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What can we learn from a two-brain approach to verbal interaction?

Lotte Schoot[a,*], Peter Hagoort[a,b], Katrien Segaert[c]

[a] Max Planck Institute for Psycholinguistics, P.O. Box 310, 6500 AH Nijmegen, The Netherlands
[b] Donders Institute for Brain, Cognition and Behaviour, P.O. Box 9101, 6500 HB, Nijmegen, The Netherlands
[c] School of Psychology, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom

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ABSTRACT

Verbal interaction is one of the most frequent social interactions humans encounter on a daily basis. In the current paper, we zoom in on what the multi-brain approach has contributed, and can contribute in the future, to our understanding of the neural mechanisms supporting verbal interaction. Indeed, since verbal interaction can only exist between individuals, it seems intuitive to focus analyses on inter-individual neural markers, i.e. between-brain neural coupling. To date, however, there is a severe lack of theoretically-driven, testable hypotheses about what between-brain neural coupling actually reflects. In this paper, we develop a testable hypothesis in which between-pair variation in between-brain neural coupling is of key importance. Based on theoretical frameworks and empirical data, we argue that the level of between-brain neural coupling reflects speaker-listener alignment at different levels of linguistic and extra-linguistic representation. We discuss the possibility that between-brain neural coupling could inform us about the highest level of inter-speaker alignment: mutual understanding.

Contents

1. Introduction

Recent advances in the field of social neuroscience suggest that in order to get at a complete understanding of the different neural processes involved in social interaction, the dynamic interplay between the brains of two interacting individuals needs to be studied (e.g. Hari et al., 2015; Hasson et al., 2012). The inter-individual neural markers of interest are inter-subject correlations in temporal and spatial patterns of brain activity, also known as *between-brain neural coupling* (Stephens et al., 2010). Assessing the level of between-brain neural coupling requires measuring brain activity for two (or more) participants involved in a social interaction, a technique called hyperscanning (brain activation is measured for both participants at the same time) or pseudo-hyperscanning (measuring brain activity for both participants in the interaction, but sequentially, one participant at a time). Since the first application of the hyperscanning method in fMRI (Montague et al., 2002), it has been applied to other neuroimaging methods as well (EEG, fNIRS and MEG) and used to investigate different aspects of social interaction (for overviews see Babiloni and Astolfi, 2014; Dumas et al., 2011; Konvalinka and Roepstorff, 2012).

In the current paper, we zoom in on what the multi-brain approach has contributed, and can contribute in the future, to our understanding of verbal interaction. Given the fact that verbal interaction is ubiquitous in our everyday lives, it is surprising

* Corresponding author at: Max Planck Institute for Psycholinguistics, P.O. Box 310, 6500 AH Nijmegen, The Netherlands.
E-mail address: Lotte.Schoot@mpi.nl (L. Schoot).

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that relatively few multi-brain studies have focused on this specific form of social interaction. So far, most multi-brain verbal communication studies have used the hyperscanning method to investigate the spatial and temporal relationship between neural mechanisms which support language production by the speaker and comprehension by the listener (see Section 2). Although these studies claim to investigate the neural correlates of verbal information transfer, they generally ignore pair-specific information about the quality of the interaction: whether information transfer was actually successful. However, it has been previously suggested that successful communication or mutual understanding can be operationalized in the form of inter-subject correlations in brain activity (Menenti et al., 2012; Stephens et al., 2010). We argue that the reason this idea has not been investigated in more detail is that although intuitive, it is not backed up by a strong theoretical framework leading to testable hypotheses.

We will discuss a recent theoretical framework (Friston and Frith, 2015a, 2015b) leading to the testable hypothesis that the strength of between-brain neural coupling reflects speaker-listener alignment at multiple representational levels (Section 3). In Section 4, we consider the possibility that between-brain neural coupling could reflect alignment at the highest representational level possible: the level of the situation model. If so, this would provide us with an inter-personal marker of successful communication. We discuss several possibilities to test this hypothesis before concluding this paper with an outlook on how the hyperscanning method may be used in future research.

2. A multi-brain approach to studying the relationship between language comprehension and production

There have been a few studies that have investigated speaker-listener neural coupling during verbal communication (Dikker et al., 2014; Jiang et al., 2012; Kuhlen et al., 2012; Silbert et al., 2014; Stephens et al., 2010). Like two-brain studies on non-verbal communication (Anders et al., 2011; Ménoret et al., 2014; Schippers et al., 2010), most of these studies have used the multi-brain approach to investigate 'information flow' from the brain of the sender (the speaker) to the brain of the receiver (the listener). In other words, to what extent is neural activity associated with encoding of information by the sender mirrored in the activity associated with the decoding of that information by the receiver? The reasoning here is as follows: if activity in area X in the brain of the sender is temporally correlated with activity in area X in the brain of the listener (perhaps with a delay), this indicates that area X is associated with encoding as well as decoding of information. More specifically, for verbal communication, such a finding would indicate that the neural infrastructures for language production and comprehension at least in part overlap, opposing the classical Wernicke-Lichtheim-Geschwind model, in which a strict division of labor is proposed. However, speaker-listener correlations in brain activity would be in line with converging evidence from patient data (e.g. Caramazza and Zurif, 1976) and one-brain neuroimaging studies (Menenti et al., 2011; Segaert et al., 2012), which support the view that the same brain regions may support language production as well as comprehension.

In the first two-brain study on verbal communication, Stephens et al. (2010) recorded a speaker telling an unrehearsed real-life story and played this recording to eleven listeners. Crucially, brain activity was measured with fMRI for both the speaker and listeners. By modeling the expected activity in the listeners' brains based on the speaker's neural activity during speech production, Stephens et al. tested whether the neural activity of the speaker was temporally and spatially coupled to the shared neural activity observed across all listeners. In other words, they tested whether there was overlap in brain areas involved in producing and listening to speech, and whether these activation patterns in the speaker and listener's brains were temporally related to each other (e.g. whether the speaker's brain activity preceded the listener's brain activity). Indeed, Stephens et al. found widespread spatial coupling between brain activity in the speaker and listener, both in areas classically associated with language processing (such as the left superior temporal gyrus and the left inferior frontal gyrus), and in areas that support processes that are generally considered to be extra-linguistic (such as the precuneus and the medial prefrontal cortex). Temporally, for most (but not all) of these areas within the listeners' brains, activity lagged behind the speaker's brain by three to six seconds. Crucially, the spatial and temporal coupling that was found when the speaker and listeners processed the same story largely disappeared when listeners were listening to a Russian speaker, or when the brain activity of the speaker that was used to model the listeners' neural responses was associated with the speaker telling a different story than the story the listeners were listening to. This indicates that between-brain neural coupling does not only depend on producing and hearing the same acoustic signal, but also on the extent to which the signal can be decoded by the listener. If the listener cannot process the linguistic input to extract meaning and structure, the underlying linguistic processes do not match and there will thus not be any coupling in areas necessary for these processes.

Other fMRI studies in which the two-brain approach has been applied to similar verbal information transfer paradigms report similar results (Silbert et al., 2014; Spiegelhalder et al., 2014). In general, these studies report enhanced between-brain neural coupling during one-way communication; when producing or listening to the same verbal information stimulus, the brain activity of the speaker is reflected in the brain of the listener. Together, these studies provide a novel type of evidence in favor of the hypothesis that language production and comprehension depend (at least in part) on the same neural mechanisms. This information is crucial for theories trying to explain behavioral phenomena in dialogue which require close coupling between language production and comprehension processes and/or shared representations at different linguistic and non-linguistic levels (see also: Pickering and Garrod, 2014). One example of such a behavioral phenomenon in dialogue is syntactic priming: hearing a specific sentence structure increases the chance that speakers will use this structure in a subsequent utterance. For this type of behavioral priming to occur from comprehension to production, one must assume some degree of shared representation and/or processing at the level of sentence structure (Menenti et al., 2012).

Most multi-brain verbal interaction studies have thus used speaker-listener between-brain neural coupling to identify neural networks associated with language production as well as language comprehension. These results have been taken as evidence to support theories which propose that a certain degree of overlap in the neural networks underlying language production and comprehension is necessary to explain inter-personal behavioral phenomena in natural conversation, such as priming. However, we would also like to make a critical observation here. By focusing research on identifying brain networks required for language production and comprehension, most of the studies discussed above have reported between-brain neural coupling common for all interaction pairs in their sample. Indeed, by comparing inter-subject correlations in pairs that produce and understand the same communicative signal to the correlations in pairs who are not coupled in this way, one can extract brain areas that are necessary to produce the signal on the one hand, and comprehend it on the other. However, by focusing on what is present across all pairs, we lose pair-specific information about the quality of the interaction, which may vary from pair to pair. In the next section, we will discuss what between-pair vari-