What Does Broca's Area Activation to Sentences Reflect?

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There is no doubt that listening to or reading sentences activates the left frontal lobe structures in and around Broca's area. The question is, what process(es) does this activation reflect? In our recent critical review of this literature (Rogalsky & Hickok, 2011) we questioned whether any of this activation reflects processes that are specific to receptive sentence processing. Specifically, we pointed out that sentence activation in the pars opercularis overlaps with activations induced by speech articulation, whereas more anterior (pars triangularis/orbitalis) and dorsal (middle frontal gyrus) sentence-elicited activations overlap with activations induced by cognitive control tasks. Given that sentence processing may be assisted by nonspecific functions such as articulatory rehearsal and cognitive control, this raises serious questions regarding the sentence specificity of activations in Broca's area and vicinity during comprehension. We concluded that the pars opercularis supports sentence comprehension via articulatory rehearsal mechanisms (phonological STM), whereas more anterior and dorsal areas may support sentence processing via some, as yet undetermined, higher-order process such as cognitive control. Additional arguments for this position were also put forward.

Federenko and Kanwisher (F&K) question our claim that there is no region within the vicinity of Broca's area that supports a sentence-specific function for comprehension. They key in on one of our arguments, namely, that listening to sentences when compared with, for example, lists of words, does not typically result in Broca's area activity. F&K suggest that these studies are flawed because they failed to take into account individual variability that washes out group level statistics. In support of their argument, they present data from individual subjects showing activity in and around Broca's area in a majority of subjects.

We agree that group level analyses can obscure important facts, and we support F&K's efforts to promote individual subject analyses. However, with respect to the content of their claims, we remain unconvinced. Although F&K do present strong evidence that Broca's area activates more for sentences than word lists in individual subjects using their stimuli and task, their study differs from previous work in that it used written stimuli and a one-back memory probe task, both of which may have influenced their findings. Specifically, both of these study features may have invoked production-related processes: Reading has been shown to involve articulatory mechanisms (e.g., articulatory suppression reduces memory span and comprehension for written but not auditorily presented stimuli; Daneman & Newson, 1992; Slowiaczek & Clifton, 1980; Baddeley, Thomson, & Buchanan, 1975), and an explicit memory probe task may induce articulatory rehearsal. There is little doubt that Broca's area and vicinity play some role in speech production, including sentence-related processes (e.g., agrammatism is a common correlate of left frontal lesions). Therefore, the differences between sentences and word lists in F&K's data may be a result of covertly producing sentences rather than comprehending them. Our claims specifically target sentence comprehension.

A previous study of ours directly assessed the role of production-related processes in driving activations in Broca's area during the performance of a complex sentence comprehension task, semantic plausibility judgment (Rogalsky, Matchin, & Hickok, 2008). We reasoned that sentences that are particularly difficult to understand, such as object-relative clauses, may induce articulatory rehearsal to assist in task performance, compared with simpler sentences, which should rely to a lesser extent on such mechanisms. We found that Broca's area responded more to complex than simple sentences, but that an articulation task, assessed within-subjects, completely overlapped the activation in posterior sectors (pars opercularis) and that the "sentence complexity effect" in this region did not emerge when subjects comprehended sentences during concurrent articulation (articulatory suppression). In other words, articulatory processes explain the Broca's area activation to sentences, at least in the posterior sector. In the anterior sector (pars triangularis), a sentence complexity effect persisted even during concurrent articulation. However, this effect disappeared during a concurrent finger-tapping task, again suggesting that the sentence activations in Broca's area are not sentence specific.

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Table 1. Proportion of Subjects Who Have Voxels Passing Threshold in Each ROI for Only Sentences > Rest ($p < .005$), Only Articulation > Rest ($p > .001$), and for Both of These Contrasts ($n = 15$, Data from Rogalsky et al., 2008)

	Sentences Only	*Articulation Only*	*Sentences and Articulation*
Broca's area (PO + Ptr)	0.33	1.0	0.27
Pars opercularis	0.27	1.0	0.33
Pars triangularis	0.13	0.8	0.27
Pars orbitalis	0.27	0.27	0.27
MFG	0.60	0.33	0.13

But perhaps, as F&K suggest, this is an artifact of group analyses. Here we present individual subject analyses of our data. For maximal sensitivity to sentence activations, we compared the complex sentences with a resting baseline (scanner noise) using an uncorrected threshold of $p = .005$ and compared subvocal articulation (in the absence of sentence listening) with a resting baseline using an uncorrected threshold of $p = .001$. We examined activity in five ROIs: Broca's area (pars opercularis + pars triangularis) pars opercularis alone, pars triangularis alone, pars orbitalis, and the middle frontal gyrus in each subject. The results are presented in Table 1, which shows the proportion of subjects who had voxels anywhere within the ROI that were activated (i) only by sentences and not articulation, (ii) only by articulation and not sentences, and (iii) by both sentences and articulation, that is, the conjunction of sentences and articulation. Figure 1 shows representative activation maps. Overall, only 33% of subjects exhibited sentence-only activation anywhere within Broca's region, only 27% in the Pars Opercularis (PO) alone, and only 13% in the Pars Triangularis (PTr) alone. The vast majority of subjects, however, showed articulation-only activity in these ROIs (100%, 100%, and 80%); about one third of our subjects had voxels that were coactivated by both conditions. Consistent with our group analyses, articulation seems to be the dominant driver of activity in the PO as well as in the PTr even when we used a more stringent threshold for articulation than sentences and even when we compared sentence activity against background scanner noise. This is inconsistent with the view that Broca's area exhibits sentence-specific responses during comprehension in most subjects.

The middle frontal gyrus seems to show a more specific sentence activation with 60% of subjects showing sentence-only activation compared with 33% with articulation-only activation. This is different than what we found in the group analysis, which showed a sentence > articulation effect in the PTr rather than the Middle Frontal Gyrus (MFG), and attests to F&K's point regarding the value of individual analyses. However, to determine whether these activations are sentence specific, they need to be compared against a range of nonsentence tasks beyond articulation, for example, tasks involving cognitive control.

The individual subject analyses reported here support our claims based on group level analyses and question the degree to which F&K's findings with written stimuli and a memory probe task generalize to auditory sentence comprehension. We again conclude that there is no compelling evidence that Broca's area plays any linguistic-specific role in sentence comprehension.

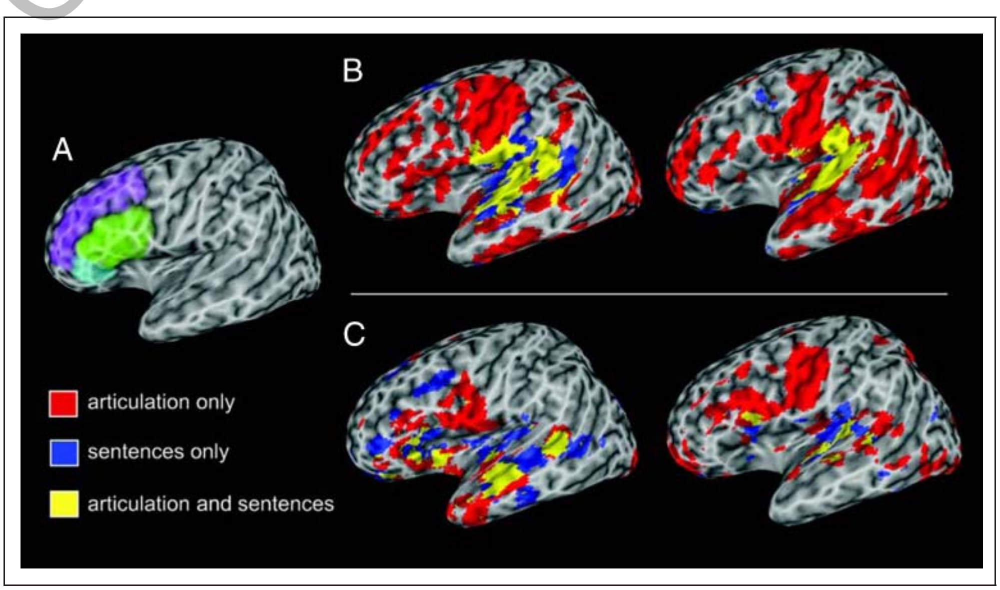

Figure 1. (A) Visualization of Broca's area (green), pars orbitalis (cyan) and middle frontal gyrus (purple). (B) Two representative subjects that have voxels in Broca's area activated during articulation (red) but not during sentence comprehension. (C) Two representative subjects that have voxels in Broca's area that were activated only during articulation (red), only during sentence comprehension (blue), or both during articulation and sentence comprehension (yellow).

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