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Research report

Generating predictions: Lesion evidence on the role of left inferior frontal cortex in rapid syntactic analysis

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ABSTRACT

A well-documented phenomenon in event-related electroencephalography (EEG) and magnetoencephalography (MEG) studies on language processing is that syntactic violations of different types elicit negativities as early as 100 msec after the violation point. Recently, these responses have been associated with activations in or very close to sensory cortices, suggesting the involvement of basic sensory mechanisms in the detection of syntactic violations. The present study investigated whether intact auditory cortices and adjacent temporal regions are sufficient to generate early syntactic negativities in the auditory event-related potential (ERP). We tested ten clinically non-aphasic patients with left inferior frontal lesions, but intact temporal cortices in a passive auditory ERP paradigm that had reliably elicited early negativities in response to violations of subject-verb agreement and word category in the past. Subject-verb agreement violations failed to elicit early grammaticality effects in these patients, whereas a group of ten age-matched controls showed a reliable early negativity. This finding supports the idea that sensory aspects of syntactic analysis as reflected in early syntactic negativities critically depend on top-down predictions generated by the left inferior frontal cortex. In contrast, word category violations elicited a small, marginally significant early negativity both in controls and patients, suggesting an additional involvement of temporal regions in early phrase structure processing. In an additional auditory oddball experiment patients showed a regular P300, but no N2b component in response to deviant tones, indicating that their deficit in generating sensory predictions extends beyond the language domain.

1. Introduction

For a long time, the human brain was seen mainly as a reactive organ, with distinct processes and hence brain areas dedicated to perception and cognition. With respect to language, neurocognitive models consequently assumed that the speech signal is processed primarily in a bottom-up fashion, with sensory cortices providing physical stimulus features to higher, specialised cortical areas that then perform syntactic and semantic analysis (Friederici, 2002; Friederici and Kotz, 2003; Hickok and Poeppel, 2007; Scott and Johnsrude, 2003). In recent years however, the conception of the brain changes

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from a reactive to a predictive organ (Bar, 2007, 2009; Bubic et al., 2010). In this light, the parameters of language processing should be reconsidered, too. One phenomenon that is particularly difficult to explain without taking major contributions of top-down predictive processes into account is the temporal concurrence of sensory and syntactic processing stages. In the present study we elaborate on the possibility that sensory processing is directly influenced by syntactic predictions, and that these predictions are generated by the left inferior frontal cortex.

A large number of studies providing real-time correlates of language processing by means of event-related potentials (ERPs) or their magnetic equivalents (event-related fields – ERF) report signal deflections starting around 100 msec after a syntactic violation has occurred. This latency coincides with the earliest cortically generated sensory components such as the N1 reflecting signal detection (Hillyard et al., 1971; Hyde, 1997; Näätänen and Picton, 1987), and the mismatch negativity (MMN), which signals the automatic detection of deviance from acoustic regularities in previous stimulation and is thus taken to reflect sensory memory (Näätänen, 2008; Näätänen et al., 1989, 2007). A classical example of such early syntactic ERP components is the early left anterior negativity (ELAN) in response to word category violations (e.g., Friederici and Kotz, 2003; Friederici et al., 1993; Neville et al., 1991). More recently, it has been shown that negativities in the 100 msec time range occur likewise in response to violations of subject-verb agreement or verb inflection errors (Brunelliere, 2011; Deutsch and Bentin, 2001; Hasting and Kotz, 2008; Kubota et al., 2003, 2004). Different types of syntactic violations have also been shown to directly modulate the amplitude of the MMN (Hasting et al., 2007; Herrmann et al., 2009; Pulvermüller and Shtyrov, 2003; Shtyrov et al., 2003). This "syntactic MMN" (sMMN) effect provides a particularly compelling link between sensory and syntactic processing, first, because it is considered highly automatic (Pulvermüller et al., 2008) and second, because it appears to be generated in auditory sensory cortices (Herrmann et al., 2009; Pulvermüller and Assadollahi, 2007; Shtyrov et al., 2003).

Outside the MMN paradigm, evidence for sensory cortex involvement in early syntactic ERP effects is less clear. Main sources of the ELAN have been identified in the anterior portion of the left superior temporal gyrus (aSTG) and in left inferior frontal cortex (Friederici and Kotz, 2003; Friederici et al., 2003, 2000). Although there are several studies that clearly show activations within or in close vicinity to primary auditory cortex even outside the MMN paradigm (Friederici et al., 2003; Gross et al., 1998; Kubota et al., 2004; Meyer et al., 2000), it was not until recently that the sensory cortices' sensitivity to syntactic cues moved into the focus of interest. In their ERF study using visually presented sentences, Dikker et al. showed that word category violations increased the M100 response in visual cortex. This effect occurred only when the target item contained an overt closed-class category marking function morpheme, leading the authors to conclude that sensory cortex may react to salient syntactic markers that are inconsistent with the predicted input (Dikker et al., 2009). Two lines of research directly followed up on this: one spatially disentangled the effects of perceptual markedness or physical deviance from genuinely syntactic effects in the auditory modality by localising the former in primary auditory cortex and the latter in adjacent regions including the aSTG (Herrmann et al., 2011, 2012), whereas the other extended the visual M100 finding by showing that it is based on word form typicality, supporting the idea that sensory cortices are provided with estimates of the predicted input and hence show increased activity in response to mismatches (Dikker et al., 2010).

The notion that syntactic predictions from higher cortical areas enable rapid sensory mismatch responses goes well with previous studies assuming structural predictions (Lau et al., 2006) or syntactic priming (Brunelliere, 2011; Hasting et al., 2007; Pulvermüller and Shtyrov, 2003) as the mechanisms underlying early syntactic ERP effects. In semantic processing, the use of predictive cues from the context to pre-activate upcoming words is a common concept (DeLong et al., 2005; Federmeier et al., 2007; Van Berkum et al., 2005). From a domain-general perspective, the idea of syntactic predictions is also consistent with recent ideas that the brain constantly generates rough estimates of to be expected input (Bubic et al., 2010). These are assumed to be based on memory representations of previous encountered analogous stimuli and to facilitate sensory processing (Bar, 2007, 2009). What is missing from previous statements is evidence as to which part(s) of the neuronal network involved in language processing generates syntactic predictions. In the following, we introduce the left inferior frontal cortex as a prime candidate for this function.

Ever since the early study by Paul Broca (1861), who reported highly disordered speech behaviour in two patients with left inferior frontal lesions, Broca's Area (BA44/45) in left inferior frontal gyrus (IFG) has been associated with language functions. Modern lesion and neuroimaging studies have shown that within the language domain, this area is particularly important for syntactic processing (Friederici and Kotz, 2003; Grodzinsky and Santi, 2008). As already mentioned above, several studies suggest that the left IFG is involved in generating the ELAN following word category violations (Friederici and Kotz, 2003; Friederici et al., 2003, 2000). More recently, it has been specified that the area in inferior frontal cortex that is most relevant for the processes of local structure building as reflected in the ELAN is in fact the left frontal operculum (FOP), a structure located ventrally and more medially to the IFG (Friederici, 2011). Due to its location the FOP is, however, most likely co-affected by lesions of the IFG, which is why it is hard to differentiate in lesion studies. Particularly relevant for the present investigation is a study, in which Broca's aphasics with lesions in the left IFG failed to show an ELAN (Friederici et al., 1999), which underlines the importance of this area for the generation of this component. In addition to its role in the detection of word category violations, the left IFG also shows increased activation in response to word order violations (Embick et al., 2000; Friederici et al., 2006) and morphosyntactic violations (Moro et al., 2001; Newman et al., 2003; Ni et al., 2000). It is important to keep in mind, however, that many of these studies also report extensive activations in the left STG containing auditory sensory cortex, at least when stimuli are presented in the auditory modality (e.g., Friederici et al., 2003, 2000; Ni et al., 2000). Thus, although Broca's area clearly is *involved* in the processing of syntactic manipulations, it does not necessarily have to be the region *generating* early syntactic negativities. The role of the IFG