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BRAIN RESEARCH

Concurrent effects of lexical status and letter-rotation during early stage visual word recognition: Evidence from ERPs

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ABSTRACT

Recent studies report that the occipito-temporal N170 component of the ERP is enhanced by letter strings, relative to non-linguistic strings of similar visual complexity, with a leftlateralized distribution. This finding is consistent with underlying mechanisms that serve visual word recognition. Conclusions about the level of analysis reflected within the N170 effects, and therefore the timecourse of word recognition, have been mixed. Here, we investigated the timing and nature of brain responses to putatively low- and high-level processing difficulty. Low-level processing difficulty was modulated by manipulating letterrotation parametrically at 0°, 22.5°, 45°, 67.5°, and 90°. Higher-level processing difficulty was modulated by manipulating lexical status (words vs. word-like pseudowords). Increasing letter-rotation enhanced the N170 led to monotonic increases in P1 and N170 amplitude up to 67.5° but then decreased amplitude at 90°. Pseudowords enhanced the N170 over left occipital-temporal sites, relative to words. These combined findings are compatible with a cascaded, interactive architecture in which lower-level analysis (e.g., word-form feature extraction) leads higher-level analysis (e.g., lexical access) in time, but that by approximately 170 ms, the brain's response to a visual word includes parallel, interactive processing at both low-level feature extraction and higher-order lexical access levels of analysis.

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1. Introduction

Fluent reading requires the extraction of multiple levels of analysis – including visual word forms, phonological, and semantic representations – within approximately half a second. Electrophysiological studies report patterns of brain activity that are modulated by visual words in the initial ~200 ms after stimulus onset, suggesting sensitivity to the processes that serve early word recognition. However, conclusions about the level of analysis reflected within these effects, and therefore about the temporal dynamics of word recognition, have been mixed. Some studies conclude that the initial ~200 ms of word recognition is dominated by low-level feature extraction within a feedforward sequence of increasingly abstract analysis (e.g., Solomyak and Marantz, 2009; Tarkiainen et al., 1999). Other recent work, however, emphasizes higher levels of analysis, such as lexical access, and recurrent interaction between lower and higher levels of analysis (Cornelissen et al., 2009; Hauk and Pulvermüller, 2004). The discrepancies between these views reflect wider

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Several ERP and MEG studies find that early, "sensory" brain responses are enhanced by letter-strings (including words and non-word strings) relative to less familiar, nonlinguistic stimuli of similar visual complexity. Tarkiainen et al. (1999) report MEG responses at ~150 ms that were larger for letter strings than for strings of letter-like symbols (letters at non-standard orientations; labeled "Type II" activity), while earlier activity at ~100 ms was modulated by visual noise but not by linguistic properties (labeled "Type I" activity). Similarly, ERP studies report that the occipital-temporal N170 component, which peaks at ~170 ms, is enhanced by the presentation of letter strings, relative to non-linguistic control stimuli (e.g., strings of alphanumeric characters), especially in the left hemisphere (Bentin et al., 1999). These effect patterns are consistent with an initial word-form "feature detector" function, which is selectively engaged by visual features contained in words or word-like stimuli and which responds less vigorously to unfamiliar, non-linguistic stimuli (Solomyak and Marantz, 2009; Tarkiainen et al., 1999). The lack of such sensitivity at earlier latencies is consistent with the conclusion that ~170 ms marks the approximate beginning of word-form analysis during word recognition; that is, word-form feature detectors are not engaged prior to ~170 ms post-stimulus-onset.

Other studies suggest faster engagement of higher levels of analysis during word recognition. A previous study reports that the N170 is enhanced by mirror-inverted words, relative to normal words¹ (Proverbio et al., 2007). This enhanced neural response to less familiar stimuli is opposite the featuredetector response pattern. There are multiple possible explanations for the finding of enhanced activity for the unfamiliar, mirror-reversed words. Proverbio et al. (2007) asked subjects to detect target letters inside letter strings (e.g., find "O" in "RIFLUSSO") that were mirror-reversed or not. Target letter shapes were always shape-reversible, looking identical in the standard and the mirror-reversed condition (e.g., "O" or "A"), while surrounding letters mostly were profoundly altered in shape by mirror-reversal (e.g., "R", "F", "S"). One possibility is that detection of target-letters is enhanced against a background of mirror-reversed letters; that is, targets may "popout" in the mirror-reversed condition, enhancing the N170. Another explanation, however, is that the N170 enhancement reflects the recruitment of additional processing resources to assist in the difficult task of recognizing words and letters under conditions of mirror-reversal. Within this account, the processing manifest in the N170 necessarily represents a more advanced level of analysis than initial feature detection. One goal of the current work was to examine the impact of manipulating letter-orientation during a task that more closely resembled normal reading, eliminating the possibility of task-mediated pop-out.

The conclusion that N170 reflects higher levels of analysis than early feature detection is also compatible with studies finding that high-level variables, such as lexical status (words vs. pseudowords) modulate the N170 and earlier activity (Bentin et al., 1999; Hauk and Pulvermüller, 2004; Hauk et al., 2006; Maurer et al., 2005; Sereno et al., 1998; Simon et al., 2007; Wydell et al., 2003). Such effects suggest access within the latency of the N170 to abstract representations that discriminate words from word-like pseudowords (e.g., lexicalsemantic representations). The pattern of effects across studies is complicated, however. Some studies report that pseudowords enhance the N170, relative to real words (Hauk and Pulvermüller, 2004; Hauk et al., 2006; Simon et al., 2007), while other studies find no effects of lexical status (Bentin et al., 1999; Wydell et al., 2003) or reductions of N170 to pseudowords relative to words (Maurer et al., 2005). These mixed effects may reflect variability in the tasks administered across studies (Maurer et al., 2005). Also relevant may be varying affordances for context-driven predictions, which can pre-activate low-level form representations, allowing very fast responses to high-level factors-several studies that presented words in sentence-contexts rather than in singleword tasks have found rapid modulation by high-level variables like syntactic or semantic congruency (e.g., Dikker et al., 2010; Kim and Lai, 2011). Overall, the effects of lexical status on the N170 are provocative but remain incompletely characterized.

Related issues have been raised within a debate over the role of the ventral occipital-temporal cortex (VOT) in reading, based largely on hemodynamic imaging (e.g., fMRI) findings that this area is recruited by visual word recognition (e.g., Ben-Shachar et al., 2011; Cohen et al., 2008; Twomey et al., 2011), and evidence that damage to this area is associated with disordered reading (Cohen et al., 2003; Leff et al., 2006). It has been suggested that this region acquires specialization for reading during development (Dehaene et al., 2005; McCandliss et al., 2003), and implements a feedforward, hierarchically organized network of "local combination detectors" (LCDs), which recognize lower and higher order visual word form features during the earliest stages of visual word recognition (Dehaene et al., 2005). This proposed reading-related specialization of VOT has sometimes been linked to the N170 ERP (McCandliss et al., 2003). The proposal that the left VOT implements a "visual word form area" has been controversial, however. One prominent alternative proposal is that the VOT is a region of recurrent interaction between higher-order semantic and phonological representations and lower-order visual feature representations (Price and Devlin, 2011; Twomey et al., 2011). Work within this area provides critical findings about the anatomical regions involved in word recognition but often cannot constrain inferences about the fine-grained temporal dynamics among regions, due to limited temporal resolution of fMRI. Progress toward understanding the neural systems of word recognition will require convergent, mutually constraining findings from high spatial resolution methods like fMRI and high temporal resolution methods like ERP and MEG.

Here, we recorded brain responses during the early stages of word recognition, while participants read words and pseudowords whose letters were manipulated through picture-plane rotation at five levels (0°, 22.5°, 45°, 67.5° and 90°; Table 1). Neither letter orientation nor lexical status was predictable from trial to trial. We used a lexical decision task,

¹ Stimuli appear as if viewed through a mirror, with left and right points in the visual field reversed.

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