Some Regions within Broca's Area *Do* Respond More Strongly to Sentences than to Linguistically Degraded Stimuli: A Comment on Rogalsky and Hickok (2011)

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Abstract

■ On the basis of their review of the literature, Rogalsky and Hickok [Rogalsky, C., & Hickok, G. The role of Broca's area in sentence comprehension. *Journal of Cognitive Neuroscience, 23,* 1664–1680, 2011] conclude that there is currently no strong evidence for the existence of "sentence-specific processing regions within Broca's area" (p. 1664). Their argument is based, in part, on the observation that many previous studies have failed to detect an effect in the left inferior frontal regions for contrasts between sentences and linguistically degraded control conditions (e.g., lists of unconnected words, lists of nonwords, or acoustically degraded sentence stimuli). Our data largely replicate this lack of activation in inferior frontal regions when traditional random-effects group analyses are conducted but crucially show robust activations in the same data for the same contrasts in almost every subject individually. Thus, it is the use of group analyses in studies of language processing, not the idea that sentences robustly activate frontal regions, that needs to be reconsidered. This reconsideration has important methodological and theoretical implications. ■

Rogalsky and Hickok (2011; henceforth R&H) argue against the role of Broca's area in sentence-level comprehension processes. One particular argument is based on the observation that several previous studies did not observe a stronger response—in regions in and around Broca's area—during the processing of sentences compared with linguistically degraded control conditions, such as lists of unconnected words or nonwords:[1] "processing a string of syntactically unstructured words produces as much activation as processing sentences containing long-distance dependencies" (p. 1667). R&H use this evidence, along with other observations, to argue against proposals according to which Broca's area (or one of its subregions) is functionally specialized for some aspect(s) of syntactic processing (e.g., Friederici, 2009; Grodzinsky & Santi, 2008). We largely agree with R&H's evaluation of such proposals (see e.g., Fedorenko & Kanwisher, 2011, for criticisms of Grodzinsky's account). However, the lack of evidence for *functional specialization* of Broca's area or its subregions for syntactic processing does not imply that these regions do not support sentence comprehension more generally. Understanding a sentence requires a complex set of cognitive processes, only some of which have to do with syntax. That said, if Broca's area indeed does not respond more strongly to sentence stimuli than, for exam-

ple, to lists of unconnected words, as R&H argue based on previous studies, then it would be difficult to argue for the role of this region in *any* aspect of sentence-level understanding. We argue here that the evidence is actually strong that Broca's area shows a greater response to sentences than to lists of unconnected words: (i) past failures to find such responses were based on group analyses that can fail to detect activations even when they are present in each subject individually (e.g., Fedorenko, Nieto-Castañón, & Kanwisher, in press; Fedorenko & Kanwisher, 2009; Saxe, Brett, & Kanwisher, 2006) and (ii) studies that analyze individual subjects do find greater activation for sentences than linguistically degraded stimuli in Broca's area consistently and robustly (Bedny, Pascual-Leone, Dodell-Feder, Fedorenko, & Saxe, 2011; Fedorenko, Hsieh, Nieto-Castañón, Whitfield-Gabrieli, & Kanwisher, 2010).

We have recently argued that because of anatomical variability between subjects, especially pronounced in the frontal lobes (e.g., Juch, Zimine, Seghier, Lazeyras, & Fasel, 2005; Amunts et al., 1999; Tomaiuolo et al., 1999), traditional group-based analyses may obscure the functional architecture of the language system because functional activations do not align well across subjects (Fedorenko & Kanwisher, 2009, 2011). This poor alignment makes it difficult to detect overlap across subjects at the voxel level, which is required for a significant effect to emerge in traditional random-effects group analyses. This situation has been seen in other cortical areas previously. For example, the fusiform face area (Kanwisher, McDermott, & Chun,

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1997) often does not emerge in group analyses, although it is easily detectable in each individual subject. Thus, failures to find greater activation in the inferior frontal regions during sentence comprehension compared with control conditions like lists of unconnected words using group analyses (e.g., Humphries, Love, Swinney, & Hickok, 2005; Friederici, Meyer, & von Cramon, 2000; Friederici, Opitz, & von Cramon, 2000; Stowe et al., 1998) leave open the possibility that robust effects are, in fact, present in each subject individually.

Indeed, in Fedorenko et al. (2010), we presented such evidence: a greater activation in the frontal regions during sentence comprehension compared with lists of words or nonwords. A functional localizer contrasting sentences and pronounceable nonwords reliably and quickly identifies key language-sensitive regions (e.g., Neville et al., 1998; Binder et al., 1997) in individual subjects, including a region in and around Broca's area (referred to as the "LIFG functional region of interest (fROI)" in Fedorenko et al.). The regions identified by this localizer contrast (a) are present in most individual subjects, (b) replicate within subjects, (c) have clear functional correspondence across subjects, (d) respond similarly to linguistic stimuli presented visually versus auditorily (see also Bedny et al., 2011), and (e) respond similarly across different sets of linguistic materials and tasks (e.g., passive reading vs. reading with a memory probe) as well as being robust to minor changes in the design or procedure. Furthermore, independent data (i.e., data not used for defining the ROIs) robustly replicate the higher response to sentences than nonword lists ($p < .0001$) and word lists ($p < .001$) in the LIFG functional ROI. These data strongly suggest that this brain region supports some aspect(s) of sentence understanding.[2]

Figure 1 shows sample activation maps for 15 subjects for the *sentences > word lists* contrast (see Fedorenko et al., 2010, for similar maps for the *sentences > nonword lists* contrast). As can be seen from the figure, although individuals vary substantially in the extent and the precise locations of the activations, the vast majority shows robust activations in and around Broca's area.[3]

Hickok (personal communication; see also R&H's response in the current issue) argues that perhaps when linguistic materials are presented visually and/or when participants have to respond to a memory probe after each stimulus, production-related processes are invoked. In particular, the hypothesis is that visual presentation and/or the memory probe task result in articulatory rehearsal: "the differences between sentences and word lists in F&K's data may be a result of covertly producing sentences rather than comprehending them" (R&H, response in the current issue). We respond to this potential concern here. First, the modality of presentation cannot account for our results. As mentioned above, Fedorenko et al. (2010; see also Bedny et al., 2011) have observed robust responses in the LIFG ROI for the contrast between sentences and word lists or nonword lists with auditory presentation. Furthermore, several other studies in the literature have reported modality-independent responses to sentence-level linguistic stimuli in the left inferior frontal regions (see Braze et al., 2011, for recent evidence and a review of previous relevant findings).

Second, let us say that the LIFG ROI does in fact support shadowing-like processes (i.e., covertly repeating the phonological forms of the incoming linguistic elements), as R&H hypothesize. Because this is a relatively low-level process, it seems unlikely that such a process would be invoked to a greater extent for sentences than for lists of unconnected words (or for jabberwocky than for lists of
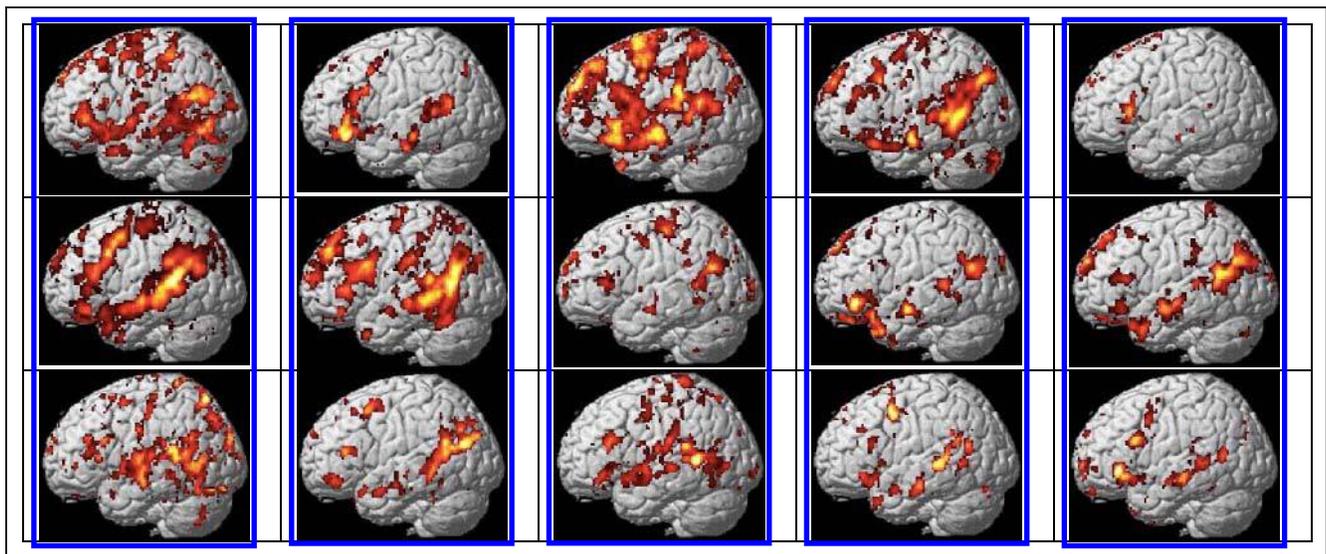

Figure 1. Sample individual activation maps from 15 subjects for the *sentences > word lists* contrast, thresholded at $p < .001$, uncorrected. These subjects performed the version of the localizer task with a memory probe task (deciding after each sentence or word list whether a probe appeared in the immediately preceding sequence; see Fedorenko et al., 2010, for details).

nonwords; see Bedny et al., 2011; Fedorenko et al., 2010, for relevant data). If anything, this process would plausibly be taxed more during the processing of, for example, non-words because the phonological forms of these elements are less familiar than those of real words and, thus, may be more difficult to repeat. So, it is unclear how the articulatory rehearsal hypothesis can explain the response profile of the LIFG region, with the greatest response to sentences, weaker response to word lists and jabberwocky sentences, and weakest response to nonword lists.

One additional point is worth making. The fact that the LIFG functional ROI responds more strongly to sentences than word lists or nonword lists does not imply that it is specialized for syntax or even for linguistic processing. In fact, our own data (Fedorenko et al., 2010; see also Bedny et al., 2011) suggest that this region supports word-level understanding in addition to higher-level linguistic processes. In particular, we observe a stronger response to word lists than to nonword lists ($p < .005$), a contrast that primarily taxes lexical-level processing. We address the question of specialization of the LIFG region for language versus various nonlinguistic processes, including domain-general cognitive control, elsewhere (Fedorenko, Behr, & Kanwisher, submitted).

In summary, sentences (presented either visually or auditorily) elicit a robust response in the left inferior frontal regions in almost every individual. This response is stronger than that elicited by linguistically degraded stimuli, such as word lists or nonword lists (e.g., Bedny et al., 2011; Fedorenko et al., 2010; Snijders et al., 2009; see also Brennan & Pylkkanen, 2010, for evidence from magneto-encephalography), suggesting that these regions support sentence-level linguistic processes, such as aspects of syntactic processing and/or compositional semantic processing. The precise nature of these regions' contribution to language production and comprehension as well as the degree of specialization of these regions for sentence understanding versus other linguistic and nonlinguistic processes remain open questions. However, without examining individual subjects' activation maps, the field will reach fundamentally wrong conclusions about the functional profile of Broca's area and its subregions.

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Notes

1. R&H further argue that a posterior portion of Broca's area (corresponding roughly to pars opercularis or Brodmann's area 44) only indirectly supports sentence comprehension via articulatory rehearsal. We do not evaluate this proposal here, largely because the regions that respond more strongly to sentences than to words or nonwords are located in the more anterior portions of Broca's area and are plausibly functionally distinct from the pars opercularis region.
2. Note also that unlike syntactic complexity contrasts, like that between object- and subject-extracted structures, the contrast

between sentences and word lists or nonword lists is not difficulty confounded. Consequently, the observed activations cannot be interpreted as reflecting general cognitive effort. In fact, when the memory-probe task is used, the word list or nonword list conditions are more difficult than the sentence condition, as evidenced by lower accuracies on the memory-probe task and the fact that the *word lists or nonword lists > sentences* contrasts activate frontal and parietal regions that have been implicated in general cognitive effort (e.g., Duncan, 2010; Duncan & Owen, 2000).

3. If a large enough number of subjects are included in a study, even a random-effects group analysis will probably detect some activation in the left inferior frontal regions for a contrast like *sentences > word lists*. However, these activations (i) will reflect only a small portion of each individual subject's activation because they only include voxels that behave consistently across subjects and (ii) will underestimate the functional selectivity of the region (see, e.g., Fedorenko et al., 2010, in press; Saxe et al., 2006, for empirical support). The latter issue is especially problematic for investigating questions of functional specialization.

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