Journal Club

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Large-Scale Network Involvement in Language Processing

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Review of Geranmayeh et al.

The human brain's proficiency for language and speech combines a vast reservoir of stored knowledge with flexibility in perceiving and producing subtle nuances of sound. A century ago, Wernicke and Broca discovered regions responsible for fluent and nonfluent aphasia, respectively (Kandel et al., 2000). More recent studies identified additional types of aphasia, such as primary progressive aphasia, with associated lesions in other regions, and noninvasive functional magnetic resonance imaging (fMRI) has identified regions involved in language and speech beyond those highlighted by neurogic pathologies. These regions include parietal cortex, insula, posterior cingulate cortex (PCC), primary sensorimotor cortex, and supplementary motor areas (Binder et al., 2009). As a result of these developments, current views of language representation within the brain, while still centered on classic frontal and temporal Broca's and Wernicke's areas, now encompass much of the cerebral cortex (Patterson et al., 2007). Many of these regions may not be specific to language, but rather may mediate domain-general processing demands such as top-down attention. Thus, two important questions remain: (1) whether these regions are language-specific, and (2) which regions interconnect to form language-relevant networks.

To answer these questions, Geranmayeh et al. (2014) examined networks involved in speech production using recent advances in fMRI analysis. Studies using fMRI commonly compare changes in blood flow within a region during psychological tasks, such as cued speech production. Techniques such as independence components analysis (ICA) are increasingly being used to identify networks of interconnected regions whose activity fluctuates in synchrony during tasks. Geranmayeh et al. (2014) used ICA to discern different networks involved in different aspects of language and cognition. In their study, healthy human subjects performed three different tasks: a speech production task in which the subject described a picture (descriptive speech), a speech task consisting of counting from one to seven (minimally linguistic control task), and a nonverbal decision-making task related to color of stimuli (general cognitive control task). The authors identified networks using ICA and compared fluctuations in network activity across tasks to identify networks of regions whose responses differed with the changing processing demands. Their primary aim was to identify regions and networks associated with linguistic aspects of speech production beyond those related to the motor control needed to produce speech or general processing demands. The contrasts between the three tasks allowed the authors to test this specificity. For example, a network specific to linguistic aspects of speech would show increased activity during the descriptive speech task compared with the counting task, due to higher semantic and syntactic demands. A network involved in sensorimotor aspects of speech would be active during descriptive speech and counting, but not during decision-making. A network involved in general cognition would be active during both descriptive speech and decision-making, but not counting.

Using these tasks, Geranmayeh et al. (2014) identified three overlapping frontotemporoparietal (FTP) networks with differential involvements in language and cognitive control. A left FTP network was primarily involved in spoken language and linguistic aspects of speech production. This network was active during the descriptive speech task and inactive during counting and decision-making. This network included the left paracingulate cortex, left lateral frontal cortex near Broca's area, and left superior and inferior parietal lobules. Decreased activity within this network during counting and decision-making, compared with descriptive speech, suggest that this network is not solely low-level motor-sensory or domain-general cognitive control in nature, but rather is involved in cognitive and linguistic processes specific to spoken language production. Additionally, a right FTP network was active during both counting and decision-making. This network mirrored the speech-specific left FTP network, but also involved the left superior and inferior

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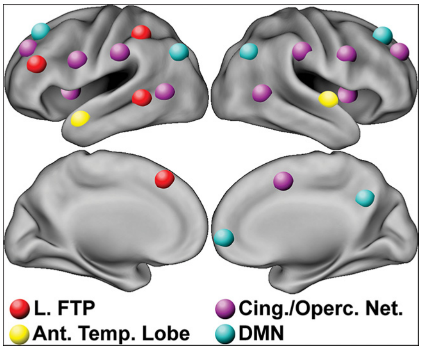

Figure 1. Large-scale networks associated with speech production. Activity in a network consisting of left frontotemporal-parietal regions (red circles), along with an anterior temporal lobe network (yellow circles), increased during descriptive speech compared with counting. Activity in networks of DMN regions (blue circles) and cingulo-opercular cognitive control regions (purple circles) were lower during speech than during rest.

parietal lobules. The authors suggest that this right FTP network is associated with automatic speech and attention. Lastly, a second left FTP network was less activated during all tasks compared with resting baseline. Regions within this network were in close anatomical proximity to the speech-specific left FTP network, with significant overlap between the two. The authors suggest that this task-deactivating left FTP may be involved in top-down attention and maintaining an externally focused, broadly vigilant state. Deactivation in this network may result from reallocation of processing resources for the narrowly focused tasks (Leech et al., 2012). All three FTP networks overlapped in the left superior parietal lobe, suggesting this region may coordinate activity between these networks and their component regions.

In addition to these overlapping FTP networks, other networks that were more or less active during descriptive speech than during counting or rest conditions received less attention in the article (Fig. 1). The remaining sections of this review will provide a detailed analysis of these networks and their relationships to language and speech.

The default mode network (DMN) is a well characterized network associated with contemplative and passive mental states (Raichle et al., 2001). The main DMN regions include the medial prefrontal cortex, PCC, and inferior parietal lobes bilaterally (Fig. 1). In general, the DMN is more active during rest and less active during most tasks. The conceptual similarity between an ongoing internal dialogue and mind wandering during the resting state suggests a possible connection between DMN regions and linguistic processing, confirmed by a meta-analysis (Binder et al., 2009). Like many fMRI studies, Geranmayeh et al. (2014) observed a decrease in DMN activity during all three tasks, with the greatest decrease occurring during descriptive speech. These results are in apparent conflict with DMN involvement in language as suggested by Binder et al. (2009). It is important to note, however, that the type of linguistic processes examined in each study differed greatly. Binder et al. (2009) investigated the connection between words, either written or spoken, and the knowledge they represent. They excluded studies involving nonlinguistic stimuli, such as knowledge-retrieval elicited by pictures. The speech production task used in Geranmayeh et al. (2014), however, asks subjects to describe a picture in detail. The relative decrease in DMN activation observed by Geranmayeh et al. (2014) during speech is consistent with distinctions made by Binder et al. (2009). Different sets of regions appear to be involved in knowledge-retrieval, depending on whether linguistic stimuli, such as a written word, or nonlinguistic stimuli, such as a picture of an object, is used to elicit a description of an object.

The cognitive control system (CCS) is a network of frontal, parietal, and insular regions involved in initiation, maintenance, and adjustment control during a wide variety of psychological tasks. Subdivisions within this larger network may separately process different types of control needed for task completion: adaptive task control by a subnetwork of frontoparietal regions, and stable task control by a subnetwork of cingulo-opercular regions (Dosenbach et al., 2007). The results of Geranmayeh et al. (2014) support this division of the CCS into two networks, which responded in opposite ways during speech and counting. Frontoparietal regions of the CCS, such as the dorsolateral prefrontal cortex and angular gyrus, were part of the descriptive speech-specific FTP network. Conversely, anterior parts of the cingulate gyrus, insula, and frontal pole comprised a second CCS network that was more active during counting compared with descriptive speech (Fig. 1). These two CCS networks and their responses mirror the behavior predicted by Dosenbach et al. (2007): a frontoparietal network active during descriptive speech (a task likely involving adaptive control) and a cingulo-operular network active during repetitive counting (likely involving more stable task control).

Perhaps the most intriguing network associated with speech production in Geranmayeh et al. (2014) was centered on the temporal poles (Fig. 1). Lesion, PET, and MEG studies suggest this region may play an important role in semantic processing (Patterson et al., 2007). However, in studies using fMRI, nearby air-filled sinuses distort the signal in the temporal poles, so task-related activity within this region is frequently missed. Consequently, its role in language may be underappreciated. The focal temporal pole lesions associated with semantic dementia or herpes encephalitis result in a focal deficit in naming objects, concepts, or people. Fluency, syntax, and working memory remain intact in these conditions (Acosta-Cabronero et al., 2011). In contrast, Alzheimer's disease involves extensive cortical atrophy, but is associated with mild language deficits that display the opposite pattern (Patterson et al., 2007). These observations suggest that the temporal poles may act as a contextual integration hub, binding together the various concepts that together underlie a word (Patterson et al., 2007). Activity within this network during descriptive speech, but not during counting, supports this theory (Geranmayeh et al., 2014). Geranmayeh et al. (2014) provided compelling evidence answering the questions posed at the beginning: a left-lateralized FTP network, including Broca's and Wernicke's areas, is specific to descriptive speech. This network is separate from those involved solely in motor control of speech and from FTP networks involved in general cognition. Furthermore, other networks, such as the temporal poles, make additional contributions to speech. Lastly, networks that were less active during descriptive speech, such as the DMN and CCS, are composed of regions previously suggested to process language. The results of Geranmayeh et al. (2014) provide important clues as to the conditions needed for involvement of these regions in language. The widespread involvement of regions from throughout the cortex suggests that the neural bases underlying language are rich, varied, and as complex as language's ability to express thought itself.

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