaction partner. INS studies not only increase the ecological validity of studies in social neuroscience but also make it possible to investigate the neural mechanisms of how human beings communicate and affect one another during reciprocal social interactions by simultaneously focusing on the social exchange at the behavioral level and linking the behavior to synchrony across brains (**Figure 1**). Grounding INS in behavioral metrics of social exchange is important to disentangle cocreated INS from the similar processing of the shared environment.

Studies measuring INS during real-time interactions demonstrate links between verbal or nonverbal behavioral features of a conversation and neural synchrony, For example, a study by Kinreich et al. (2017), used EEG hyperscanning to investigate brain-to-brain synchrony in 104 adults during a male–female naturalistic social interaction, comparing romantic couples and strangers. INS was found for couples in temporoparietal regions but not strangers, and it was linked to measures of behavioral synchrony, in particular the exchange of social gaze. In other words, using a micro-level analysis of social behavior revealed a tight link between synchrony across brains and bodies. Neural synchrony in this study was not related to speech duration or conversation content, which suggests that some aspects of INS may be driven by the nonverbal rather than the verbal aspects of social interaction.

INS also appears to be greater during periods of information sharing between partners. In a study using a complex, multimodal approach that included eye- and face-tracking as well as functional near-infrared spectroscopy (fNIRS) during conversations in which participants did or did not disclose biographical information to each other, Cañigueral et al. (2021) demonstrated a modulation of both social behavioral signals and brain activity. Specifically, participants gazed more at each other's face and produced more facial displays during disclosure. At the neural level, greater brain activity was found in the temporoparietal junction, and INS was observed during the sharing of information. In other words, the ability to communicate information to another person modulates both nonverbal behavior and brain activity patterns and, again, leads to synchrony across brains. Importantly, the analysis model used by Cañigueral et al. (2021) accounted for task- and stimulus-driven effects, which suggests that INS was not merely driven by aspects of the task or stimulus input.

A groundbreaking study further demonstrates the importance of the temporoparietal junction for INS. Bilek et al. (2015) used hyperscanning fMRI and an ingenious setup that allowed for immersive audiovisual interaction of the two participants as they were both lying inside (separate) MRI scanners. To characterize information flow between the two interacting brains, the authors adopted a data-driven approach to extract components from all participants' data and were able to identify the temporoparietal junction as a brain region specifically coupled across brains during gaze-based social interaction.

Causal Approaches to Neural Synchrony

Dynamic causal modeling (DCM) relies on effective connectivity, or the influence one neural system exerts over another, and has recently been applied to hyperscanning fMRI data (Bilek et al. 2022). In this setup, correlated neural responses become data features that have to be explained by models with and without between-brain connections. This is an important addition to measures of functional connectivity across brains, because such correlative measures of synchronization between brains can be partly explained by exposure to the same sensory information. Measures of functional connectivity per se do not evaluate whether a connection between different brains needs to be assumed and how it is measurably instantiated. Bilek et al. (2022), therefore, plausibly suggest that we have to test empirically whether INS provides a better explanation for the neural data than single-brain approaches. In their study, they use hyperscanning DCM, because DCM can be used to distinguish and quantify potential causes of correlation. In the context of two-brain hyperscanning data, this means to evaluate both shared sensory input and effective connectivity between brains. Conceptually, the approach taken by Bilek and colleagues is related to the notion of generalized synchrony, that is, the characteristic behavior of loosely coupled dynamical systems (Hunt et al. 1997), whereby knowing the state of one system would allow prediction of the state of the other (Jiruska et al. 2013). Importantly, according to Bilek et al. (2022) generalized synchrony can only occur if there is formal or structural similarity between the coupled systems. In other words, two brains can only become coupled via generalized synchrony when they share the same sort of dynamical structure. Previous work by Friston & Frith (2015) has addressed this question and used the active inference framework to generate simulations based on this premise. On this view, communication can be seen as a process between individuals that use the same model to process and attend to sensory input that is interchangeably produced by the interaction partners. Attending to sensations then allows for a shared narrative to predict sensations generated by another individual or to articulate the narrative oneself. According to Friston & Frith (2015), this produces a reciprocal exchange of sensory signals that induces a generalized synchrony between brain states in both agents. Following this logic and using hyperscanning DCM, Bilek et al. (2022) demonstrate between-brain effective connectivity that is specific to social exchange in a two-person joint attention task and directed from the sender's to the receiver's right temporoparietal junction. In other words, a causal connection was present between the two brains and was necessary to explain the data while accounting for the shared perceptual input of the two interaction partners. These findings highlight the importance and novel methodological opportunities of investigating INS beyond measures of functional connectivity and demonstrate how brain systems are dynamically coupled during reciprocal social interaction, whereby a sender's brain—in a control theoretic sense—has a causal impact on the receiver's brain. This causal connection may reflect processes of conceptual alignment to one's partner, representation of affective states, or increased prediction of a social partner's actions (see the section titled Mechanisms of Interbrain Neural Synchrony). Future exploration of the causality of cross-brain phenomena may profit from the use of multi-brain stimulation (Novembre & Iannetti 2021).

SYNCHRONY ACROSS BRAINS ENABLES AND FACILITATES SOCIAL INTERACTION AND COMMUNICATION

As discussed above, synchrony across brains comes in different forms and flavors. In this section, we focus on work that demonstrates how communication relies upon interpersonally shared similarities in brain activation patterns (i.e., neural similarity) and upon integration with neural networks that evaluate incoming information against prior and conceptual knowledge to create alignment between partners and generate a neural signature of shared experiences (i.e., INS). We also discuss possible cognitive explanations for the occurrence of INS.

Synchrony across two brains can occur when two persons who have sufficiently similar brains are being exposed to the same signal or stimuli. This synchrony emerges early and is foundational to the development of communication. As a matter of fact, human beings have the spontaneous tendency to experience (and know) the world together. Importantly, this is what the word consciousness, stemming from the Latin term *conscientia*, meaning "knowledge shared with others," used to mean. In other words, falling into synchrony with other brains appears to be an important aspect of the sharing of experiences. This sharing of experiences and understanding are fundamental to the emergence of any communication system, as a signal's meaning must be shared to allow individuals to communicate (Wittgenstein 1973). Such a shared understanding of signals and objects in the world is developed early during human development by means of various practices that can be subsumed under the term "shared intentionality" (Rakoczy & Tomasello 2007). The first instances of shared intentionality are already apparent during the first months of life, when infants demonstrate responsiveness to the reciprocity of face-to-face interactions with the caregivers. Later the interactively constituted phenomenon of joint attention emerges, whereby interaction partners actively coordinate their attention toward aspects of the environment, share experiences, and create a common ground that is known to be highly important for the development language (e.g., Mundy et al. 2007). In other words, forms of (increasingly sophisticated) communication emerge through embodied social interactions and the immediate context they create (Galantucci 2005), and typical adults continue to exert this tendency to align their behaviors and perspectives with others. This alignment or shared intentionality that emerges from repeated interactions shapes similarity between brains, leading to greater interbrain alignment in future interactions between social partners (De Felice et al. 2024) (**Figure 1**).

Conversations are characterized by various forms of synchronization: For instance, breathing patterns during conversation are correlated. Also, conversants tend to coordinate postural sway and eye gaze, even when they cannot see each other (Shockley et al. 2003, Richardson et al. 2007). During conversations, people are also likely to synchronize their word use (Garrod & Pickering 2004, Ireland et al. 2011). In other words, speech signals seem to be particularly efficient at creating interpersonal alignment at various levels, that is, the bodies of the conversation partners get coordinated in ways that they were not before the interaction started. Linguistic coordination is also an important cognitive tool that helps human beings to cooperate and reach better performance levels than an individual could (Bahrami et al. 2010).

Using neural similarity approaches, Hasson and colleagues have demonstrated that during successful communication, the speaker's and the listener's brains exhibited joint, temporally coupled response patterns (Stephens et al. 2010). Speaker–listener coupling in early auditory regions was shown to reflect shared processing of low-level acoustic properties of the stimulus. By contrast, in higher-order brain regions the responses in the listeners' brains lagged behind those in the speakers' brain. Most interestingly, speaker–listener coupling in language and higher-order social cognitive regions reflected communication and shared understanding of narratives. In addition, it was shown that neural synchrony in higher-order brain regions was not observed when communication was disrupted (Silbert et al. 2014) and that the quality of the communication correlated with the degree of interpersonal similarity in brain responses (Dikker et al. 2014). In this context of language-based communication, the development of concepts that integrate and represent our past experience is also highly important as a mechanism by which the brain gives meaning to sensations and which can be used to communicate experiences, thereby potentially leading to shared or synchronized neural activity arising from the tendency of our social brains to align thoughts and create meaning (Yeshurun et al. 2021). Indeed, the degree of neural synchrony between two social partners has been shown to predict their communication success in a communication game. In that study, neural similarity interacted with empathic abilities such that for those who were more neurally similar, empathic abilities did not impact communication; however, for those who were less neurally similar, empathic abilities were important in predicting communication success (Dziura et al. 2023).

Building on studies that use single-brain neuroimaging to investigate neural similarity, emerging work also uses hyperscanning and dual-brain neuroimaging to investigate how partners build common ground or mutual understanding during interaction. Stolk et al. (2013) asked participants to jointly reproduce a spatial configuration of two tokens on a digital board and compared a so-called communicative and an instrumental condition. In the communicative condition, the goal of the communicator was to make sure that both his token and that of the receiver were arranged according to a configuration visually presented only to the communicator. This required that the communicator used the movements of his token to signal to the receiver how she should configure her own tokens. This simple task was effective in reliably inducing dyad-specific communicative behavior. In other words, the same movements were used by different dyads to signal different meanings. Interestingly, the communicative condition elicited more mutual adjustments by the interaction partners. As a key finding, Stolk and colleagues demonstrated that the communicative condition elicited comparable neural responses in the medial prefrontal cortex and anterior temporal lobe in both communicator and receiver, which again highlights the importance of synchrony across brains. Stolk et al. (2014) followed up on their findings by using the same task for two-brain neuroimaging. Here, they found that cross-brain correlations in the superior temporal gyrus are stronger during communicative episodes, which demonstrates that INS between communicators is relevant for the development of shared meaning and concepts. Similarly, a study by Liu et al. (2023) used a coordinating symbolic communication paradigm in which two communicators were required to create an interpersonal communication system. In dyads that were able to establish communication, significantly increased levels of INS were found in the right superior temporal gyrus. Furthermore, positive correlations between INS and measures of shared intentionality and communicative accuracy were found. The authors also used transcranial alternating current stimulation (tACS) to further explore the potentially causal role of INS enhancement for communicative success. In-phase stimulation, in fact, led to an enhancement of INS in the right superior temporal gyrus and resulted in higher communicative accuracy as compared to sham or antiphase stimulation. Thus, INS appears greatest during periods of communication, and causal approaches suggest this neural synchrony may be a mechanism for communicative success.

Reciprocity of Social Interaction Affects Synchrony Across Brains

Hyperscanning studies also demonstrate how the reciprocity of social interaction contributes to synchrony across brains (e.g., Dumas et al. 2010). An fNIRS study by Fishburn et al. (2018) found greater INS in participant pairs when they completed a puzzle together in contrast to a condition where an identical puzzle was completed individually. In addition, it was shown that the time course of neural responses of one person predicted that of their partner but not that of another person completing the puzzle individually. A recent study by Koul et al. (2023) demonstrated that INS emerges spontaneously and can be predicted by the natural occurrence of dyadic behavior that is typically shown when human beings are in the presence of one another, such as reciprocated eye contact, body movement, and smiling. Importantly, Koul and colleagues ran control analyses to ensure that INS was not simply a by-product of individual EEG variation but rather reflected dyad-specific neural dynamics. They did so by comparing models in which an individual behavior of one participant would be sufficient to induce INS or, alternatively, such behavior needed to be reciprocated and occurred in both persons simultaneously. The results, indeed, demonstrate that reciprocated social behaviors predicted INS better than unreciprocated behaviors. It is important to note that the observed phenomena in Koul et al.'s (2023) study were found in the absence of a structured social interaction task, which is consistent with the idea that human beings may have a natural tendency to socially connect with others (Coan & Sbarra 2015).

In addition to the affiliative benefits of synchrony, the communicative benefits of INS might also be tractable at a computational level. According to the Bayesian brain hypothesis and predictive coding accounts, brains are probabilistic prediction machines that build up mental models of the external world to predict and explain incoming sensory information. Importantly, such mental models need to be continually updated in order to reduce the so-called prediction error, that is, the difference between the model's prediction and the observed evidence (Friston 2005). A predictive social brain should, therefore, attempt to predict another person's social behavior and observe what the person actually does (Lehmann et al. 2023). Such predictions and expectations of social behavior can sometimes be so strong that they can lead to false positive social perception (Friedrich et al. 2022). In the context of social interactions, however, behavioral synchrony might be helpful for predictive processing, because it could help to predict the interaction more easily and might allow for the relevant mental models to become more similar over time, thereby reducing prediction error and contributing to social understanding (Mayo & Shamay-Tsoory 2024).

Group Dynamics

Importantly, although most studies described above focused on dyadic synchrony, INS across members of a group is important for communication, learning, and cooperation and may feature different dynamics—for example, due to imbalance in leader versus follower roles and in-group versus out-group factors. A study by Jiang et al. (2015) has investigated whether the occurrence of INS across individuals is linked to leader emergence, that is, when and how initially leaderless small groups decide to select one person as the leader. The results demonstrate that INS for leader–follower participant pairs was higher than for follower–follower pairs. Also, INS for leader–follower participant pairs was higher during leader-initiated communication than during follower-initiated communication. INS was related to the leader's communication skills but not communication frequency, which the authors interpreted as evidence for the importance of timing and of qualitative aspects during social interaction that successful leaders seem to possess and which make them effective in having influence over others. In another important study conducted by Yang et al. (2020), measures of INS were investigated in a large fNIRS study, for which the authors organized 546 individuals into 91 three- versus three-person intergroup competitions. They used in-group bonding manipulations and demonstrated an enhancement of INS, which led participants to give more money to in-group members and to be more willing to give money to outcompete rivals. These results highlight the importance of INS but also show that synchrony across brains does not always contribute to prosocial behavior but can also accentuate in-group versus out-group behavior. Although in-group bonding can increase INS, other work with teams has shown dissociable contributions between feelings of in-group identification and INS in predicting collective team performance. Specifically, Reinero et al. (2021) had participants wear EEG caps and solve problems either working with their team or working individually. A strength of this study is that tasks were all done through a computer interface that was matched between team and individual conditions, so any stimulus entrainment should be comparable across groups. Teams outperformed individuals, and the collective performance of the team was predicted by whole-brain INS.

Respiratory sinus arrhythmia (RSA): a physiological measure of heart rate variability linked with respiration and may reflect arousal and engagement

SYNCHRONY ACROSS BRAINS SHAPES NEUROCOGNITIVE AND SOCIAL DEVELOPMENT AND LEARNING

Biobehavioral Synchrony Shapes Socioemotional Development

Biobehavioral synchrony is a defining feature of early social interactions between infants and caregivers. Already by 2 months of age, infants are sensitive to noncontingent responding from their caregiver (Murray & Trevarthen 1985). These face-to-face interactions provide a foundation for the sharing of emotions, exchange of communicative signals, understanding of others and self, and development of self-regulation abilities. The majority of work on biobehavioral synchrony has focused on parents and their children (most often, mothers and infants). Biobehavioral synchrony among parents and children is not simple mimicry but involves a coordinated attunement between parent and child to social signals, affective state, and communicative bids (Feldman 2012). Typically, this synchrony is coded in mother–infant dyads by identifying periods of coordinated positive engagement in which the mother coordinates gaze and social touch during periods of infant positive affect, vocalization, and gaze (Atzil et al. 2011, Leclère et al. 2014). Maternal sensitivity, or parental responsiveness, promotes coordinated, synchronous interactions between child and caregiver and has a significant effect on children's development of social-interactive and cognitive abilities (Landry et al. 1998, Legerstee et al. 2007) and their emotion discrimination and regulation abilities (Feldman 2012, Bell 2020, Yaniv et al. 2021). Synchrony between parent and child can be measured in terms of this behavioral coordination as well as of physiological arousal [e.g., respiratory sinus arrhythmia (RSA)] (Bell 2020). RSA synchrony between mother and child is linked to their affect during the interaction (Ham & Tronick 2009, Capraz et al. 2023), and it is affected by risk status such as a history of maltreatment (Miller et al. 2023). These effects of biobehavioral synchrony are long-lasting: Mother–infant behavioral synchrony predicts neural discrimination of emotions in adulthood (Yaniv et al. 2021). Outside of the parent–child context, synchrony between young children promotes prosocial behavior (Kirschner & Tomasello 2009), and infants are more likely to help an adult if they previously engaged in synchronous movement with that adult (Cirelli et al. 2014). Thus, synchronous coordination of behavior and affect between child and parent or peer has powerful and sustained positive effects on social, emotional, and cognitive development.

With advances in noninvasive neuroimaging technologies, including fNIRS and EEG, synchronous neural activity (or INS) can be measured between parents and children (including infants) during real-time social interactions (Nguyen et al. 2020a, Wass et al. 2020, Turk et al. 2022, Alonso et al. 2024). INS is higher when behavioral synchrony is high, including when adult and child are engaged in direct gaze (Leong et al. 2017, Piazza et al. 2020) and during turn taking in natural conversation (Nguyen et al. 2021). Affect also modulates INS, such that periods of high positive (but not negative) affect synchrony relate to high INS within medial and lateral frontal and temporoparietal brain regions (Santamaria et al. 2020). Further, maternal sensitivity, or the coordinated attunement of the mother's behavior to the child's, predicts mother–infant neural synchrony, while maternal intrusiveness, in which the mother engages the child during nonreceptive periods, predicts lower synchrony (Endevelt-Shapira & Feldman 2023). From these data, INS could be interpreted as simply a complementary approach to identifying behavioral or affective synchrony, but one that is more objective and does not require detailed frame-by-frame coding. Indeed, shared audiovisual environments and coordinated behaviors will produce similarities in neural activity that do not necessarily indicate a mutual understanding or real-time alignment between two people. However, beyond shared environments, neural synchrony can also reflect conceptual alignment that cannot be identified based on behaviors alone. This conceptual alignment includes shared perspectives, goals, or affective states as well as transfer of information (Wheatley et al. 2012, Hasson & Frith 2016) that occurs during these rich learning contexts for infants and children.

Methodological approaches can help tease apart synchrony that reflects dynamics between interaction partners beyond shared environmental features. For example, use of Granger causality and graph theory can identify directional influences between parent and child interbrain network organization (see the sidebar titled Approaches to Measure Neural Synchrony) that go beyond effects simply due to a shared environment. For example, when mothers and infants were engaged in a social referencing task during EEG data recording, greater integration was found between

Granger causality: a statistical approach to determine the influence of one time series over another, used to look at causal influences between brains during interaction

Graph theory: an approach used to characterize the brain networks based on the strength and number of connections between nodes of the network

APPROACHES TO MEASURE NEURAL SYNCHRONY

For a more extensive review and discussion of neural synchrony methods, we point readers to Hakim et al. (2023). The categories we use were taken from their systematic review. Here we highlight common analysis approaches that are discussed in this review and are used to investigate synchrony across brains.

Correlation: Correlation approaches measure the temporal relation between time series, also described as intersubject functional connectivity. This is the most common synchrony approach used with fMRI data, though other modalities use it as well. Correlations can be noninteractive (neural similarity or intersubject correlation) or interactive (INS; see **Figure 1**). They can encompass the whole interaction period or focus on time windows throughout the interaction to assess changes in synchrony over time. Correlations can be synchronous or lagged, depending on the question of interest.

Regression: Regression approaches relying on the general linear model (GLM) are more common with fMRI and fNIRS. Here one person's brain activity is used to predict the other person's in a cross-brain GLM. One can also look at time lags to identify lead-lag relationships between partners. A benefit of this approach is that behavior can also be included as a separate regressor in the prediction model.

Coherence: Coherence is a measure of the correlation in the frequency or time-frequency domains between participants. This method is most common in fNIRS studies. One common approach is wavelet transform coherence (WTC), where time series data are transformed to the time-frequency domain so that correlations in frequency bands over time can be calculated.

Phase synchrony: This method is used primarily within EEG studies due to their high temporal resolution, and it examines the extent to which two signals are in phase with each other. One instantiation of this approach is the weighted phase lag index (wPLGI). This approach allows researchers to identify synchrony that is independent of shared environment effects by examining only nonzero phase lags.

Causality: These approaches determine the causal influence of one brain on the other using approaches such as Granger causality, dynamic causal modeling, or partial directed coherence. Causal approaches are important in verifying that synchrony is an emergent property and is due to the mutual influence between brains rather than to an alignment to shared external features of the environment.

nodes of the parent and child interbrain network during positive compared to negative maternal affect (Santamaria et al. 2020). In other words, fluctuations in neural activity between regions of the child and the parent were more similar when the mother was displaying positive affect. Using directed connectivity analyses, Santamaria et al. (2020) found mothers had greater effects on interbrain density (i.e., roughly the degree of connections between brains) during positive affect, whereas infants had greater effects on interbrain density during negative affect. It is important to clarify that these neural influences during dyadic interaction occur via observable behavior (Semin & Cacioppo 2008), which then impacts conceptual models, and thus incorporating behavioral coding into models of interbrain directed connectivity in future studies will strengthen our understanding of the mechanistic role synchrony plays in emotion development. Lagged analysis approaches are another means to identify neural synchrony that goes beyond shared environment effects. Piazza et al. (2020) used lagged intersubject correlation approaches with fNIRS and detailed behavioral coding during a face-to-face interaction in which an adult experimenter read and sang to an infant, and they revealed that behavioral synchrony (e.g., periods of mutual gaze) is preceded by activation within the prefrontal cortex in the adult experimenter and child. Thus, here INS may reflect an anticipation of joint behavior rather than a result of shared behaviors. In another example, a weighted phase lag index that avoids time 0 (i.e., simultaneous neural responses) to examine cross-brain synchrony identifies EEG phase coherence between brains that is not time-locked to sensory events but rather reflects the biobehavioral attunement between social partners (e.g., Endevelt-Shapira & Feldman 2023).

Perhaps even more interesting than work on what drives INS is work demonstrating what INS predicts during development. As with behavioral evidence, synchronous neural activity during parent–child social interactions is related to the child's emotion regulation abilities (Reindl et al. 2018). Problem-solving or cooperation tasks provide a useful context to assess variation in synchrony and its relation to emotion regulation. Overall, INS is higher during cooperative compared to competitive contexts (Reindl et al. 2018, Miller et al. 2019), and neural synchrony predicts problem-solving performance beyond behavioral synchrony alone (Nguyen et al. 2020b). This improved prediction power from INS may be due to its ability to capture alignment in shared goals between partners. Further, neural synchrony is greatest during cooperation with a parent compared to cooperation with a stranger, suggesting that a preexisting understanding of, or similarity to, one's partner promotes synchrony beyond behavioral coordination alone (Reindl et al. 2018, 2022). Indeed, in sequential dual-brain studies, the similarity between parent and adolescent functional brain network organization predicts their similarity in emotional fluctuations throughout the day and the adolescent's emotional competence (Lee et al. 2017). Problem-solving tasks, such as the tangrams puzzle, can also be manipulated to induce higher or lower levels of frustration, and thus they provide an opportunity to test the hypothesis that child emotion regulation is shaped during synchronous parent–child interactions (Feldman 2012). After preschoolers and parents completed a frustrating puzzle task, they were given a recovery play period. Mother–child neural synchrony in the lateral prefrontal cortex during the recovery period predicted the child's (but not the mother's) irritable temperament, with lower INS predicting higher irritability. Higher child irritability was also related to lower behavioral synchrony between mother and child, demonstrating that child characteristics may also affect opportunities for synchronous contexts, leading to fewer opportunities to coregulate and develop self-regulation as a consequence (Quiñones-Camacho et al. 2020). Because this study was correlational and had only one time point, it is not possible to disentangle the directional effects of child irritability and interpersonal behavioral synchrony and INS between mother and child.

In the only study to date to examine longitudinal effects of neural synchrony on child socioemotional or mental health outcomes, Quiñones-Camacho et al. (2022) used the same frustration and recovery task design and demonstrated that greater parent–child prefrontal cortex neural (but not behavioral) synchrony at 4–5 years of age predicted a more rapid decrease in internalizing behaviors over the subsequent year and a half. This first longitudinal evidence of relations between parent–child neural synchrony and behavioral outcomes is important in highlighting a potential causal role of parent–child neural synchrony in developmental outcomes. Future longitudinal studies can incorporate analytic techniques examining lagged coherence or directionality of influence across multiple cross-brain regions as well as behavioral and personality measures to test whether factors reflecting alignment between brains during interaction uniquely predict child outcomes beyond shared environments or child characteristics.

Neural Synchrony Promotes Social Learning Throughout the Lifespan

One of the most powerful learning mechanisms, particularly in early life, is social learning (Herrmann et al. 2007). When caregivers and infants coordinate their attention together on objects of shared interest (i.e., engage in joint attention), infants learn about the object (e.g., the name of the object, its function, emotions toward the object, etc.) (Mundy & Newell 2007). Engaging in joint attention is itself a synchronous activity and involves ostensive and communicative cues of mutual gaze and pointing, shared affect, coordination of attention and mental states, and transfer of information between social partners. This social learning mechanism continues to shape our attention, knowledge, desires, and preferences throughout our lives (Redcay & Saxe 2013, Mundy 2018).

Interactive synchrony may facilitate learning, and social signals, such as mutual gaze, may be a mechanism driving this INS (Leong et al. 2017, Wass et al. 2020, Leong et al. 2021). Specifically, the Learning through Interpersonal Neural Coupling (LINC) hypothesis (Leong et al. 2021) suggests that ostensive cues like mutual gaze may reset the learner's (or receiver's) neuronal oscillatory rhythms to match those of the sender, which allows for optimal information transfer. This resetting would be reflected in greater interbrain phase synchrony (Leong et al. 2019, 2021). INS can, therefore, provide unique explanatory power beyond what could be learned simply from understanding single-brain learning mechanisms (e.g., Leong et al. 2019, Dikker et al. 2021, Pan et al. 2022). For example, during a social referencing task, the likelihood of learning (i.e., the emotion associated with the object) per trial was related to greater INS between parent and child, but the learning valence (i.e., the propensity of an infant to select positively or negatively labeled objects) was not. The learning valence, on the other hand, was associated with infant intrabrain connectivity but not interbrain connectivity (i.e., INS) (Santamaria et al. 2020). These findings highlight the importance of incorporating dual-brain, second-person neuroscience approaches to fully understand social processes, including social learning. How well we learn from others depends on us and them, and only dual-brain perspectives can identify and characterize that mutual influence.

While learning occurs naturally during social interactions, formal instruction, as in a classroom, also relies on social learning mechanisms such as coordination of attention and representation of mental states for successful information transfer. These coordination processes may be reflected in INS between teacher and learner. Much of the work on social learning and INS has been conducted with adults or by examining teachers and students and has shown that greater INS between teacher and student relates to greater student engagement (Dikker et al. 2017, Bevilacqua et al. 2018, Davidesco et al. 2023) and better learning outcomes (Dikker et al. 2017; Davidesco 2020; Pan et al. 2021, 2022; Zhang et al. 2022; Davidesco et al. 2023). As with the study in infants, INS predicts learning even when intrabrain metrics do not (Davidesco et al. 2023).

Several mechanisms have been proposed for why INS relates to learning. Synchrony may reflect behavioral alignment, and this alignment itself (rather than interbrain synchrony per se) may facilitate learning (Pan et al. 2022). Beyond behavioral alignment, INS may reflect two individuals in a shared attentional state. This shared attentional state may amplify processing of audiovisual input and thus facilitate learning and memory for those shared objects (Shteynberg 2015, Dikker et al. 2017). An alternative explanation is that INS represents each person's own neural activity and prediction of one's social partner. During teaching, however, the teacher's representation of and prediction of the student's mind may be more critical for effective information transfer. Examining lagged relationships can identify these leader–follower patterns. For example, using fNIRS Zheng et al. (2018) predicted that the best teaching outcomes would be reflected in a lagged coherence between teacher's and student's brains because the teacher would represent the learner's mind prior to effective transmission of information (prediction-transmission hypothesis). Specifically, coherence between the teacher's temporoparietal junction and the student's anterior temporal cortex 10 seconds later predicted better teaching outcomes (Zheng et al. 2018). Similarly, Pan et al. (2018) demonstrated during an interactive song learning task that INS predicts song learning and that the instructor's brain activity is best predicted by the learner. However, while INS may reflect these alignment and mutual prediction processes, it remains an open question as to whether interbrain synchrony plays a causal role in social learning. Novel multi-brain approaches in animals and humans are beginning to shed light on the causal role of synchrony (e.g., Liu et al. 2023). Pan et al. (2021) used multi-person transcranial alternating-current stimulation to show that INS is causally related to social learning. They synchronously stimulated the inferior frontal gyrus, an area important for song learning, of the teacher and the student during the active song learning task. This synchronous stimulation led to spontaneous synchrony of body movements and improved learning outcomes. Further spontaneous body synchrony was a partial mediator of the relation between INS and learning outcomes. While this study contained only 15 students and thus caution is warranted in the interpretation, it provides a promising approach to identify causal mechanisms.

REDUCED SYNCHRONY ACROSS BRAINS AS A CORE FEATURE OF PSYCHOPATHOLOGY OR DISORDERS OF SOCIAL INTERACTION

Psychiatric disorders are ubiquitously characterized by social difficulties. Furthermore, social interactions can either constitute a protective factor that contributes to quality of life and mental health or, in the case of social stress and exclusion, act as a risk factor that increases the probability of developing a mental health problem. Autism spectrum disorder can be considered as a paradigmatic case of a disorder of social interaction (Schilbach 2016), because it is defined by difficulties in social interaction and communication. In spite of this, most research has focused on single brains or single individuals to understand social challenges in autism. In contrast to this, we have suggested the importance of dyadic context in driving behavioral and neural responses to social stimuli and synchrony across brains in autism and other psychiatric conditions. Also, experimental tasks that focus on social interaction and are high in ecological validity are likely to be more sensitive in their objective assessment of those social impairments that are most therapeutically relevant and, when combined with computational approaches, may be used to develop more sensitive neural signatures of atypical social interaction (e.g., Lahnakoski et al. 2022). For example, social impairments have been shown to be less pronounced (or even completely absent) when two people with autism interact with each other compared to a situation in which one person with autism and one person without autism interact. These clinical observations might be related to evidence indicating that the empathy shown by autistic individuals is greatest when it is directed toward others with autism (Komeda et al. 2015), potentially due to greater mutual understanding. Similarly, individuals without autism find it easier to infer the mental states of individuals without autism than of individuals with autism (Edey et al. 2016).

At a more abstract level, these findings may be taken to suggest that social impairments in autism, but also other psychiatric conditions, could be more closely related to (dis-)similarities between interaction partners than they are to the characteristics of each individual, which we have termed the social interaction mismatch hypothesis (Bolis et al. 2017, Redcay & Schilbach 2019). Evidence of greater social difficulties in dyads with more dissimilar partners may be explained by the fact that an interaction partner's behavior can be more easily and accurately predicted when the partner is similar to oneself, as previously discussed (Friston & Frith 2015, Dziura et al. 2023). Behavioral research has, for instance, shown that interpersonal difference values of autistic traits are more closely linked to friendship quality than autistic traits per se (Bolis et al. 2021). In other words, similarity across interaction partners appears to be relevant for interaction success, which is consistent with a recent meta-analysis that demonstrates similarities across different variables for partners (Horwitz et al. 2023). Behavioral research has also shown reduced behavioral synchrony in dyads with an autistic individual (Glass & Yuill 2024; for a review, see McNaughton & Redcay 2020). Consistent with the mismatch hypothesis, evidence suggests higher behavioral synchrony among autistic pairs than among mixed neurotypes [i.e., autistic (AUT)–neurotypical (NT)] (McNaughton et al. 2023; but see Georgescu et al. 2020).

Here, hyperscanning has the potential to provide unique new insights into the disorders of social interaction and might help to address aspects of heterogeneity in autism. In recent years, a number of hyperscanning studies have, in fact, studied INS in autism, and the majority have demonstrated decreased INS for dyads consisting of AUT and NT individuals. Tanabe et al. (2012) used hyperscanning fMRI to investigate the neural correlates of live gaze-based social interactions between persons with and without autism. The results demonstrated that INS in the right inferior frontal gyrus was greater in dyads of NT individuals than AUT–NT dyads. Quiñones-Camacho et al. (2021) used fNIRS hyperscanning to investigate neural synchronization during conversations between an NT experimenter and adults with or without autism. fNIRS measures demonstrated that NT individuals showed more neural synchrony with the experimenter than autistic individuals in the temporoparietal junction. Less neural synchrony in the temporoparietal junction was associated with higher social impairments. Similarly, Key et al. (2022) have shown that lower levels of INS were associated with increased behavioral symptoms of social difficulties in autistic adolescents. Hirsch et al. (2022) have used fNIRS hyperscanning to investigate INS during in-person eye-to-eye contact and demonstrated reduced cross-brain coherence in autism. With regard to the studies that have demonstrated reduced INS in autism, the social interaction mismatch hypothesis might serve as a possible explanation for this finding, based on the assumption that interpersonal dissimilarity might disrupt processes of synchronization. In fact, recent work compared neural synchrony and behavioral patterns between dyads that were either matched or mismatched in autistic-like traits (i.e., high/high, low/low, or low/high). While dyads in which both individuals were high in autistic traits showed different communicative behaviors than the other two groups, their neural synchrony was greater than it was in the other dyad types (Peng et al. 2024). Future research may help to further address this issue by systematically manipulating interpersonal differences across dyads in order to assess their impact on social interactions and their relationship to brain structure and function of both interaction partners. In addition, future hyperscanning studies should include AUT–AUT dyads to investigate whether similar or higher levels of INS would be observed compared to AUT–NT dyads, as suggested by the social interaction mismatch hypothesis (Bolis et al. 2023).

As discussed earlier, psychiatric disorders other than autism are also characterized by social interaction difficulties that could also be related to disturbances of behavioral and/or neural synchrony. Persons with schizophrenia (SCZ), for instance, are known to exhibit a variety of abnormalities in social perception, facial emotion recognition, mentalization, and interpersonal coordination (Green et al. 2019; see Pan et al. 2023 for a recent review article). Aberrant social processing is known to negatively affect interpersonal interactions in SCZ, leading to poor social integration and quality of life (Couture et al. 2006). A recent review of studies that investigate behavioral synchrony in SCZ has demonstrated synchronization impairments across different modalities, which are also found in relatives of persons with SCZ (Dean et al. 2021). Kupper et al. (2015) have demonstrated that the severity of so-called negative symptoms of SCZ—i.e., avolition, anhedonia, social withdrawal, and affective flattening—are linked to less interpersonal synchrony. Negative symptoms are a core aspect of SCZ, do not respond well to antipsychotic medication (Correll & Schooler 2020), and account for a large part of the long-term disability and poor outcome of patients.

Other studies demonstrate that impaired behavioral synchrony between persons with and without SCZ can be improved by means of prosocial priming (Raffard et al. 2015), which may point toward an important new avenue for research. With regard to the neural correlates of social deficits in SCZ, single-brain neuroimaging studies have demonstrated connectivity differences in the DMN, but also in the action observation network that is likely to contribute to interpersonal coordination (Schilbach et al. 2016, Saris et al. 2022). Furthermore, studies have implicated the involvement of the temporoparietal cortex in the deficits in controlling representations that relate to self and other that are commonly observed in SCZ (Eddy 2016). Whether aberrant processing in the temporoparietal junction is related to INS differences in SCZ is not known. A recent study by Wei et al. (2023) has used fNIRS hyperscanning to investigate an NT cohort and a clinical high risk (CHR) group of individuals with psychosis. Here, it was found that during a cooperation task the CHR–NT dyads showed reduced INS compared to NT–NT dyads in the right inferior frontal gyrus. Interestingly, reduced levels of INS in the CHR–NT group were linked to symptom scores of suspiciousness and persecutory ideas characteristic of the CHR status. Future hyperscanning research will help to understand the relationship between previously demonstrated activation differences in SCZ and their possible contribution to INS.

Depression is one of the most prevalent mental health conditions and is known to strongly affect social interaction behavior by leading to social withdrawal. Also, cases of chronic or persistent depression have been explicitly linked to social interactional difficulties. In fact, the Cognitive Behavioral Analysis System of Psychotherapy (CBASP) has been tailored specifically to meet the demands of this patient group, who are sometimes described as disconnected from the social environment, putatively due to difficulties in formative relationships that affect their expectations of interaction partners. These difficulties can prevent chronically depressed persons from having the kinds of positive social experiences that would help to alleviate depressive symptoms and strengthen feelings of self-efficacy and self-worth. Indeed, depression at the neural level has been linked to brain networks associated with social cognition and action observation but also recall of relationship episodes (Wade-Bohleber et al. 2020; Schilbach et al. 2014, 2015). Studies of behavioral synchrony in depression have, for instance, been conducted in the field of parent–infant interactions, where it is well established that parental depression negatively affects dyadic synchrony that is important for infant development (e.g., Leclère et al. 2014, Golds et al. 2022).

As we have seen, emerging evidence demonstrates that psychiatric conditions negatively affect or are associated with lower levels of interpersonal synchronization. Consequently, restoring synchrony across patient and therapist appears to be an important goal for psychotherapy, where patients and therapists are known to spontaneously synchronize their behavior, aspects of their voice, and even physiological processes such as heart rate and where behavioral synchrony is linked to therapeutic success (see Atzil-Slonim et al. 2023 for a recent review). Koole & Tschacher have already argued in 2016 for an Interpersonal Synchrony (In-Sync) model of psychotherapy according to which synchrony plays a crucial role in shaping the so-called therapeutic alliance.

Meta-analytic assessments have demonstrated that this alliance accounts for a robust portion of outcomes in individual therapy (Flückiger et al. 2018). The model by Koole & Tschacher (2016) suggests that patient–therapist synchrony may foster the therapeutic alliance and could promote adaptive emotion regulation abilities and outcome-related variables in the patient. According to the model, the alliance is grounded in the coupling of the patient's and the therapist's brain, and behavioral synchrony helps to establish this INS. By drawing upon developmental psychology, Koole & Tschacher (2016) describe how interpersonal synchrony can be considered as a form of external emotion regulation that continues to be effective across the lifespan and constitutes an important part of psychotherapy. Work by Xie et al. (2016) in single brains has demonstrated that socially induced cognitive emotion regulation—for example, a psychotherapist helping to downregulate participants' emotions—relies upon differential activations in key nodes of the DMN. In other words, it is conceivable that the DMN might constitute a network candidate for INS in relation to psychotherapeutic interventions. INS in the DMN might facilitate those complex social cognitive processes and shared mental representations that play an important role during psychotherapy and help formulate goals and intentions needed for long-term changes. An important hyperscanning study by Bilek et al. (2017) has demonstrated that abnormalities of the DMN, in particular lower neural coupling of the temporoparietal junction in patient–control dyads in a study investigating borderline personality disorder (BPD), can no longer be found when patients remit during psychotherapeutic treatment and no longer meet the clinical criteria of BPD. This demonstrates that hyperscanning may help generate state-associated biomarkers for mental ill health, which track neural synchronization differences during treatment.

MECHANISMS OF INTERBRAIN NEURAL SYNCHRONY

As we have reviewed above, behavioral, cognitive, and personality factors drive INS between social partners (**Figure 2**). Both interactive and noninteractive synchrony are affected by how similar two individuals are in terms of their personality traits and shared perspectives or conceptual alignment (Lahnakoski et al. 2014, Yeshurun et al. 2017, Matz et al. 2022). For example, personality profiles (Matz et al. 2022), irritability (Quiñones-Camacho et al. 2020), and intolerance of uncertainty (van Baar et al. 2021) predict neural synchrony (either neural synchrony or INS) between individuals. Characteristics of the social interaction also drive interactive INS. These include perceptual-motor features such as shared audiovisual input as well as the coordination of body movements in joint action. Ostensive or social signaling behaviors, such as eye contact (Hirsch et al. 2017, Kinreich et al. 2017, Leong et al. 2017, Wass et al. 2020) or touch (Nguyen et al. 2021), are particularly powerful drivers of synchrony and may serve to reset the oscillatory rhythms of one's social partner (Leong et al. 2017) (**Figure 2**). Interestingly, while eye contact is related to greater INS, it serves to decrease pupillary synchrony (an index of shared attentional processing) during conversation (Wohltjen & Wheatley 2021), suggesting unique and potentially complementary mechanisms depending on the type of synchrony observed.

At the cognitive level, multiple nonmutually exclusive interpretations have been proposed to relate INS to cognitive processing between individuals (Wheatley et al. 2024). One group of explanations is grounded in conceptual alignment (Stolk et al. 2014, 2016; Hasson & Frith 2016). Conceptual alignment can reflect shared knowledge, shared goals, or shared affective state. During an interaction, individuals come to a mutual understanding, or common ground, through repeated probing and updating of a shared conceptual space. This shared conceptual space is reflected in similar temporal and spatial patterns of brain activity that are on different temporal scales than sensorimotor events (Stolk et al. 2013, 2014, 2016). Individuals can also come into alignment

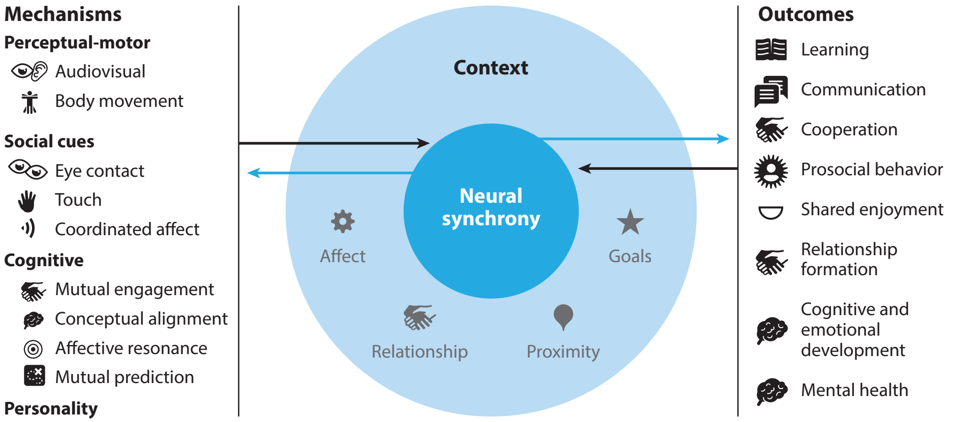

Figure 2

Correlates and consequences of neural synchrony. Shared audiovisual stimuli, behavioral coordination, social and affective cues, personality characteristics, and cognitive alignment all affect the degree of neural synchrony between partners. Contextual factors such as affect, relationship status (e.g., parent versus stranger), proximity between partners, and goals (e.g., cooperation versus competition) also influence the degree of synchrony. Synchrony also leads to many positive outcomes, including increased social learning, improved communication and cooperative performance, greater prosocial behavior, shared enjoyment of an interaction, and formation of relationship bonds as well as to the development of cognitive and affective abilities and mental health symptoms. However, most studies provide only correlational evidence of these associations, so the directionality of these effects cannot be determined. Further, these interactions are likely reciprocal; for example, dual-brain transcranial magnetic stimulation studies have shown that neural synchrony can induce coordinated body movements, suggesting bidirectional relationships between these proposed mechanisms and outcomes.

affectively through building up a shared space of affect (Anders et al. 2011) over repeated communication in which each partner's affective state is represented in the other's brain. Conceptual alignment claims are particularly compelling when synchrony is examined over the course of interaction—for example, over multiple blocks of a communicative game (Stolk et al. 2014) or using dynamic INS (Li et al. 2021, Likens & Wiltshire 2021). Otherwise, alignment may simply reflect preexisting neural similarity between partners. During any interaction, a combination of existing neural similarities in perspectives and processing style with the ability to mutually align between partners will contribute to levels of INS (**Figure 2**).

Mutual prediction frameworks, discussed above, offer a related interpretation of INS that is grounded in behavioral action and prediction. During a social interaction both partners will represent the actions of both themselves and their social partners. The INS signal reflects the summed activity of the partner's own behaviors and predictions of the other's behaviors (Hamilton 2021). Combining mutual prediction with active inference frameworks (e.g., Friston & Frith 2015, Lehmann et al. 2023), Mayo & Shamay-Tsoory (2024) propose that social partners work to minimize the prediction error of themselves and their partner. Through this active inference process, inferential models become more similar over time, and this similarity in inferential processes may be reflected in INS (Friston & Frith 2015).

BEHAVIORAL NEUROSCIENCE APPROACHES TO IDENTIFY MECHANISMS

While work in humans has begun to test causal hypotheses on the role of synchrony, this work is hampered by limits in the temporal and spatial resolution of the methods available for recording during dyadic interaction and the degree of experimental control available to test hypotheses. Behavioral neuroscience methods allow for cellular-level resolution, even while rodents are engaged in a social interaction. Behaviorally, rats and mice engage in interpersonal behavioral synchrony in ways that parallel human interactions. For example, social synchrony is seen in parent–infant or parent–pup behaviors during feeding and grooming as well as between peers as pups reach adolescence (see Ham et al. 2023 for a review). Recently, research in bats, monkeys, and mice has demonstrated that INS is reflected at the neuronal level, provides better predictive power than behavior alone, and predicts future social interactions (Tseng et al. 2018, Kingsbury et al. 2019, Zhang & Yartsev 2019). Further, recent methodological advances allow for the collection of neural responses across the entire cortical mantle at cellular resolution from freely interacting mice using optical imaging methods (Scaglione et al. 2024). While preliminary, this approach opens up avenues for more direct comparisons of human and rodent synchrony, with a greater ability to probe the mechanistic roles of synchrony in the rodent studies.

Interpersonal behavioral synchrony: the coordination of behavior between interacting individuals, which can be conscious or unconscious and involve mirroring (or imitation) or coordination of complementary actions

In an elegant series of studies with mice, Kingsbury et al. (2019) provide compelling evidence for the mutual prediction theory at the neuronal level; specifically, INS is the product of neural activity reflecting both behaviors of self and prediction of other's behaviors in both partners. Using calcium imaging to record from hundreds of dorsal medial prefrontal cortex (dmPFC) neurons across individuals simultaneously, they found correlations between dmPFC neurons when mice were engaged in social interaction. The correlation strength did not differ during periods of high compared to low concurrent behavior, suggesting that shared behaviors alone were not driving synchrony. As in human studies, synchrony was greater when the mice were in social interaction compared to when there was a barrier between them, which suggests that synchrony is not purely due to a shared environment. Importantly, using a cross-brain general linear model approach, they found that one animal's neural activity could be predicted based on the behavior of both animals, but that including the other animal's (i.e., the social partner's) neural activity in the model significantly improved prediction performance. At the level of single neurons, they found cells within dmPFC that coded for specific behaviors of the mouse during the interaction, while other neurons coded for behaviors of the interacting partner. These cells are spatially intermixed within the population, leading to synchrony at a population level between brains. In fact, the cells coding the partner's behavior had the greatest effect on interbrain synchrony. They found similar improvement in prediction when looking at the level of single-cell recording when using "behavior" cells (i.e., cells within the dmPFC ensemble that code for specific behaviors of the interaction) rather than neutral cells. Overall, these findings demonstrate a neuronal mechanism for interbrain synchrony. That is, both partners represent their own and the partner's behavior. This common behavioral repertoire leads to similar patterns of activity between brains, and the degree of INS predicts future interactions between dyads (Kingsbury et al. 2019).

CONCLUSION AND OUTLOOK

As we have reviewed in this article, emerging evidence points toward the importance of synchrony across brains in order to enable, facilitate, and realize social interaction and communication. We have seen how synchrony and shared experiences may emerge automatically during social interactions and how synchrony affects subjective experience and the views we may hold. We also see how we can work on synchronizing our brains by reaching consensus during conversations (Sievers et al. 2024) and using other forms of explicit communication to share our thoughts and mental models of the world (Frith & Frith 2024). Synchrony also waxes and wanes and is even disrupted. These disruptions are not necessarily bad, but they can also be helpful by allowing for complementary and/or independent modes of thinking (Mayo & Gordon 2020, Wohltjen &

Wheatley 2021). Rather than always swinging in synchrony like pendulums, we can also resist synchrony or intentionally break it when we try not to be influenced by the opinions and behaviors of others or by social convention, which is also an important ability in many instances of human relations. Understanding how these moment-to-moment transitions in and out of synchrony are beneficial depending on the specific context and goals of interaction will be an important area for future research (e.g., Mayo & Gordon 2020).

Whether or not brains synchronize likely relies on sufficiently large and robust similarities in brain structure and function. Research has provided striking evidence for neural homophily, that is, a tight link between familiarity and friendship between persons and similarity in brain activity when individuals are exposed to the same stimuli (Parkinson et al. 2018, Matz et al. 2022). Future research will help to further investigate how measures of brain structure and function, as well as cognitive and personality characteristics, across interacting dyads can help to predict who synchronizes with whom, how strongly, and how this relates to social interaction success. Such empirical work is needed to test hypotheses such as the dialectical misattunement theory (Bolis et al. 2017) and the double empathy problem (Milton 2012), which are consistent with the idea that communication outcomes are due to the extent to which partners align in features such as their brain organization, lived experiences, understanding of each other, and communication styles. This work could help to scientifically substantiate the notion of neurodiversity, which—originating in the autism rights movement—is tied to the idea that all brains are to a degree unique and that differences across individuals may explain disabilities rather than deficits ascribed to individuals. It has also been recognized that the study of divergence in neurodevelopment should move away from conventional categorical differences and attempt to include and model the developmental dynamics that capture the emergence of differences (Astle et al. 2024).

Another important area for future work is understanding when synchrony is a mechanism or an epiphenomenon. Progress is being made in developing theoretical models of synchrony as a mechanism of social affiliation, communication, and learning (e.g., Friston & Frith 2015, Hamilton 2021, Leong et al. 2021, Mayo & Shamay-Tsoory 2024) as well as approaches (in humans and animals) that directly test the causal role of synchrony in these processes (Kingsbury et al. 2019, Pan et al. 2021, Liu et al. 2023). Several models suggest that synchrony reflects greater predictive processing of one's partner (e.g., Friston & Frith 2015, Kingsbury et al. 2019, Hamilton 2021, Mayo & Shamay-Tsoory 2024). Studies that use computational approaches, which have been successfully employed to investigate and mathematically describe the cognitive and neural processes that underlie social perception and cognition in individuals, could be extended to study and mechanistically explain the emergence of synchrony during social interaction (Dumas et al. 2014, Pott & Schilbach 2022, Bolis et al. 2023). An important future direction will be continuing to formalize and test computational models that assess how predictive models of self and other are updated in real time during social interaction and how (or whether) this updating reflects changes in behavioral and neural synchrony between partners in real time as well as longer-term changes in neural similarity between partners. Relatedly, longitudinal studies of synchrony are critical to test whether neural synchrony between peers or between parent and child is predictive of social connection or developmental outcomes, respectively. However, currently longitudinal studies tracking the effects of synchrony are very limited (see Quiñones-Camacho et al. 2022).

Finally, most INS studies are face-to-face, but as communication increasingly occurs outside of face-to-face contexts it will be important to understand how synchrony may differ in these virtual contexts. Virtual interactions lose key aspects of copresence, including body cues, eye contact, and even smell—features that are critical to social inference and social bonding (Endevelt-Shapira et al. 2021). Further, the work reviewed above suggests that eye contact, touch, and interpersonal body coordination may drive synchrony. Indeed, preliminary work suggests that neural synchrony is decreased during virtual, texting interactions compared to face-to-face interactions, though information transfer is similar across contexts (Schwartz et al. 2024).

Taken together, social brains have the amazing ability to spontaneously and effortlessly synchronize. This capacity appears to be fundamental for the human ability to become conscious, share experiences, and communicate, which, in turn, modulates the degree of synchrony across brains. Being able to share and reflect upon our experiences of the world allows us to jointly develop mental models of the world that we can use to transmit information, educate each other, and engage in other culture-building activities that have transformed the world we live in. However, synchrony across brains (or between groups of brains) may not take place or can even go awry and lead to misunderstandings and failures of communication that can have bitter consequences. Here, differences at the interpersonal level may be relevant and should be systematically addressed in future research, including how synchronization differs depending on the neurotype match or mismatch between social partners. By doing so, future synchrony research will elucidate the factors that influence whose brains synchronize well with whom, the underlying mechanisms shared across individuals, and the compensatory strategies and techniques that might help to get communication back in sync, even when spontaneous alignment initially does not occur. In light of the many misunderstandings and conflicts that continue to characterize human existence, the potential relevance of this work is enormous and could help to alleviate human suffering by pointing toward mechanisms and techniques that support communication and reconciliation.

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