

Invariant neural representation of parts of speech in the human brain

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Abstract

Elucidating the internal representation of language in the brain has major implications for cognitive science, brain disorders, and artificial intelligence. A pillar of linguistic studies is the notion that words have defined functions, often referred to as parts of speech. Here we recorded invasive neurophysiological responses from 1,801 electrodes in 20 patients with epilepsy while they were presented with two-word phrases consisting of an adjective and a noun. We observed neural signals that distinguished between these two parts of speech. The selective signals were circumscribed within a small region in the left lateral orbitofrontal cortex. The representation of parts of speech showed invariance across visual and auditory presentation modalities, robustness to word properties like length, order, frequency, and semantics, and even generalized across different languages. This selective, invariant, and localized representation of parts of speech for nouns versus adjectives provides elements for the compositional processes of language.

Introduction

Language plays a central role in almost all of our daily activities and is at the heart of how we interact with others^{1,2}. Early neurological studies and subsequent work using electrical stimulation identified specific brain regions that play essential roles in language understanding and production³⁻⁸. Despite the critical importance of language, progress towards elucidating the neural circuits underlying its representation has remained elusive, in part due to the difficulties in investigating animal models, and in part due to the challenges associated with examining the neurophysiological responses in the human brain.

Several neurophysiological experiments have begun to investigate neural signals associated with presentation of individual words or short phrases⁹⁻¹⁶. There has been work examining the orthographic features of real versus pseudoword words¹⁷⁻¹⁹, phonetic features of word comprehension^{10,17,20,21} and production²²⁻²⁵, and retrieval of semantic information for audio-visual naming to definition task¹⁰. These studies have shed light on the early processes associated with detecting, comprehending and producing words. Beyond individual words, at the heart of linguistic structures is the notion that words serve specific functions within a sentence, including articles, nouns, adjectives, and verbs. These parts of speech are widely shared across languages, are combined according to defined grammatical rules, and play critical roles in natural language processing algorithms^{1,11,26-32}. Many studies in patients with brain lesions have focused on deficits in the retrieval of individual nouns versus verbs^{18,33-38}. However, previous studies could not identify explicit and invariant neural processes in part of speech processing due to insufficient spatial or temporal resolution³⁸. Furthermore, recent work has suggested that parts-of-speech may be implicitly learned and represented in modern large language models^{39,40}; making part of speech an important target for evaluating models of language in the brain.

What would a representation for parts of speech like nouns and adjectives in the brain look like? Consider the adjective “green” and the noun “apple”, combined to create the simple phrase “green apple.” Fundamental constraints for such a representation should include the basic invariances underlying the cognitive understanding of this phrase. The basic desiderata for the representation of parts of speech in language includes invariance to: (i) presentation modality (e.g., auditory versus visual), (ii) specific noun or adjective (e.g., green or red), (iii) position within a phrase (e.g., “green apple” versus “apple green”), (iv) specific language in bilingual speakers

(e.g., “green apple” in English versus “manzana verde” in Spanish), (v) other word properties like their written length, number of syllables, and phoneme composition.

Here we set out to investigate the representation of parts of speech in the human brain by recording intracranial field potential responses with high spatiotemporal resolution and high signal-to-noise ratio from 1,801 electrodes implanted in 20 participants with pharmacologically resistant epilepsy. We describe neural signals, especially in the left lateral orbitofrontal cortex, that selectively distinguish between nouns and adjectives. These part-of-speech selective signals are robust when words are matched for orthography (e.g., word length), phonetic features (e.g., number of syllables), word sequence (e.g., noun or adjective at first or second position within a phrase), and frequency of occurrence. Interestingly, the representation of nouns versus adjectives generalizes across audio and visual modalities, across different semantic categories within each part of speech, and across different languages.

Results

We recorded intracranial field potentials from 1,801 electrodes (840 in gray matter, 961 in white matter) implanted in 20 participants. Participants heard (auditory modality) or read (visual modality) two words that were sequentially presented and were asked to indicate whether the words were the same or not (**Figure 1a, Methods**). Participants performed the task correctly on 93.6±7.7% of the trials (here and throughout, mean±std, unless stated otherwise). All electrode locations are shown in **Figure 1b-g** (see also **Tables S1-S2** and **Methods**). We use a bipolar reference and we focus on the intracranial field potential signals filtered in the high gamma frequency band, referred to as neural responses throughout and reported in the plots as gamma power (65-150 Hz, **Methods**).

Neural signals reflect visual, auditory and multimodal inputs

We observed 565 electrodes (31.4% of the total) that responded to auditory stimuli (**Figure S1a-c, g-i**) and 532 electrodes (29.5% of the total) that responded to visual stimuli (**Figure S1d-f, g-i**). The overall proportions and dynamics of visual and auditory responsive signals are consistent with previous work^{23,41}. Of these electrodes, there were 293 electrodes that responded to *both* auditory and visual stimuli (**Figure S1g-i**). These 293 electrodes represent 16.3% of the total, 51.9% of the auditory responsive electrodes, and 55.0% of the visually responsive

electrodes. This number of audiovisual electrodes is highly unlikely to arise by chance from the number of auditory and visual electrodes ($p < 10^{-4}$, permutation test, $n = 10^6$ iterations). Of these 293 electrodes, 147 (50.2%) were in the left hemisphere and 146 (49.8%) were in the right. Of the 41 the regions in the Desikan-Killiani Atlas where we had sampling (34 defined regions and 7 extra regions representing deep gray matter structures, **Methods**, **Figure 1**, **Tables S1-S2**), 13 regions had a significantly higher number of multimodal electrodes than from the number of audio or visual electrodes ($p < 0.01$, permutation test, $n = 10^6$ iterations). These regions are indicated in bold in **Table S2**. **Figure 1h-j** shows the responses of an example audiovisual responsive electrode located in the left rostral middle-frontal gyrus (**Figure 1k**). This electrode showed strong evoked responses evident in the trial-average responses (**Figure 1h**), and even in individual trials for both auditory stimuli (**Figure 1i**) and visual stimuli (**Figure 1j**).

To compare the response dynamics of auditory and visual responses, we calculated the time at which the neural signals reached half of the max amplitude (half-maximum time, arrows in **Figure 1h**, **Methods**) and the average area under the curve (AUC) for neural responses such as those in **Figure 1h**. **Figure S2a** shows the half-maximum time for auditory-only electrodes (left), visual-only electrodes (middle), and audiovisual electrodes on audio trials (right light-gray half) or visual trials (right black half). There was no significant difference between the half-maximum time for auditory-only electrodes (329 ± 187 ms) and visual only electrodes (336 ± 174 ms) ($p > 0.05$, ranksum test). Similarly, there was no significant difference between the half-maximum time for the audio and visual responses of audiovisual electrodes (379 ± 193 ms versus 341 ± 174 ms, $p > 0.05$, ranksum test). However, there was a small but significant difference between the half-maximum time for audio only electrodes and auditory responses of audiovisual electrodes ($p < 0.01$, ranksum test).

As expected, for the audio-only electrodes, the average response AUC to auditory stimuli (108 ± 100 $\mu V^2/Hz\cdot ms$) was larger than to visual stimuli (44 ± 16 $\mu V^2/Hz\cdot ms$) ($p < 10^{-4}$, ranksum test, **Figure S2b**). Similarly, for the visual-only electrodes, the average response AUC to auditory stimuli (40 ± 23 $\mu V^2/Hz\cdot ms$) was smaller than to visual stimuli (53 ± 43 $\mu V^2/Hz\cdot ms$) ($p < 10^{-4}$, ranksum test, **Figure S2c**). For the audiovisual electrodes, the average response AUC to auditory stimuli (71 ± 72 $\mu V^2/Hz\cdot ms$) was slightly larger than the AUC of their responses to visual stimuli (54 ± 39 $\mu V^2/Hz\cdot ms$) ($p < 0.01$, ranksum test, **Figure S2d**).

Multimodal neural signals distinguish different parts of speech

We evaluated whether the neural signals differentiated between nouns and adjectives. Nouns and adjectives were matched for their number of syllables, word length, and usage frequency to control for potential confounds not specific to parts of speech (**Table S3, Methods**). **Figure 2** shows the responses of an example electrode located in the orbital H-shaped sulcus within the left lateral orbitofrontal cortex (**Figure 2i** depicts the electrode location). The orbital H-shaped sulcus lies above the bone of the eye socket where butterfly-like gyri can be seen, formed along H-shaped recessions of the sulcus. The neural responses are aligned to the word onset (vertical dashed line) for auditory presentation (**Figure 2a, b**) or visual presentation (**Figure 2c, d**), for the first (**Figure 2a, c**), or second (**Figure 2b, d**) word in each trial. This electrode showed multimodal responses triggered by both auditory and visual stimuli. The responses to nouns (blue) were stronger than to adjectives (red) across all four conditions, including both word 1 and word 2, and both for visual and auditory stimuli. The differences between nouns and adjectives can be readily appreciated even in individual trials (**Figures 2e-h**). These differences became significant at approximately 430 ms after word onset for visual presentation and about 610 ms for auditory presentation.

In all, there were 89 electrodes, 97 electrodes, and 48 electrodes that showed a difference between nouns and adjectives for auditory stimuli only, visual stimuli only, or both modalities, respectively. The 48 electrodes cannot be ascribed to randomly sampling from the total of audio and visual electrodes ($p < 10^{-4}$, permutation test, $n = 10^6$ iterations).

Neural selectivity for nouns versus adjectives was robust to word properties, phrase grammar, usage frequency, and word subcategory

Even though nouns and adjectives were matched in their average number of syllables and word length, we asked whether these variables could still contribute to the neural responses differentiating nouns and adjectives. Additionally, each trial could be grammatically correct (e.g., “green apple”), or incorrect (e.g., “apple green”) (**Methods**); therefore, we asked whether grammar could contribute to the neural differences between nouns and adjectives. To address these questions, we built a generalized linear model (GLM) for each electrode to predict its response AUC between 200 ms and 800 ms after word onset using four predictors: nouns versus adjectives, grammatically correct or not, and word length (vision) or number of syllables (audition) (**Methods**). The predictor coefficients in the GLM model for the example electrode in **Figure 2a-**

d show that only the nouns versus adjectives label significantly explained the neural responses for both auditory and visual presentation (**Figure 2j**). A total of 14 electrodes showed nouns versus adjectives as the *only* statistically significant predictor in the GLM analysis; 13/14 (93%) of these electrodes distinguished nouns versus adjectives for both auditory and visual inputs, such as the example electrode in **Figure 2a-j**.

The locations of these electrodes that robustly distinguished nouns and adjectives (orange in **Figure 2k**) and reveal a cluster enriched in the left lateral orbitofrontal cortex (LOF). Within the left LOF, 8 out of the 8 (100%) electrodes were in the posterior part of the orbital H-shaped sulcus. We recorded from a total of 113 electrodes in the lateral orbitofrontal region, 38 electrodes in the left hemisphere and 75 electrodes in the right hemisphere (**Figure 1b-g, Table S1**). Of the 38 left hemisphere electrodes, 21% distinguished nouns from adjectives during both audio and visual presentation. In stark contrast, only 1.3% of the 75 electrodes in the right hemisphere distinguished nouns from adjectives in both audio and vision (these hemispheric differences were statistically significant: $p < 10^{-4}$, permutation test, $n = 10^6$ iterations). **Table S4** shows the distribution of electrodes distinguishing part of speech between the left and right hemispheres for all brain regions and **Table S5** shows the distribution of electrodes separating nouns versus adjectives in different participants.

We had initially assumed that distinguishing parts of speech constitutes a core component of language and would therefore be reflected exclusively in *both* visual and auditory modalities. Indeed, 13/14 (93%) of electrodes differentiating nouns from adjectives in the GLM did so in both modalities. In addition to these 13 electrodes there was a small number of electrodes (2 auditory only and 1 visual only) that showed differences between nouns and adjectives in one modality but not the other. Unlike the electrodes in **Figure 2k**, for the 2 auditory-only electrodes, the number of syllables also significantly contributed towards explaining the neural responses. **Figure S3** shows the responses of an example electrode located in the right insula that showed a difference between nouns and adjectives during auditory presentation but *not* during visual presentation. Conversely, **Figure S4** shows the responses of an example electrode located in the left lateral orbitofrontal cortex that showed a clear difference between nouns and adjectives during visual presentation but *not* during auditory presentation. **Figure S4 k,l** shows the locations of auditory only (white circles) and visual only electrodes (black circle) in the left and the right hemispheres, respectively.

Nouns and adjectives differ in their usage frequency. We asked whether the differences in the neural responses to nouns versus adjectives depended on usage frequency. To address this question, we randomly subsampled the trials to match the distribution of Google Ngram frequency (**Methods**). The Google Ngram database reports the frequency of words (and word sequences) in the corpora of printed sources published between 1500 and 2019. **Figure S5a** shows matched noun and adjective distributions for the example electrode shown in **Figure 2a-k**. This electrode showed differential responses between parts of speech for auditory (**Figure S5 b,c**) and visual (**Figure S5 d,e**) stimuli during word1 (**Figure S5 b,d**) and word2 (**Figure S5 c,e**), even after nouns and adjectives were matched for their frequency of occurrence. Of the 13 audiovisual electrodes where nouns versus adjectives was the only significant predictor in the GLM analysis, 6 electrodes (43%, 4 in the left-LOF, and 2 in left superior temporal gyrus) robustly distinguished nouns and adjectives matched for their frequency of occurrence, like the example electrode in **Figures 2** and **S5** whereas the other electrodes maintained their selectivity in most but not all conditions.

Within our stimulus set, there were two subcategories of nouns, animals and food, and there were two subcategories of adjectives, concrete and abstract (**Table S3**). We asked whether the electrodes that showed differential responses generalized across different word subcategories. The example electrode in **Figure 2a-j** did not show differences between the two noun or adjective subcategories for either auditory stimuli (**Figure S6 a, b, f, g**), visual stimuli (**Figure S6 c, d, h, i**), word 1 (**Figure S6 a, c, f, h**), or word 2 (**Figure S6 b, d, g, i**). Of the 13 audiovisual electrodes where nouns versus adjectives was the only significant predictor in the GLM analysis, 8 electrodes (62%) showed generalization across different noun or adjective subcategories. The remaining 6 electrodes (38%) showed a significant difference between the two noun subcategories or between the two adjective subcategories (**Table S5**). **Figure S7** shows one of the exceptions, i.e., an electrode in the left LOF which showed a significant response only for food nouns. This selectivity was particularly pronounced for the visual stimuli (**Figure S7 c, d, h, i**), but was also apparent for auditory stimuli (**Figure S7 a, b, f, g**), and was evident both for word 1 and word 2.

In sum, differences in selective responses to nouns versus adjectives were particularly prominent and clustered in the left lateral orbitofrontal cortex, persisted across different word lengths, whether the word was used in a grammatically correct phrase or not, after equalizing word occurrence frequency, and generalized across different noun or adjective subcategories.

Neural signals enhanced for nouns versus adjectives were anatomically segregated

Of those electrodes uniquely selective for part of speech, 77% showed responses that were significantly stronger for nouns compared to adjectives ($\beta_{NvsA} > 0$) as illustrated by the example in **Figure 2a-j**. The remaining 23% showed responses that were stronger for adjectives compared to nouns ($\beta_{NvsA} < 0$) as illustrated by the example in **Figure S8 a-i (Table S5)**. For auditory stimuli, the difference in the onset time between nouns and adjectives was larger for noun-preferring electrodes (550 ± 107 ms) than adjective-preferring electrodes (312 ± 94 ms, ranksum test, $p < 0.05$). For visual stimuli, the difference in the onset time between nouns and adjectives was not different between noun-preferring electrodes (425 ± 107 ms) and adjective-preferring electrodes (437 ± 134 ms, ranksum test, $p > 0.05$). There was a significant correlation between auditory and visual difference onset times for noun-preferring electrodes (Pearson $R^2 = 0.80$, $p < 0.01$) but not for adjective preferring electrodes (Pearson $R^2 = -0.70$, $p > 0.05$).

When we displayed the electrode locations on the brain, we observed an anatomical separation between these two groups of responses (**Figure 2l,m**). We compared noun- versus adjective- preferring electrodes along 3 axes of Montreal Neurological Institute 305 Coordinates (MNI305, units abbreviated as m.u.)⁴². Along the lateral to medial axis (x-axis in **Figure 2l,m**, zero being more medial), noun-preferring electrodes had a mean of 25.3 ± 6.2 m.u. and adjective-preferring electrodes had a mean of 47.3 ± 7.7 m.u. ($p < 0.01$, ranksum test). Along the ventral-dorsal axis (y-axis in **Figure 2l**), noun electrodes had a mean of -12.17 ± 5.3 m.u. and adjective electrodes had a mean of -3.7 ± 1.7 m.u. ($p < 0.05$, ranksum test). Along the posterior-anterior axis (y-axis in **Figure 2m**), noun electrodes had a mean of 21.4 ± 18.9 m.u. and adjective electrodes had a mean of -2.7 ± 25.8 m.u. ($p < 0.05$, ranksum test). Hyperplanes generated from a support vector machine (SVM) with a linear kernel, shown in black on the frontal plane in **Figure 2l** and on the axial plane in **Figure 2m**, separated noun-preferring electrodes from adjective-preferring electrodes with $97.8 \pm 3.7\%$ and $94.8 \pm 9.3\%$ accuracy on the training data (no cross-validation due to the small number of electrodes). **Table S6** summarizes the locations of noun- vs adjective-preferring electrodes across brain regions. A permutation test combining all brain regions for these electrodes showed that that electrodes in the LOF tended to show stronger responses to nouns ($\sim 90\%$ $\beta_{NvsA} > 0$, $p < 10^{-4}$, permutation test, $n = 10^6$ iterations, **Methods**).

A population of electrodes in the lateral orbitofrontal cortex can distinguish nouns from adjectives in individual trials and generalizes across words and modalities

To assess whether information about part of speech was available in individual trials, we used a machine learning pseudopopulation approach by combining electrodes within anatomically defined brain regions in the Desikan-Killiany Atlas⁴³. We binned the response in 100 ms time bins and used the top-N principal components that explained more than 70% of the variance in the training data for all the electrodes. We trained an SVM classifier with a linear kernel to distinguish between nouns and adjectives and tested the classifier on held-out data (**Methods**). **Figure 3** shows decoding accuracy for the left (**Figure 3a, d, g**) and the right (**Figure 3b, e, h**) LOF as a function of time from word onset. When trained using data from both word1 and word2 with combined auditory and visual features, there was a statistically significant decoding performance starting approximately at ~300 ms after word onset and reaching a peak of $63.6 \pm 1.1\%$ at ~500 ms after word onset in the left LOF (**Figure 3a**). Statistical significance was assessed by comparing with a control where noun and adjective labels were randomly shuffled (**Methods**). Even though there were almost twice as many electrodes in the right LOF compared to the left LOF (**Table S2, Figure 1b-g**), decoding performance was much higher for the left LOF compared to the right LOF (compare **Figure 3a** versus **Figure 3b**). The differences between the left and right LOF persisted after randomly subsampling to equalize the number of electrodes across hemispheres for all regions (**Figure S9 a, b**).

In **Figure 3 a, b**, word 1 and word 2 are combined. Decoding performance in the left LOF was also high when separately considering word 1 (**Figure S10 a-c**) and word 2 (**Figure S10 d-f**). Furthermore, the machine learning classifier was able to generalize across words, as evidenced by the decoding performance when training on word 1 and testing on word 2 (**Figure 3 d, e**), and vice versa (**Figure 3 g, h**). Similarly, auditory and visual trials are combined in **Figure 3a, b**. Decoding performance in the left LOF was also high when separately considering auditory trials (**Figure S10 g-i**) and visual trials (**Figure S10 j-l**). Furthermore, the machine learning classifier was able to generalize across modalities as evidenced by the decoding performance when training on auditory trials and testing on vision trials (**Figure S10 m-o**) and vice versa (**Figure S10 p-r**).

We extended the analyses in **Figure 3a,b,d,e,g,h** to all other regions in the Desikan-Killiany atlas. In addition to the left LOF, the left superior temporal cortex and the left fusiform

cortex also showed statistically significant decoding performance (**Figure 3c**). However, in contrast to the results for the left LOF, the decoding results for other regions were less robust (**Figure S9c**) and did not generalize across words (**Figure 3f, i**) or across modalities (**Figure S10 o, r**).

Multimodal neural signals distinguishing different parts of speech are conserved across languages

One of the participants was fluent in two languages, English and Spanish. Therefore, this patient provided an opportunity to ask whether the neural signals discriminating between different parts of speech were language-specific or showed invariance across languages. All the words were translated into Spanish by a native Spanish speaker and the task was repeated in both languages. **Figure 4a-h** shows the responses of an example electrode located in the left LOF (**Figure 4k**). This electrode showed a stronger response to nouns compared to adjectives for auditory stimuli (**Figure 4 a, b, e, f**), for visual stimuli (**Figure 4 c, d, g, h**), for Word 1 (**Figure 4 a, c, e, g**), and for Word 2 (**Figure 4 b, d, f, h**). Interestingly, the separation between nouns and adjectives was evident both when the words were presented in English (**Figure 4a-d**) and when the words were presented in Spanish (**Figure 4e-h**). The GLM analysis showed that nouns versus adjectives was the only significant predictor in English trials (**Figure 4i**), and Spanish trials (**Figure 4j**). All in all, there were three electrodes in this participant that showed a multimodal response selective for part of speech. All three of these electrodes were in the left orbital H-shaped sulcus within the LOF (**Figure 4k**, green).

In addition to this bilingual participant, the task was run in monolingual participants who spoke English (n=16 participants) and monolingual participants who spoke Taiwanese (n=3 participants, **Table S1**). In **Figure 4k**, we show all electrodes from the left LOF that showed part-of-speech encoding from different participants (**Table S7**). We also indicate the language in which this difference was observed whether it be English (pink), Taiwanese (brown) or bilingual English/Spanish (green). All participants in **Figure 4k** were right-handed. Electrodes separating parts of speech from monolingual participants were also clustered in the same region. Thus, the left LOF distinguished between parts of speech for both auditory and visual presentations of stimuli across participants speaking different languages.

Discussion

We described neurophysiological signals that selectively discriminate between two parts of speech, nouns and adjectives (**Figure 2**). This selectivity was robust to orthographic variables such as word length, phonetic features such as number of syllables, and word occurrence statistics (**Figure 2**). This selectivity for part of speech generalized across sensory modalities (**Figures 2, 3, 4**), word positions, grammatical correctness and motor outputs (**Figures 2, 3, 4**), and semantic groups of nouns and adjectives (**Figure S6**). These neurophysiological signals enable discrimination between parts of speech even in single trials (**Figures 2, 3**). Electrodes that uniquely distinguished nouns from adjectives were particularly clustered within a small, circumscribed region of the lateral orbitofrontal cortex, lateralized to the left hemisphere (**Figure 2, 4**). Neural discrimination of nouns from adjectives was apparent in the LOF in English-speaking and Taiwanese-speaking participants (**Figure 4**). In addition, in a bilingual participant, the same electrodes within the left LOF distinguished nouns and adjectives in both English and in Spanish (**Figure 4**).

In English and other languages, some words can be used both as a noun or as an adjective (e.g., long *race* versus *race* horse). One usage is typically more frequent than the other. In particular, the nouns and adjectives in this study are highly overrepresented in their labeled part of speech (**Table S8**). Similarly, some words can be used both as a noun or as a verb (e.g., long *race* versus *race* you to the top); all the nouns in this study are highly overrepresented in their usage as nouns (**Table S8**). Thus, the words used in this study had a prototypical interpretation as either a noun or an adjective. The distinction between nouns and adjectives includes their grammatical roles but also their associated semantic connotations (nouns refer to things and adjectives to the attributes of those things).

In languages like English, nouns and adjectives follow a specific grammatical order (i.e., adjectives precede nouns). Other languages reverse this order. In Spanish, adjectives typically follow nouns, though the English order can also be used. It is thus interesting to observe that many electrodes demonstrated strong selectivity for nouns

versus adjectives, irrespective of their position within the two-word phrases. Furthermore, in the bilingual participant, the neural responses separated nouns and adjectives in both languages even though the grammatical order is typically reversed between English and Spanish. It is conceivable that the strong part-of-speech selectivity independent of grammar shown here could be linked to the two-word phrase structures. The results could be different when considering natural sentences. Another possibility is that the representation of nouns versus adjectives is invariant to grammatical usage rules.

Non-invasive scalp electroencephalography and magnetoencephalography signals have revealed correlates of language processing with a wide range of onset times from approximately 100 ms all the way to well over 600 ms (for a review, see⁴⁴). The earliest onset signals commencing between 100 and 300 ms after stimulus onset, sometimes referred to as early left anterior negativity, have been associated with grammatical violations, but previous studies have not documented any invariance in the representation of parts of speech and there is disagreement about whether these early signals are even associated with language⁴⁴. Our work reports an invariant distinction between nouns and adjectives in the LOF commencing at approximately 400 ms after stimulus onset, which is consistent with part-of-speech being represented well after the onset of modality-specific purely visual and auditory signals.

A remarkable hallmark of language is its universality. We can interpret the word *cat* when uttering the word, writing it, listening to it, reading it, and even when examining a photograph of a cat. It is therefore tempting to speculate that there may be an invariant representation of language concepts in the brain. Several studies have examined putative correlates of language processing using only unimodal signals (e.g.,^{11-15,17,23,26,31,32}). While we observed electrodes that distinguished between parts of speech only in the auditory stimuli or only in the visual stimuli, the responses of those electrodes could be partly explained by other variables including number of syllables, word frequency, or grammar. Using strict criteria and after controlling for confounding variables, most electrodes that distinguished nouns from adjectives showed selectivity during both auditory and visual presentation. Future work should evaluate whether the same

electrodes also distinguish parts of speech when participants utter words, write them, or when examining photographs. An intriguing study described neurons in the human medial temporal lobe that respond selectively to images and their corresponding text and sound descriptions^{45,46}. However, these medial temporal lobe neurons do not seem to distinguish between different parts of speech and their responses seem to be connected with the formation of memories rather than the internal representation of language⁴⁷. Indeed, there exist strong anatomical and functional connections between the medial temporal lobe and frontal regions that could link language and memory formation⁴⁸.

The lateral orbitofrontal (LOF) cortex constitutes a large expanse of neocortex within the frontal lobe, spanning Brodmann areas (BA) 10, 11, 12 (called BA47 in humans due to cytoarchitectural differences from monkeys) and 13⁴⁹⁻⁵¹. Neurobiological tracings from rats, mice, and macaques have identified LOF as a nexus of many inputs⁵¹ conveying olfactory, gustatory, visual, auditory, somatosensory, and visceral-sensory information. The LOF has been associated with a bewildering plethora of cognitive functions, including multisensory integration, working memory, long-term memory consolidation, reward processing, social interactions, memory, decision making, and emotion processing^{48,50,52-56}. This heterogeneity might be partly ascribed to investigations probing different cognitive tasks, as in the case of the proverbial blind men sampling different parts of an elephant. Given the prominent role of language in cognition, it is conceivable that previous studies that describe other roles of the LOF did not probe its possible associations with language. However, it is even more likely that descriptors like LOF that refer to such large brain areas would inevitably fail to uncover specific functionality. The current results point to a rather well circumscribed location within LOF, the posterior part of the H-shaped sulcus in the left hemisphere. In humans, this location overlaps with BA13-lateral and BA 47-medial and has been shown to have a strong convergence of auditory and visual inputs^{50,51,57}. Interestingly, work on Primary Progressive Aphasia and frontotemporal lesions implicate the orbitofrontal cortex in word and sentence comprehension deficits^{7,57-59}. These studies also reveal language-related deficits associated with lesions in the left anterior temporal lobe and left dorsomedial prefrontal cortex where we also found selective but not invariant responses. Consistent

with extensive work documenting the lateralization of language functions, the results presented here also show a strong predominance of the left hemisphere in the representation of part of speech, despite the fact that there were more electrodes sampling signals from the right hemisphere.

All the results reported here are derived from patients with epilepsy. The invasive study of epilepsy patients constitutes the predominant way to access neurophysiological signals from the human brain^{60,61}. Neurophysiological studies in other patient populations (e.g., paraplegic patients, Parkinson's patients, brain tumor patients), typically target specific regions that are not known to be associated with language processing. Caution should be exercised in the interpretation of results from patient populations. To the best of our knowledge, all patients used language fluently and had no language impediments, but one should be aware of the possibility that epilepsy could potentially impact the representation of language. Second, the electrode locations are strictly dictated by clinical criteria. Our sampling of brain activity is extensive but not exhaustive (**Figure 1, Tables S1-S2**). It is quite possible that other areas not examined here may also reveal neural correlates of parts of speech and that the regions we found interact with other relevant brain areas. A critical goal of cortical resections in epilepsy patients is to cure seizures without interfering with cognitive function. As such, given the strong lateralization and ubiquitous role for language in cognition, it is extremely important to precisely understand the neural structures that support language in these patients and the current results could help guide surgical approaches for epilepsy. Another limitation worth emphasizing is that the current work focuses on two parts of speech. Nouns and adjectives do not constitute an exhaustive list of parts of speech and future work should examine the representation of pronouns, verbs, adverbs, prepositions and conjunctions.

These results provide initial glimpses into highly localized structures that represent a fundamental component of language that has been extensively studied by linguists for decades, the functional role of different words within a sentence. The representation of nouns versus adjectives in the human brain is invariant to the presentation modality, word properties, grammar, and semantics. Furthermore, the representation even generalizes

462 across different languages. These observations open the doors to begin to elucidate the
463 neural representation of more complex language concepts and to bridge the extensive
464 work in language and linguistics to their underlying neural representations.

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Methods

Preregistration

This study was preregistered on the Open Science Framework (OSF) website. The preregistration DOI is: <https://doi.org/10.17605/OSF.IO/8TU2G>.

Data availability

All data and code will be made publicly available through the following link:
https://klab.tch.harvard.edu/resources/Misraetal_POS.html

Participants

We recorded data from 20 participants (9 male, 9-60 years old, 2 left-handed, 2 ambidextrous, **Table S1**) with pharmacologically resistant epilepsy. All experiments were conducted while participants stayed at Children's Hospital Boston (CHB), Brigham and Women's Hospital (BWH), or Taipei Veterans General Hospital (TVGH). All studies were approved by each hospital's institutional review boards and were carried out with the participants' informed consent.

Recordings and Electrode Locations

Participants were implanted with intracranial depth electrodes (Ad-Tech, Racine, WI, USA). Neurophysiological data were recorded using XLTEK (Oakville, ON, Canada), Bio-Logic (Knoxville, TN, USA), Nihon Kohden (Tokyo, Japan), and Natus (Pleasanton, CA). The sampling rate was 2048 Hz at BCH and TVGH, and 1024 Hz or 512 Hz at BWH. All data were referenced in a bipolar montage. There were no seizure events in any of the sessions. Electrode locations were decided based on clinical criteria for each participant. Electrodes in the epileptogenic foci, as well as pathological areas, were removed from analyses. The total number of electrodes after bipolar referencing and removing electrodes with no signal, line noise or recording artifacts was 1,801.

Following implantation, electrodes were localized by co-registration of pre-operative T1 MRI and post-operative CT scans using the iELVis software⁴². We used FreeSurfer to segment MRI images, upon which post implant CT was rigidly registered⁶². Electrodes

were marked in the CT aligned to pre-operative MRI using the Bioimage Suite⁶³. The Desikan-Killiany (DK) atlas was used to assign the electrodes locations. **Figure 1b-g** and **Table S2** show the locations of all the electrodes.

Experiment Design

A schematic of the task is shown in **Figure 1**. Participants were presented two words, 875 ms presentation time, with a 400 ms blank screen between them. At the end of each trial, participants were asked to indicate via a button press whether the two words were same or different. Word presentation was either visual or auditory. All visual stimuli were displayed on a 15.4 inch 2,880 × 1,800 pixel LCD screen using the Psychtoolbox in MATLAB (Natick, MA) and a MacBook Pro laptop (Cupertino, CA). The stimuli were positioned at eye level at about 80 cm from the participant and each word subtended approximately 3 degrees of visual angle. Sounds were played from the speakers of a MacBook Pro 15.4 at 80% loudness using the Psychtoolbox in MATLAB⁶⁴. We used the USB-1208FS-Plus device from Measurement Computing Corporation (Norton, Massachusetts) to send trigger pulses that enabled us to align stimuli onsets and behavioral responses to neural recordings. On average, we presented 1500 ± 710 trials (**Table S1** shows the number of trials per participant).

There were three types of trials: Noun followed by Adjective (42% of trials, e.g., “apple green”), Adjective followed by Noun (42% of trials, e.g., “green apple”), Repeated Noun (8% of trials, e.g., “apple apple”), and Repeated Adjective (8% of trials, e.g., “green green”). The order of trials (stimulus presentation modality and noun/adjective structure) was randomly interleaved. Each word combination was presented in a randomized manner 5 times in the audio modality and 5 times in the visual modality. The nouns belonged to two categories, animals (e.g., “cat”) and food (e.g., “apple”). The adjectives belonged to two categories, concrete adjectives (e.g., “big”) and abstract adjectives (e.g., “good”). A list of all the nouns and adjectives is included in **Table S3**. We selected only high frequency English words that were more frequent than 10^{-6} in Google Ngram and were shorter than 7 letters and had more 1 or 2 syllables. We used the max frequency of a word between 2006 and 2019. Finally, we created a balanced selection of nouns and

adjectives such that noun and adjectives were indistinguishable from each other using word length or number of syllables ($p > 0.05$ ranksum test). We conducted the experiment in 3 languages, English (16 monolingual and 1 bilingual participants), Spanish (1 bilingual participants) and Taiwanese (3 monolingual participants). Two bilingual international scholars whose native language was Spanish (MAG) and Taiwanese (YLK) translated the words in the task. For non-English languages, we also kept nouns and adjectives indistinguishable based on word-length and number of syllables.

Participants had to indicate whether the two words in a trial were the same or not. The motor responses were the same for nouns or adjectives. The motor responses were also the same for noun followed by adjective or adjective followed by noun trials. Thus, the motor responses were orthogonal to parts of speech and grammar and differences between nouns and adjectives cannot be attributed to motor signals.

Data Analyses

Preprocessing

A total of 2,428 electrode contacts were implanted, 627 of which were excluded from analysis due to bipolar referencing, presence of line noise or recording artifacts⁶⁵. We removed 60 Hz line noise and its harmonics using a fifth-order Butterworth filter. We focus on the high-gamma band of the intracranial field potential signals obtained by bandpass filtering raw data of each electrode in the 65–150 Hz range (fifth-order Butterworth filter). The high gamma band (65-150 Hz) power was computed using the Chronux toolbox⁶⁶. We used a time-bandwidth product of 3 and 4 leading tapers, a moving window size of 200 ms, and a step size of 5 ms. For every trial, we computed the normalized high gamma activity by subtracting the mean activity from -150 to 50 ms from the onset of the first fixation and then dividing by the standard deviation. This normalized response is reported as “gamma power” on the y-axis when showing electrode responses.

Responsive Electrodes

We evaluated whether an electrode was responsive to visual or auditory stimuli by comparing the 100 to 400 ms post stimulus onset to the -400 to -100 ms before stimulus onset (e.g., **Figure S1**). The responsiveness threshold was set using Cohen's d prime coefficient and based on the number of trials for a statistical power of 80% and $p < 0.01$ (one-tailed z-test). We also computed the time at which the neural signals reach half of the maximum amplitude.

Part-of-speech selectivity

We compared the neural responses to nouns versus adjectives. Periods of significant selective activation were tested using a one-tailed t-test with $p < 0.05$ at each time point to differentiate between nouns and adjectives and were corrected for multiple comparisons with a Benjamini-Hochberg false detection rate (FDR) corrected threshold of $q < 0.05$, separately for auditory and visual trials. After fixing the FDR with $q < 0.05$, an electrode was considered to be selective for part of speech if there was a significant difference between nouns and adjectives for a minimum contiguous window of 65 ms.

General Linear Model (GLM)

We created a GLM to tease out the experiment variables that significantly contribute for explaining the responses of a given channel. The equation for a GLM is as follows:

$$AUC = \beta_0 + \beta_{NvsA}NvsA + \beta_{GvsUG}GvsUG + \beta_{NSyllables}NSyllables + \beta_{WordLength}WordLength \quad (1)$$

where AUC is the area under the response curve (e.g., **Figure 2a**) from 200 ms to 800 ms after the onset of word1 and word2, β_0 is a constant additive term, NvsA is 1 for Nouns and -1 for Adjectives, GvsUG is 1 for Grammatical trials and -1 for Ungrammatical trials, NumberOfSyllables is 1 or 2 (and 0 for visual trials), or WordLength goes from 3 to 7 (and 0 for auditory trials) as the task predictors. We fit this GLM model for each electrode separately using the MATLAB function fitglm and report the corresponding β coefficients (e.g., **Figure 2j**). We assessed whether each coefficient was significantly different from zero when compared to β coefficients generated from shuffled labels ($p < 0.01$, corrected for multiple comparisons).

Anatomical comparisons

To assess the degree of anatomical specificity in the neural responses, we compared the percentage of significant electrodes in each brain region to the null distribution expected given the number of electrodes in each area using a permutation test ($p < 0.01$, 10^6 iterations). A similar approach was followed to compare the same region between the left and right hemispheres.

Decoding Analysis

We performed a machine learning decoding analysis⁶⁷ to decode parts of speech in individual words combining all the electrodes in each brain region as defined by the Desikan-Killiany atlas⁴³ (**Figure S9**). The top-N principal components of all electrodes that explained more than 70% of the variance in the training data for the area under curve of non-overlapping 100 ms time-windows of the signal following word onset were used for decoding. The signal for decoding comprised of features from different frequency bands (beta:12-30 Hz, low gamma:30-65 Hz, and high gamma power: 65-150Hz). The analysis was repeated for 100 random splits of the data with 80% of the data used for training a Support Vector Machine with a linear kernel. Significant decoding performance was found by comparing performance from the original data at each time-window with a null distribution obtained by shuffling labels ($p < 0.01$, ranksum test). Regions with statistically significant decoding performance were found by comparing the average of the maximum decoding performance across time for 100 random iterations of the original data with that of the null distribution, separately for both hemispheres ($p < 0.01$, ranksum test corrected for multiple comparisons) (**Figure 3c,f,i, Figure S9c, Figure S10c,f,i,l,o,r**).

We also applied a threshold such that for a given region R

$$[\mu_R - 3 * \sigma_R]_{original\ data} > [\mu_R + 3 * \sigma_R]_{null\ data}$$

where μ and σ represent the average and standard deviation in region R. For the significant regions, the average max-performance between the left and right hemispheres was compared to find if decoding performance was lateralized ($p < 0.01$, ranksum test, corrected for multiple comparisons).

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References

- 1 Chomsky, N. *The minimalist program*. (MIT Press, 1995).
- 2 Scott, S. K. From speech and talkers to the social world: The neural processing of human spoken language. *Science* **366**, 58-62, doi:10.1126/science.aax0288 (2019).
- 3 Heilman, K. M. & Valenstein, E. *Clinical Neuropsychology*. (Oxford University Press, 1993).
- 4 Ojemann, G., Ojemann, J., Lettich, E. & Berger, M. Cortical language localization in left, dominant hemisphere. An electrical stimulation mapping investigation in 117 patients. *J Neurosurg* **71**, 316-326, doi:10.3171/jns.1989.71.3.0316 (1989).
- 5 Petrides, M. *Neuroanatomy of language regions in the human brain*. (Elsevier, 2014).
- 6 Mahon, B. Z. & Caramazza, A. Concepts and categories: a cognitive neuropsychological perspective. *Annual review of psychology* **60**, 27-51, doi:10.1146/annurev.psych.60.110707.163532 (2009).
- 7 Mesulam, M. M., Thompson, C. K., Weintraub, S. & Rogalski, E. J. The Wernicke conundrum and the anatomy of language comprehension in primary progressive aphasia. *Brain* **138**, 2423-2437, doi:10.1093/brain/awv154 (2015).
- 8 Warrington, E. & Shallice, T. Category specific semantic impairments. *Brain* **107**, 829-854 (1984).
- 9 Nourski, K. V. *et al.* Gamma Activation and Alpha Suppression within Human Auditory Cortex during a Speech Classification Task. *J Neurosci* **42**, 5034-5046, doi:10.1523/JNEUROSCI.2187-21.2022 (2022).
- 10 Forseth, K. J. *et al.* A lexical semantic hub for heteromodal naming in middle fusiform gyrus. *Brain* **141**, 2112-2126, doi:10.1093/brain/awy120 (2018).
- 11 Murphy, E. *et al.* Minimal Phrase Composition Revealed by Intracranial Recordings. *J Neurosci* **42**, 3216-3227, doi:10.1523/JNEUROSCI.1575-21.2022 (2022).
- 12 Keshishian, M. *et al.* Joint, distributed and hierarchically organized encoding of linguistic features in the human auditory cortex. *Nat Hum Behav* **7**, 740-753, doi:10.1038/s41562-023-01520-0 (2023).
- 13 Sinai, A. *et al.* Electrocorticographic high gamma activity versus electrical cortical stimulation mapping of naming. *Brain* **128**, 1556-1570, doi:10.1093/brain/awh491 (2005).
- 14 Ding, N., Melloni, L., Zhang, H., Tian, X. & Poeppel, D. Cortical tracking of hierarchical linguistic structures in connected speech. *Nat Neurosci* **19**, 158-164, doi:10.1038/nn.4186 (2016).
- 15 Cometa, A. *et al.* Event-related causality in stereo-EEG discriminates syntactic processing of noun phrases and verb phrases. *J Neural Eng* **20**, doi:10.1088/1741-2552/accaa8 (2023).
- 16 Artoni, F. *et al.* High gamma response tracks different syntactic structures in homophonous phrases. *Sci Rep* **10**, 7537, doi:10.1038/s41598-020-64375-9 (2020).
- 17 Woolnough, O. *et al.* Spatiotemporal dynamics of orthographic and lexical processing in the ventral visual pathway. *Nat Hum Behav* **5**, 389-398, doi:10.1038/s41562-020-00982-w (2021).
- 18 Vigliocco, G., Vinson, D. P., Druks, J., Barber, H. & Cappa, S. F. Nouns and verbs in the brain: a review of behavioural, electrophysiological, neuropsychological and imaging studies. *Neurosci Biobehav Rev* **35**, 407-426, doi:10.1016/j.neubiorev.2010.04.007 (2011).

- 669 19 Castellucci, G. A., Kovach, C. K., Howard, M. A., 3rd, Greenlee, J. D. W. & Long, M. A.
670 A speech planning network for interactive language use. *Nature* **602**, 117-122,
671 doi:10.1038/s41586-021-04270-z (2022).
- 672 20 Yi, H. G. *et al.* Learning nonnative speech sounds changes local encoding in the adult
673 human cortex. *Proc Natl Acad Sci U S A* **118**, doi:10.1073/pnas.2101777118 (2021).
- 674 21 Gwilliams, L., King, J. R., Marantz, A. & Poeppel, D. Neural dynamics of phoneme
675 sequences reveal position-invariant code for content and order. *Nat Commun* **13**, 6606,
676 doi:10.1038/s41467-022-34326-1 (2022).
- 677 22 Forseth, K., Pitkow, X., Fischer-Baum, S. & Tandon, N. What the brain does as we speak.
678 *bioRxiv* **bioRxiv** **2021.02.05.429841**, doi:<https://doi.org/10.1101/2021.02.05.429841>
679 (2021).
- 680 23 Forseth, K. J., Hickok, G., Rollo, P. S. & Tandon, N. Language prediction mechanisms in
681 human auditory cortex. *Nat Commun* **11**, 5240, doi:10.1038/s41467-020-19010-6 (2020).
- 682 24 Bhaya-Grossman, I. & Chang, E. F. Speech Computations of the Human Superior
683 Temporal Gyrus. *Annual review of psychology* **73**, 79-102, doi:10.1146/annurev-psych-
684 022321-035256 (2022).
- 685 25 Hamilton, L. S., Oganian, Y., Hall, J. & Chang, E. F. Parallel and distributed encoding of
686 speech across human auditory cortex. *Cell* **184**, 4626-4639 e4613,
687 doi:10.1016/j.cell.2021.07.019 (2021).
- 688 26 Chomsky, N., Gallego, A. & Ott, D. Generative grammar and the faculty of language:
689 insights, questions, and challenges. *Catalan Journal of Linguistics*, 226-261 (2019).
- 690 27 OpenAI. GPT-4 Technical Report. *arXiv* **2303.08774** (2023).
- 691 28 Hagoort, P. The neurobiology of language beyond single-word processing. *Science* **366**,
692 55-58, doi:10.1126/science.aax0289 (2019).
- 693 29 Hagoort, P. & Indefrey, P. The neurobiology of language beyond single words. *Annu Rev*
694 *Neurosci* **37**, 347-362, doi:10.1146/annurev-neuro-071013-013847 (2014).
- 695 30 Calinescu, L., Ramchand, G. & Baggio, G. How (not) to look for meaning composition in
696 the brain: A reassessment of current experimental paradigms. *Frontiers in Language*
697 *Sciences* **2**, 1096110 (2023).
- 698 31 Goldstein, A. *et al.* Shared computational principles for language processing in humans
699 and deep language models. *Nat Neurosci* **25**, 369-380, doi:10.1038/s41593-022-01026-4
700 (2022).
- 701 32 Cai, J., Hadjinicolaou, A., Paulik, A., Williams, Z. & Cash, S. Natural language processing
702 models reveal neural dynamics of human communication. *Biorxiv* **2023.03.10.531.095**
703 (2023).
- 704 33 Rapp, B. & Caramazza, A. Selective difficulties with spoken nouns and written verbs: A
705 single case study. *Journal of neurolinguistics* **15**, 373-402 (2002).
- 706 34 Caramazza, A. & Hillis, A. E. Lexical organization of nouns and verbs in the brain. *Nature*
707 **349**, 788-790, doi:10.1038/349788a0 (1991).
- 708 35 Woolnough, O., Forseth, K. J., Rollo, P. S., Roccaforte, Z. J. & Tandon, N. Event-related
709 phase synchronization propagates rapidly across human ventral visual cortex. *Neuroimage*
710 **256**, 119262, doi:10.1016/j.neuroimage.2022.119262 (2022).
- 711 36 Aflalo, T. *et al.* A shared neural substrate for action verbs and observed actions in human
712 posterior parietal cortex. *Sci Adv* **6**, doi:10.1126/sciadv.abb3984 (2020).

- 37 Damasio, A. R. & Tranel, D. Nouns and verbs are retrieved with differently distributed neural systems. *Proc Natl Acad Sci U S A* **90**, 4957-4960, doi:10.1073/pnas.90.11.4957 (1993).
- 38 Crepaldi, D., Berlingeri, M., Paulesu, E. & Luzzatti, C. A place for nouns and a place for verbs? A critical review of neurocognitive data on grammatical-class effects. *Brain Lang* **116**, 33-49, doi:10.1016/j.bandl.2010.09.005 (2011).
- 39 Tenney, I., Dipanjan, D. & Pavlick, E. BERT rediscovers the classical NLP pipeline. *arXiv* **1905.05950** (2019).
- 40 Elazar, Y., Ravfogel, S., Jacovi, A. & Goldberg, Y. Amnesic probing: behavioral explanation with amnesic counterfactuals. *arXiv* **2006.00995** (2021).
- 41 Bansal, A. *et al.* Neural Dynamics Underlying Target Detection in the Human Brain. *Journal of Neuroscience* **34**, 3042-3055, doi: 10.1523/JNEUROSCI.3781-13.2014 (2014).
- 42 Groppe, D. M. *et al.* iELVis: An open source MATLAB toolbox for localizing and visualizing human intracranial electrode data. *J Neurosci Methods* **281**, 40-48, doi:10.1016/j.jneumeth.2017.01.022 (2017).
- 43 Desikan, R. S. *et al.* An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *Neuroimage* **31**, 968-980 (2006).
- 44 Tager-Flusberg, H. & Seery, A. in *Neural circuit development and function in the brain* (eds JLR Rubenstein & P Rakic) 315-330 (Elsevier, 2013).
- 45 Quian Quiroga, R., Reddy, L., Kreiman, G., Koch, C. & Fried, I. Invariant visual representation by single neurons in the human brain. *Nature* **435**, 1102-1107, doi:10.1038/nature03687 (2005).
- 46 Quian Quiroga, R., Kraskov, A., Koch, C. & Fried, I. Explicit encoding of multimodal percepts by single neurons in the human brain. *Current biology : CB* **19**, 1308-1313, doi:10.1016/j.cub.2009.06.060 (2009).
- 47 Quian Quiroga, R., Kreiman, G., Koch, C. & Fried, I. Sparse but not 'Grandmother-cell' coding in the medial temporal lobe. *Trends in Cognitive Science* **12**, 87-91 (2008).
- 48 Geva-Sagiv, M. *et al.* Augmenting hippocampal-prefrontal neuronal synchrony during sleep enhances memory consolidation in humans. *Nat Neurosci* **26**, 1100-1110, doi:10.1038/s41593-023-01324-5 (2023).
- 49 Wojtasik, M. *et al.* Cytoarchitectonic Characterization and Functional Decoding of Four New Areas in the Human Lateral Orbitofrontal Cortex. *Front Neuroanat* **14**, 2, doi:10.3389/fnana.2020.00002 (2020).
- 50 Kringelbach, M. L. The human orbitofrontal cortex: linking reward to hedonic experience. *Nat Rev Neurosci* **6**, 691-702, doi:10.1038/nrn1747 (2005).
- 51 Ongur, D. & Price, J. L. The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cereb Cortex* **10**, 206-219, doi:10.1093/cercor/10.3.206 (2000).
- 52 Xiao, Y. *et al.* Integration of recognition, episodic, and associative memories during complex human behavior. *Biorxiv* **2023.03.27.534384**, doi:<https://doi.org/10.1101/2023.03.27.534384> (2023).
- 53 Hunt, L. T. *et al.* Triple dissociation of attention and decision computations across prefrontal cortex. *Nat Neurosci* **21**, 1471-1481, doi:10.1038/s41593-018-0239-5 (2018).
- 54 Nogueira, R. *et al.* Lateral orbitofrontal cortex anticipates choices and integrates prior with current information. *Nat Commun* **8**, 14823, doi:10.1038/ncomms14823 (2017).

- 55 Noonan, M. P. *et al.* Separate value comparison and learning mechanisms in macaque medial and lateral orbitofrontal cortex. *Proc Natl Acad Sci U S A* **107**, 20547-20552, doi:10.1073/pnas.1012246107 (2010).
- 56 de Araujo, I. E., Rolls, E. T., Kringelbach, M. L., McGlone, F. & Phillips, N. Taste-olfactory convergence, and the representation of the pleasantness of flavour, in the human brain. *Eur J Neurosci* **18**, 2059-2068, doi:10.1046/j.1460-9568.2003.02915.x (2003).
- 57 Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Jr., Redfern, B. B. & Jaeger, J. J. Lesion analysis of the brain areas involved in language comprehension. *Cognition* **92**, 145-177, doi:10.1016/j.cognition.2003.11.002 (2004).
- 58 Mesulam, M. M. *et al.* Neuropathological fingerprints of survival, atrophy and language in primary progressive aphasia. *Brain* **145**, 2133-2148, doi:10.1093/brain/awab410 (2022).
- 59 Mesulam, M. M. *et al.* Primary progressive aphasia and the evolving neurology of the language network. *Nat Rev Neurol* **10**, 554-569, doi:10.1038/nrneurol.2014.159 (2014).
- 60 Fried, I., Cerf, M., Rutishauser, U. & Kreiman, G. *Single neuron studies of the human brain. Probing cognition.*, 408 (MIT Press, 2014).
- 61 Mukamel, R. & Fried, I. Human intracranial recordings and cognitive neuroscience. *Annual review of psychology* **63**, 511-537, doi:10.1146/annurev-psych-120709-145401 (2012).
- 62 Dale, A. M., Fischl, B. & Sereno, M. I. Cortical surface-based analysis. I. Segmentation and surface reconstruction. *Neuroimage* **9**, 179-194 (1999).
- 63 Joshi, A. *et al.* Unified framework for development, deployment and robust testing of neuroimaging algorithms. *Neuroinformatics* **9**, 69-84, doi:10.1007/s12021-010-9092-8 (2011).
- 64 Brainard, D. The Psychophysics Toolbox. *Spatial Vision* **10**, 433-436 (1997).
- 65 Wang, J., Tao, A., Anderson, W. S., Madsen, J. R. & Kreiman, G. Mesoscopic physiological interactions in the human brain reveal small-world properties. *Cell Rep* **36**, 109585, doi:10.1016/j.celrep.2021.109585 (2021).
- 66 Mitra, P. & Bokil, H. *Observed brain dynamics* (Oxford University Press, 2008).
- 67 Bansal, A., Golby, A., Madsen, J. & Kreiman, G. in *COSYNE*.

Figure Captions

Figure 1. Task schematic, electrode locations, and multimodal responses. **a.** Task schematic. Two words were sequentially presented either in visual modality or auditory modality. Participants indicated whether the two words were the same (e.g., “apple apple” or “green green”, 8% of trials of each type) or different (e.g., “green apple” or “apple green”: 42% of trials of each type, **Methods**). In the 84% of trials where the two-words were different, there was an adjective followed by a noun or a noun followed by an adjective. **b-f.** Location of all electrodes overlayed on the Desikan-Killiany Atlas shown with different views. Each white circle shows one electrode. **b.** Left lateral view (n=693), **c.** Left medial view (n=693), **d.** Superior, whole brain view (n=1,801), **e.** Inferior, whole brain view (n=1,801), **f.** Right lateral view (n=1108) **g.** Right medial view (n=1108). **h.** Trial-averaged ($\pm$ SEM) gamma power for responses to auditory (light grey) or visual (black) presentations for an example electrode in the left rostral middle frontal gyrus (electrode location shown in **k**). Responses are aligned to word onset (vertical dashed line). The arrows indicate the half-maximum time. **i, j.** Raster plots showing each individual trial for the same electrode for each of the 1,496 words for auditor (**i**) and visual (**j**) presentations (see color scale on right).

Figure 2. Neural signals distinguish between different parts of speech. **a-d.** Trial-averaged normalized gamma-band power of responses from an example electrode in the left lateral orbitofrontal cortex (see location in **i**) to nouns (blue) or adjectives (red) during presentation of auditory stimuli (**a, b**, n=435 grammatical and 432 ungrammatical trials) or visual stimuli (**c, d**, n=435 grammatical and 432 ungrammatical trials) aligned to the onset (vertical dashed line) of the first word (**a, c**) or second word (**b, d**). Shaded areas denote s.e.m. Horizontal gray lines denote windows of statistically significant differences between responses to nouns versus adjectives (t-test $p < 0.05$, Benjamini-Hochberg false detection rate, $q < 0.05$). **e-h.** Raster plots showing the responses in each individual trial (see color scale on bottom right). The red and blue curves in **a-d** correspond to the averages of noun and adjective trials, respectively, in **e-h**. **i.** Location of the example electrode in the left lateral orbitofrontal cortex. **j.** Z-scored β coefficients for Generalized Linear Model used to predict area under the curve between 200 ms and 800 ms post word onset, using four task predictors: Noun versus Adjectives, Grammatically correct versus incorrect, number of syllables (auditory presentation) and word

length (visual presentation). Asterisks denote statistically significant coefficients, corrected for multiple comparisons (**Methods**).

k. Inferior axial view of both hemispheres showing electrodes that revealed statistically significant differences between nouns and adjectives for both audio and visual presentation (orange circles, $n=13$ electrodes). All the electrodes whose responses were significantly explained *only* by the Nouns versus Adjective task predictor in the GLM are included in this plot.

l, m. All electrodes from **k** projected onto the left hemisphere are shown on the frontal plane (**l**) and the axial plane (**m**, same plane as **k**). Electrodes that respond more strongly to nouns, i.e., Nouns versus Adjectives $\beta > 0$ ($n=10$ electrodes), are shown in blue and electrodes that responded more strongly to adjectives ($\beta < 0$, $n=3$ electrodes), are shown in red. All units are in MNI305 coordinates. Linear support vector machines separating these electrodes are shown with a thick black line. Kernel density curves (bandwidth 2) outline the marginal distributions of noun-preferring (blue) and adjective-preferring (red) electrodes along the lateral-medial axis (**l**: top x-axis), ventral-dorsal axis (**l**: right y-axis) and anterior-posterior axis (**m**: right y-axis). P-values indicate significant differences between the coordinates for noun- and adjective-preferring electrodes (ranksum test).

Figure 3. Neural signals distinguishing nouns and adjectives in single trials generalize across word1 and word2.

a, b, d, e, g, h. Average cross-validated performance of a support vector machine classifier (SVM, 80% training/20% test) decoding nouns versus adjectives for all electrodes in the left lateral orbitofrontal cortex (LOF) (**a, d, g**) or the right LOF (**b, e, h**). The dotted horizontal black line shows the chance level. Shaded areas denote s.e.m. Solid horizontal black bar shows time points where performance significantly differed from chance (100 random shuffles, ranksum test, $p < 0.01$). The inputs to the SVM included the top-N principal components of the electrode response that explained $>70\%$ variance for the training data at each time bin (**Methods**). **a, b:** Features from auditory and visual responses were combined and used for training and testing on a dataset of both Word1 and Word2 trials. **c, d:** Generalization across word order was evaluated on a dataset where Word1 trials were used for training and word2 trials were used for testing. **g, h:** Training on Word2 and testing on Word1. Black: original labels; Gray: shuffled labels.

c, f, i. Summary of average of max-decoding performance for distinguishing nouns versus adjectives in each hemisphere (dark: left; white: right)) for different brain regions. Bottom asterisks denote regions with significant decoding performance with respect to chance and performance from the real and null distribution do not overlap within 3 standard deviations of each other

($p < 0.01$, ranksum test, corrected for multiple comparisons, **Methods**). Shaded box: maximum of the mean $\pm$ SD. for the null distribution across all regions. Top asterisks with a U-bracket denote significant differences between decoding accuracy of the left versus the right hemisphere ($p < 0.01$, ranksum test, corrected for multiple comparisons). Regions are sorted in descending order of performance in panel **c**. **c**: Classifiers were trained and tested with features from both Word1 and Word2 trials. **f**: Classifiers were trained on Word1 trials and tested on Word2 trials. **i**: Classifiers were trained on Word2 trials and tested on Word1 trials.

Figure 4. Neural signals in left LOF generalize across languages in a bilingual subject and in monolingual subjects.

a-h. Trial averaged responses of an electrode in the left lateral orbitofrontal cortex from a bilingual patient. The format follows **Fig. 2a-d**. (**a-d**) English words (audio: $n=190$ grammatical and 185 ungrammatical trials; vision: $n=189$ grammatical and 191 ungrammatical trials). (**e-h**) Spanish words (audio: $n=184$ grammatical and ungrammatical trials; vision: 184 grammatical and 186 ungrammatical trials). Auditory responses (**a, b, e, f**). Visual responses (**c, d, g, h**). Word 1 (**a, c, e, g**) and Word 2 (**b, d, f, h**).

i, j. Z-scored β coefficients for Generalized Linear Model to predict area under the curve (AUC) for the English experiment (**i**) and for the Spanish experiment (**j**). The AUC computed between 200 ms and 800 ms post word onset using four task predictors: Noun versus Adjectives, Grammatical versus Ungrammatical, number of syllables (auditory presentation) and word length (visual presentation). Asterisks denote statistically significant coefficients corrected for multiple comparisons (**Methods**). The word order for grammatically correct trials in English is an adjective followed by a noun, such as “green apple”. This word order gets flipped in grammatically correct Spanish trials.

k. Inferior view of the 9 out of 38 electrodes (8 audiovisual: **Figure 2k**, 1 visual-only: **Figure S4**, see **Table S4** and **S7**) in the left lateral orbitofrontal cortex that showed noun versus adjective differences across different languages in which the experiment was conducted (significant Nouns versus Adjectives β , $p < 0.01$ corrected for multiple comparisons). These electrodes come from 4 different subjects. Electrodes from the bilingual patient are in green with a black arrow indicating the example electrode. Electrodes from one monolingual English patient are in pink and those from 2 monolingual Taiwanese patients are in brown.

Figure 1

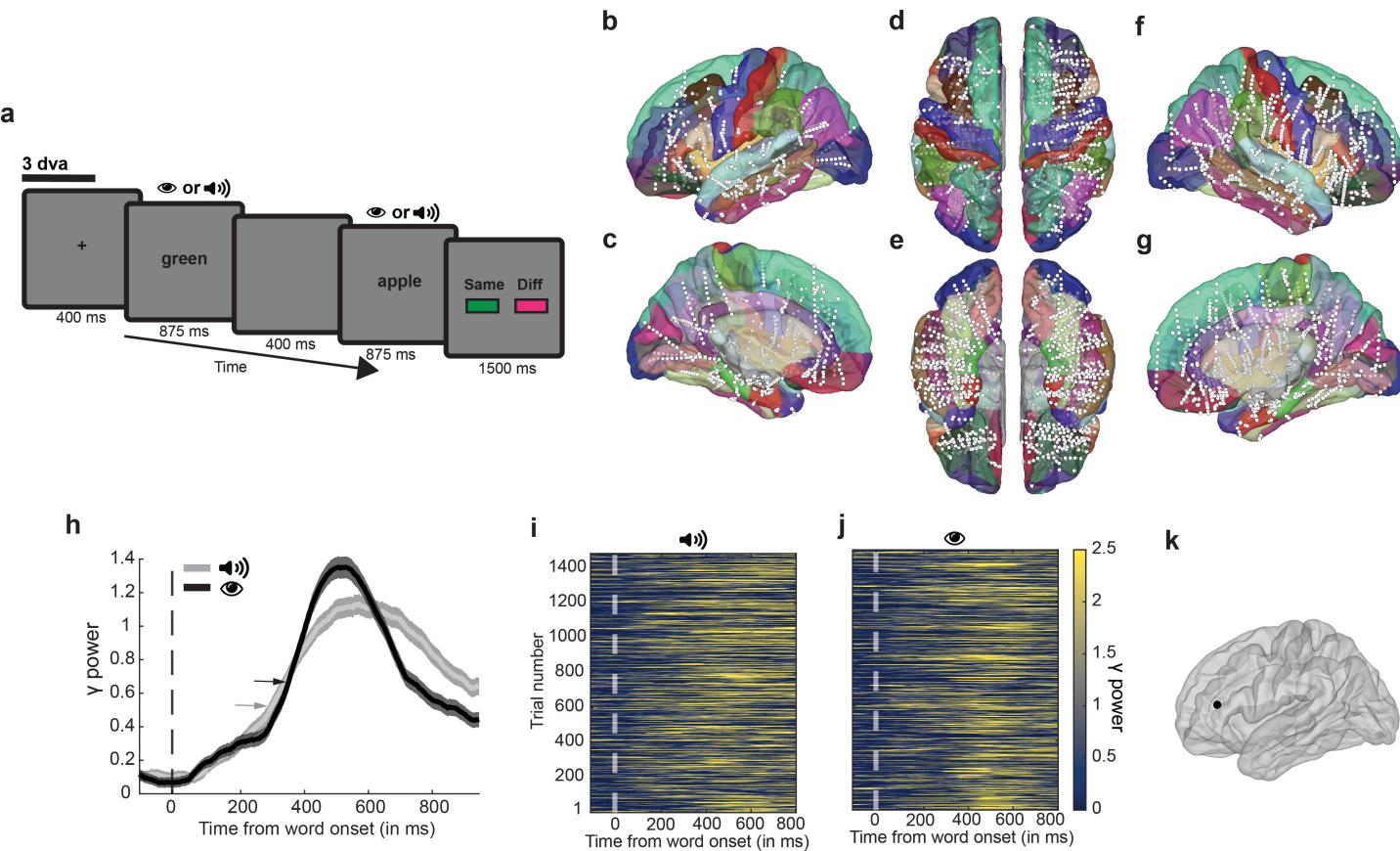


Fig. 1 | Task design, electrode locations and multimodal responses.

a. Task schematic. Two words were sequentially presented either in visual modality or auditory modality. Participants indicated whether the two words were the same (e.g., “apple apple” or “green green”, 8% of trials of each type) or different (e.g., “green apple” or “apple green”: 42% of trials of each type, Methods). In the 84% of trials where the two-words were different, there was an adjective followed by a noun or a noun followed by an adjective. **b-f.** Location of all electrodes overlaid on the Desikan-Killiany Atlas shown with different views. Each white circle shows one electrode. **b.** Left lateral view (n=693), **c.** Left medial view (n=693), **d.** Superior, whole brain view (n=1,801), **e.** Inferior, whole brain view (n=1,801), **f.** Right lateral view (n=1108), **g.** Right medial view (n=1108). **h.** Trial-averaged ($\pm$ SEM) gamma power for responses to auditory (light grey) or visual (black) presentations for an example electrode in the left rostral middle frontal gyrus (electrode location shown in **k**). Responses are aligned to word onset (vertical dashed line). The arrows indicate the half-maximum time. **i, j.** Raster plots showing each individual trial for the same electrode for each of the 1,496 words for auditor (**i**) and visual (**j**) presentations (see color scale on right).

Figure 2

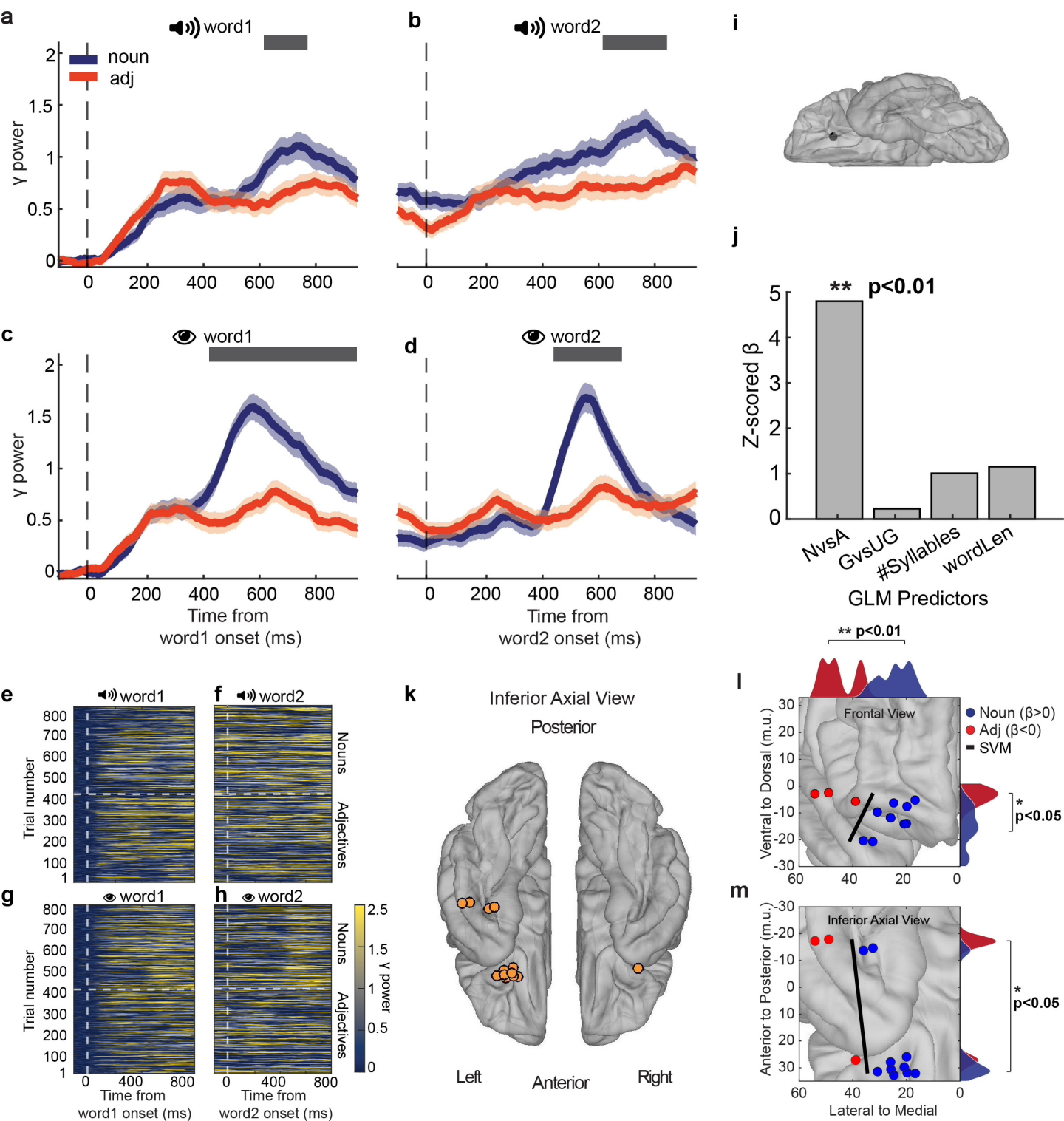


Fig. 2 | Neural signals distinguish between different parts of speech.

a-d. Trial-averaged normalized gamma-band power of responses from an example electrode in the left lateral orbitofrontal cortex (see location in **i**) to nouns (blue) or adjectives (red) during presentation of auditory stimuli (**a, b**, $n=435$ grammatical and 432 ungrammatical trials) or visual stimuli (**c, d**, $n=435$ grammatical and 432 ungrammatical trials) aligned to the onset (vertical dashed line) of the first word (**a, c**) or second word (**b, d**). Shaded areas denote s.e.m. Horizontal gray lines denote windows of statistically significant differences between responses to nouns versus adjectives (t-test $p<0.05$, Benjamini-Hochberg false detection rate, $q<0.05$).

e-h. Raster plots showing the responses in each individual trial (see color scale on bottom right). The red and blue curves in **a-d** correspond to the averages of noun and adjective trials, respectively, in **e-h**.

i. Location of the example electrode in the left lateral orbitofrontal cortex.

j. Z-scored β coefficients for Generalized Linear Model used to predict area under the curve between 200 ms and 800 ms post word onset, using four task predictors: Noun versus Adjectives, Grammatically correct versus incorrect, number of syllables (auditory presentation) and word length (visual presentation). Asterisks denote statistically significant coefficients, corrected for multiple comparisons (**Methods**).

k. Inferior axial view of both hemispheres showing electrodes that revealed statistically significant differences between nouns and adjectives for both audio and visual presentation (orange circles, $n=13$ electrodes). Electrodes whose responses were significantly explained only by the Nouns versus Adjective task predictor in the GLM are included in this plot.

l, m. All electrodes from **k** projected onto the left hemisphere are shown on the frontal plane (**l**) and the axial plane (**m**, same plane as **k**). All the electrodes that respond more strongly to nouns, i.e., Nouns versus Adjectives $\beta>0$ ($n=10$ electrodes), are shown in blue and electrodes that responded more strongly to adjectives ($\beta<0$, $n=3$ electrodes), are shown in red. All units are in MNI305 coordinates. Linear support vector machines separating these electrodes are shown with a thick black line. Kernel density curves (bandwidth 2) outline the marginal distributions of noun-preferring (blue) and adjective-preferring (red) electrodes along the lateral-medial axis (**l**: top x-axis, zero being more medial), ventral-dorsal axis (**l**: right y-axis) and anterior-posterior axis (**m**: right y-axis). P-values indicate significant differences between the coordinates for noun- and adjective-preferring electrodes (ranksum test).

Figure 3

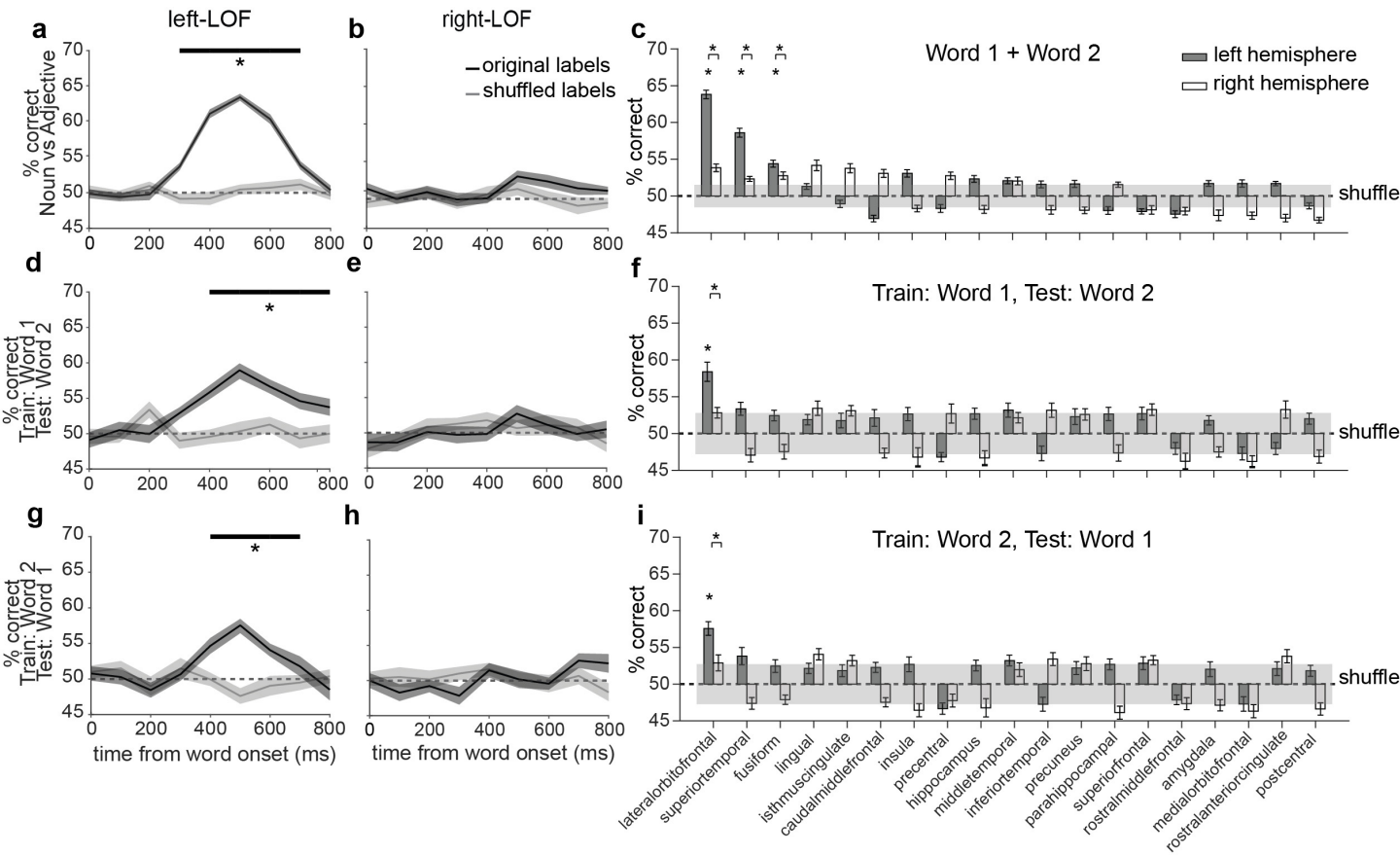


Fig. 3 | Neural signals distinguishing nouns and adjectives in single trials generalize across Word1, and Word2.

a, b, d, e, g, h. Average cross-validated performance of a support vector machine classifier (SVM, 80% training/20% test) decoding nouns versus adjectives for all electrodes in the left lateral orbitofrontal cortex (LOF) (**a, d, g**) or the right LOF (**b, e, h**). The dotted horizontal black line shows the chance level. Shaded areas denote s.e.m. Solid horizontal black bar shows time points where performance significantly differed from chance (100 random shuffles, ranksum test, $p < 0.01$). The inputs to the SVM included the top-N principal components of the electrode response that explained $> 70\%$ variance for the training data at each time bin (**Methods**). **a, b:** Features from auditory and visual responses were combined and used for training and testing on a dataset of both Word1 and Word2 trials. **c, d:** Generalization across word order was evaluated on a dataset where Word1 trials were used for training and word2 trials were used for testing. **g, h:** Training on Word2 and testing on Word1. Black: original labels; Gray: shuffled labels.

c, f, i. Summary of average of max-decoding performance for distinguishing nouns versus adjectives in each hemisphere (dark: left; white: right) for different brain regions. Bottom asterisks denote regions with significant decoding performance with respect to chance and performance from the real and null distribution do not overlap within 3 standard deviations of each other ($p < 0.01$, ranksum test, corrected for multiple comparisons, **Methods**). Shaded box: maximum of the mean $\pm$ SD. for the null distribution across all regions. Top asterisks with a U-bracket denote significant differences between decoding accuracy of the left versus the right hemisphere ($p < 0.01$, ranksum test, corrected for multiple comparisons). Regions are sorted in descending order of performance in panel **c**. **c:** Classifiers were trained and tested with features from both Word1 and Word2 trials. **f:** Classifiers were trained on Word1 trials and tested on Word2 trials. **i:** Classifiers were trained on Word2 trials and tested on Word1 trials.

Figure 4

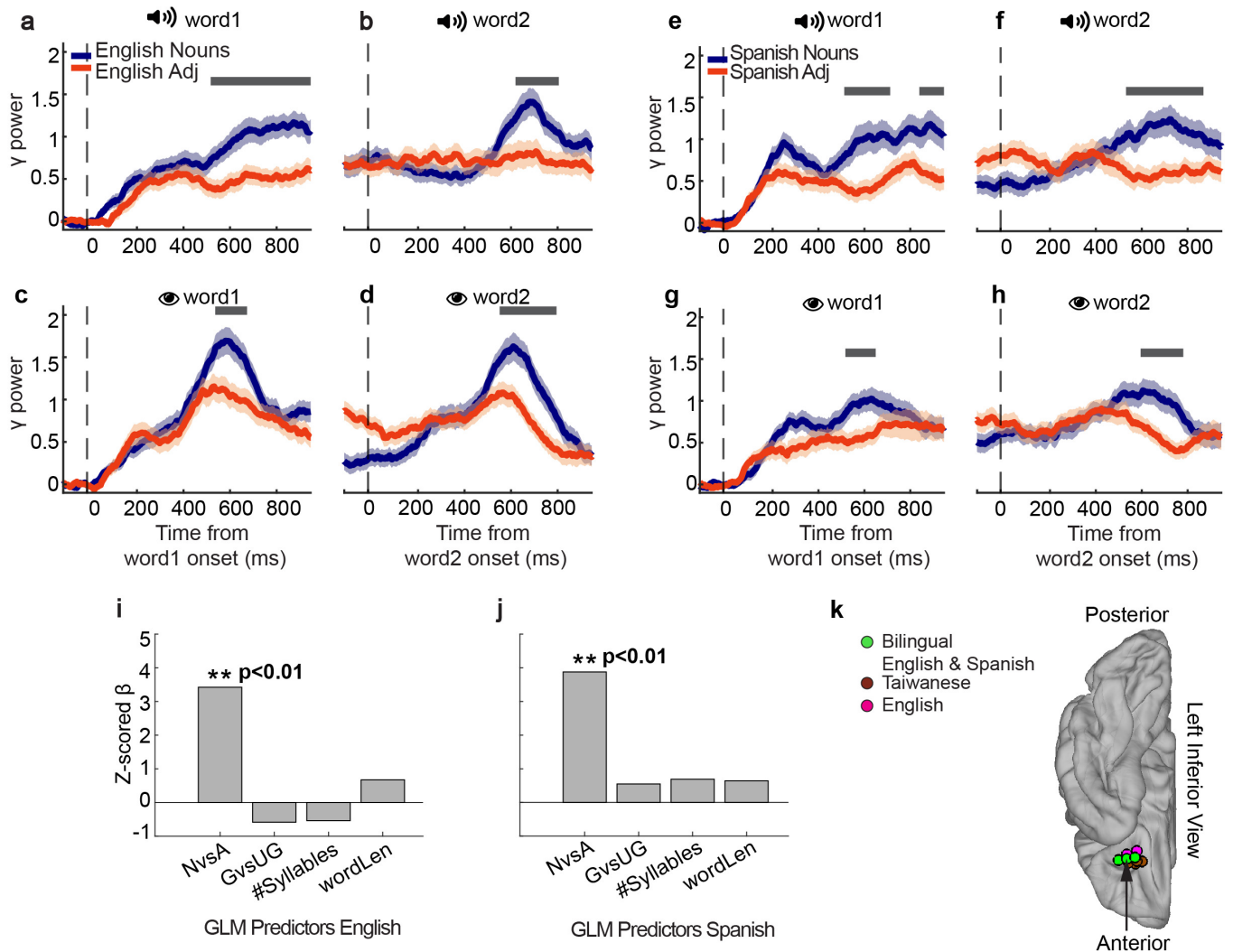


Fig. 4 | Neural signals in left LOF generalize across languages in a bilingual subject and in monolingual subjects. a-h. Trial averaged responses of an electrode in the left lateral orbitofrontal cortex from a bilingual patient. The format follows **Fig. 2a-d**. (**a-d**) English words (audio: $n=190$ grammatical and 185 ungrammatical trials; vision: $n=189$ grammatical and 191 ungrammatical trials). (**e-h**) Spanish words (audio: $n=184$ grammatical and ungrammatical trials; vision: 184 grammatical and 186 ungrammatical trials). Auditory responses (**a, b, e, f**). Visual responses (**c, d, g, h**). Word 1 (**a, c, e, g**) and Word 2 (**b, d, f, h**). **i, j.** Z-scored β coefficients for Generalized Linear Model to predict area under the curve (AUC) for the English experiment (**i**) and for the Spanish experiment (**j**). The AUC computed between 200 ms and 800 ms post word onset using four task predictors: Noun versus Adjectives, Grammatical versus Ungrammatical, number of syllables (auditory presentation) and word length (visual presentation). Asterisks denote statistically significant coefficients corrected for multiple comparisons (**Methods**). The word order for grammatically correct trials in English is an adjective followed by a noun, such as “green apple”. This word order gets flipped in grammatically correct Spanish trials. **k.** Inferior view of all the 9 out of 38 electrodes (8 audiovisual: **Figure 2k**, 1 visual-only: **Figure S4**, see **Table S4** and **S7**) in the left lateral orbitofrontal cortex that showed noun versus adjective differences across different languages in which the experiment was conducted (significant Nouns versus Adjectives β , $p < 0.01$ corrected for multiple comparisons). These electrodes come from 4 different subjects. Electrodes from the bilingual patient are in green with a black arrow indicating the example electrode. Electrodes from one monolingual English patient are in pink and those from 2 monolingual Taiwanese patients are in brown.

FIGURE S1

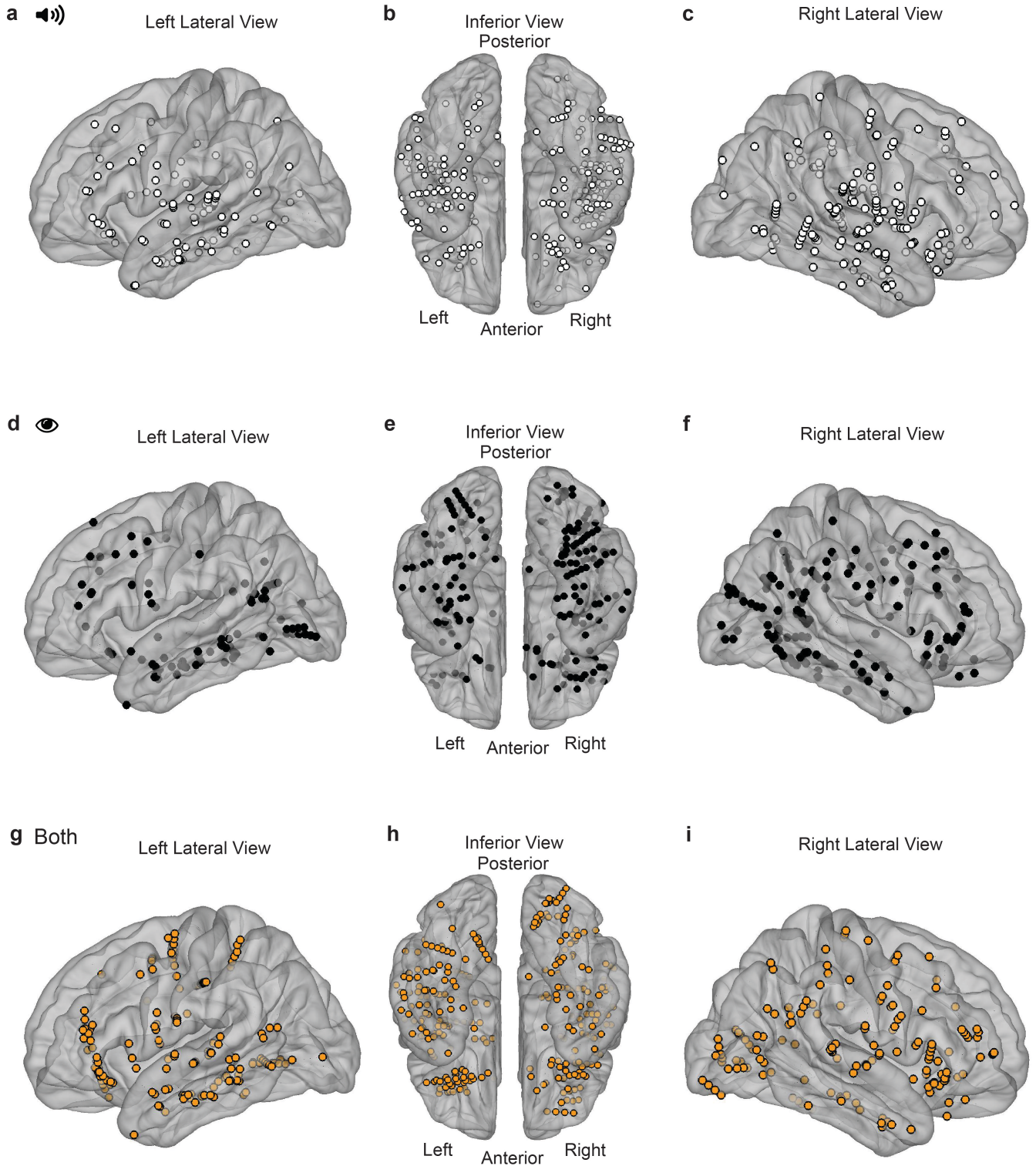


Fig. S1 | Location of responsive electrodes. **a-c.** Only audio responsive electrodes (**a:** left hemisphere lateral view, $n=102$; **b:** inferior view ($n=272$); **c:** right hemisphere lateral view, $n=170$). **d-f.** Only visually responsive electrodes (**d:** $n=85$; **e:** $n=239$; **f:** $n=154$). **g-i.** Audiovisual responsive electrodes (**g:** $n=147$; **h:** $n=293$; **i:** $n=146$). The same color scheme is followed throughout the paper to indicate vision-only, audio-only or audiovisual electrodes. iELVis pullout factor=20, opaqueness=0.6.

FIGURE S2

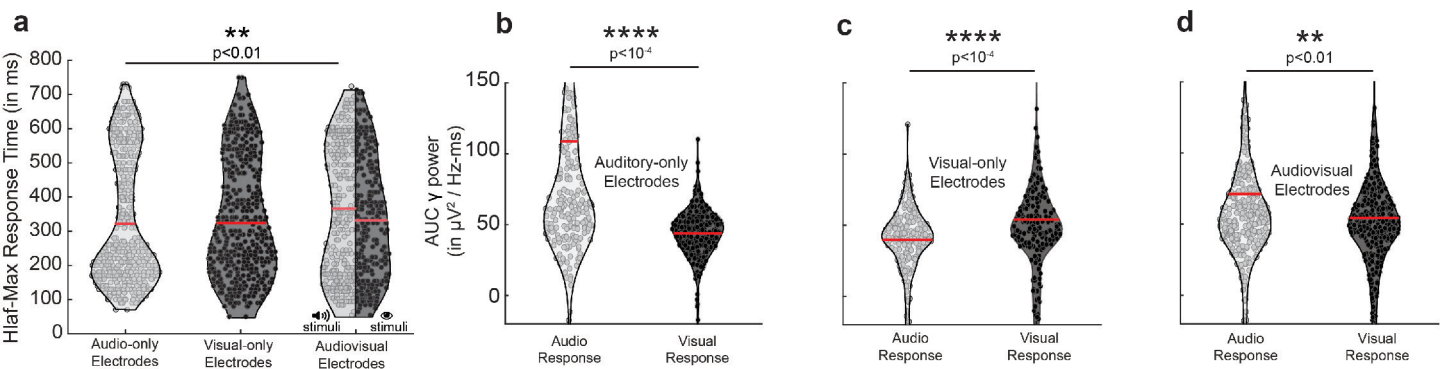


Fig. S2 | Half-maximum time and area under the curve for responsive electrodes. a.. Half-maximum time for audio-only electrodes (left, light-gray: 329 ± 187 ms), visual-only electrodes (middle, black: 336 ± 174 ms), and audiovisual electrodes (right; auditory stimuli in light-gray: 379 ± 193 ms, visual stimuli in black: 341 ± 174 ms). There was a small but significant difference between the half-maximum time for auditory-only electrodes and for auditory responses of audiovisual electrodes ($p < 0.01$, ranksum test). Horizontal red bars indicate mean. Horizontal black bars indicate significant differences.

b-d. Area under the curve for the trial averaged response to auditory stimuli (light-gray violin plots) and visual stimuli (black violin plots) for audio-only electrodes (**b**, auditory stimuli: $108 \pm 100 \mu V^2 / \text{Hz-ms}$, visual stimuli: $44 \pm 16 \mu V^2 / \text{Hz-ms}$; $p < 10^{-4}$, ranksum test), visual-only electrodes (**c**, auditory stimuli: $40 \pm 23 \mu V^2 / \text{Hz-ms}$, visual stimuli: $53 \pm 43 \mu V^2 / \text{Hz-ms}$; $p < 10^{-4}$, ranksum test), and audiovisual electrodes (**d**, auditory stimuli: $71 \pm 72 \mu V^2 / \text{Hz-ms}$, visual stimuli: $54 \pm 39 \mu V^2 / \text{Hz-ms}$; $p < 0.01$, ranksum test). Horizontal red bars indicate mean. Horizontal black bars indicate significant differences.

FIGURE S3

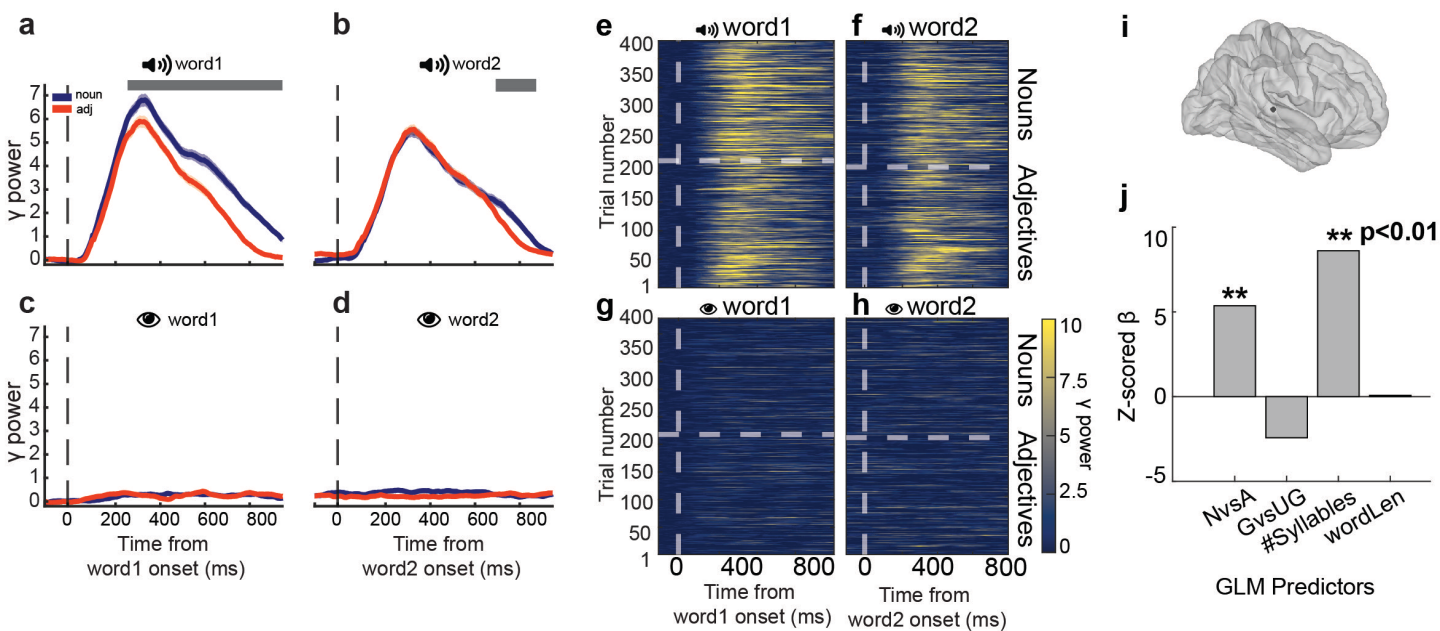


Fig. S3 | Example electrode distinguishing parts of speech only for auditory stimuli. a-d. Trial averaged γ -power of neural responses to Taiwanese words, separated by nouns (blue) and adjectives (red). Neural responses are shown for auditory presentation (**a**, **b**), and visual presentation (**c**, **d**), aligned to word1 onset (**a**, **c**) or word2 onset (**b**, **d**). The vertical dashed lines show word onsets. Shaded areas represent s.e.m. Horizontal lines indicate time periods of statistically significant differences between nouns and adjectives (t-test, $p < 0.05$, Benjamini-Hochberg false detection rate, $q < 0.05$). There was a significant differences between noun and adjectives for auditory presentations shown with a gray horizontal line but no difference for visual presentations.

e-h. Raster plots showing the responses in individual trials (see color scale on bottom right).

i. Electrode location in the right insula.

j. Z-scored β coefficients for Generalized Linear Model used to predict area under the curve between 200 ms and 800 ms post word onset using four task predictors: Noun versus Adjectives, Grammatically Correct versus Ungrammatical, number of syllables (auditory presentation) and word length (visual presentation). Asterisks denote statistically significant coefficients.

FIGURE S4

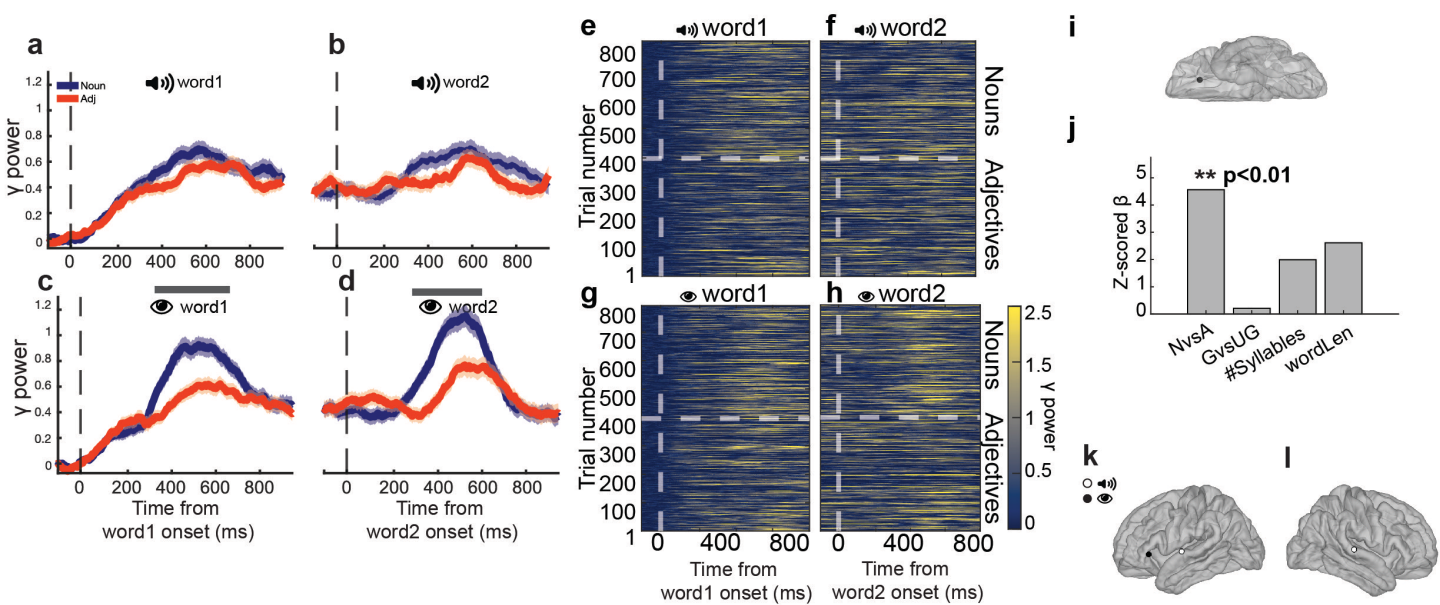


Fig. S4 | Example electrode distinguishing parts of speech only for visual stimuli. **a-d.** Trial averaged γ -power of neural responses to Taiwanese words, separated by nouns (blue) and adjectives (red). Neural responses are shown for auditory presentation (**a, b**), and visual presentation (**c, d**), aligned to word 1 onset (**a, c**) or word 2 onset (**b, d**). The vertical dashed lines show word onsets. Shaded areas represent s.e.m. Horizontal lines indicate time periods of statistically significant differences between nouns and adjectives (t-test, $p < 0.05$, Benjamini-Hochberg false detection rate, $q < 0.05$). There was a significant differences between noun and adjectives for visual presentations shown with a gray horizontal line but no difference for auditory presentations.

e-h. Raster plots showing the responses in individual trials (see color scale on bottom right).

i. Electrode location in the left lateral orbitofrontal.

j. Z-scored β coefficients for Generalized Linear Model used to predict area under the curve between 200 ms and 800 ms post word onset using four task predictors: Noun versus Adjectives, Grammatically Correct versus Ungrammatical, number of syllables (auditory presentation) and word length (visual presentation). Asterisks denote statistically significant coefficients.

k, l. Electrodes in the left (**k**) and right (**l**) hemispheres that showed significant differences between nouns and adjectives either only for auditory trials (white circles) or visual trials (black circles).

FIGURE S5

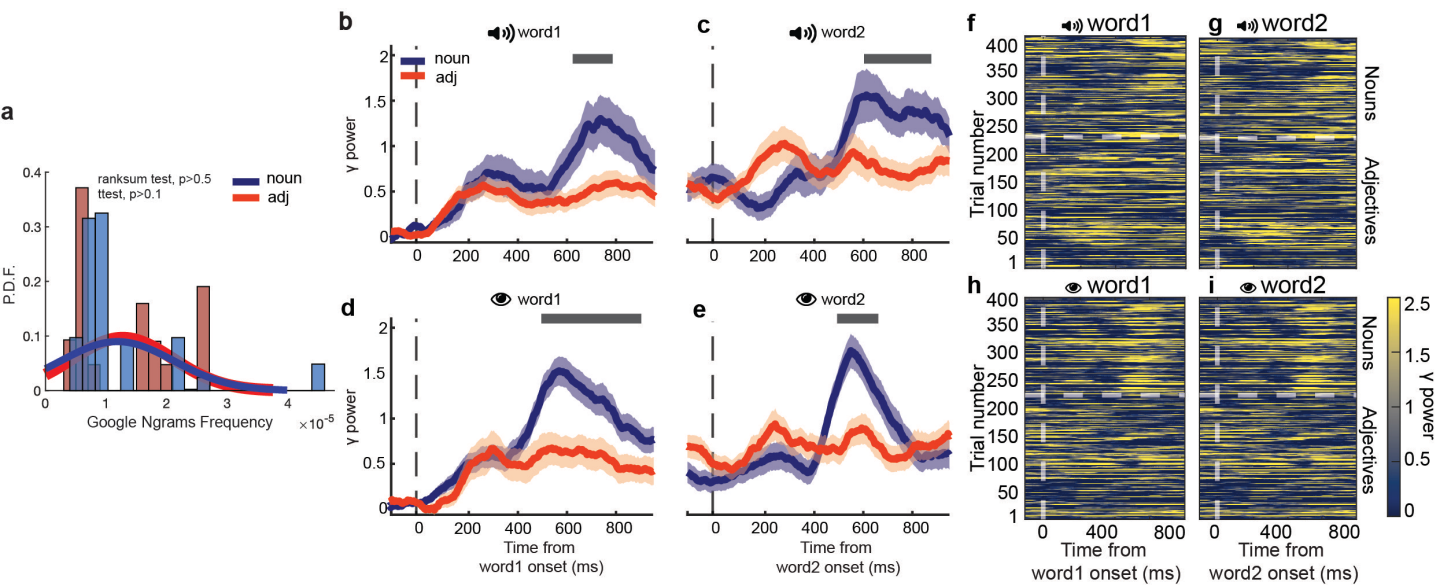


Fig. S5 | Example electrode distinguishes parts-of-speech for nouns and adjectives matched for their frequency of occurrence. **a.** Google Ngrams frequency distribution of nouns (blue) and adjectives (red) that were matched for their median ($p > 0.05$, ranksum test) and mean ($p > 0.05$, t-test)

b-e. Trial averaged γ -power of neural responses to word onsets, separated by nouns (blue) and adjectives (red). Neural responses are shown for auditory presentation (**b, c**), and visual presentation (**d, e**), aligned to word 1 onset (**a, c**) or word 2 onset (**c, e**). The vertical dashed lines show word onsets. Shaded areas represent s.e.m. Horizontal lines indicate time periods of statistically significant differences between noun subcategories and adjective subcategories (t-test, $p < 0.05$, Benjamini-Hochberg false detection rate, $q < 0.05$).

f-i. Raster plots showing the responses in individual trials (see color scale on bottom right).

FIGURE S6

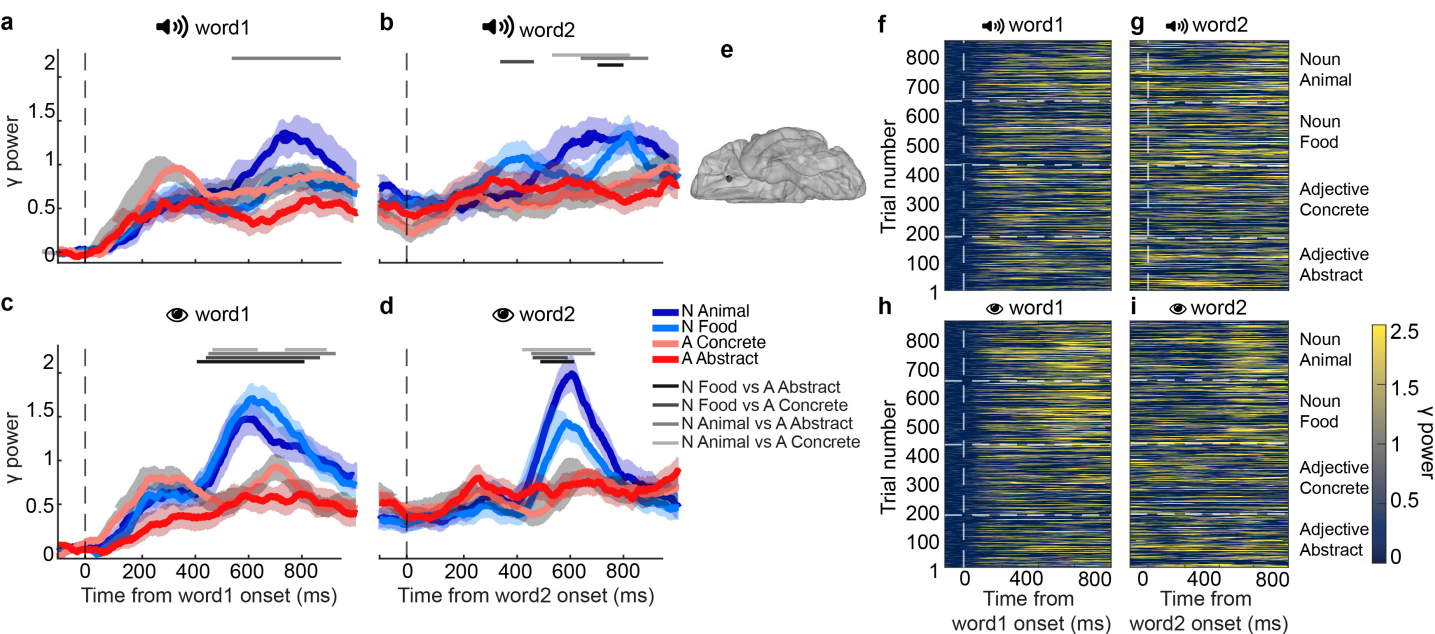


Fig. S6 | Selective responses to nouns versus adjectives across different noun and adjective categories. **a-d.** Trial averaged γ -power of neural responses to Taiwanese words, separated by animal nouns (dark blue), food nouns (light blue), concrete adjectives (light red), and abstract adjectives (dark red). Neural responses are shown for auditory presentation (**a**, **b**), and visual presentation (**c**, **d**), aligned to word 1 onset (**a**, **c**) or word 2 onset (**b**, **d**). The vertical dashed lines show word onsets. Shaded areas represent s.e.m. Horizontal lines indicate time periods of statistically significant differences between noun subcategories and adjective subcategories (t-test, $p < 0.05$, Benjamini-Hochberg false detection rate, $q < 0.05$). There were no significant differences between noun sub-categories or between adjective sub-categories.

e. Electrode location in left lateral orbitofrontal.

f-i. Raster plots showing the responses in individual trials (see color scale on bottom right).

FIGURE S7

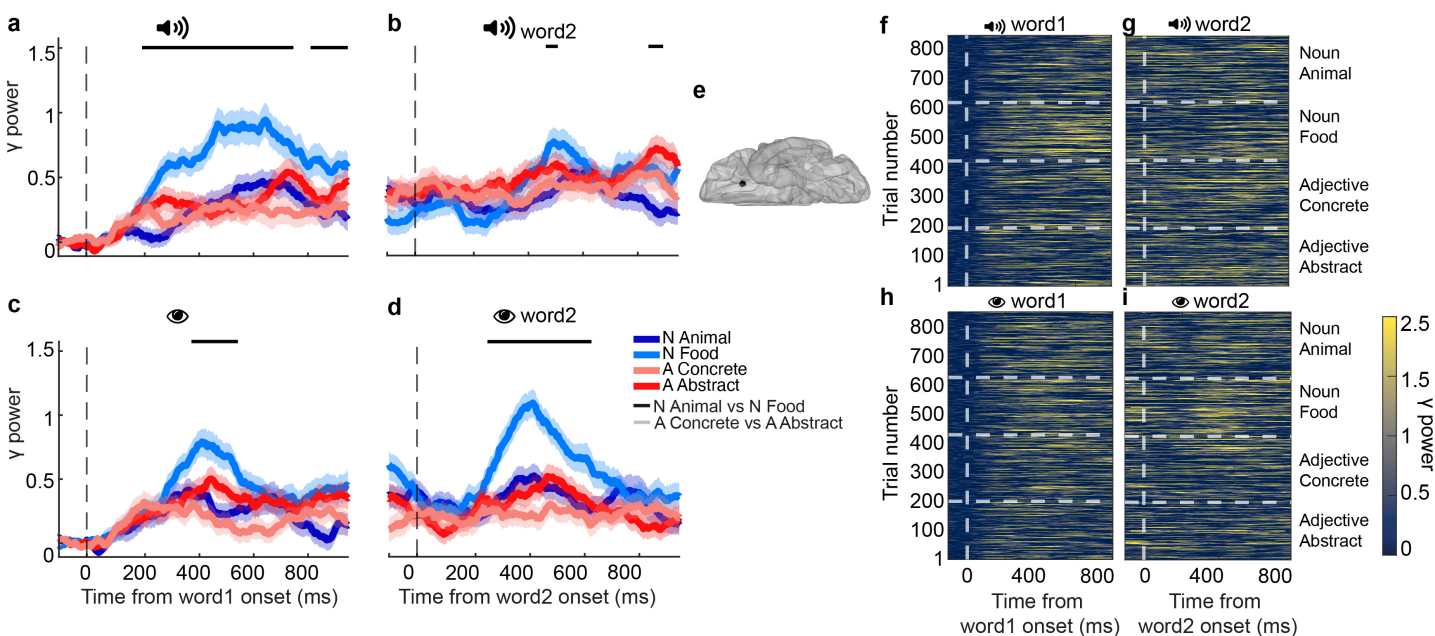


Fig. S7 | Example electrode distinguishing different types of nouns. **a-d.** Trial averaged γ -power of neural responses to English words, separated by animal nouns (dark blue), food nouns (light blue), concrete adjectives (light red), and abstract adjectives (dark red). Neural responses are shown for auditory presentation (**a, b**), and visual presentation (**c, d**), aligned to word 1 onset (**a, c**) or word 2 onset (**b, d**). The vertical dashed lines show word onsets. Shaded areas represent s.e.m. Horizontal lines indicate time periods of statistically significant differences between noun subcategories and adjective subcategories (t-test, $p < 0.05$, Benjamini-Hochberg false detection rate, $q < 0.05$). There was a significant differences between noun sub-categories shown with a black horizontal line but no difference between adjective sub-categories.

e. Electrode location in the left lateral orbitofrontal.

f-i. Raster plots showing the responses in individual trials (see color scale on bottom right).

FIGURE S8

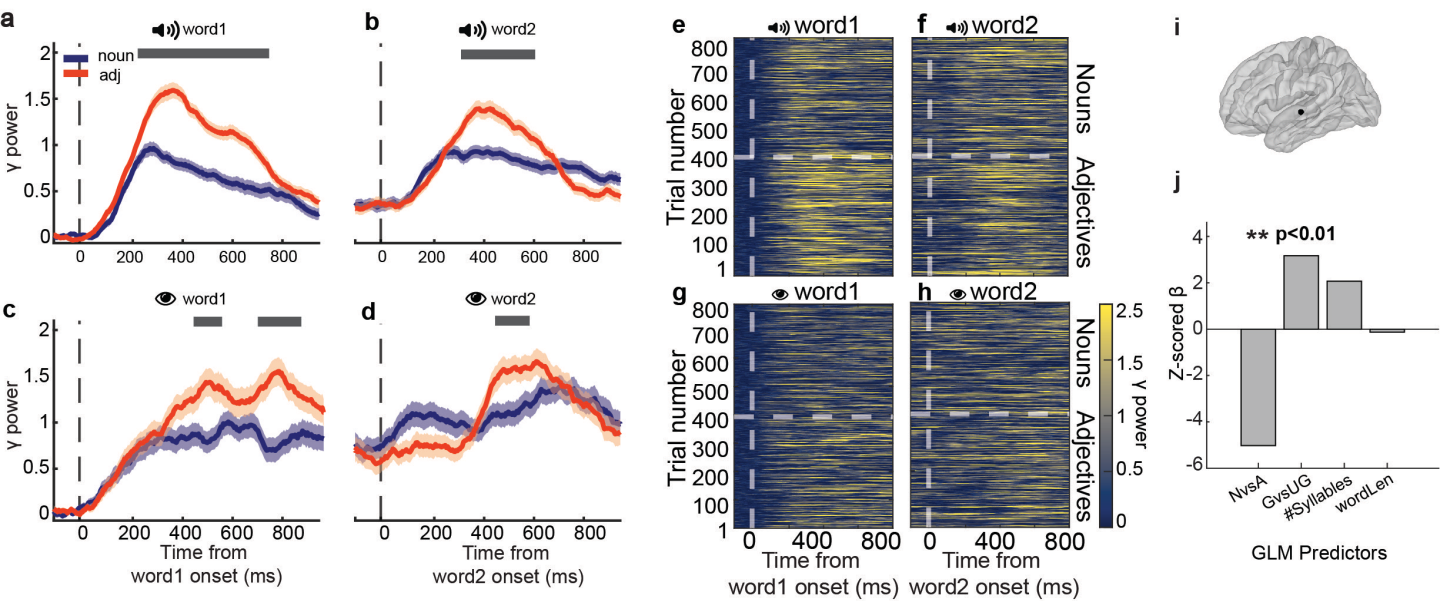


Fig. S8 | Example electrode distinguishing nouns from adjectives with a preference for adjectives. a-d. Trial averaged γ -power of neural responses to English words, separated by nouns (blue), and adjectives (red). Neural responses are shown for auditory presentation (**a**, **b**, $n=442$ grammatical and 438 ungrammatical trials), and visual presentation (**c**, **d**, $n=432$ grammatical and 434 ungrammatical trials), aligned to word 1 onset (**a**, **c**) or word 2 onset (**b**, **d**). The vertical dashed lines show word onsets. Shaded areas represent s.e.m. Horizontal lines indicate time periods of statistically significant differences between nouns and adjectives (t-test, $p < 0.05$, Benjamini-Hochberg false detection rate, $q < 0.05$).

e-h. Raster plots showing the responses in individual trials (see color scale on bottom right).

i- Electrode location in the left superior temporal gyrus.

j-k. Z-scored β coefficients for Generalized Linear Model used to predict area under the curve between 200 ms and 800 ms post word using four task predictors: Noun versus Adjectives, Grammatical versus Ungrammatical, number of syllables (auditory presentation) and word length (visual presentation). Asterisks denote statistically significant coefficients. Only the Nouns vs Adjective task predictor was significant and showed a preference for adjectives ($p < 0.01$, corrected for multiple comparisons and $\beta_{NvsA} < 0$).

FIGURE S9

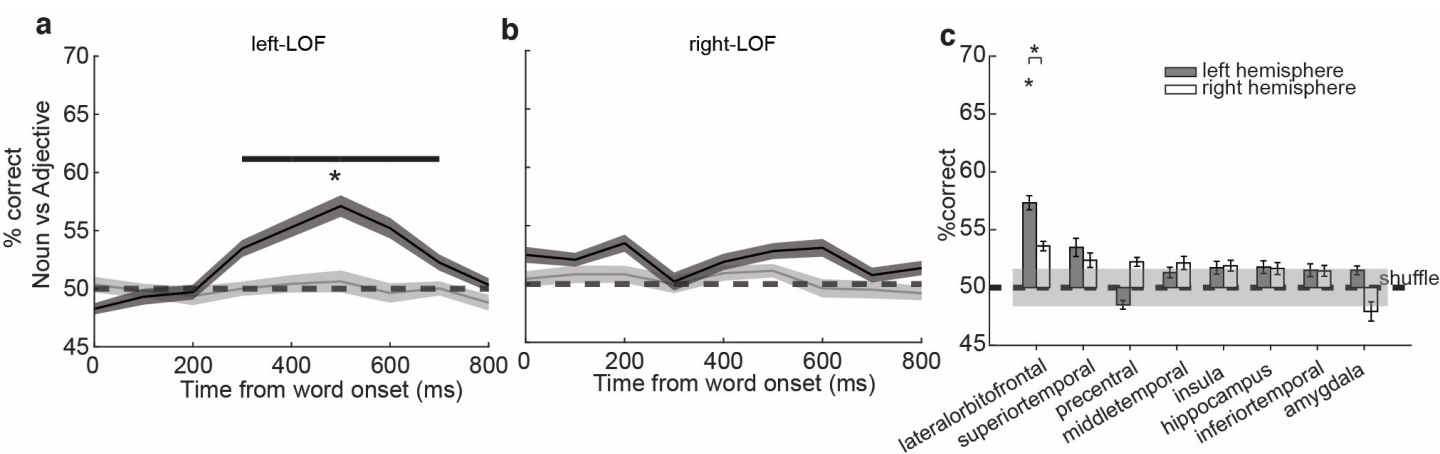


Fig. S9 | Neural signals from left-LOF distinguish nouns and adjectives when number of electrodes were normalized across all regions and both hemispheres. a-b. Average cross-validated performance of a support vector machine classifier (SVM, 80% training/20% test) decoding nouns versus adjectives for 8 randomly subsampled electrodes in the left lateral orbitofrontal cortex (LOF) (**a**), and in the right LOF (**b**).

Black: original labels; Gray: shuffled labels. The dotted horizontal black line shows the chance level. Solid horizontal gray bar shows time points where decoding from correct labels significantly differed from that of shuffled labels (100 random shuffles of the data, ranksum test, $p < 0.01$). The inputs to the SVM were 100 ms time bins from word onset containing the top-N principal components of the electrode response at each bin that explained $> 70\%$ variance for the training data (**Methods**).

c. Summary of average of max-decoding performance for distinguishing nouns versus adjectives across both hemispheres (left hemisphere: dark gray bars; right hemisphere: white bars) for different brain regions when a total of 8 electrodes was taken from each hemisphere in each region for the decoding. Regions with less than 8 electrodes in either hemisphere were omitted.

Asterisk: significant hemisphere within a Desikan-Killiani defined brain region ($p < 0.01$, ranksum test, corrected for multiple comparisons, and performance from the real and null distribution do not overlap within 3 standard deviations of each other) (**Methods**). Gray box: maximum mean $\pm$ s.t.d. for the null distribution across all regions. Asterisk with a U-bracket: significant difference between decoding accuracy of the left versus the right hemisphere ($p < 0.01$, ranksum test, corrected for multiple comparisons). Regions are sorted in descending order of performance in panel **c**.

FIGURE S10

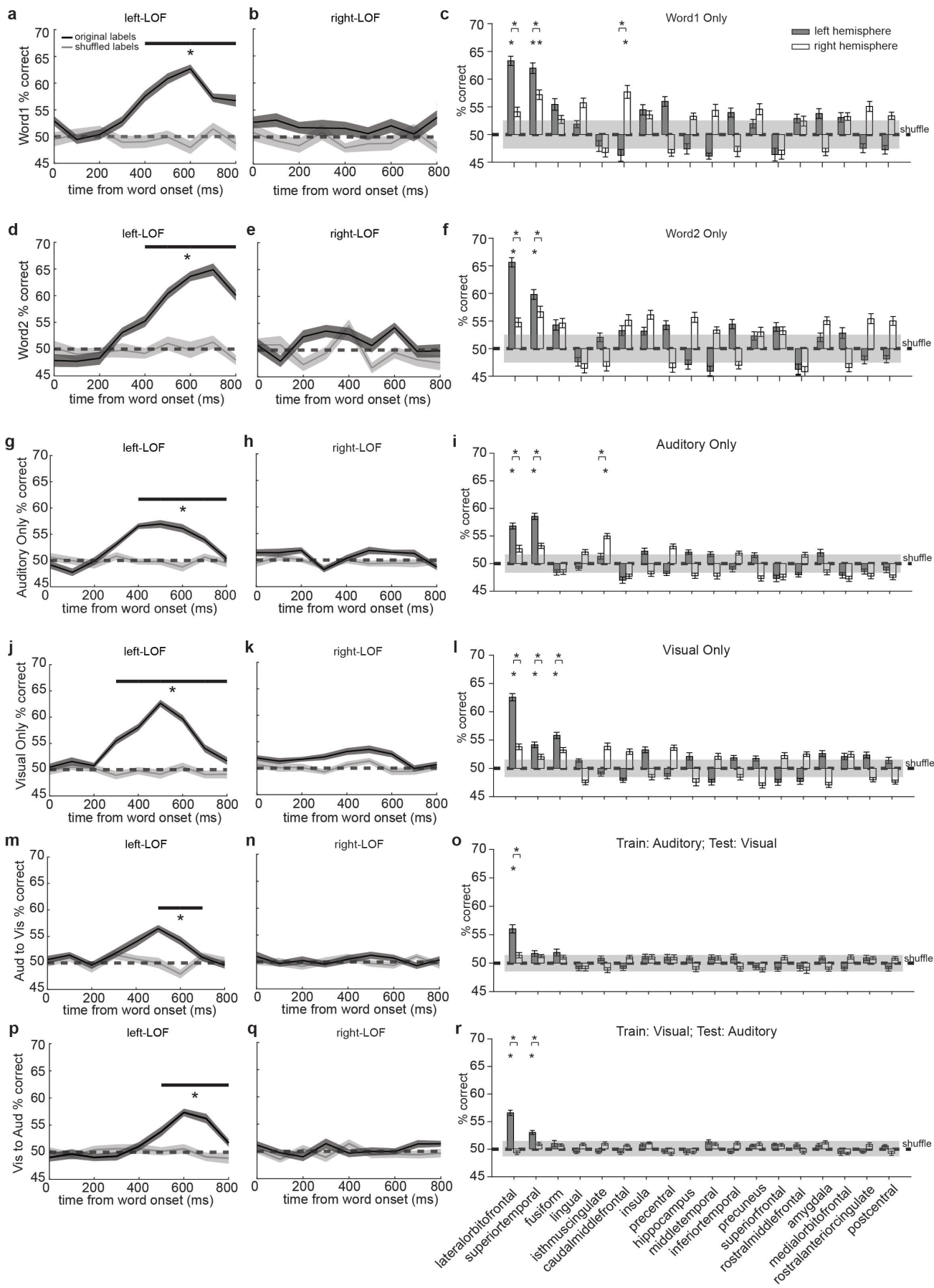


Fig. S10 | Neural signals distinguish nouns and adjectives in single trials for word1-only, word2-only, audio-only features, vision-only features, and generalization from audio to vision or vice versa.

a, b, d, e, g, h, m, n, p, q. Average cross-validated performance of a support vector machine classifier (SVM, 80% training/20% test) decoding nouns versus adjectives for all electrodes in the left lateral orbitofrontal cortex (LOF) (**a,d,g,j,m,p**), and in the right LOF (**b,e,h,k,n,q**). The dotted horizontal black line shows the chance level. Shaded areas denote s.e.m. Solid horizontal black bar shows time points where performance significantly differed from chance (100 random shuffles, ranksum test, $p < 0.01$). The inputs to the SVM included the top-N principal components of the electrode response that explained $>70\%$ variance for the training data at each time bin (**Methods**). Features from auditory and visual responses were combined and used for training and testing on datasets of word1 (**a,b**) and word2 trials (**d,e**). Using a combined dataset of word1 and word2 trials, the decoding performance was evaluated for audio-only (**g,h**) and vision-only features (**j,k**). The decoding performance generalized for audio to vision (**m,n**) and vice versa (**p,q**).

c, f, i, l, o, r . Summary of average of max-decoding performance for distinguishing nouns versus adjectives in each hemisphere (dark: left; white: right) for different brain regions. Bottom asterisks denote regions with significant decoding performance with respect to chance and performance from the real and null distribution do not overlap within 3 standard deviations of each other ($p < 0.01$, ranksum test, corrected for multiple comparisons, Methods). Shaded box: maximum of the mean $\pm$ SD. for the null distribution across all regions. Top asterisks with a U-bracket denote significant differences between decoding accuracy of the left versus the right hemisphere ($p < 0.01$, ranksum test, corrected for multiple comparisons). **c**: Classifiers were trained and tested on Word1 trials. **f**: Classifiers were trained and tested on Word2 trials. **i**: Classifiers were trained and tested on audio trials. **l**: Classifiers were trained and tested on visual trials. **o**: Classifiers were trained on audio trials and tested on visual trials. **r**: Classifiers were trained on visual trials and tested on audio trials.

Subject	Age	Gender	Language	Handedness	#Trials	%Correct	#Electrodes
1	9	M	EN	R	1178	98.5	142
2	14	F	EN	R	1332	94.7	100
3	22	M	EN	R	1520	97.5	212
4	49	F	EN	L	760	83.3	44
5	18	F	EN	R	3573	99.6	100
6	20	M	EN	R	760	99.3	139
					760	67.5	
7	16	F	EN	L	760	97.9	88
8	12	F	EN	R	760	92.9	131
9	37	F	EN	R	1900	89.3	51
10	47	F	EN	R	1895	98.3	75
11	12	M	EN	R	950	95.5	135
12	13	F	EN	R	950	99.3	121
13	25	M	EN	L write, R throw	1520	99.3	84
14	26	F	EN	L write, R other	1900	97.4	32
15	32	F	EN	R	1521	98.4	29
					EN:950		
16	22	M	EN & SP	R	SP:950	97.3	77
17	42	M	TW	R	1068	89	57
18	36	M	TW	R	2429	87.1	59
19	53	F	EN	R	950	90.5	73
20	44	M	TW	R	1900	NA	52
TOTAL							1801

Table S1 | Information about each participant including age, gender, language (English, Spanish, Taiwanese), handedness, number of trials, behavioral performance and number of electrodes.

Region\nelecs	Total	GMLeft	WMLeft	Left	GMRight	WMRight	Right	rAud	rVis	rAV
Amygdala	52	21	0	21	31	0	31	9	7	1
Cerebellum-Cortex	4	3	0	3	1	0	1	2	1	1
Hippocampus	59	33	0	33	26	0	26	15	14	5
Inf-Lat-Vent	1	1	0	1	0	0	0	0	1	0
Lateral-Ventricle	4	0	0	0	4	0	4	0	1	0
Putamen	2	1	0	1	1	0	1	1	0	0
VentralDC	1	1	0	1	0	0	0	0	0	0
bankssts	24	2	4	6	9	9	18	20	11	9
caudalanteriorcingulate	17	3	1	4	3	10	13	0	0	0
caudalmiddlefrontal	52	2	12	14	21	17	38	11	14	7
cuneus	16	0	3	3	10	3	13	6	8	5
entorhinal	6	1	1	2	2	2	4	0	1	0
frontalpole	1	0	0	0	1	0	1	1	1	1
fusiform	108	19	32	51	27	30	57	40	41	21
inferiorparietal	73	3	17	20	31	22	53	14	35	11
inferiortemporal	119	14	38	52	31	36	67	22	26	15
insula	109	18	29	47	29	33	62	45	24	12
isthmuscingulate	32	7	4	11	11	10	21	6	4	1
lateraloccipital	41	2	8	10	13	18	31	16	26	9
lateralorbitofrontal	113	7	31	38	38	37	75	45	40	29
lingual	45	6	13	19	8	18	26	21	33	17
medialorbitofrontal	47	10	8	18	14	15	29	6	9	5
middletemporal	117	27	39	66	24	27	51	28	20	8
paracentral	4	0	0	0	2	2	4	0	0	0
parahippocampal	27	12	4	16	6	5	11	3	3	1
parsopercularis	18	5	4	9	4	5	9	10	7	5
parsorbitalis	20	2	5	7	7	6	13	4	7	4
parstriangularis	34	3	4	7	16	11	27	9	10	7
pericalcarine	13	3	2	5	3	5	8	8	8	6
postcentral	37	2	6	8	10	19	29	13	12	7
posteriorcingulate	16	4	3	7	1	8	9	6	4	4
precentral	87	10	10	20	33	34	67	47	40	29
precuneus	80	12	24	36	14	30	44	6	15	3
rostralanteriorcingulate	16	3	4	7	5	4	9	0	0	0
rostralmiddlefrontal	94	16	22	38	24	32	56	27	28	18
superiorfrontal	85	17	16	33	19	33	52	18	18	9
superiorparietal	49	4	6	10	15	24	39	13	16	7
superiortemporal	108	20	38	58	15	35	50	69	28	26
supramarginal	56	0	0	0	30	26	56	15	12	5
temporalpole	4	3	1	4	0	0	0	1	2	0
transverse temporal	10	2	5	7	2	1	3	8	5	5
TOTAL	1801	299	394	693	541	567	1108	565	532	293

Table S2 | Distribution of electrodes over the Desikan-Killiany Atlas

The number of electrodes for different brain regions of the DK atlas (rows) for different conditions (columns). From the left to right the columns represent the following: (1) Total electrodes, (2) Gray Matter Left, (3) White Matter Left, (4) Total Left, (5) Gray Matter Right, (6) White Matter Right, (7) Total Right, (8) Responsive Audio, (9) Responsive Visual, (10) Responsive Audiovisual. The regions that showed a significant percent of audiovisual electrodes that was statistically unlikely to get from a random intersection of audio or visual electrodes are highlighted in bold ($p < 0.01$, permutation test, $n = 10^6$ iterations, total electrodes ≥ 20)

(a) ENGLISH

Noun Animal	Length	Syll.	Ngram Freq	Noun food	Length	Syll.	Ngram Freq
'fish'	4	1	6.42E-05	'water'	5	2	3.39E-04
'horse'	5	1	6.07E-05	'oil'	3	1	8.64E-05
'bear'	4	1	5.56E-05	'coffee'	6	2	3.94E-05
'dog'	3	1	5.33E-05	'salt'	4	1	3.70E-05
'bird'	4	1	3.20E-05	'fruit'	5	1	3.59E-05
'cat'	3	1	2.91E-05	'milk'	4	1	3.58E-05
'mouse'	5	1	2.31E-05	'sugar'	5	2	3.40E-05
'sheep'	5	1	1.95E-05	'tea'	3	1	3.33E-05
'turkey'	6	2	1.92E-05	'rice'	4	1	3.13E-05
'fox'	3	1	1.84E-05	'bread'	5	1	3.07E-05
'bull'	4	1	1.63E-05	'eggs'	4	1	2.13E-05
'rat'	3	1	1.49E-05	'corn'	4	1	2.00E-05
'wolf'	4	1	1.47E-05	'apple'	5	1	1.65E-05
'seal'	4	1	1.40E-05	'cheese'	6	1	1.53E-05
'lion'	4	2	1.36E-05	'butter'	6	2	1.51E-05
'deer'	4	1	1.24E-05	'pepper'	6	2	1.26E-05
'cow'	3	1	1.14E-05	'olive'	5	1	1.14E-05
'snake'	5	1	1.12E-05	'bean'	4	1	9.08E-06
'penguin'	7	2	1.05E-05	'garlic'	6	2	8.59E-06
'eagle'	5	2	9.73E-06	'salad'	5	2	8.55E-06
'dragon'	6	2	9.54E-06	'lemon'	5	2	8.49E-06
'pig'	3	1	9.35E-06	'onion'	5	2	6.42E-06
'bat'	3	1	9.28E-06	'berry'	5	1	6.39E-06
'tiger'	5	2	8.53E-06	'cherry'	6	1	6.27E-06
'rabbit'	6	2	8.41E-06	'pizza'	5	2	5.60E-06
'monkey'	6	2	6.86E-06	'nut'	3	1	5.20E-06
'duck'	4	1	6.70E-06	'pasta'	5	2	4.50E-06
'goat'	4	1	6.34E-06	'grape'	5	1	3.86E-06
'whale'	5	1	5.77E-06	'peas'	4	1	3.61E-06
'hawk'	4	1	5.56E-06	'peach'	5	1	3.22E-06
'spider'	6	2	5.46E-06	'plum'	4	1	2.78E-06
'ant'	3	1	5.33E-06	'lettuce'	7	2	2.68E-06
Adj concrete	Length	Syll.	Ngram Freq	Adj abstract	Length	Syll.	Ngram Freq
'long'	4	1	5.04E-04	'good'	4	1	5.76E-04
'small'	5	1	3.48E-04	'best'	4	1	2.69E-04
'large'	5	1	3.21E-04	'better'	6	2	2.63E-04
'low'	3	1	2.09E-04	'free'	4	1	2.17E-04
'short'	5	1	1.80E-04	'real'	4	1	2.10E-04
'clear'	5	1	1.74E-04	'poor'	4	1	1.42E-04
'hard'	4	1	1.59E-04	'bad'	3	1	1.09E-04
'strong'	6	1	1.47E-04	'serious'	7	2	8.12E-05
'big'	3	1	1.40E-04	'happy'	5	2	7.47E-05
'deep'	4	1	1.07E-04	'rich'	4	1	6.90E-05

'dark'	4	1	1.00E-04	'holy'	4	2	6.65E-05
'cold'	4	1	9.21E-05	'pretty'	6	2	5.84E-05
'round'	5	1	8.84E-05	'evil'	4	2	5.71E-05
'heavy'	5	2	6.79E-05	'wild'	4	1	5.37E-05
'hot'	3	1	6.75E-05	'pure'	4	1	4.79E-05
'fast'	4	1	6.44E-05	'sick'	4	1	3.45E-05
'dry'	3	1	5.33E-05	'busy'	4	2	2.96E-05
'soft'	4	1	5.22E-05	'sad'	3	1	2.54E-05
'slow'	4	1	4.84E-05	'proud'	5	1	2.53E-05
'solid'	5	2	4.74E-05	'calm'	4	1	2.47E-05
'huge'	4	1	4.71E-05	'gentle'	6	1	2.04E-05
'warm'	4	1	4.71E-05	'strict'	6	1	2.02E-05
'fat'	3	1	4.18E-05	'mad'	3	1	2.02E-05
'bright'	6	1	4.17E-05	'smart'	5	1	2.01E-05
'weak'	4	1	4.16E-05	'crazy'	5	2	1.70E-05
'thin'	4	1	4.10E-05	'brave'	5	1	1.55E-05
'sweet'	5	1	4.08E-05	'cheap'	5	1	1.49E-05
'silent'	6	1	3.65E-05	'ugly'	4	2	1.12E-05
'oval'	4	2	5.71E-06	'clever'	6	1	1.10E-05
'tiny'	4	2	2.93E-05	'jealous'	7	2	7.70E-06
'dirty'	5	2	1.58E-05	'shy'	3	1	7.70E-06
'massive'	7	2	2.52E-05	'lazy'	4	2	6.09E-06

(b) SPANISH

Noun Animal	Length	Syll.	Ngram Freq	Noun food	Length	Syll.	Ngram Freq
buho	4	2	6.00E-08	ajo	3	2	5.00E-06
burro	5	2	3.50E-06	arroz	5	2	1.30E-05
dragon	6	2	8.00E-08	café	4	2	5.00E-05
gallo	5	2	6.00E-06	coco	4	2	3.00E-06
gato	4	2	1.40E-05	frijol	6	2	4.50E-06
leon	4	1	2.20E-07	huevo	5	2	1.00E-05
lobo	4	2	7.80E-06	jamon	5	2	2.50E-08
mono	4	2	6.00E-06	jugo	4	2	5.90E-06
oso	3	2	4.80E-06	limon	5	2	6.40E-08
pato	4	2	2.50E-06	maiz	4	1	1.70E-06
pavo	4	2	3.00E-06	mango	5	2	4.50E-06
perro	5	2	3.70E-05	melon	5	2	3.00E-08
pez	3	1	8.00E-06	pan	3	1	3.70E-05
pulpo	5	2	1.00E-06	pastel	6	2	4.80E-06
raton	5	2	2.50E-08	postre	6	2	7.60E-06
tigre	5	2	5.00E-06	queso	5	2	1.10E-05
topo	4	2	1.60E-06	vino	4	2	8.00E-05
toro	4	2	9.30E-06	yogur	5	2	1.98E-06
Adj concrete	Length	Syll.	Ngram Freq	Adj abstract	Length	Syll.	Ngram Freq

alto	4	2	1.20E-04	bello	5	2	1.40E-05
ancho	5	2	2.50E-05	bueno	5	2	7.57E-05
bajo	4	2	2.88E-04	cruel	5	2	1.40E-05
claro	5	2	1.35E-04	feliz	5	2	4.84E-05
debil	5	2	1.20E-07	feo	3	2	5.56E-06
dulce	5	2	3.00E-05	guapo	5	2	7.44E-06
duro	4	2	3.30E-05	lindo	5	2	4.53E-06
fino	4	2	1.00E-05	listo	5	2	1.25E-05
frio	4	2	6.00E-07	loco	4	2	2.44E-05
fuerte	6	2	1.10E-05	malo	4	2	3.00E-05
grande	6	2	1.00E-04	pobre	5	2	5.00E-05
largo	5	2	2.22E-04	puro	4	2	2.50E-05
lento	5	2	1.70E-05	rico	4	2	2.32E-05
rojo	4	2	3.77E-05	sabio	5	2	1.38E-05
seco	4	2	1.80E-05	serio	5	2	3.96E-05
suave	5	1	3.00E-05	tonto	5	2	7.94E-06
sucio	5	2	6.78E-06	triste	5	2	3.36E-05
verde	5	2	3.78E-05	vago	4	2	5.00E-06

(c) TAIWANESE

Noun Animal	Length	Syll.	Ngram Freq	Noun food	Length	Syll.	Ngram Freq
乳牛-cow	2	2	1.00E-07	咖啡-coffee	2	2	4.60E-05
企鵝-penguin	2	2	1.40E-06	大蒜-garlic	2	2	8.00E-07
兔子-rabbit	2	2	3.30E-06	奶油-butter	2	2	7.60E-07
海豹-seal	2	2	5.10E-07	桃子-peach	2	2	4.60E-07
熊-bear	1	1	4.00E-06	水-water	1	1	2.00E-04
狐狸-fox	2	2	1.60E-06	沙拉-salad	2	2	3.80E-06
狗-dog	1	1	2.20E-05	洋蔥-onion	2	2	1.50E-06
狼-wolf	1	1	1.00E-05	牛奶-milk	1	1	7.80E-06
猴子-monkey	2	2	9.00E-06	玉米-corn	1	1	1.40E-05
獅子-lion	2	2	6.20E-06	米-rice	1	1	6.00E-05
綿羊-sheep	2	2	1.80E-06	糖-sugar	1	1	8.40E-06
老虎-tiger	2	2	7.00E-06	茶-tea	1	1	2.20E-05
老鼠-mouse	2	2	8.60E-06	葡萄-grape	2	2	3.70E-06
蜘蛛-spider	2	2	5.00E-06	蘋果-apple	2	2	2.30E-05
螞蟻-ant	2	2	4.60E-06	蛋-eggs	1	1	7.70E-06
貓-cat	1	1	9.10E-06	豆子-bean	2	2	4.70E-07
馬-horse	1	1	8.20E-05	辣椒-chili	2	2	9.00E-07
鯨魚-whale	2	2	1.80E-06	鳳梨-pineapp	2	2	4.50E-07
鳥-bird	1	1	1.30E-05	鹽-salt	1	1	1.20E-05
龍-dragon	1	1	2.00E-05	麵包-bread	2	2	2.50E-05
Adj concrete	Length	Syll.	Ngram Freq	Adj abstract	Length	Syll.	Ngram Freq
乾的-dry	2	2	1.00E-04	假的-fake	2	2	4.00E-05
低的-low	2	2	2.00E-04	傻的-silly	2	2	4.00E-06

冷的-cold	2	2	1.50E-05	壞的-bad	2	2	4.30E-05
大的-large	2	2	1.40E-03	好的-good	2	2	6.00E-04
小的-small	2	2	4.50E-04	帥的-handsor	2	2	2.50E-06
快的-fast	2	2	9.60E-05	忙的-busy	2	2	1.50E-05
慢的-slow	2	2	3.00E-05	怒的-angry	2	2	5.50E-06
濕的-wet	2	2	8.10E-06	懶的-lazy	2	2	3.80E-06
熱的-hot	2	2	5.50E-05	新的-new	2	2	1.40E-03
甜的-sweet	2	2	5.00E-06	病的-sick	2	2	4.30E-04
瘦的-thin	2	2	4.00E-06	瘋的-mad	2	2	4.50E-06
短的-short	2	2	5.00E-05	真的-real	2	2	1.40E-04
硬的-hard	2	2	2.00E-05	窮的-poor	2	2	1.80E-05
胖的-fat	2	2	6.30E-06	笨的-stupid	2	2	2.20E-06
軟的-soft	2	2	2.60E-05	累的-tired	2	2	1.70E-05
輕的-light	2	2	3.00E-05	美的-beautifu	2	2	2.00E-04
酸的-sour	2	2	3.80E-06	舊的-old	2	2	8.00E-05
重的-heavy	2	2	2.20E-04	貴的-expensi	2	2	2.70E-05
長的-long	2	2	3.00E-04	醜的-ugly	2	2	6.30E-06
高的-tall	2	2	5.00E-04	難的-difficult	2	2	1.40E-04

Table S3 | List of all the words used in the experiment, their lengths, number of syllables, and occurrence frequency. (a) English. (b) Spanish. (c) Taiwanese

Region	Total	Left	Right
hippocampus	1	1	0
fusiform	1	1	0
lateralorbitofrontal	10	9	1
superiortemporal	2	2	0
TOTAL	14	13	1

Table S4 | Distribution of electrodes that showed modulation by part of speech across brain regions. Significant regions showing lateralization shown in bold. ($p < 10^{-5}$, permutation test, $n = 10^6$ iterations, regions with less than 4 electrodes were excluded).

subject#	#Total	NounEnhanced ($\beta > 0$)	AdjEnhanced ($\beta < 0$)	Generalize	SubCategory (=Total- Generalized)
5	2	2	0	0	2
14	3	2	1	1	2
16	3	3	0	3	0
18	2	2	0	2	0
20	4	2	2	2	2
TOTAL	14	11	3	8	6

Table S5 | Distribution of nouns- versus adjective-preferring electrodes and electrodes that generalize for parts-of-speech versus those that do not.

Distribution across different subjects of electrodes that are more noun enhanced (column 3) versus more adjective enhanced (column 4), and that of electrodes that generalize to nouns and adjectives (column 5) versus those that showed differences between noun subcategories or adjective subcategories (column 6).

Region	RegionTotal	Noun	Adjective
hippocampus	1	1	0
fusiform	1	1	0
lateralorbitofrontal	10	9	1
superiortemporal	2	0	2
TOTAL	14	11	3

Table S6 | Distribution of nouns- versus adjective-preferring electrodes across brain regions. A permutation test combining all brain regions for these electrodes showed that that LOF was significantly noun preferring. ($p < 10^{-5}$, permutation test, $n = 10^6$ iterations, regions with less than 4 electrodes were excluded).

subject#	nLeftLOF	nPOS	%POS
6	6	0	0
9	3	0	0
13	6	0	0
14	4	3	75
15	4	0	0
16	5	3	60
18	5	2	40
20	5	2	40
Total	38	10	Mean%All = 27 ± 31
Mean%POSsubjects = 54 ± 17			

Table S7 | Distribution of part of speech encoding electrodes in the left lateralorbitofrontal cortex across subjects

Noun Animal	#N	#A	#V	(#N+1)/ (#A+1)	(#N+1)/ (#V+1)	Noun food	#N	#A	#V	(#N+1)/ (#A+1)	(#N+1)/ (#V+1)
'fish'	105	0	11	106.0	8.8	'water'	372	0	0	373	373
'horse'	126	0	0	127.0	127.0	'oil'	110	0	0	111	111
'bear'	11	0	93	12.0	0.1	'coffee'	68	0	0	69	69
'dog'	124	0	0	125.0	125.0	'salt'	33	0	0	34	34
'bird'	93	0	0	94.0	94.0	'fruit'	51	0	0	52	52
'cat'	55	0	0	56.0	56.0	'milk'	48	0	0	49	49
'mouse'	28	0	0	29.0	29.0	'sugar'	38	0	0	39	39
'sheep'	30	0	0	31.0	31.0	'tea'	88	0	0	89	89
'turkey'	0	0	0	-	-	'rice'	16	0	0	17	17
'fox'	13	0	0	14.0	14.0	'bread'	38	0	0	39	39
'bull'	12	0	0	13.0	13.0	'eggs'	62	0	0	63	63
'rat'	24	0	0	25.0	25.0	'corn'	12	0	0	13	13
'wolf'	12	0	0	13.0	13.0	'apple'	35	0	0	36	36
'seal'	15	0	15	16.0	1.0	'cheese'	30	0	0	31	31
'lion'	21	0	0	22.0	22.0	'butter'	21	0	0	22	22
'deer'	0	0	0	-	-	'pepper'	11	0	0	12	12
'cow'	26	0	0	27.0	27.0	'olive'	0	0	0	-	-
'snake'	12	0	0	13.0	13.0	'bean'	18	0	0	19	19
'penguin'	0	0	0	-	-	'garlic'	0	0	0	1	1
'eagle'	18	0	0	19.0	19.0	'salad'	14	0	0	15	15
'dragon'	13	0	0	14.0	14.0	'lemon'	14	0	0	15	15
'pig'	25	0	0	26.0	26.0	'onion'	12	0	0	13	13
'bat'	13	0	0	14.0	14.0	'berry'	0	0	0	-	-
'tiger'	13	0	0	14.0	14.0	'cherry'	0	0	0	-	-
'rabbit'	25	0	0	26.0	26.0	'pizza'	0	0	0	-	-
'monkey'	11	0	0	12.0	12.0	'nut'	15	0	0	16	16
'duck'	19	0	0	20.0	20.0	'pasta'	0	0	0	-	-
'goat'	12	0	0	13.0	13.0	'grape'	0	0	0	-	-
'whale'	13	0	0	14.0	14.0	'peas'	33	0	0	34	34
'hawk'	0	0	0	-	-	'peach'	0	0	0	-	-
'spider'	10	0	0	11.0	11.0	'plum'	0	0	0	-	-
'ant'	10	0	0	11.0	11.0	'lettuce'	0	0	0	-	-
Adj concrete	#A	#N	#V	(#A+1)/ (#N+1)	(#A+1)/ (#V+1)	Adj abstract	#A	#N	#V	(#A+1)/ (#N+1)	(#A+1)/ (#V+1)
'long'	392	0	0	393.0	393.0	'good'	1276	25	0	49.1	1277.0
'small'	518	0	0	519.0	519.0	'best'	0	0	0	-	-
'large'	471	0	0	472.0	472.0	'better'	0	0	0	-	-
'low'	286	0	0	287.0	287.0	'free'	200	0	23	201.0	8.4
'short'	198	0	0	199.0	199.0	'real'	227	0	0	228.0	228.0

'clear'	239	0	55	240.0	4.3	'poor'	166	0	0	167.0	167.0
'hard'	176	0	0	177.0	177.0	'bad'	264	0	0	265.0	265.0
'strong'	196	0	0	197.0	197.0	'serious'	124	0	0	125.0	125.0
'big'	338	0	0	339.0	339.0	'happy'	129	0	0	130.0	130.0
'deep'	97	0	0	98.0	98.0	'rich'	79	0	0	80.0	80.0
'dark'	104	31	0	3.3	105.0	'holy'	30	0	0	31.0	31.0
'cold'	103	25	0	4.0	104.0	'pretty'	30	0	0	31.0	31.0
'round'	28	47	0	0.6	29.0	'evil'	15	16	0	0.9	16.0
'heavy'	105	0	0	106.0	106.0	'wild'	55	0	0	56.0	56.0
'hot'	94	0	0	95.0	95.0	'pure'	36	0	0	37.0	37.0
'fast'	50	0	0	51.0	51.0	'sick'	44	0	0	45.0	45.0
'dry'	56	0	28	57.0	2.0	'busy'	53	0	0	54.0	54.0
'soft'	66	0	0	67.0	67.0	'sad'	36	0	0	37.0	37.0
'slow'	56	0	23	57.0	2.4	'proud'	32	0	0	33.0	33.0
'solid'	35	0	0	36.0	36.0	'calm'	14	0	0	15.0	15.0
'huge'	79	0	0	80.0	80.0	'gentle'	29	0	0	30.0	30.0
'warm'	70	0	0	71.0	71.0	'strict'	24	0	0	25.0	25.0
'fat'	20	28	0	0.7	21.0	'mad'	32	0	0	33.0	33.0
'bright'	62	0	0	63.0	63.0	'smart'	16	0	0	17.0	17.0
'weak'	45	0	0	46.0	46.0	'crazy'	18	0	0	19.0	19.0
'thin'	56	0	0	57.0	57.0	'brave'	18	0	0	19.0	19.0
'sweet'	36	0	0	37.0	37.0	'cheap'	68	0	0	69.0	69.0
'silent'	38	0	0	39.0	39.0	'ugly'	14	0	0	15.0	15.0
'oval'	0	0	0	-	-	'clever'	25	0	0	26.0	26.0
'tiny'	56	0	0	57.0	57.0	'jealous'	0	0	0	-	-
'dirty'	27	0	0	28.0	28.0	'shy'	11	0	0	12.0	12.0
'massive'	44	0	0	45.0	45.0	'lazy'	0	0	0	-	-

Table S8 | List of all the words used in the experiment, the number of times they occurred in the British National Corpus as a noun (#N), as an adjective (#A), or a verb (#V), and the ratios of their frequency of occurrence in their assigned part of speech versus their usage in other parts of speech. Dashes indicate words that were missing in the corpus.