SPECIAL ISSUE: POSITION PAPER

BROCA'S AREA AND THE VENTRAL PREMOTOR CORTEX IN LANGUAGE: FUNCTIONAL DIFFERENTIATION AND SPECIFICITY

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Abstract

The idea is put forward that Broca's area (BA 44/45) and the left ventral premotor cortex (BA 6) together with the frontal operculum support different functions during language processing. While BA 44/45 is seen to be increasingly activated whenever the internal re-construction of a hierarchical structure from a sequential input is necessary, BA 6 is involved in the processing of local structural dependencies. This functional differentiation is discussed in the context of the neurocytoarchitectonical differentiation between agranular structure characterizing BA 6 and a dysgranular cortical structure characterizing BA 44/45. This differentiation is exemplified in the domain of language, but is possibly applicable to non-language domains.

Key words: Broca's area, ventral premotor cortex, frontal operculum, syntax

Broca's area (BA 44/45) and the left ventral premotor cortex (BA 6) both show increased levels of activation as a function of syntactic processes during language comprehension. When considering imaging studies which investigate syntax at sentential level a recent metanalysis suggests a functional dissociation between activation in BA 44/45 on the one hand and in BA 6 and laterally adjacent frontal operculum on the other (Friederici, 2004). Increased activation in BA 44/45 is observed for the processing of non-canonical sentences in which words are moved out of their original position as compared to sentences of canonical word order. This has been reported for English object relative clauses (Just et al., 1996) and for cleft object sentences (Caplan et al., 1999) as compared to their subject initial counterparts and also for sentences containing transformations in German (Fiebach et al., 2004; Röder et al., 2002) and in Hebrew as compared to their canonical counterparts (Ben-Shachar et al., 2003). Moreover, activation in BA 44/45 is reported for the processing of grammatical rules defined in terms of hierarchical phrase structure as compared to non-grammatical rules based on sequential cues (Tettamanti et al., 2002). Thus, these data suggest that BA 44/45 is supporting the processing of syntactic hierarchies.

There appear to be two exceptions to this general pattern, one study in English (Cooke et al., 2001) and one study in German (Fiebach et al., 2005). Both of these studies not only varied the factor canonicity of word order, but, moreover, the factor length between the crucial element's position and its reference position in the sentence. Fiebach et al. (2005), for example, used wh-sentences (see Table I) in which the length between the crucial wh-element (object wh-element marked by accusative case) and its original object position in the sentence (see Table I) was varied. Interestingly, both studies found activation in the inferior frontal gyrus to increase as a function of the factor length of syntactic dependency, and as an interaction of length and canonicity, but not as a function of canonicity alone. A closer look reveals that Cooke et al. (2001) reported increased activation in the left inferior frontal gyrus located, however, anterior to the core region of BA 44/45, namely in BA 47, for the comparison between long and short object relative sentences as well as for the canonicity-length interaction. Fiebach et al. (2005) found an activation increase in the core region of BA 44/45, i.e., in left BA 44/45 and in the inferior tip of BA 44 due to an interaction between length and canonicity. Although the two factors length and canonicity do not reflect the same level of representation according to linguistic theories, they may be considered as two sides of the same coin, namely, an increase in demands on the syntactic parser. The parser's performance is not only determined by the syntactic structure to be processed (non-canonical vs. canonical word order), but, moreover, by the fact that language processing is realized as a sequential process in time. The latter fact leads to a dependence of the parser's performance on the length of the distance of a moved element between its original (base) position in the syntactic hierarchy and its actual position in the non-canonical sentence. Once a word in a non-canonical position has been identified as a moved element, the parser has to keep this element active in working memory,

TABLE I

Examples of stimulus items in the study by Fiebach et al. (2002)

Short, SUBJECT-first **Thomas fragt sich, wer den Doktor am Dienstag nachmittag nach dem Unfall verständigt hat.** Thomas asks himself, who$_{NOM}$ the doctor on Tuesday afternoon after the accident called.
Short, OBJECT-first **Thomas fragt sich, wen$_i$ der Doktor ____$_i$ am Dienstag nachmittag nach dem Unfall verständigt hat.** Thomas asks himself, who$_{ACC}$ the doctor____$_i$ on Tuesday afternoon after the accident called.
Long, SUBJECT-first **Thomas fragt sich, wer am Dienstag nachmittag nach dem Unfall den Doktor verständigt hat.** Thomas asks himself, who$_{NOM}$ on Tuesday afternoon after the accident the doctor called.
Long, OBJECT-first **Thomas fragt sich, wen$_i$ am Dienstag nachmittag nach dem Unfall der Doktor ____$_i$ verständigt hat.** Thomas asks himself, who$_{ACC}$ on Tuesday afternoon after the accident the doctor____$_i$ called.

The subject in these sentences is marked by the nominative case (NOM), whereas the object is marked by accusative case (ACC). ____$_i$ indicates the position of the object noun phrase in the canonical (base) structure from which it has moved into the actual initial position. The error indicates the movement.

probably a working memory specialized for syntactic features, until the original position in the syntactic structure can be specified. Evidence for the latter process has been provided by a recent event-related brain potential experiment demonstrating a left anterior negative going brain wave starting with the identification of the moved element and ending at the element's original sentential position (Fiebach et al., 2002).

The most general aspect common to all these sentence processing studies is that the parser has to deal with incoming sequences which can only be understood once the underlying hierarchical structures and the non-local dependencies they entail are rebuilt from the sequential input. Processing demands increase as a function of non-canonicity and as a function of the length of the distance between non-local dependencies. These processes appear to be supported by the core region of BA 44/45.

In a number of studies on syntactic processing, activation was observed in BA 6 and the adjacent frontal operculum (FO). The region was found in some of those studies which investigated syntactic processes by comparing correct with incorrect sentences containing syntactic violations (Fiebach et al., 2004; Friederici et al., 2003; Newman et al., 2003). There are, however, also a number of imaging studies which do not report such an activation for the processing of syntactic violations. It may well be possible that the non-activation in BA 6/FO in these studies is a function of the particular comparisons conducted (i.e., often comparisons between violations of different types, e.g., such as comparisons between syntactic errors and spelling errors [Embick et al., 2000] or between syntactic errors and phonological errors [Moro et al., 2001]). The exact function of BA 6/FO has yet to be defined. It is not clear whether this cortical region is involved in error detection of local structures or in the processing of local structural dependencies in general and only increases in activation once a local structure is violated. Clearly, more data are needed before this issue can be resolved. The finding, however, that local violations within phrases (or across adjacent phrases) during on-line sentence parsing is more likely to activate BA 6/FO than BA 44/45, whereas BA 44/45 is more likely to be activated by the processing of non-local dependencies in syntactic hierarchies, points to a functional dissociation of these two adjacent brain areas.

This functional dissociation could be connected to the principle difference between simple probabilistic grammar processing and phrase structure grammar processing as proposed by Hauser et al. (2002). Only the latter allows and actually requires the build-up and processing of hierarchical structures (Fitch & Hauser, 2004; Friederici, 2004). Fitch and Hauser (2004; see also Hauser et al., 2002) argue that the ability to process hierarchical structures is particularly human, as humans appear to be able to easily learn both types of grammars, whereas monkeys can only learn probabilistic grammars.

Taking these results demonstrating a principle difference between monkeys and humans into account, one might speculate about the relation between the observed difference in the two species and its possible neural basis. It was proposed that the processing of local syntactic dependencies that can be mastered on the basis of local probabilities may possibly be based on a phylogenetically older cortex, namely BA 6 and the adjacent frontal operculum, whereas the processing of syntactic hierarchies may rather be supported by a phylogenetically younger cortex, namely BA 44/45 (Friederici, 2004). Here, I refrain from going into the long standing discussion concerning which brain areas in the monkey are the analogue counterparts in humans (for details see Petrides and Pandya, 1994; Rizolatti and Arbib, 1998). The argument put forward is rather based on the cyto- and myelo-architectonic observations of Sanides (1962) and his notion of gradiation of the cortical structure during phylogeny. Following the principle of gradiation from agranular to dysgranular