Single-cell Encoding of Linguistic Features in the Human Brain

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According to psycholinguistic theories, during the processing of spoken and written sentences processing, spoken and written words are first encoded along independent phonological and orthographic dimensions, then enter into modality-independent syntactic and semantic codes. Non-invasive brain imaging has isolated several cortical regions putatively associated with those processing stages, but lacks the resolution to identify the corresponding neural codes. Here, we describe the firing responses of over x hundred neurons in 20 people with implanted electrodes prior to surgery, awake humans during written and spoken sentence comprehension. Using forward modeling of temporal receptive fields, we determine which sensory or abstract dimensions are encoded. We observe a basic dissociation between (1) superior temporal neurons sensitive to phonemes and phonological features (2) ventral occipito-temporal neurons sensitive to letters and orthographic features; and (3) previously unreported neurons, primarily located in middle temporal and inferior frontal

areas, which are modality-independent and sensitive to linguistic theoretical constructs such as part of speech, end-of-sentence wrap-up effects, or syntactic dimensions such as affirmatives declarative sentences versus questions.

Introduction

Results

Methods and Materials

Participants

We recorded single-unit activity from 20 patients at the UCLA neurosurgical centre with intractable epilepsy, who were implanted with Behnke-Fried electrodes (fried$_{c}erebral_{1}999$-1) as part of their clinical evaluation.

Stimuli

The stimuli in the experiment were English sentences with length between two to five words. The sentences were created such that they contrast various linguistic features by creating minimal comparisons. For example, to contrast the two values of grammatical number (singular vs. plural), the design contains minimal-pair contrasts, such as: "He smiles" vs. "They smile"; for gender "He smiles" vs. "She smiles"; for tense "He smiles" vs. "He smiled", etc. (Figure **??**). These contrasts along various grammatical dimensions allow to study, with a relatively small set of stimuli, neural activity in response to various linguistic features. Table **??** shows the full list of stimuli.

The stimuli were presented to the participants both (1) Visually, using Rapid Serial Visual Presentation (RSVP) on a computer screen, with a stimulus onset asynchrony (SOA) of 500ms;

and (2) auditorily, via standard computer speakers (Figure **??**). The experiment had six blocks in total, three visual and three auditory, which were presented intermittently, starting with a visual block. Each block contained the full set of stimuli, 152 sentences in total, repeated across blocks, each time in a random order. The participants were asked to perform a semantic task, and to press a button each time a word related to food was presented (which was the case in 5% of the stimuli; all removed from further analyses).

Data acquisition

Electrophysiological signals were recorded with Neuralynx or BlackRock devices, at high sampling rate for microwires (30,000-40,000Hz), required for extracting spiking data, and 2,000Hz for macro contacts.

Data analysis

Preprocessing

Spike sorting

High-gamma activity

Decoding models

Encoding models

Discussion

References

fried$_{c}erebral_{1}999I. \quad Fried, et\ al., Journalofneurosurgery\mathbf{91}, 697(1999).Publisher \quad : JournalofNeurosurgeryPublishingGroup.$

Acknowledgments

TBC

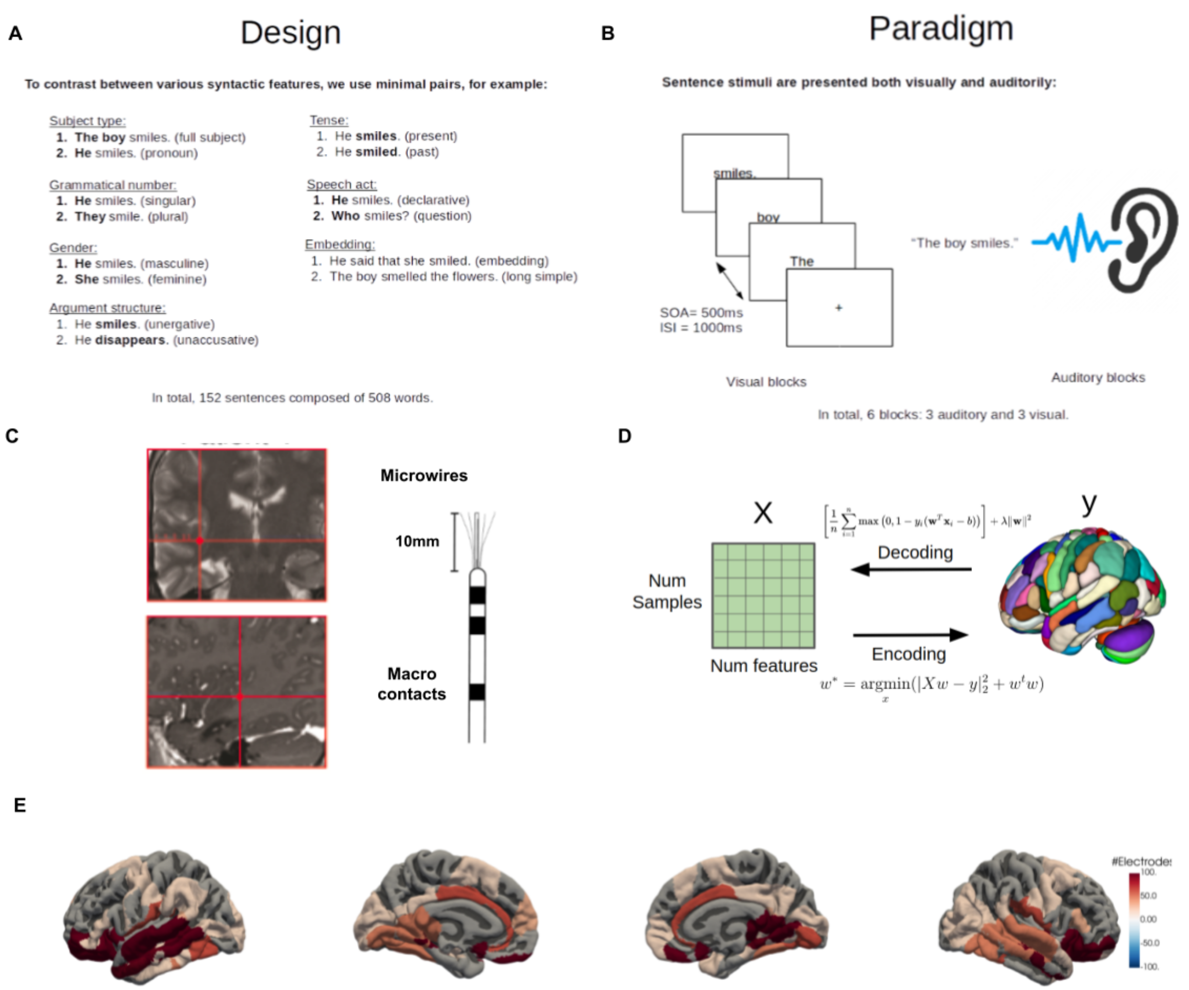

Figure 1: **Neural responses during language processing - from single cells to large neuronal populations:** (A) Examples for minimal pairs that define contrasts across various linguistic dimensions. (B) Stimuli were presented to participants both visually, in rapid serial visual presentation (RSVP), and auditorily, via computer speakers. The experiment was composed of six blocks, three from each modality. (C) An example of a Behnke-Fried electrode (fried$_{c}erebral_{1}$999-1). (D) Encoding and decoding models. (E) Electrode coverage. Color scale represents the number of microwires within each region of interest.

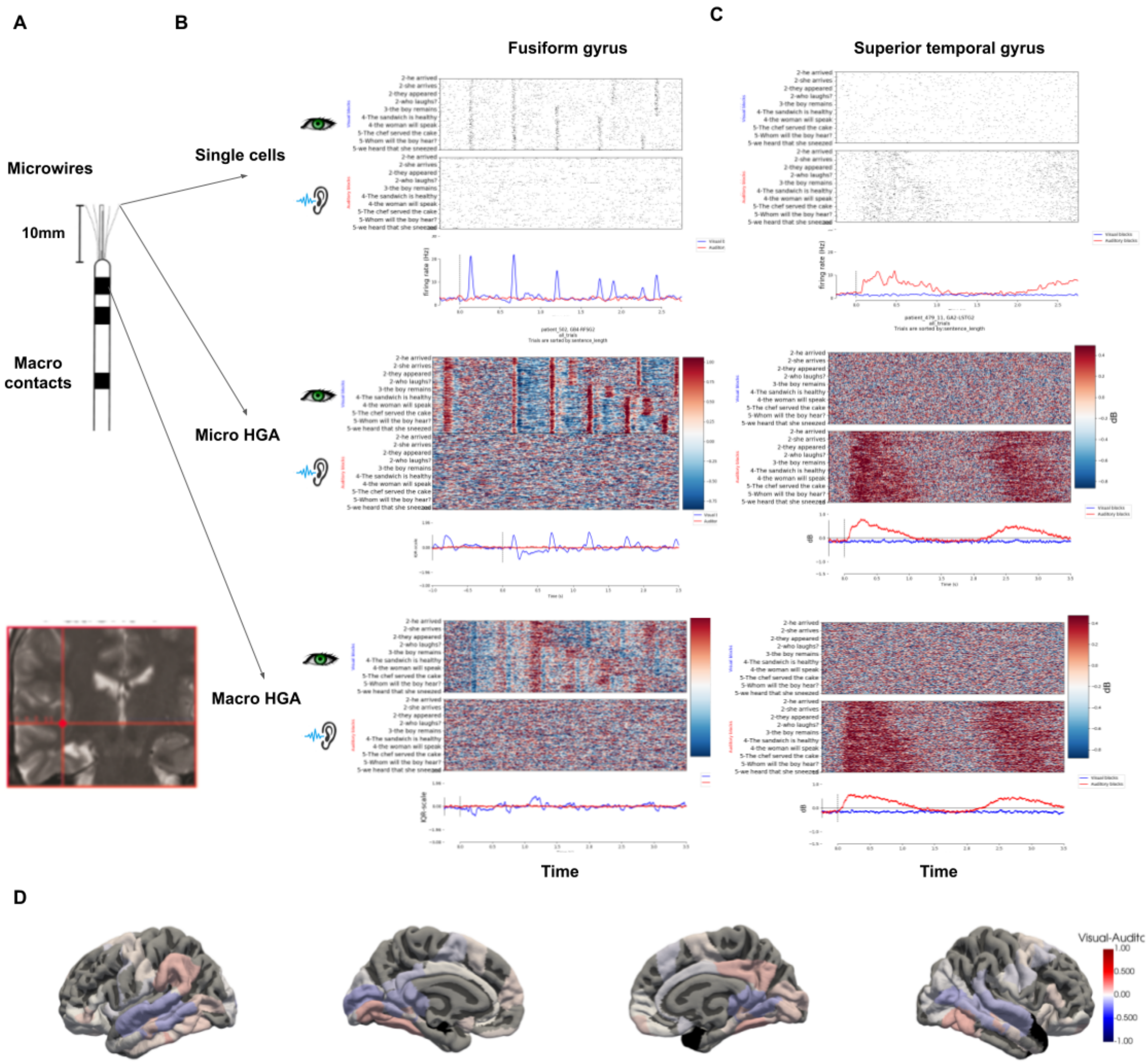

Figure 2: **Neural responses during language processing - from single cells to large neuronal populations:** (A) single-cell (top) high-gamma activity in an example microwire (middle) and macro contact (bottom) from the fusiform gyrus, during the processing of all stimuli in the experiment . In each plot, the top (bottom) panel shows activity during the visual (auditory) blocks - see cartoons on the left. The firing rate (mean HGA) is presented below. (B) Same for an example single cell, microwire and macro contact from the superior temporal gyrus. (C) Modality specificity.

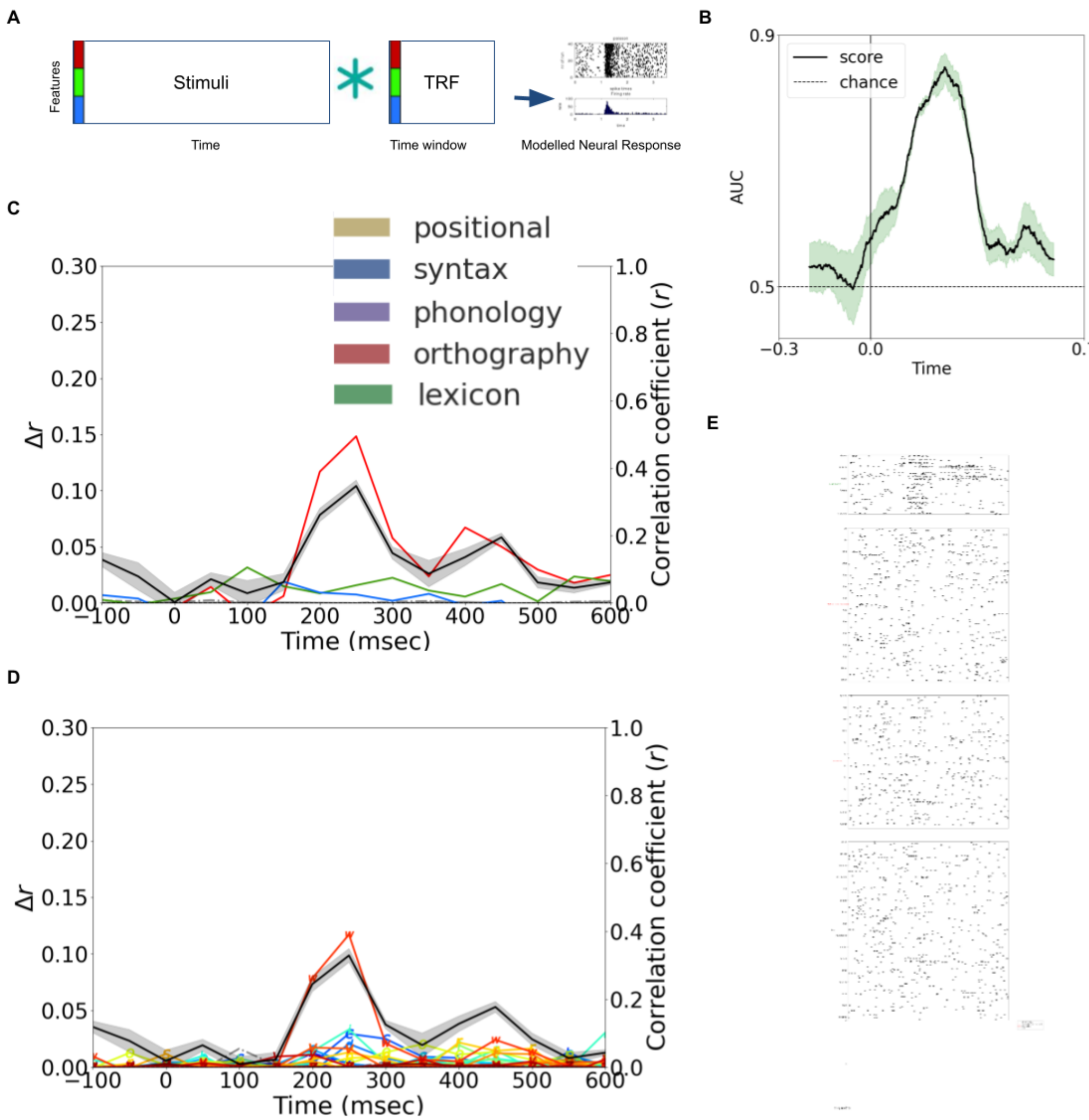

Figure 3: **Selective encoding of orthographic features in the fusiform cortex:** (A)

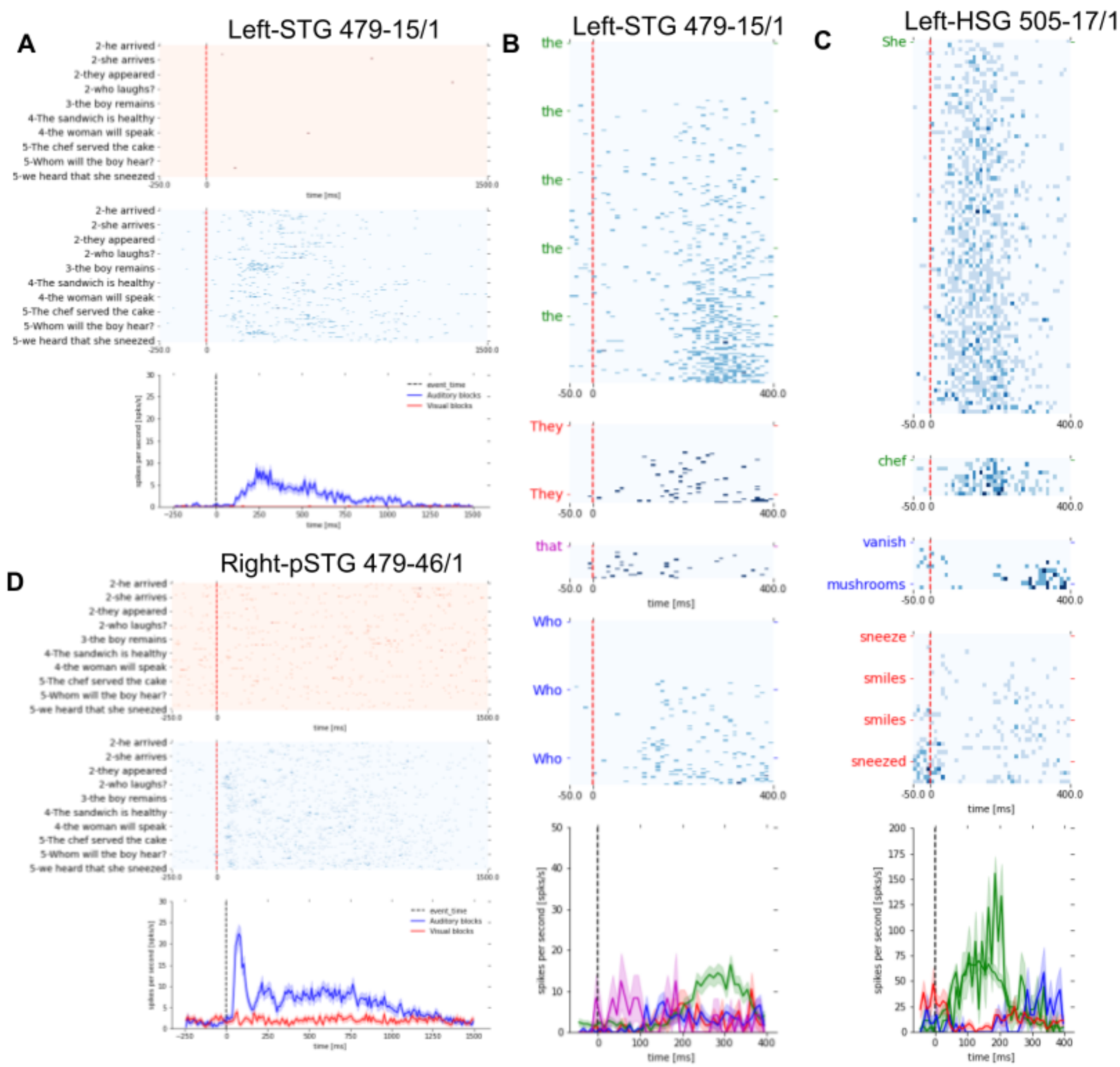

Figure 4: **Selective encoding of during auditory processing:** (A)

Supplementary materials

Materials and Methods

Supplementary Text

Figs. S1 to S3

Tables S1 to S4

References *(4-10)*

Fig. 1. Please do not use figure environments to set up your figures in the final (post-peer-review) draft, do not include graphics in your source code, and do not cite figures in the text using LaTeX `\ref` commands. Instead, simply refer to the figure numbers in the text per *Science* style, and include the list of captions at the end of the document, coded as ordinary paragraphs as shown in the `scifile.tex` template file. Your actual figure files should be submitted separately.