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Dynamic Functional Organization of Language: Insights from Functional Neuroimaging

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Abstract

One of the oldest questions in cognitive science is whether cognitive operations are modular or distributed across domains. We propose that fMRI has made a unique contribution to this question by elucidating the nature of structure/function relations. We discuss language, the classic domain for arguments in favor of domain specificity and a fixed neural architecture. We will argue that fMRI has provided evidence for the idea that rather than a ‘fixed neural architecture’, there is a dynamic functional architecture that emerges across the lifespan, pursuant to injury, and in response to language experience. We use empirical examples to highlight how fMRI has helped restructure theory by shedding light on how functionally distinct modular components of the grammar can recruit some of the same neural regions, how areas considered to be domain-specific may be recruited in a domain general fashion, and how language network specialization and left lateralization dynamically emerge in response to experience. FMRI provides a window into neural plasticity and dynamic functional organization not easily afforded by behavior alone.

This article considers the nature of brain structure and cognitive function relations through the lens of functional magnetic resonance imaging (fMRI). We will argue that fMRI provides unique insights not afforded by behavioral studies alone or by examining the behavioral consequences of structural lesions. Specifically, we argue that fMRI has provided strong support for a dynamic functional and neural architecture underlying language processes. We provide evidence suggesting that this neural architecture is shared across components of language and other cognitive domains and changes across early deprivation, recovery after brain injury, development and learning. These insights challenge the classic view of the theory of modularity, which has influenced current theories of the functional and neural architecture of language.

There are a number of defining characteristics of a theory of modularity. We provide here fMRI evidence that challenges two of these properties - domain specificity and fixed neural architecture (Fodor, 1983). Domain specificity proposes that the mind is comprised of separate, specialized modules. Each module represents one content area and operates on specific types of input. For example, language is one module, separate and distinct from other cognitive domains, such as music. Moreover, some views of the functional architecture of language propose that the components of the grammar - phonetics/phonology, lexicon, syntax, semantics - are themselves separate modules as they operate over different types of

representations and hence inputs (Fodor, 1983; Levelt, 1989; Pinker, 1994). Fixed neural architecture refers to the notion that there are ‘distinct neural structures’ that operate over each module.

We provide evidence from fMRI showing that the structural components of language are not domain specific but rather recruit a broadly distributed neural network, that often the same neural areas are recruited across these different components of the grammar, and that language draws on at least some neural mechanisms and computational properties shared across other cognitive domains. We then turn to issues of neural plasticity drawing from brain injury and developmental studies of language that show not a ‘fixed’ but rather a changing and in this sense ‘dynamic’ functional and structural organization underlying cognitive operations over time and experience.

To be clear, we are not claiming that there is no neural architectural predisposition for language and its organization. Studies have shown that the newborn brain has a bias to respond to spoken language (Dehaene-Lamberg, Hertz-Pannier, & Dubois, 2006). What we are claiming is that the system is not fixed and immutable, but rather is flexible, dynamically organizes over development and language exposure, and is plastic pursuant to injury.

The Modularity of Language or Not?

There is little debate that language is left hemisphere dominant and recruits a distributed neural system involving frontal, temporal, and parietal structures. What is less clear is whether within this neural architecture, there are domain specific modules associated with different components of the grammar, whether such modules recruit distinct neural structures that are solely dedicated to the processing of that module, and whether the neural systems associated with language are different from those recruited across other cognitive domains.

fMRI results in general have failed to show focal activation related to a particular component of the grammar but rather have shown distributed neural activation patterns within each component of the grammar (Hickok, 2009; Hickok & Poeppel, 2007; Price, 2012). In particular, the fMRI literature has shown consistent distributed neural activation patterns for speech processing (Hickok & Poeppel, 2007; Scott & Wise, 2004), lexical processing (Blumstein, 2009; Indefrey & Levelt, 2004; Paulesu, Frith, & Frackowiak, 1993), syntactic/sentence processing (Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Kaan & Swaab, 2002) and semantic processing (Binder, 2009). The identification of such distributed neural systems associated with a particular module is not *prima facie* evidence against a modular view. Each component of the grammar could potentially have a dedicated neural architecture distinct from other components of the grammar but current neuroimaging methods may not be able to provide a sufficiently fine-grained picture of the neural structures associated with particular language functions.

What is challenging to the claim that there is a fixed neural architecture for each component of the grammar is evidence that many of the same neural areas within these distributed neural networks are recruited across components of the grammar. Studies on language processing typically focus on a particular linguistic domain and map out the neural structure

recruited within that domain. However, looking at the findings of this research *across* linguistic domains reveals that many of the same neural areas are recruited. For example, different functional roles have been ascribed to the inferior frontal gyrus and these roles are associated with different components of the grammar including syntactic processing (Grodzinsky & Friederici, 2006), speech processing (Myers, Blumstein, Walsh, & Eliassen, 2009), semantic processing (Binder, 2009), the unification of lexical and sentence level information (Snijders, Vosse, Kempen, et al., 2009), and the selection among semantic alternatives (Thompson-Schill, D'Esposito, Aguirre, & Farah M., 1997) (but see Poldrack, Wagner, Prull, et al., 1999 for proposal of a functional subdivision between phonology and semantics within the IFG).

There is also evidence to suggest that some neural areas recruited for language processing are also recruited across other cognitive domains. One such area is the superior temporal sulcus (STS). In a recent paper, Hein and Knight (2008) reviewed results from fMRI studies that have claimed a critical role for this region in a particular cognitive domain including speech perception, face processing, biological motion, social perception, theory of mind, and audiovisual integration. Analysis of focal activation associated with these domains revealed that, rather than there being a functional subdivision of the STS, this area appears to be recruited in the service of each of these cognitive functions depending on 'task-dependent network connections' with other areas including frontal cortex and medial temporal lobe (p. 2125) (but see Federenko & Kanwisher, 2009).

Taken together, these findings suggest that although language recruits specific neural areas, these areas are not domain specific. Nonetheless, these claims have not gone unchallenged. In a recent study, Federenko, Behr & Kanwisher (2011) used a language localizer to map out language regions on an individual subject basis. Their findings showed little or no overlap between the language network and nonlinguistic processes, thus supporting a modular view of language. To identify the language network, they used a localizer task comparing activation patterns of sentences to nonwords. In this task, participants determined whether a probe appeared in a preceding sentence or list of pronounceable nonwords. The language network was defined as those areas in which there was greater activation for sentences than for nonwords. As designed, this localizer fails to uniquely define the language network as 1) the task is not a language task, 2) nonwords are linguistic stimuli, and 3) speech, a critical part of language, is not included (for other critiques see Grodzinsky, 2010).

Neural Plasticity After Early Deprivation and Brain Injury

Studies examining neural plasticity after early deprivation or brain injury provide strong evidence that language does not have an immutable neural architecture but rather that the neural system is flexible and can change and reorganize in response to a number of factors. Turning first to early deprivation, fMRI findings show that congenitally blind individuals recruit occipital areas in processing Braille, a system used for tactile reading, whereas sighted individuals show deactivation in these areas when doing somatosensory tasks (Sadato et al., 1996; Sadato, 2005). Perhaps more interestingly, occipital areas are also recruited when congenitally blind individuals are processing language (Bedny, Pascual-Leone, Dodell-Feder, Fedorenko, & Saxe, 2011; Burton, Snyder, Diamond, & Raichle,

2002). In particular, visual cortex in congenitally blind individuals is recruited across a number of components of the grammar, including phonological, lexical-semantic, and sentence processing. Of importance, the language network in this population involves neural areas that are not typically involved in these cognitive functions.

There is also a growing body of literature examining the neurobiology of language recovery in aphasia. Of interest, there appear to be multiple stages in this process, each recruiting different brain structures, consistent with a dynamic process of language recovery and reorganization (Saur, Lange, Baumgaertner et al., 2006). Their findings suggest that in the acute phases (several days post-stroke), there is reduced left hemisphere activation, even in non-infarcted language areas. Within two weeks, there is an increase in activation of right hemisphere structures in homologous language areas, which correlate with the degree of recovery. In the chronic stages (close to a year post-stroke), there is an increase of activation in left hemisphere language areas, again correlated with degree of recovery.

There has been considerable question in the literature whether the increased activation on the right side seen in chronic aphasics reflects a compensatory or pathological role (cf. Crinion & Price, 2005; Naeser, Martin, Thereot, et al., 2011; Thompson, 2008; Turkeltaub, Coslett, Thomas, et al., 2011). What does seem to be the case is that those aphasics who do show the most recovery recruit left hemisphere structures including perilesional areas and, as well, neural areas that are not typically involved in language processing (Buckner, Corbetta, Schatz et al., 1996; Thompson, 2000; Turkeltaub, Messing, Norise, & Hamilton, 2011). As we elucidate below, developmental studies and studies of adult language learning show analogous patterns of dynamic change in network architecture.

Dynamic Organization As A Function of Language Development and Learning

Healthy adult language processing is left lateralized and subserves a network of fronto-temporo-parietal cortical regions. Arguably, a fixed neural architecture for language is one that would be present and robust at birth and constant over the lifespan. Recent fMRI data from newborn infants challenges this notion. Perani et al. (2011) paired whole brain fMRI, functional connectivity analyses, and diffusion tensor imaging (DTI) during auditory language input in 1–2 day-old newborns. While they found involvement of bilateral temporal regions as well as the left IFG in newborns in response to speech, the activations were less lateralized in newborns. Indeed there was greater activation in primary and secondary auditory cortex on the right side, not as one might expect from a strictly modular view on the left side. Moreover, functional connectivity data showed that infants displayed greater interhemispheric connectivity as compared to intrahemispheric connectivity in the language network characteristic of adults (Oleser, Wise, Dresner, & Scott, 2007). Other work, which examined sentence processing in 6 year-old children, has shown that these developmental differences in hemispheric connectivity for the default language network extend well into childhood (Friederici, Brauer, & Lohmann, 2011). In particular, children's default language network is comprised of strong interhemispheric connectivity between superior temporal regions in contrast to the adult network which shows intrahemispheric connectivity between left IFG (BA 44) and left posterior STG/STS. Thus, hemispheric

lateralization seen in adults for the auditory processing of speech is not fixed or present at birth.

Additional evidence shows that this dynamic process of organization and specialization to an adult stable state is dependent on language experience and knowledge. Redcay, Haist, & Courchesne (2008) recently used fMRI to examine speech processing in early childhood, a time marked by significant advances in language development. They compared 1–2 year-old toddlers with little language to 3-year-old children with better language proficiency on passive perception of backward and forward speech. Toddlers with immature language skills showed involvement of a broad frontal, parietal, and occipital network in response to forward relative compared to speech. In contrast, 3 year-olds with better language recruited the classic left lateralized language STG area, in addition to parietal and occipital regions. These data point to a key interaction between language learning and brain organization.

It can be argued, however, that something ‘triggers’ a language module to engage in this narrow age range. An even stronger argument for organization subsequent to language exposure then comes from adult studies of language learning that show a similar pattern of organization as that described above. The ‘trigger’ hypothesis is unlikely to explain these data in adults. Rather than seeing recruitment of only the left hemisphere language network as one might expect if language in the mature adult had a ‘fixed neural architecture’, there appears to be a progression from bilateral to left hemisphere dominance during the learning process and changes in patterns of functional connectivity in the language network (Sheppard, Wang, & Wong, 2012; Wong, Perrachione, & Parrish, 2007). The extent of these changes correlates with the success of language learning. Thus, although there is considerable individual variation, adults also display dynamic neural plasticity, and this plasticity appears to reflect the intersection of language learning ability with the computational and cognitive processes required for learning and ultimately internalizing a new language system. These patterns of change are similar to those described in the newborn studies discussed above (Perani et al., 2011). Taken together, these neuroimaging data argue for a dynamic functional language architecture that cortically specializes with language experience.

Conclusions

How then have fMRI studies informed cognitive theory? We argue that evidence from cognitive neuroscience challenges the strong form of a theory of modularity. A theory of modularity typically draws from data focusing only on a single snapshot in time for any particular cognitive operation. This increases the likelihood of concluding that there is a static, fixed, and specialized neural architecture for a given cognitive process. The biological data, as revealed through the lens of fMRI, do not support a view that language is domain specific or is dependent on a fixed neural architecture. In the end, cognitive systems allow for neural plasticity and adaptive function.

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