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Syntactic processing is distributed across the language system

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ABSTRACT

Language comprehension recruits an extended set of regions in the human brain. Is syntactic processing localized to a particular region or regions within this system, or is it distributed across the entire ensemble of brain regions that support high-level linguistic processing? Evidence from aphasic patients is more consistent with the latter possibility: damage to many different language regions and to white-matter tracts connecting them has been shown to lead to similar syntactic comprehension deficits. However, brain imaging investigations of syntactic processing continue to focus on particular regions within the language system, often parts of Broca's area and regions in the posterior temporal cortex. We hypothesized that, whereas the entire language system is in fact sensitive to syntactic complexity, the effects in some regions may be difficult to detect because of the overall lower response to language stimuli. Using an individual-subjects approach to localizing the language system, shown in prior work to be more sensitive than traditional group analyses, we indeed find responses to syntactic complexity throughout this system, consistent with the findings from the neuropsychological patient literature. We speculate that such distributed nature of syntactic processing could perhaps imply that syntax is inseparable from other aspects of language comprehension (e.g., lexico-semantic processing), in line with current linguistic and psycholinguistic theories and evidence. Neuroimaging investigations of syntactic processing thus need to expand their scope to include the entire system of high-level language processing regions in order to fully understand how syntax is instantiated in the human brain.

Introduction

Language processing is supported by an extended system of brain regions, primarily in the left frontal and temporal lobes (e.g., Binder et al., 1997; Fedorenko et al., 2010). Whereas evidence from both the patient and neuroimaging literatures strongly suggests that this system is selectively engaged in linguistic processes and not in other cognitive processes (e.g., Dronkers et al., 1998; Varley et al., 2005; Fedorenko et al., 2011; Willems et al., 2011; Fedorenko et al., 2012a; Monti et al., 2012), the division of linguistic labor among its constituent regions is still heavily debated. A key question for understanding the internal structure of the language system is to what extent different aspects of language comprehension are localized to particular regions within the system versus distributed across the entire system. The answer to this question will reveal which functions are implemented in distinct neural circuits and which functions share neural resources. These organizational principles of neural architecture might, in turn, illuminate the cognitive architecture of the human language faculty (for similar inferences from neural to cognitive architectures in perception, see e.g., Kanwisher, 2010). In the current paper, we specifically focus on syntactic processing: is it localized or distributed across the language system?

Prior literature addressing this issue provides conflicting evidence, such that neuropsychological evidence – on the whole – supports a distributed view of syntactic processing whereas neuroimaging evidence appears to support a more localized view. On the one hand, investigations of patients with brain damage have revealed that lesions to many different parts of the language system can cause similar syntactic comprehension difficulties. Such regions include Broca's region in the inferior frontal gyrus (e.g., Caramazza and Zurif, 1976; Schwartz et al., 1980; Caplan and Futter, 1986; Zurif et al., 1993; Grodzinsky, 2000), the arcuate fasciculus and/or the extreme capsule (e.g., Caramazza and Zurif, 1976; Papoutsi et al., 2011; Rolheiser, Stamatakis, and Tyler, 2011; Tyler et al., 2011; Wilson et al., 2011), posterior temporal regions (e.g., Samuels and Benson, 1979; Selnes et al., 1983; Basso et al., 1985; Tramo et al., 1988; Caplan et al., 1996; Bastiaanse and Edwards, 2004; Wilson and Saygin, 2004; Amici et al., 2007; Tyler et al., 2011; Thothathiri et al., 2012), and anterior temporal regions (e.g., Dronkers et al., 1994; Dronkers et al., 2004; Magnusdottir

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et al., 2013). For instance, lesions in all of these regions can impair the interpretation of semantically reversible sentences, such as *The boy is chased by the girl*, whose meanings (who did what to whom) depend on their syntactic form (i.e., word order, function words, and functional morphology). Consequently, some have argued that syntactic processing is supported by the language system as a whole (e.g., Caplan et al., 1996; Dick et al., 2001; Wilson and Saygin, 2004; Mesulam et al., 2015).

On the other hand, many neuroimaging studies employing syntactic manipulations have found activations not across the entire language system but, instead, restricted to a subset of the system, most commonly in the inferior frontal and posterior temporal regions (e.g., Just et al., 1996; Stromswold et al., 1996; Cooke et al., 2001; Ben-Shachar et al., 2003; Wartenburger et al., 2003; Constable et al., 2004; Bornkessel et al., 2005; Fiebach et al., 2005; Caplan et al., 2008; Meltzer et al., 2009; Peelle et al., 2010; Christensen et al., 2012; see Friederici, 2011, for a recent meta-analysis). These studies suggest a localized view of syntactic processing, in line with many proposals that link syntax to Broca's area (e.g., Bornkessel and Schlesewsky, 2006; Grodzinsky and Friederici, 2006; Grodzinsky and Santi, 2008; Friederici, 2009, 2011, 2012; Baggio and Hagoort, 2011; Tyler et al., 2011; Duffau et al., 2014; Ullman, 2012).

How can we reconcile these two sets of conflicting findings? One possibility is that the localized activation patterns in neuroimaging studies result from (i) the use of group analyses, which suffer from sensitivity loss due to inter-subject variability in the precise locations of activation peaks (e.g., Nieto-Castañon and Fedorenko, 2012); and (ii) differences across brain regions in the overall strength of response to language stimuli. In highly language-responsive regions one might expect relatively wide neighborhoods of strong activation, so that overlap across subjects could be evident despite individual variability in peak location. In regions that are language-selective but respond only weakly to language stimuli, however, one might expect smaller and shallower activation neighborhoods surrounding the (low) peaks, so that overlapping activations across subjects are less likely to emerge. Such reasoning suggests that neuroimaging methods that take into account inter-individual variability may be able to find evidence for distributed, rather than localized, syntactic processing. Therefore, here we use an individual-subjects approach (Fedorenko et al., 2010) that allows us to narrow in on the high-level language processing regions in each individual brain. We measure the effect of syntactic complexity on the response of these individually localized regions and show that, in fact, syntactic complexity modulates neural responses throughout the language system, consistent with the evidence from the patient literature.

Materials and methods

To test for sensitivity to syntactic demands, we chose a commonly used syntactic complexity manipulation: the contrast between subject- and object-extracted relative clauses, as in (1) (See also Fig. 1).

(1)

a. Subject-extracted relative clause: *the star that is greeting the circle*
b. Object-extracted relative clause: *the circle that the star is greeting*

In both (1a) and (1b), the verb phrase *is greeting* has two arguments (i.e., dependents): a subject who is doing the greeting (the star), and an object who is being greeted (the circle). However, the two sentences critically differ in the distance separating the verb phrase from its two dependents. Specifically, in the subject-extracted relative clause (1a), the dependencies are local: both the word *that* (which refers to *the star*) and the object *the circle* connect locally to the verb phrase *is greeting*. In contrast, the object-extracted relative clause (1b) has a more complex dependency structure: the verb phrase *is greeting* is separated from its object, *the circle*, by the subject *the star*. An appealing feature of this contrast is that a variety of factors that have been shown to affect sentence comprehension (e.g., Tanenhaus and Trueswell, 1995; Gibson and Pearlmutter, 1998) are matched across the two conditions, including lexical-level factors (the words are identical) and plausibility. So, only the dependency structure (i.e., syntax) varies.

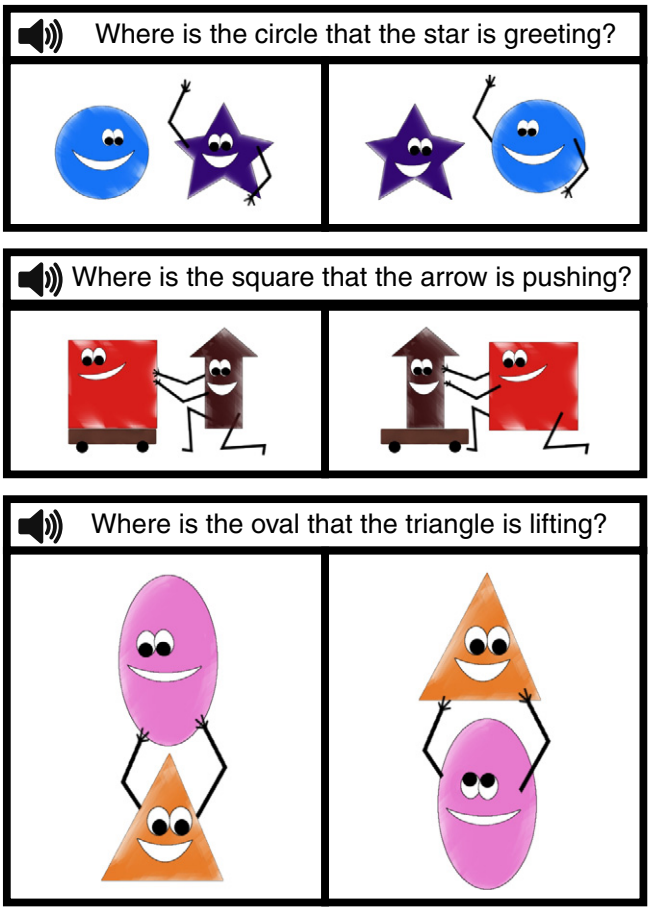

Fig. 1. Schematic illustration of sample trials in the object-extracted condition. In these instances, the picture matching the sentence is on the left.

Across many languages, object-extracted relative clauses like (1b) have been shown to cause comprehension difficulty compared to subject-extracted relative clauses like (1a), as reflected in a variety of dependent measures including reading times and response accuracies to comprehension questions (e.g., *English*: Wanner and Maratsos, 1978; King and Just, 1991; Gibson, 1998; Grodner and Gibson, 2005; *French*: Holmes and O'Regan, 1981; Baudiffier et al., 2011; *German*: Mecklinger et al., 1995; Schriefers et al., 1995; *Dutch*: Frazier, 1987; Mak et al., 2002, 2006; *Japanese*: Miyamoto and Nakamura, 2003; Ishizuka et al., 2003; Ueno and Garnsey, 2008; *Korean*: O'Grady et al., 2003; Kwon et al., 2006; Kwon et al., 2010; *Russian:* Levy et al., 2013). Therefore, the contrast between object- and subject-extracted relative clauses is considered by many to be a marker of syntactic processing, and has been used widely in both investigations of individuals with aphasia and brain imaging studies.

As mentioned above, in previous neuroimaging work, such contrasts between object- and subject-extractions as well as other, similar contrasts have produced activations largely restricted to Broca's area, the surrounding regions in the inferior frontal gyrus and the posterior parts of the middle (and sometimes superior) temporal gyrus. Other regions in the language system – such as the orbital portions of the inferior frontal gyrus or the anterior temporal regions – did not show reliable responses. However, this data pattern does not necessarily imply that the former regions are significantly more sensitive to the syntactic