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Research report

Hierarchical functional connectivity between the core language system and the working memory system

*Michiru Makuuchi and Angela D. Friederici**

Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

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ABSTRACT

Language processing inevitably involves working memory (WM) operations, especially for sentences with complex syntactic structures. Evidence has been provided for a neuroanatomical segregation between core syntactic processes and WM, but the dynamic relation between these systems still has to be explored. In the present functional magnetic resonance imaging (fMRI) study, we investigated the network dynamics of regions involved in WM operations which support sentence processing during reading, comparing a set of dynamic causal models (DCM) with different assumptions about the underlying connectional architecture. The DCMs incorporated the core language processing regions (pars opercularis and middle temporal gyrus), WM related regions (inferior frontal sulcus and intraparietal sulcus), and visual word form area (fusiform gyrus). The results indicate a processing hierarchy from the visual to WM to core language systems, and moreover, a clear increase of connectivity between WM regions and language regions as the processing load increases for syntactically complex sentences.

1. Introduction

The arcuate fasciculus (AF), a white matter fiber bundle connecting Broca's area to Wernicke's area, has been considered to play a central role in language processing for more than a century (Dejerine, 1901; Geschwind, 1965a, 1965b; Wernicke, 1874). Using diffusion tensor imaging (DTI) to enable the visualization of white matter fibers, a comparative study among humans, chimpanzees, and macaques revealed that humans possess the most developed AF (Rilling et al., 2008), which appears to be consistent with the fact that only the humans enjoy fully developed language.

After applying DTI to humans, the classical view of the AF and its role in language processing was revised. The first novel finding was the existence of direct and indirect (relayed by the inferior parietal lobe) dorsal connections between Broca's and Wernicke's areas (Catani et al., 2005). The two dorsal connections which also differ in their termination regions in the prefrontal cortex appear to serve different functions. The connection that terminates in the premotor cortex supports sound-to-motor mapping (Hickok and Poeppel, 2007; Saur et al., 2008) and the connection that terminates in the posterior portion of Broca's area subserves the processing of syntactically complex sentences (Friederici, 2009; Brauer et al., 2011; Wilson et al., 2011). The second eminent finding was the reappraisal of a ventral pathway connecting Broca's and Wernicke's areas via the extreme capsule fibers system (ECFS; Makris et al., 2009; Petrides and Pandya, 2009) and its possible

* *Corresponding author*. Max Planck Institute for Human Cognitive and Brain Sciences, Department of Neuropsychology, Stephanstraße 1a, 04103 Leipzig, Germany.
E-mail address: angelafr@cbs.mpg.de (A.D. Friederici).
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role as part of the semantic processing system (Hickok and Poeppel, 2007; Rolheiser et al., 2011; Saur et al., 2008; Weiller et al., 2009).

More recently, studies revealed that both the dorsal and the ventral pathways are involved in syntactic processing (Friederici et al., 2006; Tyler et al., 2011). The ventral pathway appears to support local combinational processes while the dorsal pathway subserves the processing of complex syntax in particular (Friederici et al., 2006) as indicated by developmental (Brauer et al., 2011) and patient studies (Wilson et al., 2011). These latter studies showed that the processing of syntactically complex sentences is deficient when the dorsal pathway connecting to the posterior portion of Broca's area is not fully matured or lesioned by degenerative processes.

The full merit of the anatomical connections will become obvious when the effective connectivity among the language-relevant brain regions during processing is identified. Effective connectivity analysis of functional magnetic resonance imaging (fMRI) data, especially dynamic causal model (DCM) (Friston et al., 2003; Stephan and Friston, 2010) can estimate inter-regional relationships in a neural network, such as the direction of the causal influence and its change due to experimental interventions.

Here we investigated the dynamics of the neural network supporting the processing of sentences with varying syntactic complexity. Syntactic complexity was chosen as a focus of interest since many prior studies on language processing have reported activation increase in Broca's area, in particular the pars opercularis (PO) and middle and superior temporal regions for syntactically complex object-first compared to subject-first sentences (e.g., Stromswold et al., 1996; Bornkessel et al., 2005; Santi and Grodzinsky, 2007; Caplan et al., 2008; Friederici et al., 2009; Newman et al., 2010). In object-first sentences, the object noun is dislocated from its original position leaving a trace behind, thus creating a distance between the new and the original positions which needs to be dealt with during processing. The processing of syntactically complex sentences has long been considered to be an interplay between working memory (WM) and syntactic processing (Caplan and Waters, 1999; Fiebach et al., 2001; Cooke et al., 2002; Novais-Santos et al., 2007; Santi and Grodzinsky, 2007; Makuuchi et al., 2009).

In this context, two WM components have been discussed: syntactic WM with its main focus located in the inferior frontal gyrus (IFG) (Caplan and Waters, 1999) and phonological WM with its main focus located in the parietal cortex (Novais-Santos et al., 2007). The syntactic WM is taken to be syntax-specific (Caplan and Waters, 1999) whereas the phonological WM is viewed to be involved in memory for word lists (Owen et al., 2005) as well as for memory-demanding sentence structures (Meyer et al., 2012). A recent fMRI experiment has located the syntactic WM, i.e., the region directly related to syntactic complexity in the inferior frontal sulcus (IFS) (Makuuchi et al., 2009). This study had used embedded sentence structures requiring the storage of multiple subject-noun phrases of the different embedded sentences. Another fMRI experiment investigated the storage of one subject or object-noun phrase across a number intervening words in a sentence and found the temporo-parietal cortex to activate as a function of storage distance (Meyer et al., 2012). Relating the localization to findings in the literature (Owen et al., 2005), this storage component was identified as phonological WM.

In the present study, DCM was applied to fMRI data from an experiment (Makuuchi et al., 2013) varying syntactic complexity (subject-first canonical structures *vs* object-first non-canonical structures) and the concomitant WM demands. The WM demands are resulted from the non-canonical structures in which the object-noun phrase is encountered early in the sentence but has to be kept in memory before the subject-noun phrase and the verb are perceived. This may recruit the phonological WM as the object-noun phrase has to be stored in memory, but also the syntactic WM as structure-building is required while holding the object-noun phrase. In the original fMRI study object-first sentences which resulted from different syntactic operation compared to subject-first sentences led to increased activations in a number of brain region: the PO and the IFS as well as the middle part of the middle temporal gyrus (mMTG), and the intraparietal sulcus (IPS) of the left hemisphere. Based on the functional data, we included these regions in the DCM analysis. Activations were also observed in the two right hemisphere regions, PO and IPS, which are homolog areas to activated regions in the left hemispheric network. Such right hemispheric homolog activations are often reported in language studies without discussing their specific function. They may reflect inter-hemispheric coactivation mediated by the corpus callosum. To keep the number of possible models at a reasonable level, we decided to take only the left hemispheric network into account. We further added the fusiform gyrus (FG) since it is assumed to represent the visual word form area (Cohen et al., 2000, 2002) and to act as the initial cerebral gate of the visual linguistic information. With these regions we constructed and estimated fifteen alternative DCMs.

2. Methods

The present study used data collected in a previous fMRI study. The details of the experimental stimuli and procedure of this study are found in the paper published elsewhere (Makuuchi et al., 2013). For a comprehensive description of stimuli and procedure see also below.

2.1. *Participants*

Twenty-two young, right-handed, healthy participants were examined (eleven females). Handedness (mean 93.9, range 80–100) was assessed with the Edinburgh Inventory (Oldfield, 1971). The mean age was 25.0 years old (range 20–33 years). All participants were native German speakers. Reading span was measured by a German version of the Daneman and Carpenter (1980) reading span test (mean 4.0, range 3–5.5). No participant had a history of neurological disorders. One participant who had low performance was excluded from the group analysis as in the previous report (Makuuchi et al., 2013), and also excluded from the DCM analysis. The experimental procedures were approved by the Research Ethics Committees of the University of Leipzig. Written informed consent was given by all participants.