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Citation

Sahin, N. T., S. Pinker, S. S. Cash, D. Schomer, and E. Halgren. 2009. Sequential Processing of Lexical, Grammatical, and Phonological Information Within Broca's Area. *Science* 326, no. 5951: 445–449. doi:10.1126/science.1174481.

Published version

<https://doi.org/10.1126/science.1174481>

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Sequential Processing of Lexical, Grammatical, and Articulatory Information within Broca's Area

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Words, grammar, and articulation are linguistically distinct, yet their neural substrates cannot be clearly distinguished in macroscopic brain regions. We investigated whether they can be separated in time and space at the circuit level by recording from populations of neurons using electrodes implanted in traditional language areas while people read words verbatim or produced them with context-appropriate grammatical inflection (present/past, singular/plural). Neighboring probes within Broca's area revealed neuronal activity separated in time for lexical (~200 ms), grammatical (~320 ms), and articulatory (~450 ms) processing, identically across nouns and verbs. This suggests that a linguistic processing sequence predicted on computational grounds may be implemented in the brain in fine-grained spatiotemporally patterned activity.

Within cognitive neuroscience, language is understood far less well than sensation, memory, or motor control, because language has no animal homologues, and noninvasive methods appropriate to human subjects (fMRI, lesions, and scalp-recorded potentials) are far coarser in space or time than the underlying causal events in neural circuitry. Moreover, language involves several kinds of abstract information (lexical, grammatical, phonological) that are difficult to manipulate independently. This has left a gap between the computational structure of language suggested by linguistics and the neural circuitry that implements language processing. We attempt to narrow this gap using a technique with high spatial, temporal, and physiological resolution, and a task that distinguishes three components of linguistic computation.

On computational grounds, the ability to identify words, to combine them grammatically, and articulate their sounds should be distinct (1). Though the clinical literature contains reports of double dissociations, where a patient is impaired on grammar but not articulation or vice-versa (2), in most studies both abilities are linked to similar regions in the left inferior prefrontal cortex, particularly Broca's area (3). Broca's area has been variously hypothesized to be the seat of articulation, grammar, and even particular grammatical operations (4,5,6,7). Yet both lesion and neuroimaging studies have tied it to a variety of linguistic and nonlinguistic processes (8), and its function remains unclear. Nor do standard methods reveal the degree to which components of language are processed sequentially or in parallel. It remains possible that linguistic components are processed distinctly, even sequentially, in the microcircuitry of the brain, but standard methods which sum over seconds and centimeters necessarily blur them.

In a rare procedure, multi-contact depth electrodes are implanted in the brains of patients with epilepsy for clinical evaluation. Recordings of local field potentials (LFP) during periods of normal brain activity afford simultaneous millisecond resolution in time and millimeter resolution in space, a finer-grained combination than other techniques. We recorded from three patients whose electrodes were located in traditional language areas (9) while they read words verbatim or converted them to an inflected form (past/present tense, singular/plural number). The task engages inflectional morphology, which is like syntax in combining meaningful elements according to grammatical rules, but the units are shorter and semantically simpler, making fewer demands on working memory and conceptual integration and allowing greater experimental control.

In each trial, participants saw either the instruction "Repeat word," or a sentence frame that dictated a particular inflected form (*Every day they ____; Yesterday they ____; That is a ____; Those are the ____*). Next they saw a target verb or noun and produced the appropriate form silently (Fig. 1A) (10). The target word was presented in uninflected form in a phrase: "*a [noun]*" or "*to [verb]*" (11) (Fig. 1B). Half the target words were regular (e.g. *link/linked*) and half irregular (e.g. *think/thought*), to ensure that participants had to access the word and determine its inflectional form rather than automatically appending the regular suffix (12). Note that a present-tense verb and a singular noun are not overtly marked ("Null Inflect" condition), and thus require the same output form to be articulated as in the Read condition, though differing from it in requiring that the suitable inflectional form be selected. The difference between these two conditions thus implicates the process of inflection. In contrast, a past-tense verb or plural noun require that a suffix be added (regular) or the form changed (irregular). It thus differs from the Null-Inflect condition in requiring computation of a different articulatory output (Fig. 1B). The design was fully crossed, with trials of all conditions presented in a pseudorandom order.

To ensure that these patients did not have radically reorganized language systems, , and to correlate LFP with regions activated in fMRI during this task, we scanned two of the patients preoperatively and confirmed that their activation

patterns were similar to 18 healthy controls (**Fig. 2A-C**) (for other fMRI results see [13](#)). Most of the 168 channels from which we recorded LFP ([14](#)) were in fMRI-activated regions (**Fig 2A-G**). About half the channels (86/168) recorded LFP that was significantly correlated with the task ([15](#)). Of these channels, 49 (56%) were within Broca’s area or the anterior temporal lobes, and most (20/26) of those in Broca’s area yielded a strong triphasic (3-component) LFP waveform (**Fig. 1D, Fig. 3D, Fig. S5**). The mean peaks of the population activity fell ~200, ~320, and ~450 ms after the target word appeared (**Fig. 1D**). Using anatomical MRI, the neuronal generators of word production assessed from the LFP were mapped onto specific gyral anatomy (**Fig. 2I-J, Fig. S2**).

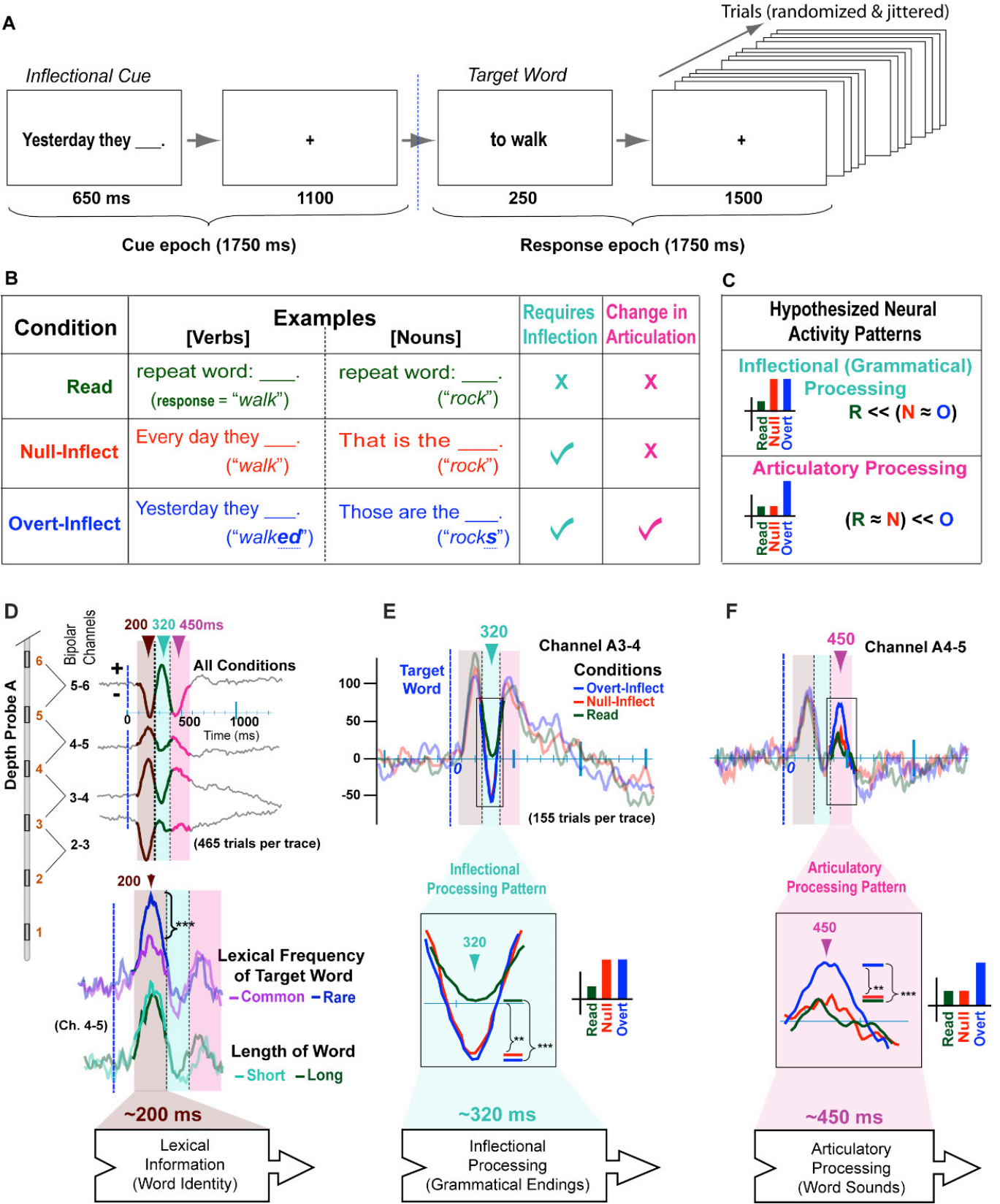


Fig. 1. Experimental task and neural responses. **(A)** Structure of trials. **(B)** Experimental design (columns 1-3) and psycholinguistic processes required (columns 4-5). **(C)** Hypothesized neural activity differences for inflectional and articulatory processing. **(D) Top:** Neural activity recorded from several channels in Broca's area (Patient A) shows three LFP components that were consistently evoked by the task (~200, ~320, ~450 ms). **Bottom:** The ~200 ms component is sensitive to word frequency but not word length, suggesting it indexes lexical access, not simply perception. **(E)** At ~320 ms the LFP pattern suggests inflectional processing. **(F)** At ~450 ms, in a channel 5 mm distant, the complementary pattern suggests articulatory processing.

A clear pattern of separation among processing stages was displayed by Patient A's LFP components (16). The component peaking at ~200 ms did not vary by task condition, presumably because it indexes a processing stage common to all conditions, *i.e.*, lexical access. Its latency is similar to word-specific activity elicited in the visual word form area (17,18, but see 19), which becomes phase-locked with Broca's area at this time(20). To confirm that this component represents conveyance of information about word identity from the visual stream, we examined effects of word frequency, which indexes lexical access (21) (scalp-ERP studies have shown lexical frequency effects in this temporal range (22)). As predicted, rare words (log frequency 1-4) yielded a significantly higher amplitude in the ~200 ms component ($t(204)=3.32$, $p < .001$) than common words (log frequency 9-12). Later components were unaffected by frequency (Fig. 1D). Rarer words tend to be longer, but we found no significant difference at ~200 ms between short (2-4 character) and long (6-11 character) words (Fig. 1D). We also found no significant differences between one-morpheme and two-morpheme responses.(23)

The subsequent two temporal components did vary by task condition (Fig. 1E-F). In one channel (probe A, contact pair 3-4, in probable Brodmann 45), the conditions significantly differed only for the ~320 ms component: Overt-Inflect and Null-inflect significantly differed from the baseline and the Read condition, but not from each other, even though only Overt-Inflect required a change in the word's articulation (Fig. 1E). This pattern suggests grammatical computation, independent of articulation (Fig. 1C). In a second channel (A4-5, 5 mm further lateral) the conditions significantly differed only for the ~450 ms component, and in the complementary pattern: greater amplitude during the Overt-Inflect than the Null-Inflect and Read conditions, which did not differ from each other (Fig. 1F). This pattern suggests articulatory computation. We confirmed this by comparing trials requiring the patients to articulate different numbers of syllables: only in the ~450 ms component did longer words yield a significantly higher LFP amplitude (Fig. 3C).

The fact that each difference among conditions was found only in a specific time window and channel (with the waveforms superimposing elsewhere; Fig. 1D-F, Fig 3C) shows that the activity patterns do not simply index global difficulty. Moreover, the pattern of sign inversions across neighboring bipolar channels (Fig. 1D) suggest that the computations occurred within millimeters of those channels (see SOM), and the slight difference in inversions across components indicate their generators were slightly separated in space (Fig. 2I-J). Thus the overall LFP pattern suggests a fine-grain spatiotemporal progression of lexical, grammatical, and articulatory processing within Broca's area during word production.

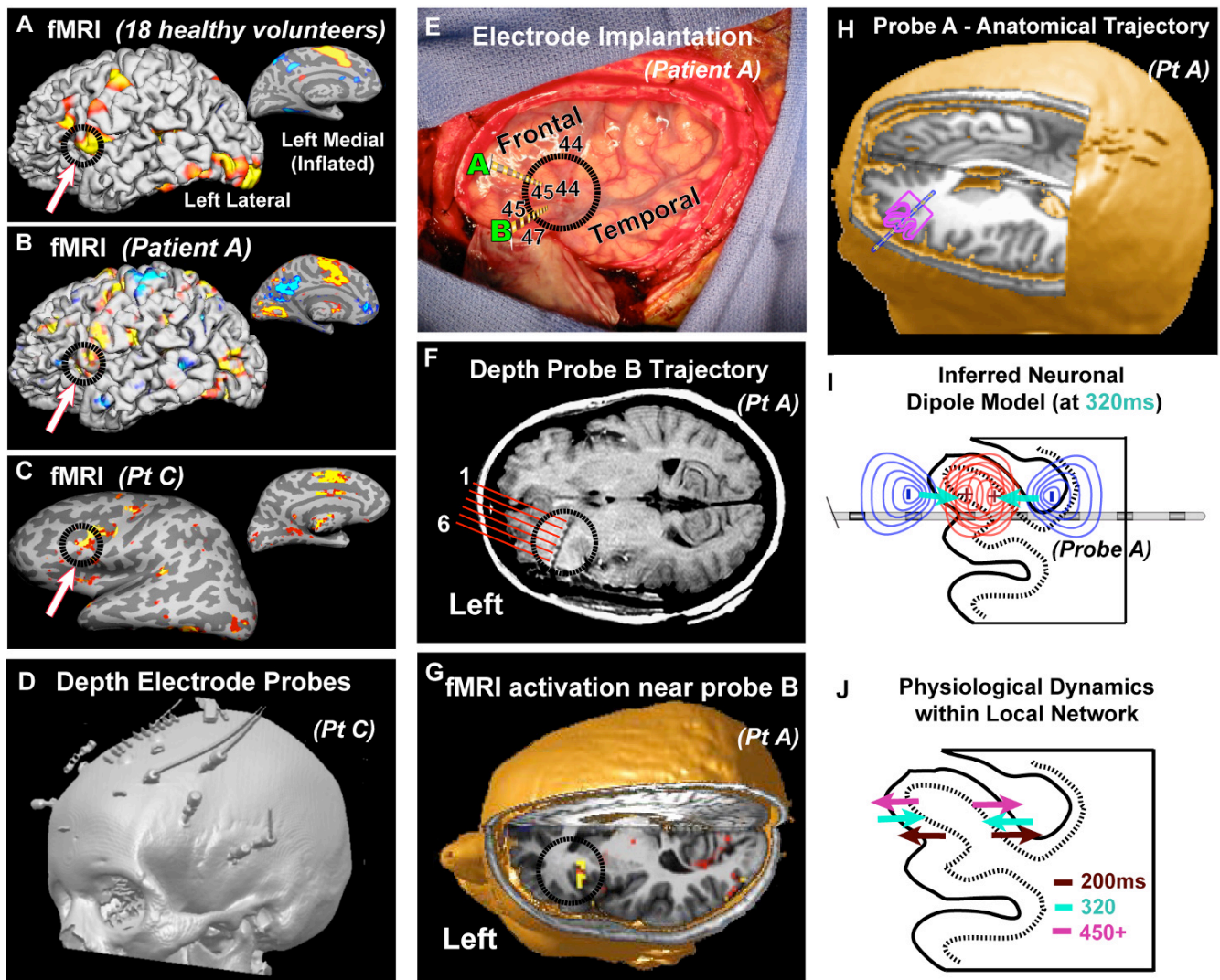


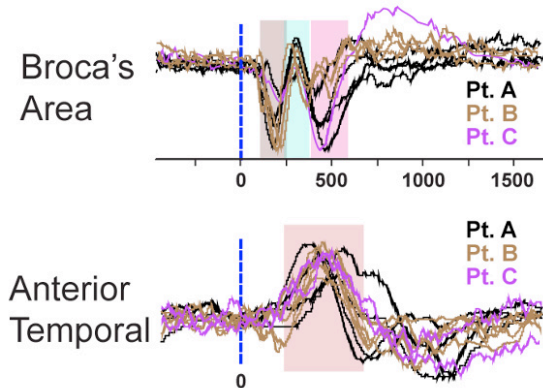
Fig. 2. Neural activity in patients and healthy controls. **(A)** fMRI in 18 controls showing the task engages classical language areas (Broca's, speech-related motor cortex, medial supplementary motor area, anterior cingulate) and visual-reading circuits (visual wordform area, primary and ventral visual cortex). Contrast (task conditions vs. visual-fixation baseline) rendered on Patient A's brain. Broca's area is circled. **(B-C)** Single-patient fMRI for the identical contrast. **(D)** CT of Patient C showing depth probes inserted through the skull. Some surfaces are inflated to reveal activations within sulci. **(E)** Left perisylvian language areas shown intra-operatively. Letters: insertion points of the probes; dashed lines: surface projections of their intra-cortical trajectories. Brodmann areas are labeled. **(F)** Location of Probe B in dorsal Broca's area, with pre-operative fMRI **(G)** demonstrating the region is activated in this patient. **(H)** Location of Probe A. **(I-J)** Neural dipoles around Probe A that generated the LFP components, inferred from their polarities, amplitudes and locations (see Fig. S2).

The triphasic temporal pattern aligned tightly across all three patients (**Fig. 3A**), though in patients B and C, the key contrasts in amplitude were less well defined. The word-frequency effect on the ~200 ms component was significant in Patient B but not recorded on any channel in Patient C; the Read-Overt difference was significant but earlier (~270 ms) in Patient B, and visible but not significant in Patient C; the Overt-Null difference (~450 ms) was visible in both patients but not significant in Patient B. The triphasic pattern shared by all patients was found only in Broca's area; in contrast, anterior temporal lobe sites consistently showed a slow and late monophasic pattern (peak ~500-600 ms) (**Fig. 3A**, **Fig. S4h-i**) (24).

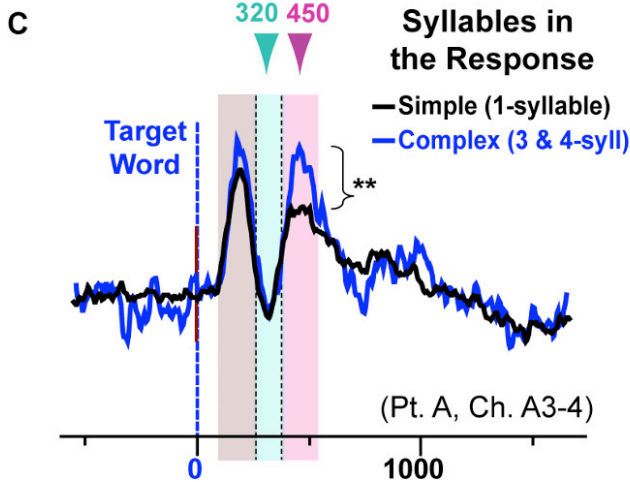
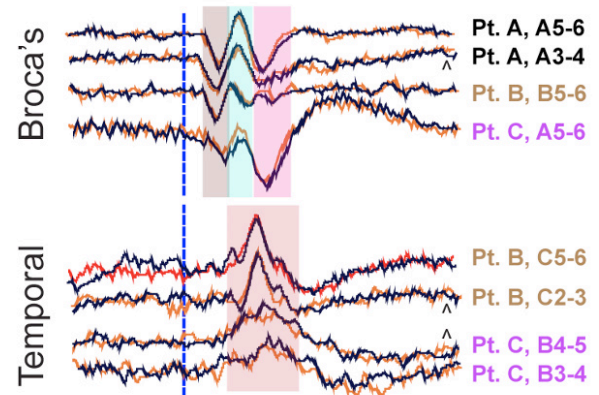
Though nouns and verbs differ semantically, grammatically, and neurophysiologically (25-26), the LFP waveforms for nouns and verbs (averaged across conditions) superimposed tightly (**Fig. 3B**). Furthermore, the contrasts in amplitude across conditions (**Fig. 1**) were highly similar (**Fig. S6**). These parallels suggest that words from different lexical classes feed a common process of grammatical inflection.

Further evidence that the LFP patterns reflect linguistic computation is that they are triggered by presentation of the word to be inflected or repeated, not by the cue (even though the cue involved more complex material) (Fig. 3D, Fig. S3) (27). Furthermore, activity to the cue showed little modulation by condition.

A Regional Specificity of Triphasic LFP



B Noun vs Verb Inflection



D Cue Epoch vs. Response Epoch

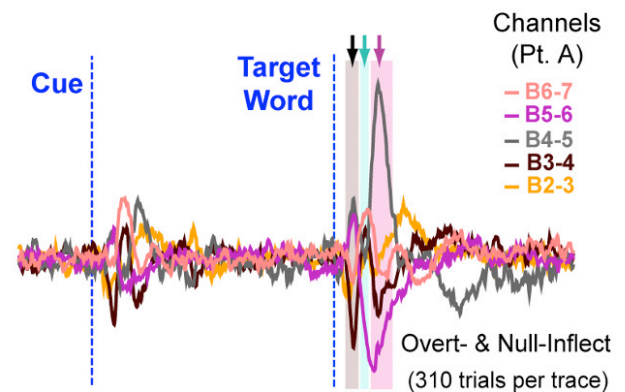


Fig. 3. Specificity of the lexical-inflectional-articulatory waveform. (A) Triphasic activity is specific to Broca's area, and consistent across patients (the three patients' waveforms are superimposed after amplitude and polarity normalization to channel A3-4 in Patient A). (B) Noun (black) and verb (red) inflection involved nearly identical neuronal activity, across sites and patients. (C) The ~450 ms component, which is sensitive to articulatory differences among task conditions, is also sensitive to articulatory complexity (syllable count) of the target word across conditions ($p < 0.01$, corrected). (D) Neural activity in Broca's area is evoked primarily by processing the target word, not the cue.

The LFP patterns are consistent with the computational nature of the task and with independent estimates of the timing of its subprocesses. Inflectional processing cannot occur before the word is identified (especially whether it is regularly or irregularly inflected), and articulation cannot be programmed before the sound form is identified. Word identification has been shown at ~170-250 ms (28-29), consistent with our ~200 ms component. At the other end, we measured the behavioral response at around ~600 ms. Since motor neuron commands producing speech occur about 50 ms prior, articulatory specification must have been complete by ~550 ms, consistent with the hypothesized articulation component at ~400-500 ms. Notably, the present components vary only by amplitude across conditions, even though the response can vary in time. Evidently the stages identified here are consistently timed, and other processes (simultaneous or subsequent) produce the differences in latency.

Though articulation depends upon information computed by inflection, the two processes could have been a single interacting stage, with progressive definition of the articulatory output while the inflectional choice is gradually defined. This would be consistent with the suggestion that Broca's area relates to language functions in a holistic, distributed, or mass-action way. However, it is unlikely that macroscopic areas such as Broca's, comprising hundreds of millions of neurons, would have a unitary function. Instead, the higher-resolution data presented here suggest a degree of temporal and spatial

modularity, where adjacent but distinct neuronal populations within Broca's area sequentially compute inflection and articulation.

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