BRAIN RESEARCH 1468 (2012) 52–62

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Research Report

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

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ARTICLE INFO

Article history:
Accepted 5 April 2012
Available online 14 April 2012

Keywords:
P1
N170
Letter rotation
Lexical access
Visual word recognition
Pseudowords
Visual word form area

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 left-lateralized 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 letter-rotation 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.

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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0006-8993/$ – see front matter © 2012 Published by Elsevier B.V.
doi:10.1016/j.brainres.2012.04.008

debates within cognitive neuroscience over the speed and interactivity of the cortical and subcortical systems involved in perception and object recognition.

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, non-linguistic 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 words[1] (Proverbio et al., 2007). This enhanced neural response to *less* familiar stimuli is opposite the feature-detector 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 “pop-out” 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., lexical-semantic 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 single-word 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,

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

Table 1 – Examples of word and pseudoword stimuli at the five rotation angles.

		word	pseudoword
0°	r0	BLADE	BLAGE
22.5°	r1		
45°	r2		
67.5°	r3		
90°	r4		

which does not explicitly focus participants on low-level physical features of the input and which becomes more difficult with the degree of letter-rotation; thus, early effects of letter-rotation should not be attributed to easier discrimination under letter-rotation. We examined early visual ERPs (the P1 and N170 components) for effects of these two manipulations of stimulus familiarity (letter-rotation and pseudowords). If word recognition includes an initial "feature-detector" response, we expected unfamiliar stimuli to depress neural responding, reducing ERP amplitudes, relative to upright letter words If the difficulty of recognizing unfamiliar stimuli recruits additional processing resources, we expected unfamiliar stimuli to enhanced neural responding, relative to upright-letter words. These two effect patterns could both occur, with unfamiliar stimuli initially depressing neural responses at the level of initial feature-detection and later enhancing neural responses as additional processing resources are recruited. The manipulation of letter-rotation and lexical status allowed a comparison of their effects on word recognition with respect to timecourse and directionality, under identical processing conditions. Since sensitivity to lexical status involves a more abstract level of representation than sensitivity to letter-rotation, we examined the ERP for evidence that effects of letter-rotation would precede those of lexical status in time, consistent with an architecture that processes letter-level representations on a faster time-scale than higher-level representations that correlate with lexical status.

2. Results

2.1. Behavioral data

Lexical decision accuracy and reaction time (regardless of accuracy) are shown in Fig. 1. Mean decision accuracy, across all conditions was 96.43% and mean lexical decision latency across all conditions was 344.64 ms. Lexical decision accuracy decreased non-linearly with the eccentricity of letter rotation, with the greatest drop in accuracy at the 67.6–90° rotation step. This was reflected in a significant linear ($t_{134}=-9.6$, $p<0.00001$) and quadratic contrasts ($t_{134}=-5.0$, $p<0.00001$). Lexical decision reaction time increased non-linearly with the eccentricity of letter rotation, with the greatest increase in reaction time for the 67.6–90° rotation step. This was reflected in a significant linear ($t_{134}=7.2$, $p<0.00001$) and quadratic contrasts ($t_{134}=3.0$, $p<0.01$). Furthermore, subjects took longer to make lexical decisions about pseudowords (395.68 ms) than words (370.33 ms; $F_{1,33}=17.42$, $p<0.001$).

2.2. ERPs

Grand-average ERPs to the stimuli at the five rotation levels, averaging words and pseudowords together, are shown in Fig. 2. All experimental conditions elicited a positive P1 peak at 95–125 ms, followed by a negative-going N170 component, which was largest at occipito-temporal channels, and peaked on average across all conditions at 176 ms post-stimulus, with considerable variability in the peak latency across conditions. Amplitude differences between levels of letter rotation were apparent at both the P1 and the N170 (Fig. 2). Lexical-status also appeared to modulate the N170, although only when letters were upright (Figs. 6 and 7).

We analyzed mean voltages and peak latencies in two 30 ms windows centered on the peaks of the P1 (95–125 ms) and N170 (160–190 ms). We also analyzed mean voltages in a later, 195–225 ms window, reflecting numerical differences among conditions that continued after the N170 peak. Analysis focused on a left occipital-temporal (PO5, PO7, CB1,

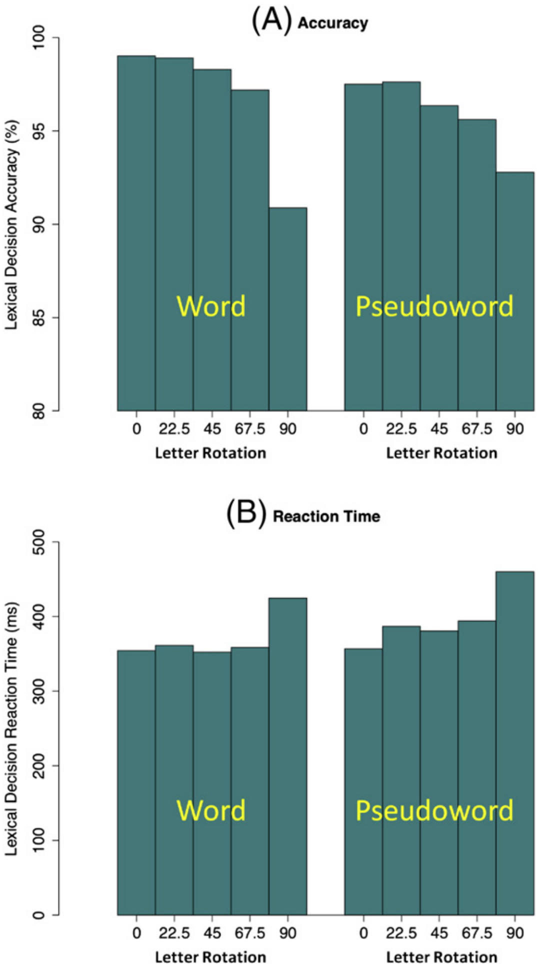

Fig. 1 – Accuracy (A) and reaction time (B) for real words and pseudowords at each of the five rotation levels.

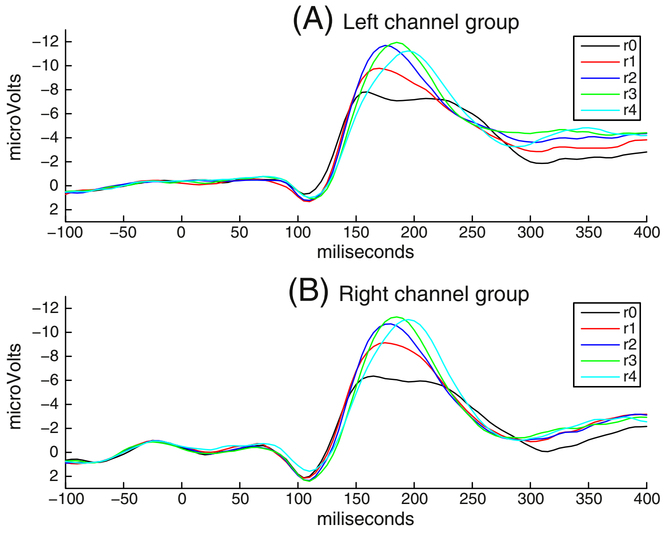

Fig. 2 – Grand averaged ERP waveforms for (A) the left channel-group (averaging channels P5, P7, PO5, PO7 and CB1) and (B) the right channel-group (averaging channels P6, P8, PO6, PO8 and CB2). ERPs are plotted separately for each of the five rotation levels. Word and pseudoword ERPs are averaged together at each rotation level. Negative is plotted up.

P5 and P7) and a right occipital-temporal channel-group (PO6, PO8, CB2, P6 and P8). Fig. 3 shows mean voltages within the three time windows.

2.2.1. *Letter-rotation effect*

2.2.1.1. P1 component. In the 95–125 ms window, letter-rotation delayed the P1 peak (Fig. 4A, B) This was reflected in a significant linear ($t_{134}=3.91$, $p<0.0001$) but not a quadratic contrast for peak latency. Letter-rotation had a non-linear impact on P1 amplitude (Fig. 3A, B) reflected in a significant quadratic ($t_{134}=4.58$, $p<0.00001$), but not a linear contrast for mean voltage. Pairwise comparisons at adjacent levels of letter-rotation showed that P1 amplitude increased (mean voltage became more positive) with letter-rotation in the 0–22.5° step ($F_{1,33}=12.5$, $p<0.01$), did not change in the 22.5–45° or 45–67.5° steps (Fs<1), and then decreased in the 67.6–90° step ($F_{1,33}=15.4$, $p<0.001$); see Fig. 3A, B.

2.2.1.2. N170 component. In the 160–190 ms time window, letter-rotation delayed the N170 peak (Fig. 4C, D). This was reflected in a significant linear contrast for peak latency ($t_{134}=9.24$, $p<0.00001$). Letter-rotation had a non-linear impact on N170 amplitude (Fig. 3C, D), reflected in significant linear ($t_{134}=-12.04$, $p<0.00001$) and quadratic ($t_{134}=12.5$, $p<0.00001$) contrasts for mean voltage. Pairwise comparisons at adjacent levels of letter-rotation showed that N170 amplitude increased (mean voltage became more negative) with letter rotation in the 0–22.5° step ($F_{1,33}=138.4$, $p<0.001$), and the 22.5–45° step ($F_{1,33}=50.0$, $p<0.001$), did not change in the 45–67.5° step ($F<1$), and decreased in the 67.5–90° step ($F_{1,33}=35.9, p<0.001$). These effects were concentrated at occipital-temporal sites bilaterally (Fig. 5A–D).

2.2.1.3. N170, later portion, 195–225 ms. In the later portion of the N170, amplitude increased (mean voltage became more negative) linearly with rotation (Fig. 3E, F), reflected in a significant linear ($t_{134}=-13.67$, $p<0.00001$) but no significant quadratic contrast. Pairwise comparisons showed that N170 amplitude increased at each step in rotation angle (0–22.5°: $F_{1,33}=16.44$, $p<0.001$; 22.5–45°: $F_{1,33}=12.3$, $p<0.01$; 45–67.5°: $F_{1,33}=17.4$, $p<0.001$; 67.5–90°: $F_{1,33}=21.8$, $p<0.001$). The effect of rotation was larger in the right than the left hemisphere, reflected in an interaction between rotation and hemisphere at the 0–22.5° comparison ($F_{1,33}=6.8$, $p<0.05$) and at the 67.5–90° comparison ($F_{1,33}=4.7$, $p<0.05$); see Fig. 5E, H.

2.2.2. *Lexical status effect*

2.2.2.1. P1 component. In the 95–125 ms window, lexical status did not affect voltages, either in mean voltage ($F<1$) or peak latency ($F<2$).

2.2.2.2. N170 component. Visual inspection suggested enhanced ERPs for pseudowords relative to words in the left hemisphere, when letters were upright (Fig. 6). In the 160–190 ms time window, lexical status did not affect voltages in a three-way lexical-status × rotation × hemisphere analysis ($F<1$). However, ANOVAs for upright-letter words revealed a marginal effect of lexical status on mean voltage ($F_{1,33}=3.8$, $p=0.06$). Examination of each channel-group separately showed that this effect was significant in the left hemisphere ($F_{1,33}=4.66$, $p<0.05$) but not in the right-hemisphere channel-group ($F<1$). At other rotation angles (22.5°, 45°, 67.5°, 90°), words and pseudowords were not different. Fig. 7 shows the topographic distribution of the lexical status effect in four time windows from 125 to 260 ms.

2.2.2.3. N170, later portion, 195–225 ms. In the later N170 window, upright pseudowords again elicited more negative-going ERPs than words ($F_{1,33}=10.9$, $p<0.01$). This effect was significant in the left-hemisphere channel-group ($F_{1,33}=9.82$, $p<0.01$) but not in the right-hemisphere channel-group ($F_{1,33}=2.5$).

3. Discussion

Letter rotation and lexical status both modulated brain responses within the first 200 ms of word recognition. Letter rotation enhanced and delayed both the P1 component (95–125 ms) and the N170 component of the ERP beginning around 155 ms. P1 and N170 amplitudes responded non-monotonically to letter-rotation, such that both components increased in amplitude with eccentricity of letter rotation up to a point (22.5–67.5°) but then decreased as rotation was increased beyond that level (67–90°)—though not below the level of activity elicited by upright words. 90°-rotation also drove a non-linear increase in reaction time and a decrease in accuracy. Pseudowords elicited greater N170 amplitude than real words, when letters were upright, beginning at 160 ms.

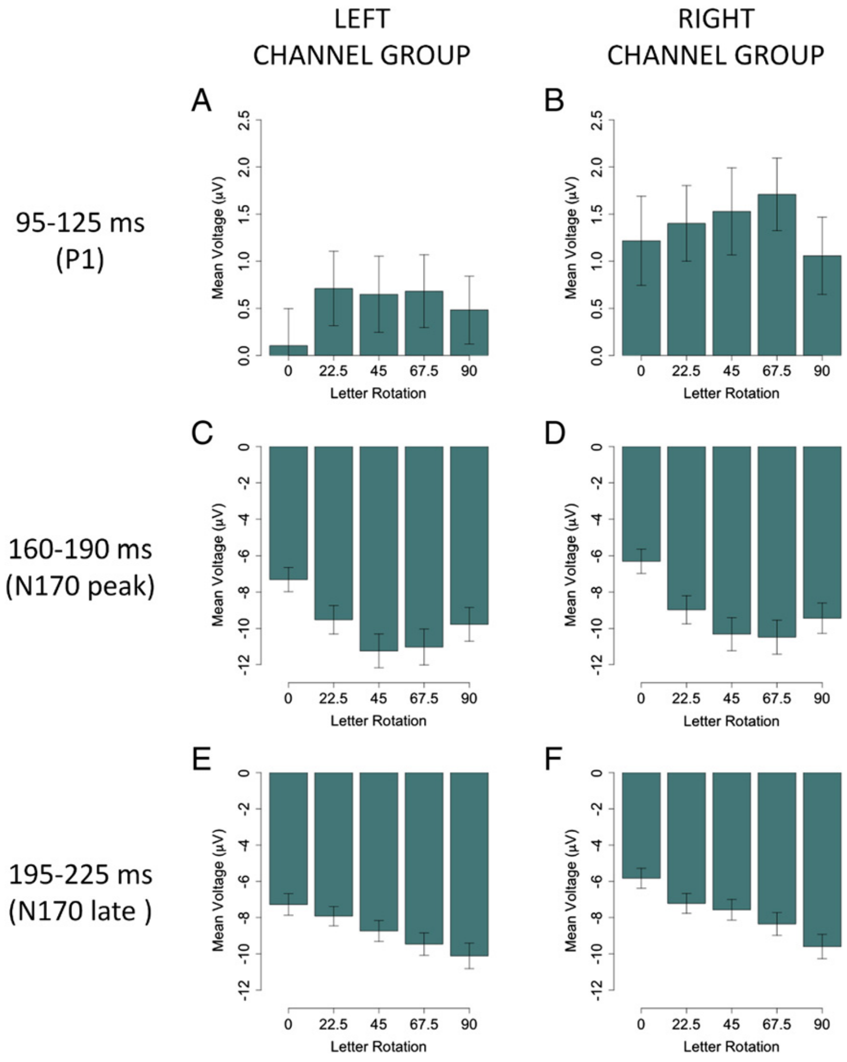

Fig. 3 – Mean voltages at each of the five rotation levels. Panels show data averaged within the 95–125 ms window (A: left channel group; B: right channel group); the 160–190 ms window (C: left channel group, D: right channel group); and the 195–225 ms window (E: left channel group, F: right channel group). Word and pseudoword ERPs are averaged together at each rotation level. Error bars indicate standard error within each rotation level.

3.1. *Letter-rotation effects*

The enhancement of P1 and N170 by letter-rotated strings relative to letter-upright strings, is consistent with rapidly increased visual system neural activity in response to the difficulty of recognizing words constructed from rotated letters. This effect pattern contrasts with previous findings of depressed early brain responses to unfamiliar stimuli, such as non-linguistic symbol strings, relative to real words (Tarkiainen et al., 1999). Response depression by unfamiliar stimuli has been associated with the failure of unfamiliar stimuli to engage specialized word-form detection mechanisms (Tarkiainen et al., 1999). The discrepancy between these prior results and the current findings may reflect different task demands and stimuli. In the Tarkiainen et al. (1999) study, non-linguistic symbol strings and letter-strings appeared in separate blocks and under passive viewing conditions. These task conditions may allow participants to process non-linguistic symbol stimuli shallowly, without engaging word-recognition mechanisms. The current experiment rendered a shallow processing strategy unlikely for the rotated-letter words, because 1) the rotated stimuli were recognizable as Roman letters, making them likely to engage letter-recognition mechanisms (as opposed to non-linguistic stimuli), 2) letter-rotation was not predictable across trials, and 3) the lexical decision task required attempting to extract lexical-semantic representations from the input. Under these circumstances, we suggest that rotated letters rapidly engage letter-recognition systems and in fact recruit additional processing resources to assist in analysis difficulty, relative to upright-letter words—by ~100 ms. Rotated letters may drive activation of units that are consistent with the input letters and also erroneous units representing other letters, resulting in competition between letter-representations, and recruiting top-down feedback that aids selection of the appropriate letter-level representations.

Previous findings of enhanced N170 to mirror-inverted (Proverbio et al., 2007) or picture-plane inverted words (Rossion

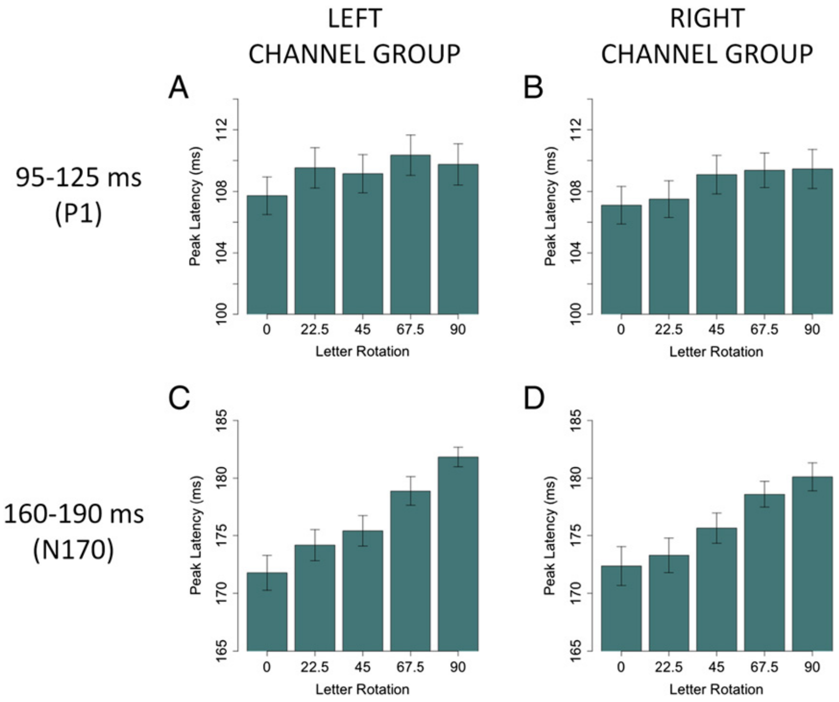

Fig. 4 – Latencies of peak voltages within the 95–125 ms window (A: left channel group; B: right channel group) and the 160–190 ms window (C: left channel group, D: right channel group). Error bars show standard error within each rotation level.

et al., 2003) are like the current study in manipulating letter orientation (not in the same manner as done here) and also in presenting stimulus conditions randomly rather than in blocks. These prior studies used tasks that potentially facilitated early sensitivity to the orientation manipulation via mechanisms that are not typical of normal word recognition (see Introduction). The current study used a high-level task that did not focus subjects on low-level input features. The effects we obtained at P1 are even earlier than in the prior studies. We suggest that high-level tasks such as lexical decision may increase top-down feedback to low-level form processing, enhancing the sensitivity of early word-recognition processes to disturbances in orientation.

Some aspects of our data are compatible with response depression by unfamiliar stimuli. The non-linearity in our P1 and N170 amplitude effects could reflect limited tolerance for letter-rotation in the word-recognition system, such that rotations beyond a certain eccentricity (e.g., 67–90°) yields diminished engagement of word-recognition systems. Dehaene et al. (2005) have proposed that “local combination detectors” in the ventral occipital-temporal cortex respond to visual word form features in a manner that is invariant across variability in case, location, size, and rotation until some threshold of degradation, beyond which responses are reduced (Dehaene et al., 2005, p. 6). This invariance-with-limits perspective does not explain why moderate levels of rotation (22.5–67.5°) enhance brain responses but could explain why highly eccentric rotations (90°) decrease response amplitude, relative to moderate rotations. Thus, we see, within the N170 time window, evidence both that deviation from preferred stimulus properties can recruit additional processing resources and also that deviation beyond a certain level reduces activity.

A potentially related fMRI study associated with the LCD proposal reports that rotating whole words (not individual letters, as investigated here) at five levels (0°, 22.5°, 45°, 67.5°, 90°) caused reaction time effects similar to our own, with nonlinear increases that were largest for 90°-rotations (Cohen et al., 2008). fMRI BOLD signal in occipital-temporal cortex increased linearly with rotation angle, while in parietal cortex, effects were non-linear, such that 90° rotation drove a larger increase in activity than other stimuli. This effect pattern was interpreted as reflecting two pathways to reading: 1) a whole-word recognition system based in the ventral visual system (VOT), which is engaged by words displayed in a familiar format (foveal horizontal words with normally spaced letters), and 2) a letter-by-letter serial reading system, controlled by dorsal (parietal) attention systems, which is engaged by words displayed in unfamiliar formats. The dorsal system appears to be most strongly engaged by 90°-rotations, coinciding with the greatest increases in behavioral measures of processing difficulty.

An interesting question for further investigation is whether our ERP effects reflect interactions between dorsal and ventral systems, of the kind observed by Cohen et al. (2008). In particular, the drop in N170 amplitude around the peak (160–190 ms) for 90°-rotations could reflect a drop in occipital-temporal engagement as rotation exceeds some threshold of eccentricity, while the monotonic increase in the later portion of the N170 (195–225 ms) could reflect the onset of top-down feedback from dorsal mechanisms, which upregulates VOT responses. The right-lateralization of the late N170 effects could reflect influences of right-hemisphere-dominant dorsal-attentional systems (e.g., Shulman et al., 2010) over right-hemisphere ventral areas. The LCD model focuses on feedforward information flow and does not predict top-down modulatory

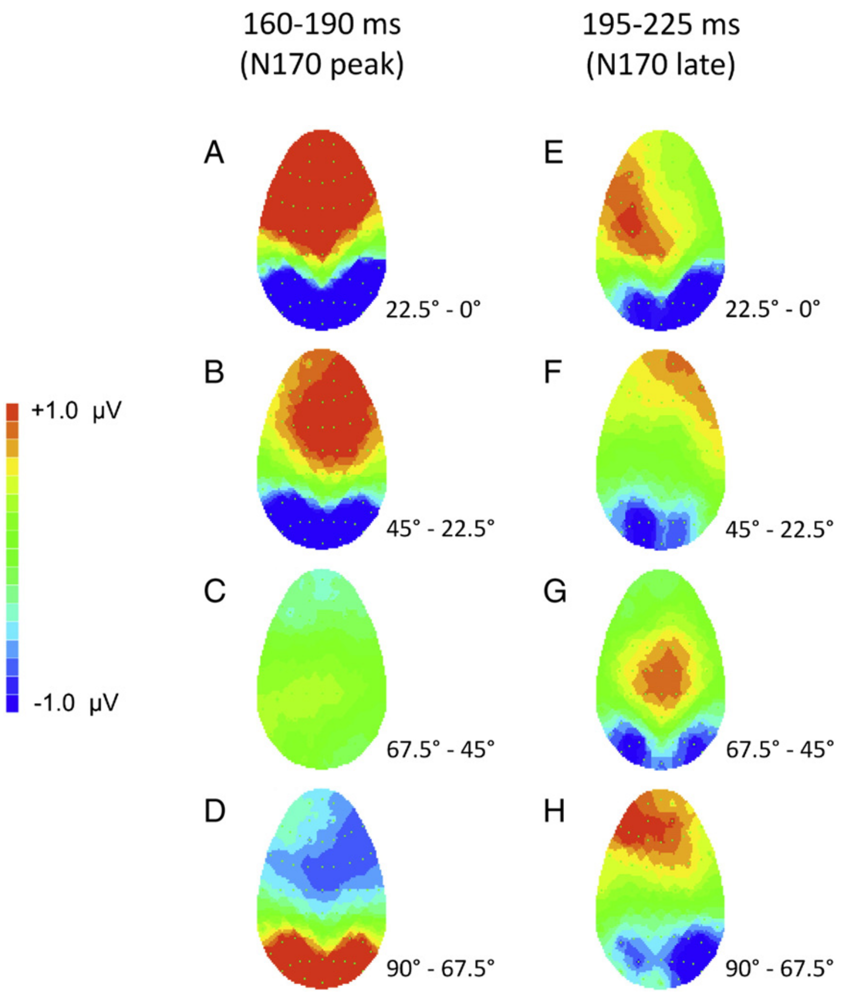

Fig. 5 – Scalp distributions of voltage differences due to each increasing step in letter-rotation in the 160–190 ms window (N170 peak): 22.5–0° (A), 45–22.5° (B), 67.5–45° (C), and 90–67.5° (D) and in the 195–225 ms window (N170 late): 22.5–0° (E), 45–22.5° (F), 67.5–45° (G), and 90–67.5° (H). Each panel shows the result of subtracting the low rotation from the high rotation ERP. Blue regions indicate more negative-going ERPs with increasing rotation. Red regions indicate more positive-going ERPs with increasing rotation.

effects. However, the architecture is compatible with extensions to include top-down feedback. And top-down modulation, perhaps from parietal mechanisms, would account for the increasing BOLD signal in VOT by rotation in Cohen et al. (2008). In contrast, a rotation-invariant feature detector, without top-down feedback, should maintain a constant level of activity across upright and mildly rotated words, with diminished responses for eccentric rotations. These speculative suggestions will require further investigation to test, including source-estimation analyses and perhaps longer epochs of ERP. An inspection of ERP scalp topographies across rotation did not indicate an obvious shift toward activity at parietal channels for 90° stimuli (see Fig. 5); however, it is not possible to rule out parietal generators based on ERP scalp-distributions. It is also possible that all the effects that we observe here precede the engagement of dorsal systems observed by Cohen et al. (2008), and their findings include dorsal activations that accumulate across the long analysis epoch used by fMRI, which are not detected within the short timeframe of early ERPs investigated here. Relatedly, Cohen et al. (2008) did not see diminution of neural responses at 90° as we did, and this might reflect the insensitivity of fMRI to transient changes in brain activity.

The speculative possibilities listed here need to be investigated further.

3.2. *Lexical status effects*

The enhanced N170 for pseudowords, relative to words, is consistent with access of high-level representations, which distinguish between words and visually very similar but meaningless stimuli, by ~160 ms. This effect corroborates previous reports that pseudowords enhance N170 or earlier activity (Hauk and Pulvermüller, 2004; Hauk et al., 2006; Sereno et al., 1998; Simon et al., 2007). As with letter-rotation, the effect-pattern is not consistent with an initial “feature detector” response, because unfamiliar pseudowords enhanced rather than reduced activity. We suggest that pseudowords

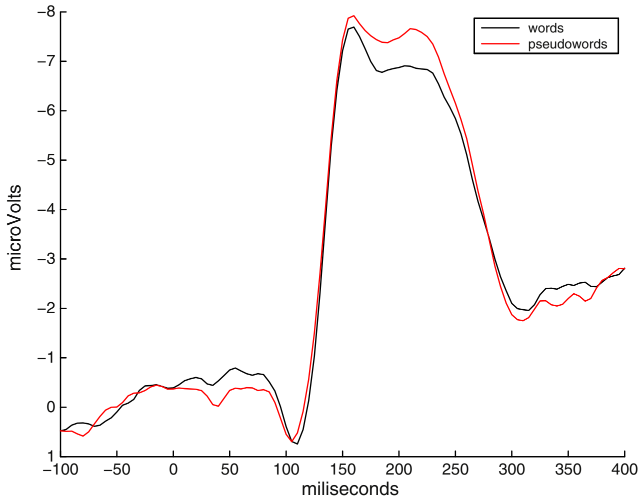

Fig. 6 – Grand averaged ERP waveforms for word (black) and pseudoword stimuli (red) for the left occipital-temporal channel-group (averaging channels P5, P7, PO5, PO7 and CB1). ERPs are for upright-letter stimuli.

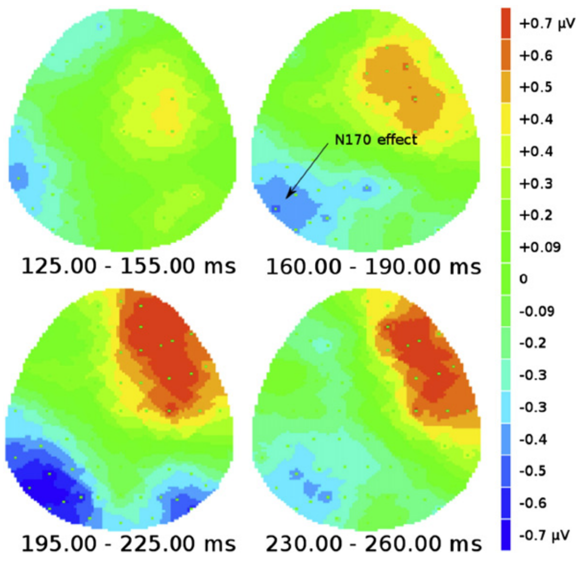

Fig. 7 – Topographic distribution of lexical status effect at four time windows. Plots show difference between word and pseudoword ERPs (words minus pseudowords) in the upright condition (0°) in four 30 ms windows, 125–155, 160–190, 195–225, and 230–260 ms post-stimulus onset. Blue regions show where pseudoword ERPs were numerically more negative than word ERPs. The 160–190 and 195–225 ms time window reflects data used in the lexical status N170 effect described in the text.

drive rapid partial activation of lexical representations with which they are partially consistent. Holcomb and Grainger (2006) have argued that such overactivation may explain enhancement of the later N400 component by pseudowords; here we suggest that such over-activation occurs earlier, within the N170 latency window. The resulting activation of multiple, alternatives at the lexical level may generate feedback to lower-level word-form representations, increasing word-form processing activity, which manifests in enhanced N170.

3.3. *Cascaded, interactive processing*

Several aspects of the data are consistent with a faster timescale for the processing of letter-level than higher-level (lexical) analysis. First, the effects of letter-rotation began earlier than those of lexical status, at the P1.[2] Second, at the N170, the effects of letter-rotation were much larger than that of lexical status. Finally, lexical status effects occurred only when words were upright, consistent with the possibility that letter-rotation disrupts low-level form processing in a way that has downstream consequences on the activation of lexical representations.

While letter-rotation effects lead the lexical-status effects in time, effects of letter-rotation and lexical-status were not discretely separated in time. The general pattern of letter-rotation effects at the P1 continued and was much more robust at the later N170. It appears that rotation effects are quite extended in time and overlap substantially with access to higher level variables. The concurrence of lexical-status and letter-rotation effects on N170 indicate that, by ~160 ms, parallel processing of these levels of analysis is underway. Within the letter rotation effects, there is also evidence of concurrence of higher and lower-order processing. At both the P1 and the N170, we see evidence that highly deviant stimuli (e.g., 90°-rotated letters) exceed the tolerance of word-form feature detectors and reduce brain responses. At the same time, moderately unfamiliar stimuli (22.5–67°-rotated letters) enhanced brain responses, suggesting recruitment of additional processing resources. It appears that initial feature detection and recruitment of additional processing resources for difficult analyses occur within the same "stage" of processing; that is, they are not staged. This pattern of effects is consistent with a cascaded, interactive processing architecture (e.g., Grainger and Holcomb, 2009), in which low-level (letter-recognition) analysis leads high-level (lexical) analysis in time, but in which the two levels also engage in parallel, interactive processing.

Our conclusions assume that, by ~160 ms, the word recognition system has initiated critical interactions within cortex between sensory representations and higher-level lexical representations that encode lexically specific information. The idea that word recognition is highly interactive is widely accepted within cognitive models of word recognition (McClelland and Rumelhart, 1981; Price and Devlin, 2011), but the timecourse of interaction has remained unclear and controversial. Neuroimaging investigations of word recognition have often assumed that the initial ~150 ms of word recognition is dominated by low-level sensory analysis in early visual cortical areas (Bentin et al., 1999; Tarkiainen et al., 1999). But recent physiological and anatomical findings have supported new thinking about the speed and direction of

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[2] We do not necessarily infer qualitatively separable processes underlying P1 and N170. Rather these two prominent components offer convenient points for analyzing ERP responses at different time points in the evolution of the brain's response to the input.

information flow between lower and higher levels within the visual system (Foxe and Simpson, 2002; Lamme and Roelfsema, 2000). (Foxe and Simpson, 2002) report human ERP evidence that occipital cortex responds to visual stimuli by 56 ms, and that frontal cortex is active by 80 ms. Monkey intracranial recordings show that feedforward information flow from V1 to the highest levels of the ventral visual system (inferotemporal cortex, IT) occurs in ~23 ms (Schroeder et al., 1998; Schroeder et al., 2001) and that robust selectivity for complex stimuli (e.g., faces) occurs at latencies of ~100 ms (e.g., Rolls and Tovée, 1994). A number of studies indicate that transmission time for information flowing along a single synaptic distance is 10–15 ms, both between and within cortical regions (Tovée, 1994). In the context of such estimates, recent ERP studies have increasingly concluded that high level representations are accessed within the initial 200 ms (Cornelissen et al., 2009; Dikker et al., 2009; Hauk and Pulvermüller, 2004; Hauk et al., 2006), consistent with our own conclusions here.

4. Experimental procedures

4.1. *Participants*

Thirty-five native English-speaking students at the University of Colorado participated in this study. Participants were right-handed, with normal or corrected-to-normal vision and had no history of neurological disease. Participants received credit or cash for their participation. All participants gave written informed consent to participate. The experimental protocol was approved by the University of Colorado Institutional Review Board.

4.2. *Materials*

Stimuli were 240 words and 240 pseudowords (lexical status), each 5 characters in length. Each pseudoword was an orthographically regular string derived by altering one letter in one of the real words. The letters in words and pseudowords were presented in five levels of rotation: 0°, 22.5°, 45°, 67.5°, and 90° (r0, r1, r2, r3, r4; letter-rotation). See Table 1. The spacing between the centers of characters within stimuli was constant and was sufficient to accommodate the rotation of all letters in the alphabet through the full range of rotations. Stimuli were in white font on gray background. Five experimental lists were constructed. In each list, 48 words and 48 pseudowords occurred in each rotation level. Rotation-levels were assigned to different sets of words and pseudowords across lists in a Latin-square design. Within each list, each word and its associated pseudoword were assigned to different rotation levels and appeared in different halves of the list. Furthermore, within each block of 48 trials, half of the items were pseudowords. Stimuli appeared pseudorandomly, subject to the constraints listed above.

4.3. *Procedure*

The participants were seated in a comfortable chair in a dimly lit room in front of an LCD screen. The experimental session took 1–1.5 h including the initial setup. Each trial consisted of a fixation prompt, followed by a single word or pseudoword presented at the center of the computer screen. The fixation prompt appeared on screen for 300 ms, followed by a 200 ms blank screen. The word was presented on screen for 200 ms, followed by an 850 ms blank screen, and finally a prompt indicating that the participant should judge whether the previously displayed stimulus was a word or a nonword ("Word/NonWord"). Letter rotation and lexical status both varied pseudo-randomly across trials.

4.4. *EEG recording*

Continuous EEG was recorded from 64 sintered Ag/Ag–Cl electrodes embedded in an elastic cap (Neuroscan QuikCaps) arranged according to the extended 10–20 system. Vertical eye movements and blinks were monitored with two electrodes placed above and below the left eye, and horizontal eye-movements were monitored by electrodes placed at the outer canthi of each eye. EEG was also recorded over left and right mastoid sites. Impedances were maintained below 10 kΩ. EEG was referenced on-line to a vertex electrode and later re-referenced to linked mastoids. EEG was amplified and digitized at 1000 Hz (Neuroscan Systems). After recording, data was down-sampled to 200 Hz and filtered with a bandpass of 0.1–30 Hz. Eye-blink artifact was corrected using a subject-specific regression-based algorithm (Semlitsch et al., 1986). Any remaining voltages exceeding ±100 μV were rejected. On average, 90.78% trials were accepted, with similar rejection-rates across conditions (90.59% and 90.97% of trials accepted in the word and pseudoword conditions, respectively; 90.56, 90.35, 91.33, 91.21, 90.4% of trials accepted in rotation levels 0–4, respectively). One subject's data was excluded from the analysis due to excessive artifact ERPs were averaged in epochs of activity spanning −100 to 600 ms relative to the onset of the target stimulus.

4.5. *EEG analysis*

Two channel-groups (electrode groups) were selected, encompassing left occipital-temporal (PO5, PO7, CB1, P5 and P7) and right occipital-temporal electrodes (PO6, PO8, CB2, P6 and P8). These channels were selected for analysis by identifying the electrode sites with the maximum grand-averaged N170 amplitude across all conditions. Channels in this occipital-temporal region have previously shown sensitivity to cognitive variables (Dien, 2009). Data was averaged across electrodes within each channel-group.

ERPs were quantified for analysis as mean voltages and latencies in time windows of 95–125, 160–190, and 195–225 ms post-stimulus-onset. The effect of parametrically increasing letter-rotation on mean voltage and latency was analyzed with linear mixed effects models with Rotation as a fixed factor and Subjects as a random factor. We included quadratic in addition to linear contrasts to capture non-monotonic patterns apparent in visual inspection of the P1 and N170 amplitudes. All other analyses were within-subject analysis of variance (ANOVA). Mean voltages at adjacent rotation levels (0–22.5°, 22.5–45°, 45–67.5°, 67.5–90°) were analyzed by ANOVA with factors rotation (low/high) and hemisphere (left/right).

Lexical status effects were analyzed by ANOVA with factors lexical status (word/pseudoword) and hemisphere (left/right). Significant main effects were followed by simple effects analysis.

4.6. *Behavioral data analysis*

Lexical decision times greater than 2.5 *SDs* from each participant's mean decision time were dropped. This affected 2.8% of the data. The effect of parametrically increasing letter-rotation on lexical decision time and accuracy were analyzed with linear mixed effects models with Rotation as a fixed factor and Subjects as a random factor. We included linear and quadratic contrasts to capture non-monotonic patterns apparent in visual inspection of the data.

5. Conclusion

Our findings provide support for a hierarchical model of word recognition in which analysis proceeds from low to higher levels of analysis in a cascaded, interactive dynamic. At the early latency of ~100 ms and continuing through the initial 200 ms, we find evidence that letter rotation causes analysis difficulty that recruits additional processing resources. We do not find evidence of an initial "feature detection" stage at which real, standard-oriented words enhance brain responses over other stimuli. By ~160 ms, letter recognition has advanced to a level where processing difficulty reflects the degree of letter rotation and also access of lexical representations. At this timepoint, we also see evidence of concurrent processing of both letter-level and lexical-level representations.

Acknowledgments

This work has been partially supported by MŠMT ČR Výzkumná centra, č. LC536 (Centrum komputační lingvistiky), by MŠMT ČR, č. ME09008 (Mnohojazyčná univerzální anotace lingvistických dat) and by Project MŠMT ČR LM2010013 LINDAT-Clarin.

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