

## ERPs Reveal Predictive Activation of Word Form Features in Sensory Cortex

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Sentence comprehension is increasingly viewed as a process that actively predicts linguistic input rather than passively responding to the input after it arrives. Although this view is generally supported by numerous recent findings, much remains unknown about what information is predicted during sentence processing and by what neurocognitive mechanisms. We investigated how fine-grained predictions can be, asking whether people predict the sensory features of individual words.

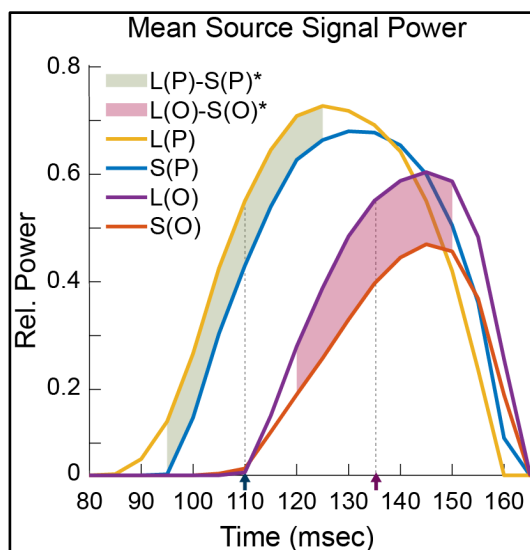
We developed a paradigm in which participants read sentences with words occasionally omitted from presentation. EEG activity during omitted word events provided evidence about predictions related to the omitted word. 26 young adult participants read 200 sentences like (1)–(2) below, one word at a time on a computer screen. Each sentence contained a target noun that was predictable given its context. Half of the target nouns were short (range=3 to 6 characters; mean=4.5) and half were long (range=7 to 14 characters; mean=8.9). Each sentence could appear in full (present-word events) or with the target word omitted (omitted-word events), leaving a crosshair in its place.

1. Short target word sentence: *The comedian told a joke and ...*
2. Long target word sentence: *Sherlock Holmes was a detective and ...*

EEG was recorded from 64 scalp electrodes, and event related potentials (ERPs) were computed from epochs of EEG time-locked to the target word position for both present-word and omitted-word events. Our analyses focused on the P1 ERP, a widely observed visual sensory response over occipital-temporal electrodes, which has been associated with early stages of visual word recognition in numerous studies. The P1 amplitude, averaged over occipital-temporal electrodes and in a time window of 85 to 165 msec increased in proportion to the length of the eliciting word, for both present-word and omitted-word events. In the omitted word condition, because there was no bottom-up stimulus, we conclude that the correlation between brain activity and the omitted word's physical properties (length) must reflect prediction of the word's form features.

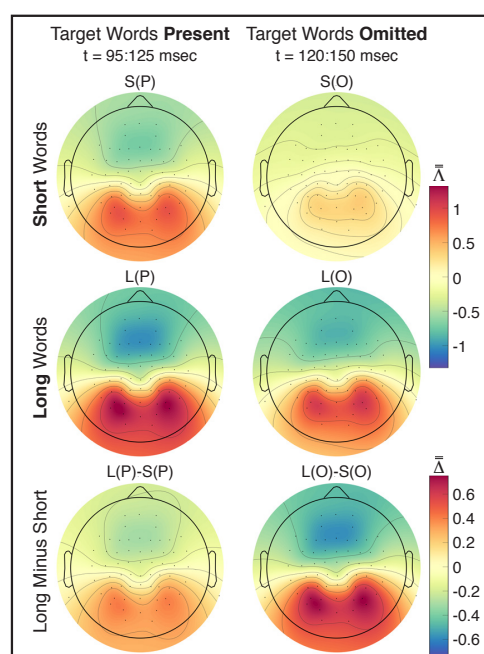
We modeled the neural sources underlying these prediction-related ERP effects by conducting a spatiotemporal multidimensional scaling (MDS) analysis of the P1 ERPs, separately for each participant and for each of the four conditions. We aggregated the individual participants' MDS analyses using a method known as DISTATIS, which yielded a constrained source space. For each participant, we computed an individual source signal, constrained by DISTATIS. Figure 1A shows the mean (across participants) power of the MDS-scaled source signal projected to each of four target word conditions: Long(Present), Short(Present), Long(Omitted), and Short(Omitted), and Figure 1B shows the scalp distribution of each projected condition. Two important patterns were present in this source signal's activity. First, the peak latency,  $t$ , was later ( $t(\text{present})=130$  msec;  $t(\text{omitted})=145$  msec) and peak magnitude,  $a$ , was smaller ( $a(\text{present})=0.68$ ;  $a(\text{omitted})=0.51$ ) for omitted-word events than present-word events. Second, the source signal's activity was greater in magnitude for long than short words, for both present-word events (range=95 to 125 msec; median=110 msec;  $p<0.05$ ) and omitted-word events (range=120 to 150 msec; median=135 msec;  $p<0.05$ ). Shaded areas in Figure 1A highlight windows of consecutive significant long-vs-short differences, after testing at every time sample, for the present-word and omitted-word conditions. These effects of word length corroborate our observations of the P1 ERP described above.

In order to explore the neuroanatomical systems underlying these effects of prediction, we modeled the neural generators of the P1 ERP sources described above using standardized low-resolution brain electromagnetic tomography (sLORETA). We then examined how the P1's neural generators were affected by length by calculating the difference in activity between generators for short and long words in the present-word condition (L(P)-S(P)) and omitted-word condition (L(O)-S(O); Figure 2). Three neural regions showed significant effects of word length, whether the word was presented or not: 1) inferior parietal cortex, which has been associated with grapheme-to-phoneme mappings during visual word recognition; 2) inferior temporal cortex, which has been associated with visual word-form processing; and 3) medial parietal lobe, which is heavily interconnected with the medial-temporal lobe memory system and has been implicated in perceptual predictions. Our findings indicate that these regions are part of a neural network of mechanisms involved not only in the bottom-up response to a word but also in predictions about word-forms during comprehension.



**Figure 1 (left).** Mean source signal power for all participants across four target word conditions: L(P) (long present, gold), S(P) (short present, blue), L(O) (long omitted, magenta), and S(O) (short omitted, orange). The shaded regions represent consecutive significant differences between long and short target words ( $p < 0.05$ ,  $n\text{-perms} = 1009$ , FDR corrected for comparisons at multiple time samples). The shaded green region represents the area between the L(P) and S(P) curves with consecutive significant differences in power, and the shaded pink region represents the area between the L(O) and S(O) curves with significant differences in power. The dashed lines and arrows represent the median significant latency values: L(P)-S(P) (range=95 to 125 msec, median=110) and L(O)-S(O) (range=120 to 150 msec, median=135). The scalp maps (Figure 2) and brain source estimates (Figure 3) are plotted as the mean values within these significant ranges.

**Figure 2 (right):** Topographic scalp maps of the mean P1 source signal for each of the four target word conditions and each of the two difference conditions. The upper colorbar represents the mean relative amplitudes ( $\bar{\Lambda}$ ) for all participants and the lower colorbar represents the mean difference amplitudes ( $\Delta\bar{\Lambda}$ ) for the two comparisons conditions.



**Figure 3 (below):** Mean estimated brain sources for L(P)-S(P) (95 to 125 msec, left panel) and L(O)-S(O) (120 to 150 msec, right panel). Sources are shown in nine views as labeled below each brain image. Sources were computed for each P1 source signal from each participant using standardized low-resolution brain electromagnetic tomography (sLORETA) constrained to the pial surface of a realistic (3-shell BEM) head model using the ICBM159 averaged MRI. The colorbar represents the mean sLORETA T-values for all participants constrained to the upper 15% of all T-values ( $\beta \geq 0.85$ ). Three neural regions showed significant effects of word length and were identified by mapping the peak T-values to a co-registered model of the Desikan-Killiany brain atlas: medial parietal (left and right), inferior parietal cortex (left and right), and inferior temporal cortex (left and right). Each significant region is delineated with a colored arrow as described in the figure legend and serves only for visualization.

