Opinion

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Brain-to-brain coupling: a mechanism for creating and sharing a social world

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Cognition materializes in an interpersonal space. The emergence of complex behaviors requires the coordination of actions among individuals according to a shared set of rules. Despite the central role of other individuals in shaping one's mind, most cognitive studies focus on processes that occur within a single individual. We call for a shift from a single-brain to a multi-brain frame of reference. We argue that in many cases the neural processes in one brain are coupled to the neural processes in another brain via the transmission of a signal through the environment. Brain-to-brain coupling constrains and shapes the actions of each individual in a social network, leading to complex joint behaviors that could not have emerged in isolation.

Why two (or more) brains are better than one

Although the scope of cognitive neuroscience research is vast and rich, the experimental paradigms used are primarily concerned with studying the neural mechanisms of one individual's behavioral processes. Typical experiments isolate humans or animals from their natural environments by placing them in a sealed room where interactions occur solely with a computerized program. This egocentric framework is reminiscent of the Ptolemaic geocentric frame of reference for the solar system. From the early days of civilization, stars were not thought to have any influence on the geophysical processes on Earth. The present understanding of gravity, orbits and the tides came about only after the Copernican revolution, which brought about the realization that the Earth is just another element in a complex, interacting system of planets. Along the same lines, we argue here that the dominant focus on single individuals in cognitive neuroscience paradigms obscures the forces that operate between brains to shape behavior.

Verbal communication is an excellent example to illustrate the role that other individuals play in one's cognitive processes. As Wittgenstein argued, the meaning of a word is defined by its use [1]. The word's correct use, however, can vary across eras, cultures and contexts. Thus, the appropriate use of a word is grounded in a set of inter-related norms shared by a community of speakers. To master a language, one has to learn the correct uses of words by interacting with other members of the community. Such interactions fundamentally shape the way individuals think and act in the world [2,3]. This is by no means limited to language. Several other nonverbal social and cognitive skills, such as courting, dancing or tool manipulation, require the collaboration of multiple agents that coordinate their behavior according to a shared set of rules and customs. With so many cognitive faculties emerging from interpersonal space, a complete understanding of the cognitive processes within a single individual's brain cannot be achieved without examining and understanding the interactions among individuals [4]. In this article, we call for a shift from a single-brain to a multi-brain frame of reference.

Brain-to-brain coupling

The premise of brain-to-brain coupling is that the perceptual system of one brain can be coupled to the motor system of another. This binding mechanism builds on a more rudimentary ability of brains to be coupled to the physical world (stimulus-to-brain coupling, Figure 1a). Different objects in the environment emit different forms of energy (mechanical, chemical, electromagnetic), and receptors convert these signals into electrical impulses that the brain can use to infer information about the state of the world and generate appropriate behaviors. Furthermore, organisms are not passive receivers of sensory input but rather actively move their sensory receptor surfaces (hands, eyes, tongues, etc.) to sample information from the environment [5,6]. Thus, stimulus-to-brain coupling is fundamental to the ability to retrieve information about the world to guide actions.

Brain-to-brain coupling also relies on stimulus-to-brain coupling as a vehicle for conveying information. However,

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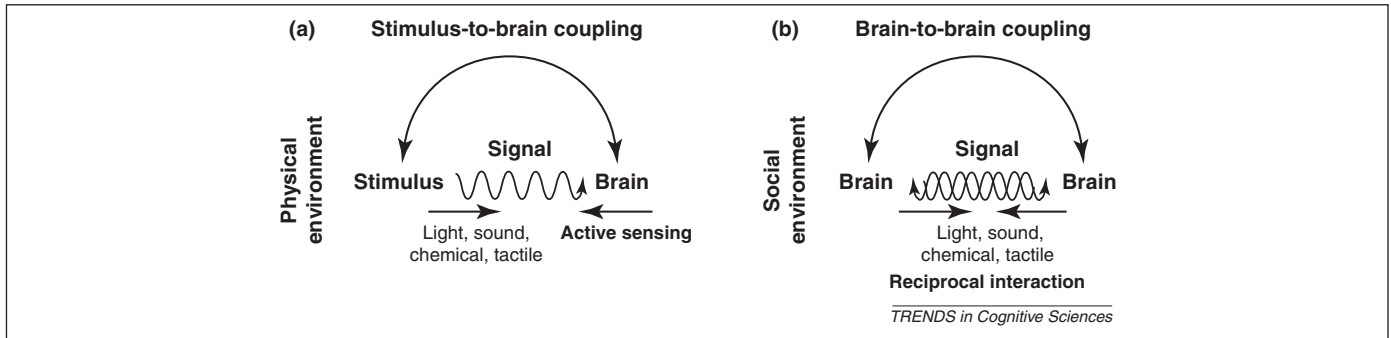
Figure 1. Two types of coupling: **(a)** stimulus-to-brain coupling; **(b)** brain-to-brain coupling.

in brain-to-brain coupling, the signal is generated by another brain and body that resemble one's own, rather than by inanimate objects in the physical environment (Figure 1b). Brain-to-brain coupling is analogous to a wireless communication system in which two brains are coupled via the transmission of a physical signal (light, sound, pressure or chemical compound) through the shared physical environment.

The coordination of behavior between the sender and receiver enables specific mechanisms for brain-to-brain coupling unavailable during interactions with the inanimate world. For example, seeing or hearing the actions, sensations or emotions of an agent trigger cortical representations in the perceiver (so-called vicarious activations [7,8]). If the agent has a similar brain and body, vicarious activations in the perceiver will approximate those of the agent, and the neural responses will become coupled [7]. If the agent, however, has a brain and body that are fundamentally different from those of the witness, this vicarious activation pattern will look fundamentally different from that in the agent and the brain responses will not be coupled. Vicarious activation, of course, is only one particular mechanism by which the neural responses can be coupled across two brains. In other cases, the neural responses in the receiver can be coupled to the neural responses in the sender in a lawful, but more complex, manner [9].

Acquiring communication
The emergence of any communication system, as Wittgenstein suggested [1], requires a shared understanding of the signals' meaning (i.e. uses) within a particular context among a community of users. Such common ground is established through learning, which often takes place in the form of early interactions between a tutor's brain and a learner's brain. This hypothesis is supported by developmental evidence.

Many joint behaviors such as mating, group cohesion and predator avoidance depend on accurate production and perception of social signals. As a result, the development of these behaviors is strongly influenced by interactions with other group members. Developmental processes ultimately must result in coupling between the sensory systems of one individual with the signals produced by the motor system of another individual. How might this coupling occur? We demonstrate how a multi-brain frame of reference might provide an answer to this question using studies of birds and human infants.

Early studies of song learning in captive birds explicitly excluded social factors, in line with a single-brain frame of reference approach. Young birds were only exposed to taped recordings of adult songs. This practice enabled great experimental control and reflected the assumption that song learning was based on an imprinting mechanism. However, it occluded the fact that songbirds learn much more effectively in social contexts, to the extent that one species of bird can learn the song of another species provided that the tutor is a live bird as opposed to a tape-recording [10]. Perhaps the best evidence that social interactions mediate vocal learning in birds comes from studies of cowbirds [11]. Male cowbirds learn to sing a potent (attractive) song by watching the reactions of females [12]. When female cowbirds (who do not sing) hear an attractive song or a song element, they produce a small wing movement. The visual signal reinforces the males' behavior so that they are more likely to repeat the song elements that elicited the female wing movement. This ultimately leads males to sing a more advanced song that will successfully attract many females. Females, in turn, learn their preferences for certain male songs by watching and hearing the responses of other females in the group [13,14]. Thus, both song production and preferences emerge through social interactions.

In human infant communication, it is typically assumed that social interactions primarily have a role in children's language learning after they learn how to produce words. It turns out, however, that the social environment also influences infants' earliest prelinguistic vocalizations. The babbling of a 7–12-month-old infant exhibits a pitch, rhythm and even a syllable structure that is similar to the ambient language [15]. This acoustic shift in babbling towards the ambient language occurs through interactions with caregivers [15]. Consistent caregiver responses to babbling can reinforce certain acoustic structures, allowing infants to learn from the consequences of their vocalizations. For this type of learning, there are two reciprocal requirements: (i) adult caregivers must be sensitive to the acoustic characteristics of babbling and respond to them, and (ii) infants must perceive the reactions of caregivers and adjust their vocalizations accordingly. Indeed, caregivers respond readily to babbling during the first year of life, often by mimicking the infants' vocalizations and establishing turn-taking during face-to-face interactions. Furthermore, caregivers are more likely to respond to vocalizations that contain

more speech-like elements, such as consonant–vowel structured syllables [16]. We know from studies of contingent versus non-contingent social reinforcement that infants care about these reactions; these studies have demonstrated robust effects of caregiver responses on infant vocal production [17,18].

Perhaps the most compelling data showing that communication emerges through interaction come from adults trying to communicate with wholly original signals [19]. In a set of experiments looking at the emergence of novel communication systems, pairs of human participants were invited to play cooperative games through interconnected computers. The games required players to communicate, but players could not see, hear or touch each other. The only means of contact were devices that allowed for the exchange of visual signals but could not be used to exchange standard graphic forms (such as letters or numbers). Thus, to communicate with each other, players had to craft a novel visual communication system [20]. Such experiments showed that, when there was direct interaction between two (or more) players, symbols (i.e. signs that bear a conventionalized relation to their referents) quickly emerged [19,21–23]. However, these trademarks of human communication did not emerge when the signs were developed by isolated individuals who played with an offline partner [22]. Moreover, the abstraction of the signs increased as they were

transmitted through generations of players [23]. Finally, bystanders watching the novel communication system develop, but not actively involved in its creation, were not as effective at using the system [22,24]. This provides clear evidence for the crucial role of behavioral interaction for the generation of a novel communication system.

Together, these data from songbirds, human adults and infants show that the development of communication is fundamentally embedded in social interactions across individual brains.

Speech emerges through coupled oscillations

In the typical human scenario, much of communication is mediated by speech. How are speech signals transmitted and received when two adult individuals communicate? Notably, the transmission of information between two individuals is similar to reafferent forms of transmission of information between two areas within a single brain. Whereas it is typically thought that signals between parts of the brain require anatomical connections, neural states can also be influenced by physical signals that were generated by another part of the brain and transmitted through the environment. For example, a speaker delivering a monologue, without any awareness of doing so, adjusts the production of their speech patterns by monitoring how they sound in a given context. The motor areas of the brain
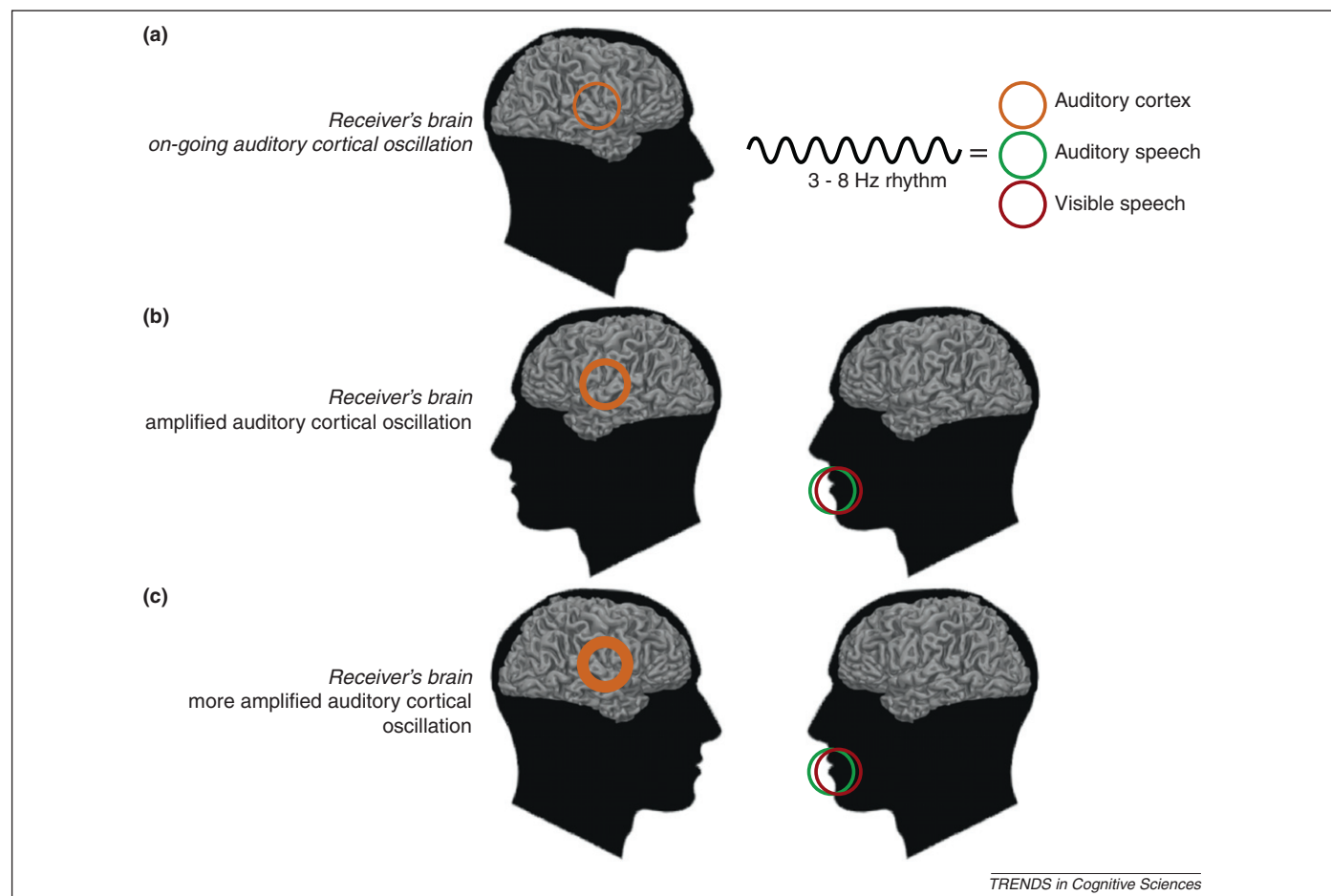
Figure 2. The 3–8-Hz rhythm of speech couples with the ongoing auditory cortical oscillations that have a similar frequency band. **(a)** Even in silence, there are ongoing auditory cortical oscillations in the receiver's brain. **(b)** The signal-to-noise of this cortical oscillation increases when it is coupled to the auditory-only speech of the signaler. **(c)** In humans, the mouth moves at the same rhythmic frequency of the speech envelope, hence audiovisual speech can further enhance the signal-to-noise ratio of the cortical oscillation.

generate a program for speech, and the body produces an acoustic signal that mixes in the air with ambient noise. This sound travels back to the speaker's ears and auditory system, and thus acts as a feedback signal directing the motor system to adjust vocal output if necessary. This is the reason why humans (and other primates) reflexively raise their voices in noisy environments. In this scenario, communication between the motor and the auditory parts of the brain is coordinated through the vocal signal, with the air as a conduit. This idea naturally extends to both sides of a conversation – the speaker and the listener.

During speech communication two brains are coupled through an oscillatory signal. Across all languages and contexts, the speech signal has its own amplitude modulation (i.e. it goes up and down in intensity), consisting of a rhythm that ranges between 3 and 8 Hz [25–27]. This rhythm is roughly the timescale of the speaker's syllable production (three to eight syllables per second). The brain, in particular the neocortex, also produces stereotypical rhythms or oscillations [28]. Theories of speech perception point out that the amplitude modulations in speech closely match the structure of the 3–8 Hz theta oscillation [25,29,30] (Figure 2a). This suggests that the speech signal could be coupled [30] or resonate (amplify) [25] with ongoing oscillations in the auditory regions of a listener's brain [31,32] (Figure 2b). Resonance, for example, could increase the signal-to-noise ratio of neural signals and thus help to improve hearing. In addition, disruption of the speech signal by making it faster than 8 Hz reduces the intelligibility of speech [33–35] and decreases the entrainment of the auditory cortex [36,37].

The coupling hypothesis also extends to the visual modality [25] (Figure 2c). Human conversations, which typically occur face to face, are perceived through both visual and auditory channels. It is well established that watching a speaker's face improves speech intelligibility [38]. Indeed, in noisy situations such as a cocktail party, watching a speaker's face is the equivalent of turning up the volume by 15 decibels. This amplification of speech by vision is due, at least in part, to the fact that mouth movements during speech are tightly coupled with the speech signal's amplitude modulations [25]. Thus, the speaker's mouth oscillations at a rate of 3–8 Hz are captured by the listener's visual system, and amplify (via numerous multisensory neural pathways [39]) the auditory signals in the listener's brain [25,30,40].

In the scenario described above, the speaker is like a radio station broadcasting an AM speech signal via the mouth, and this signal and background noises are picked up by the antenna-like ears of the listener. The listener's brain is pretuned, so to speak, to the specific AM frequency of the speech signal and thus amplifies the speech signal alone through resonance. The structure of the speech signal is modulated with a 3–8-Hz frequency that resonates (or samples, or entrains) with ongoing oscillations in the auditory regions of the listener's brain that are also 3–8 Hz in frequency. To further amplify this vocal signal in noisy environments, the brain takes advantage of the coupling between visible mouth movements and the oscillatory speech sound waves. Thus, the mouth motion helps to divide up or 'chunk' the speech into syllables so that the

listener's brain can efficiently extract meaningful information from the signal. According to the brain-to-brain coupling framework, vocal communication emerges through the interactions or entrainment between the brains and bodies of signaler and receiver.

## Coordinated, hierarchical alignment during speech

Once brains are coupled to each other via speech signals, information can be shared and exchanged more efficiently. Human communication protocols can be divided into two types: monologues, in which only one speaker sends information and listeners receive it, and dialogues, in which interlocutors have to interweave their activities with precise timing. Garrod and Pickering argue that communication protocols in general, and dialogues in particular, are made easy because of the largely unconscious process of 'interactive alignment' [41,42]. In this scheme, two interlocutors simultaneously align their representations at different linguistic levels and do so by imitating each other's choices of speech sounds [43], grammatical forms [44], words and meanings [45]. For example, if Peter says to Mary with reference to their child, 'I handed John his lunch box today', Mary is more likely to respond with 'And I handed him his coat' than with 'And I gave him his coat', even though the two alternative responses have equivalent meaning.

Interactive alignment occurs for two related reasons. First, within an individual's brain, production (speaking) and comprehension (listening) are coupled to each other and rely on shared linguistic representations [46]. Second, accordingly, when a speaker produces a particular representation, it primes (activates) both the comprehension and the corresponding production of the same representation in listeners, making them more likely to use it in their speech [42]. Crucially, interactive alignment occurs at all linguistic levels, from the phonological and syntactic up to the semantic and the contextual. Additionally, alignment at one linguistic level leads to greater alignment at other levels [44,47]. For example, 'low-level' alignment of words or grammatical forms can lead to alignment at the critical level of the situation model (i.e. the level at which the speaker and the listener understand that they are referring to the same state of affairs [48]). This interactive alignment, as we argue below, is achieved by coupling the speaker's brain responses during speech production with the listener's brain responses during speech comprehension.

Coupling of two brains via verbal communication

The coupling between the speaker's and listener's brain responses during natural communication relies on speaker–listener brain coupling. Using functional MRI, Stephens *et al.* recently recorded the brain activity of a speaker telling an unrehearsed real-life story [49]. Next, they measured the brain activity of a subject listening to the recorded audio of the spoken story, thereby capturing the time-locked neural dynamics from both sides of the communication. Finally, they asked the listeners to complete a detailed questionnaire that assessed their level of comprehension.

Using a dynamic model of neural coupling based on intersubject correlation analysis (Figure 3a), the authors found that, during successful communication,
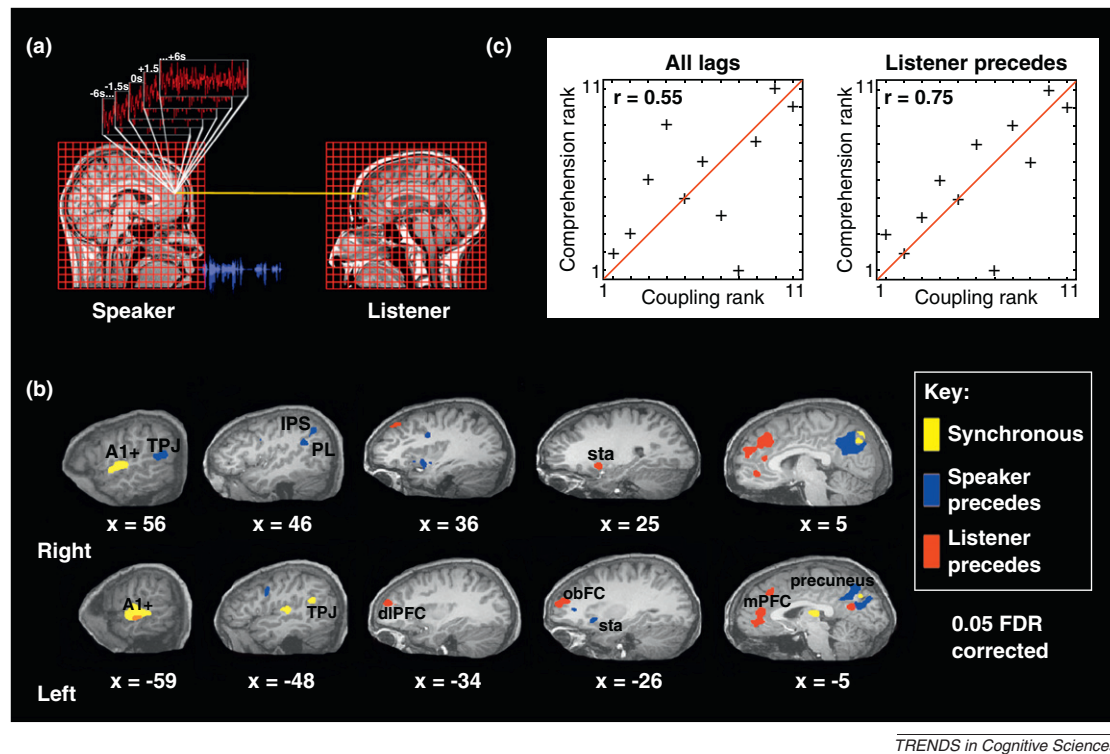
Figure 3. Speaker–listener brain-to-brain coupling. **(a)** The speaker–listener neural coupling was assessed through the use of a general linear model in which the time series in the speaker's brain are used to predict the activity in the listeners' brains. **(b)** The speaker–listener temporal coupling varies across brain areas. In early auditory areas (A1+) the speaker–listener brain coupling is time locked to the moment of vocalization (yellow). In posterior areas the activity in the speaker's brain preceded the activity in the listeners' brains (blue), whereas in the mPFC, dlPFC and striatum the listeners' brain activity preceded (red). **(c)** The listeners' behavioral scores and the extent of significant speaker–listener brain coupling was found to be strongly correlated ($r = 0.54$, $p < 0.07$). These results suggest that the stronger the neural coupling between interlocutors, the better the understanding. The extent of brain areas where the listeners' activity preceded the speaker's activity (red areas in **b**) provided the strongest correlation with behavior ($r = 0.75$, $p < 0.01$). These results provide evidence that prediction is an important aspect of successful communication. Adapted from [49].

the speaker's and listener's brains exhibited joint, temporally coupled, response patterns. This 'brain-to-brain' coupling substantially diminished in the absence of communication, for instance when the speaker told the story in a language the listener did not know. On average, the listener's brain responses mirrored the speaker's brain responses with some temporal delays (Figure 3b, blue). The delays matched the flow of information across interlocutors, implying a causal relationship by which the speaker's production-based processes induce and shape the neural responses in the listener's brain. However, the analysis also identified a subset of brain regions in which the responses in the listener's brain in fact preceded the responses in the speaker's brain (Figure 3b, red). These anticipatory responses suggest that the listeners are actively predicting the speaker's upcoming utterances. Such predictions may compensate for problems with noisy or ambiguous input [41]. Indeed, the more extensive the coupling between a speaker's brain responses and a listener's anticipatory brain responses, the better the comprehension (Figure 3c).

The speaker–listener neural coupling reveals a shared neural substrate that exhibits temporally aligned response patterns across interlocutors. Previous studies showed that, during free viewing of a movie or listening to a story, shared external input can induce similar brain responses across different individuals [50–55]. Verbal communication enables us to directly convey information across brains, even when the information is unrelated to the

current external environment. Thus, whereas stimulus-to-brain coupling (Figure 1a) is mostly locked to momentary states of affairs in the environment, brain-to-brain coupling (Figure 1a) can provide a mechanism for transmitting information regarding temporally and spatially remote events. This mechanism works by directly inducing similar brain patterns in another listening individual in the absence of any stimulation other than speech. Such freedom from the immediate physical environment is one of the prime benefits of the human communication system.

Coupling of two brains via nonverbal communication
Brain-to-brain coupling is also possible through hand gestures and facial expressions. This was first demonstrated in an experiment in which participants played the game 'charades' in the fMRI scanner. A signaler had to transmit nonverbal cues about the identity of a word while her brain activity was measured and her hand gestures were video recorded [56]. Later, an observer was shown the video footage while his brain activity was measured. Using between-brain Granger causality (Figure 4), the study found that the temporal variation in the brain activity of the observer carried information about the temporal variation in that of the signaler, demonstrating brain-to-brain coupling during gestural communication. Furthermore, between-brain Granger causality identified two networks in the observer's brain that, coupled with activity in the signaler's motor system (regions associated with the mirror neuron system and regions associated with theory-of-mind
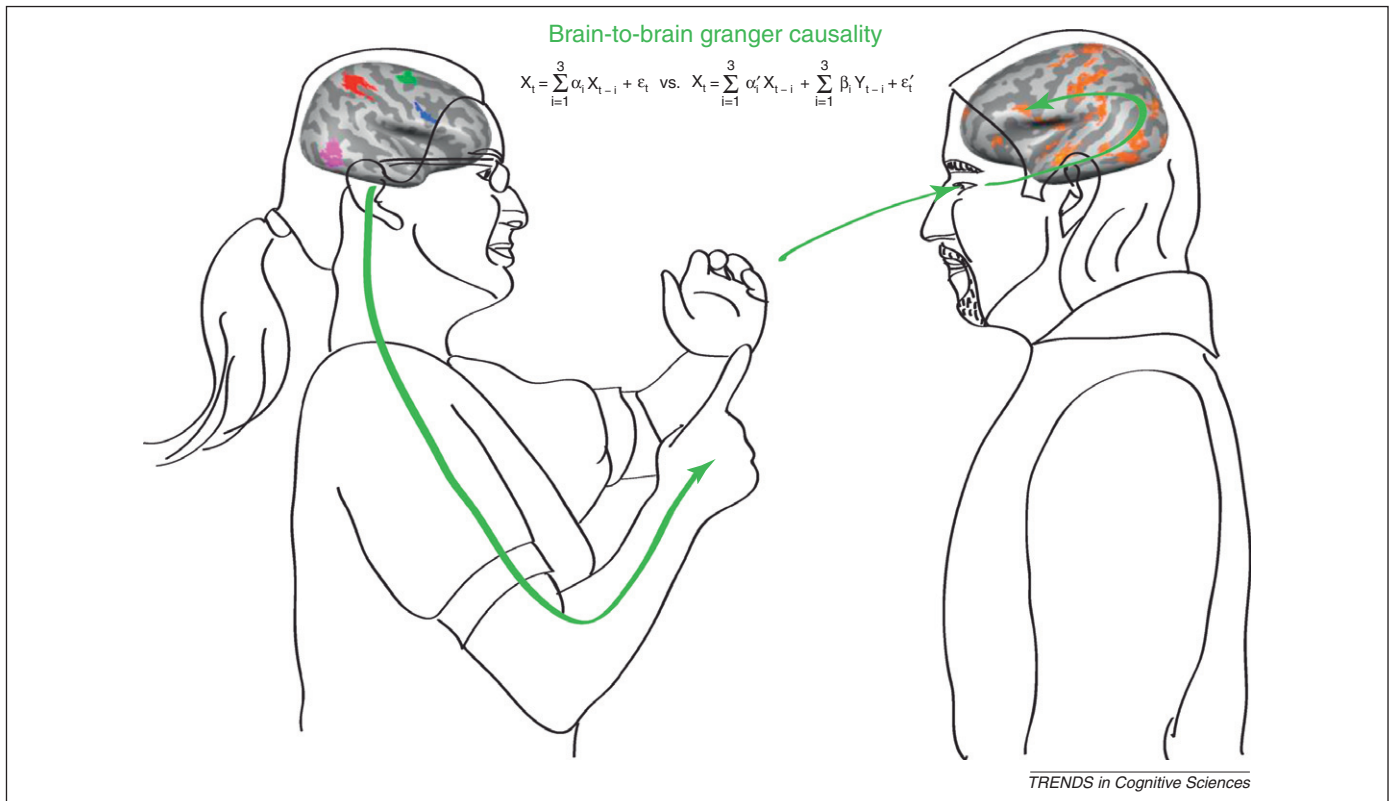
Brain-to-brain granger causality

$$X_t = \sum_{i=1}^{3} \alpha_i X_{t-i} + \varepsilon_t \quad \text{vs.} \quad X_t = \sum_{i=1}^{3} \alpha_i' X_{t-i} + \sum_{i=1}^{3} \beta_i Y_{t-i} + \varepsilon_t'$$

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Figure 4. Gesturer–observer brain-to-brain coupling. During gestural communication, in the game of charades, brain activity in the gesturer triggers muscle movements (gestures) that are seen by the receiver and trigger activity in brain regions of the observer that are similar to those that caused the gestures in the gesturer. Brain-to-brain Granger causality can map such information transfer by calculating how much brain activity in the gesturer helps to predict brain activity in the viewer.

processes), provide support for the idea that these two networks collaborate during social perception [57]. Interestingly, separate analyses of the brain activity of the signaler and observer failed to identify the full extent of the networks involved, illustrating the power of brain-to-brain approaches to advance understanding of brain function [58].

In another study, Anders *et al*. had women express emotions in the fMRI scanner and then showed movies of their expressions to their romantic partners [59]. They found that the temporal sequence of activation was coupled across the brains of the women and their partners, and analyses provided evidence for a 'shared coding' of emotion-specific information in a distributed network across the brains of the signaler and observer.

In both the gesture and emotion experiments, each pair of participants was free to choose idiosyncratic signals, ensuring that the interaction was unique. Indeed, control analyses in both experiments revealed that the brain-to-brain coupling was tighter within a pair than across pairs [56,59]. Thus, brain-to-brain approaches can provide an exciting new tool to study the idiosyncratic aspects of human interactions that emerge between a dyad in the context of a communicative act.

Synergy through joint action
Coupled systems can generate complex behaviors that cannot be performed in isolation. Many human actions, such as playing basketball or operating a sailboat, require tight spatiotemporal coordination across team members [60]. Moreover, even actions that can be performed in isolation, such as playing a musical instrument or dancing, are faster and more accurate when performed within an ensemble.

An increasing body of evidence shows that, during joint actions, people become implicitly coupled at motor, perceptual and cognitive levels [61]. At a motoric level, for example, two people on rocking chairs synchronize their rocking as if they were mechanically coupled [62]. Pianists synchronize their playing during a duet with accuracies that rival those of the two hands of a single musician [63]. Moreover, interpersonally coordinated actions of pairs of guitarists playing a short melody together are accompanied by between-brain oscillatory couplings [64]. At a perceptual level, when two people view an object from different sides and are asked to mentally rotate the object, they adopt the perspective of their partner [65]. At a cognitive level, implicit coupling occurs when two people respond to different aspects of a stimulus using either the same effectors (e.g. the same hand, compatible condition) or different effectors (e.g. the opposite hand, incompatible condition). Although the assigned stimulus–response tasks did not require participants to coordinate their responses, the response times sped up when the other participants' responses were compatible and slowed down when they were incompatible [66].

A recent proposal views joint action as the linking of degrees of freedom across individuals' motor systems into synergies [9]. In this scheme, two motor systems working together in joint action result in dimensional compression (the two individuals constrain each other's degrees of freedom) and reciprocal compensation (whereby one

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component of the synergy can react to changes in other components).

Joint decision making

The choices an individual makes are often influenced and modified by the decisions of others. Individuals playing a strategy game keep track not only of the actions of the opponent but also of how opponents are influenced in response to their own actions [67]. For example, while playing the game 'rock–paper–scissors', players automatically imitate each other's strategic decisions when competing, although imitation does in fact reduce the chance of winning [68]. The influence of one brain on the decision-making processes of another brain was measured concurrently using a hyperscanning fMRI setup [64,69–72]. In one study, subjects played an investor–trustee economic exchange game [69]. Neural responses, as well as the decisions, of the trustee were influenced by the social signal expressed by the investor. In particular, responses in the caudate nucleus were stronger for benevolent reciprocity than for malevolent reciprocity. Moreover, after playing a few games together, caudate brain activity in the trustee predicted the investor's expected behavior, responding even before the investor revealed their decision.

However, it is not always the case that two brains are better than one [73–75]. A first step toward modeling the way in which two individuals accurately combine information that they communicate with each other was made in an elegant study in which two observers performed a collective low-level perceptual decision-making task [73]. The experiment revealed that sharing information among two observers with equal visual sensitivity improved their performances whereas sharing information among individuals with different levels of visual sensitivity worsened their performances.

Concluding remarks

The structure of the shared external environment shapes neural responses and behavior. Some aspects of the environment are determined by the physical environment. Other aspects, however, are determined by a community of individuals, who together establish a shared set of rules (behaviors) that shape and constrain the perception and actions of each member of the group. For example, human infants undergo a period of perceptual narrowing whereby younger infants can discriminate between social signals from multiple species and cultures, but older infants fine-tune their perception following experience with their native social signals [76]. Coupled brains can create new

phenomena, including verbal and nonverbal communication systems and interpersonal social institutions, that could not have emerged in species that lack brain-to-brain coupling. Thus, just as the Copernican revolution simplified rather than complicated understanding of the physical world, embracing brain-to-brain coupling as a reference system may simplify understanding of behavior by revealing new forces that operate among individuals and shape one's social world (Box 1).

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Box 1. Questions for future research

- How to further develop principled methods to explore information transfer across two (or more) brains?
- What is the full range of neural transformations that could govern or characterize brain-to-brain coupling (e.g. 'mirroring', entrainment, synergy, etc.)?
- How does the tuning between brains emerge during development?
- Why can some individuals better couple to other individuals?
- What are the minimum brain-to-brain coupling requirements for interspecies interactions?

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