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Research Report

Neural circuits of hierarchical visuo-spatial sequence processing

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ABSTRACT

Sequence processing has been investigated in a number of studies using serial reaction time tasks or simple artificial grammar tasks. Little, however, is known about higher-order sequence processing entailing the hierarchical organization of events. Here, we manipulated the regularities within sequentially occurring, non-linguistic visual symbols by applying two types of prediction rules. In one rule (the adjacent dependency rule), the sequences consisted of alternating items from two different categories. In the second rule (the hierarchical dependency rule), a hierarchical structure was generated using the same set of item types. Thus, predictions about non-adjacent elements were required for the latter rule. Functional Magnetic Resonance Imaging (fMRI) was used to investigate the neural correlates of the application of the two prediction rules. We found that the hierarchical dependency rule correlated with activity in the pre-supplementary motor area, and the head of the caudate nucleus. In addition, in a hypothesis-driven ROI analysis in Broca's area (BA 44), we found a significantly higher hemodynamic response to the hierarchical dependency rule than to the adjacent dependency rule. These results suggest that this neural network supports hierarchical sequencing, possibly contributing to the integration of sequential elements into higher-order structural events. Importantly, the findings suggest that Broca's area is also engaged in hierarchical sequencing in domains other than language.

1. Introduction

Sequence processing is inherent in several cognitive domains. In the field of language, sequencing is necessary, e.g. for concatenating letters to words, words to phrases, and phrases to sentences. Similarly, sequential organization is also required in non-language domains such as goal-directed behavior or action perception and prediction. Accordingly, experiments dealing with the sequential structure of stimuli are rooted in different research domains (cf. Fiebach and Schubotz, 2006; Schubotz and Fiebach, 2006). Recently, efforts have been directed to the investigation of hierarchical sequence processing not only in the field of language, but also in non-language domains.

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Some language processing studies used fMRI to determine which cognitive processes were involved in the processing of sentences with different hierarchical structures. In these linguistic structures, the syntactic complexity was manipulated, while the meaning (semantics) of the sentences was kept constant. For example, the syntactic structure was varied by manipulating the hierarchical order of phrases within sentences, and this manipulation resulted in increased brain activity in Broca's area. It was suggested that Broca's area, among other brain regions, played an important role in parsing syntactically complex natural sentences (e.g. Roder et al., 2002; Santi and Grodzinsky, 2007).

Hierarchical sequencing was also examined in studies that used the serial reaction time task (Koch and Hoffmann, 2000), the serial prediction task (Schubotz and von Cramon, 2002) and in a study that applied abstract, hierarchically organized action plans (Koechlin and Jubault, 2006). Schubotz and von Cramon (2002) suggested that a premotor–parietal network plays a crucial role in predicting and planning in the motor domain. Importantly, this study did not differentiate between hierarchical and non-hierarchical sequences. In contrast, Koechlin and Jubault (2006) found Broca's area and its right hemispheric homologue to be sensitive to the start and the end states of hierarchically organized event sequences.

Recent PET and fMRI studies that investigated the learning and processing of artificial grammar (AG) rules addressed the question of explicit versus implicit rule learning (Fletcher et al., 1999; Forkstam et al., 2006; Peigneux et al., 2000; Seger et al., 2000; Skosnik et al., 2002) or chunk versus pattern learning (Lieberman et al., 2004). Most of these imaging studies, applied Reber's artificial grammar (Reber, 1967). Brain activations reported for the processing of Reber's artificial grammar varied as a function of the type of the design used, and of the type of the comparison conducted. Several different regions were reported to be involved in the learning of a Reber grammar. Most common activations were found in different parts of the left prefrontal cortex (Forkstam et al., 2006; Lieberman et al., 2004; Peigneux et al., 2000; Seger et al., 2000). Moreover, the basal ganglia were also engaged in artificial grammar learning. Activation in the caudate nucleus was reported by Peigneux et al. (2000), Lieberman et al. (2004), and Forkstam et al. (2006). Another group of studies working with artificial grammars used rules containing a more language-like structure than the Reber grammar (Bahlmann et al., 2008; Opitz and Friederici, 2003; Opitz and Friederici, 2004). Opitz and Friederici (2003) found that learning of the artificial language came along with activation in the hippocampal formation in the early learning stage; the left inferior frontal gyrus was engaged during the later part of the task.

A growing number of behavioral and fMRI studies have been published which have focused on the processing of hierarchical structure (Bahlmann et al., 2008; de Vries et al., 2008; Friederici et al., 2006; Gentner et al., 2006; Opitz and Friederici, 2007; Perruchet and Rey, 2005). The hierarchical stimulus structure employed in these experiments comprised center-embedded stimuli also present in natural sentences (e.g. [the football player [who scored the goal] was praised]). Studies on hierarchical sequence processing suggest that Broca's area plays an important role whenever language-related stimuli (e.g. letters, syllables, words, or sentences) are to be processed. Beyond this, in a theoretical article, Fiebach and Schubotz (2006) recently proposed that Broca's area plays a crucial role in hierarchical sequence processing, independent of the cognitive domain. In a similar vein, based on their fMRI data, Koechlin and Jubault (2006) suggested that Broca's area is involved in hierarchical sequence processing in non-language domains, for example, the executive control of the hierarchical organization of goal-directed behavior.

In a recent fMRI study, we used two AG rules that varied in complexity in an fMRI setting (Bahlmann et al., 2008). The 'lexicon' of this language consisted of consonant–vowel syllables. The less complex structure followed the rule $(AB)^n$ and employed an adjacent dependency rule. It involved the generation of sequences of alternating, adjacent category pairs. The more complex structure was coded as A^nB^n. That is, sequence structuring was governed by a hierarchical dependency rule, since individual items related to each other according to non-adjacent, hierarchically organized sequences of stimuli. The direct comparison of hierarchical versus adjacent dependency syllable sequences revealed activity in a network comprising Broca's area, the ventral premotor cortex (BA 44/6) and other cortical and sub-cortical areas.

In the present study we aimed to identify brain regions involved in hierarchical sequence processing in the visuo-spatial domain. We applied a hierarchical and a non-hierarchical AG to non-linguistic stimuli (see Fig. 1). These materials consisted of abstract visual stimuli that were characterized by their spatial orientation and surface pattern. Importantly, these stimuli were considered to be novel because they were not associated with a linguistic label or any conceptual knowledge (cf. Koester and Prinz, 2007). If Broca's area is engaged in domain-general hierarchical sequencing, we expect this region to also be activated for hierarchical structures in an AG using non-linguistic stimuli.

2. Results

2.1. Behavioral results

In the present study two different sequencing rules (factor RULE) were applied to abstract visual stimuli (see Fig. 1). The sequences consisted of four or six stimuli (factor LENGTH) and were grammatical or ungrammatical (factor GRAMM). Participants entered the scanner after they successfully learned the two rule types. Each participant learned and processed both rules in two separate fMRI sessions, with one week delay between the sessions. A grammaticality judgment task was applied.

An ANOVA on errors rates was conducted with the factors RULE (adjacent dependency, hierarchical dependency rule), LENGTH (short sequences, long sequences), and GRAMM (grammatical sequences, ungrammatical sequences; see the Experimental procedures section for a detailed description of the factors). A significant main effect of RULE was found [$F(1,14)=12.7$, $p<.01$], indicating that the hierarchical dependency rule induced more errors (5.9%, SD=6.1) than the adjacent dependency rule (1.4%, SD=2.5; see Fig. 2). The interaction between RULE and GRAMM also reached significance [$F(1,14)=12.0$, $p<.01$].