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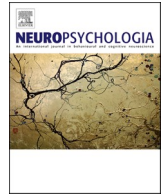
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On letter-specific crowding and reading: Evidence from ERPs

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ABSTRACT

We compared processing of letter and symbol stimuli presented briefly in the right or left visual field, and either in isolation or surrounded by two flanking characters of the same category. The flankers could be arranged horizontally or vertically. Participants performed a two-alternative forced choice (2AFC) task with the isolated character or the central character in flanked displays as target. Alternatives in the 2AFC task were characters from the same category as the target that were not present in the display. We recorded EEG in order to investigate the timing of crowding effects (isolated vs. flanked conditions) and the hypothesized differential impact of crowding on letters and symbols. Behavioral results showed no significant difference between isolated letters and symbols, but significantly higher accuracy to flanked letters compared with flanked symbols – and the effect of stimulus type was significantly greater with horizontally aligned stimuli. Likewise, amplitude of the N170 and a following negativity (identified here as the N250) did not differ significantly when comparing isolated letters and symbols but did differ for flanked stimuli. Flanked letters showed significantly greater N170 and N250 amplitudes compared with flanked symbols. N170 and N250 amplitudes were also significantly greater for flanked vs. isolated letters whereas symbols showed a significant difference in the opposite direction for the N250. We conclude that the processing of compact strings of letters is optimized for skilled reading via changes in the mapping of visual features onto letter identities in multi-letter arrays in order to reduce the interfering effects of excessive crowding.

1. Introduction

In the quest to understand the efficiency with which skilled readers retrieve word identities from highly complex visual displays during reading, one essential goal is to describe the processing involved in the very first stages of mapping visual information onto the most elementary linguistic representations. For readers of written languages that use an alphabetic orthography, the first step in the transition from purely visual sensory processing to the processing of perceptual linguistic information involves mapping visual features onto linearly arranged letter identities. This assertion assumes that visual word recognition is primarily letter-based, and indeed the evidence for this assumption is overwhelming (see Grainger and Dufau, 2012; Grainger and Hannagan, 2014, for reviews). As argued by Grainger (2018), letter-level processing provides the starting point for all higher-order linguistic processing during reading, enabling access to phonological, morphological, and whole-word orthographic representations.

The theoretical background for the present study is the proposal that,

assuming letter-based word recognition, then during the initial stages of learning to read the status of letter stimuli changes radically. Since most children learn the alphabet prior to learning to read, or at least prior to becoming efficient readers, letters as individual visual objects must take on a different role when reading words (see Grainger and Hannagan, 2014b, for a more detailed description of this general theory). Letters are converted into the parts of word objects, becoming the equivalent of the complex visual features that are the basis of visual object identification (e.g., Biederman, 1987). The central idea here is that although letters maintain their status as individual objects, there is a change in the impact of neighboring letters when processing written words and other multi-letter arrays. This change is thought to primarily involve the impact of visual clutter, otherwise referred to as crowding (Pelli and Tillman, 2008; Whitney and Levi, 2011).

1.1. Behavioral studies of crowding

Crowding is thought to be a major bottleneck for visual object

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identification in general, with ease of identification dropping in the presence of other objects as a function of their proximity with the target object (Whitney and Levi, 2011). The interfering effects of crowding increase linearly with target eccentricity – a phenomenon referred to as Bouma's law (Pelli and Tillman, 2008, in reference to the pioneering work of Herman Bouma on crowding and letter identification, Bouma, 1970). Thus, crowding severely limits the ability to recognize objects in the visual periphery (where crowding effects are typically examined), but crowding effects are also present in the fovea (Coates et al., 2018). Hence crowding affects the visibility of letters in words that are fixated (Grainger et al., 2016), as well as for words in the parafovea which is also used during reading (see Schotter et al., 2012, for a review). Indeed, given the compact nature of written words, with minimal spacing between the component letters, identification of these component letters will be subject to extreme levels of crowding. So, how does the reading system overcome such effects of crowding? Here we suggest that in order to optimize letter-based word recognition, learning to read causes modifications in the most elementary mechanisms involved in identifying letters when presented in multi-letter arrays. This leads to major changes in the way multi-letter arrays are processed in skilled readers (i. e., at the end point of reading acquisition) compared with the processing of other stimulus arrays. More specifically, we propose that the process of mapping visual features onto letter identities when letters are presented in strings is modified in order to reduce the interfering effects of crowding. Thus, the central hypothesis to be tested in the present study, is that the basic processing of crowded letter strings in skilled readers differs fundamentally from the processing of crowded arrays of other kinds of visual objects that are not typically processed in strings, and these processing differences should disappear when the stimuli are presented in isolation.

In line with this hypothesis, prior behavioral research has revealed differences in letter-string processing relative to the processing of other kinds of stimulus arrays, and notably in terms of crowding effects (Chanceaux et al., 2013; Vejnović & Zdravković, 2015). Crowding effects can be revealed in two different ways: either by comparing flanked stimuli with isolated stimuli (the strategy we adopt in the present work), or by increasing the distance separating the target items and flanking stimuli (a critical spacing manipulation). The first key finding with respect to the present study is that crowding effects have been found to be greater for arrays of symbols compared with arrays of letters (Grainger et al., 2010). The mechanism that presumably allows this type of particular, category-specific favored processing is the lifetime of intensive experience reading arrays of letter strings. According to one account, the modified receptive field hypothesis (Chanceaux and Grainger, 2012; Chanceaux et al., 2013, 2014; Tydgat and Grainger, 2009), this experience is thought to specifically tune individual letter detectors in order to facilitate letter processing under circumstances that might otherwise result in low visibility due to crowding. Other comparable stimuli such as ASCII symbols (as tested in the present study) are not typically encountered in such specific crowded contexts (i.e., during reading), and generally do not combine to form a higher-order representation in the way that letters combine to form words. Therefore, the visual system is not likely to be optimized or tuned to process such stimuli under crowded conditions.

1.2. ERP studies of crowding

Few studies have examined the effects of crowding on ERP signals which is perhaps curious given the advantages that such continuous online measures offer in terms of unraveling the time course of early sensory and perceptual processing (Luck, 2014). The ERP studies that have looked at crowding have painted a mixed picture, suggesting multiple possible foci for crowding effects, perhaps operating in tandem. Using sinusoidal grating stimuli presented in peripheral vision a study by Chen et al. (2014) reported that the early sensory C1 component was suppressed under crowded conditions. This finding is consistent with

fMRI data showing that the BOLD signal is suppressed for crowded stimuli as early as V1 (Millin et al., 2014). Based on these data Chen et al. argued that crowding at least partially results from the loss of visual information due to receptive field pooling in early visual areas. Another study (Bacigalupo and Luck, 2015) investigated the effects of crowding on letter perception using a later ERP component related to attentional engagement, the N2pc. They found N2pc amplitude increases with crowding but under extreme crowding N2pc effects disappear. These results suggest that increased attention is involved in resolving crowded targets. Another group of ERP studies have focused on the N1 – an early perceptual component generated in response to visual stimuli. Here, crowding has been shown to decrease the amplitude of the N1 when a target stimulus (line segments in these experiments) is crowded compared to when there is less crowding of targets (Chicherov et al., 2014; Ronconi et al., 2016). These studies concluded that crowding results from a failure in a post-sensory feature integration or grouping stage of processing (see Herzog et al., 2015). These N1 results are the most directly related to the component of interest in the current study, the N170.

The N170 is typically thought of as either a subtype of N1 or as reflecting activity that summates with the N1 as a result of perceptual processing of specific kinds of visual stimuli (e.g., Bentin et al., 1999). For example, there is substantial evidence that ERPs to different categories of visual objects such as faces, cars and visual words generate distinctly different patterns of N170 across the scalp (e.g., Sehyr et al., 2020). The conclusion of much of the research on the N170 is that it is sensitive to overlearned classes of stimuli such as faces and words, and that differences in the amplitude and scalp distribution of this component reflects subtle differences in the featural makeup of these stimuli (Bentin et al., 1999; Maurer et al., 2008). In fact, a number of studies have already shown that the amplitude and scalp distribution of the N170 differs for strings of stimuli made up of letters and common ASCII symbols presented to the fovea, with a larger amplitude on the left side of the head for letter-based stimuli (typically short 4 to 5 letter words) compared to strings of symbols (e.g., Bentin et al., 1999; Emmorey et al., 2017). This left lateralization has been proposed to reflect the proximity of left sided occipito-temporal networks and pre-existing phonological codes used in speech perception ((Sacchi and Laszlo, 2016; Emmorey et al., 2017). The idea is that during learning to read letter expertise develops as a function of mapping developing orthographic codes onto preexisting phonological codes (Sacchi and Laszlo, 2016). Consistent with this argument is that fact that children learning to read only show the left sided N170 pattern to letter strings once they have become relatively competent readers (Maurer et al., 2005b). Furthermore, children with poor phonological skills (Sacchi and Laszlo, 2016) and congenitally deaf adults who also have weak phonological skills, show less left lateralization of the N170 to letter strings (Emmorey et al., 2017). Together these results suggest that the N170 to word-like stimuli reflects activity in an expertise-tuned system specialized for letter processing even years later in adult readers. If reading expertise serves to tune the orthographic system, might this system also be the locus of attenuated visual crowding effects? The behavioral crowding studies reviewed above suggest this might be the case as accuracy for crowded letter strings in parafoveal vision has been shown to be better than it is for strings of symbols (Chanceaux et al., 2013; Vejnović & Zdravković, 2015).

Two other ERP components have been examined in previous letter/word processing studies, the P1 which precedes the N170, and a later negativity that varies in the period between 200 and 300 ms (here referred to as the N250). The P1 typically does not show the same sensitivity as the N170 to differences in stimulus type (e.g., letters vs. symbols) but has been shown to vary in amplitude as a function of stimulus size/complexity (larger more complex stimuli produce larger P1s, e.g., Emmorey et al., 2017). Yum et al. (2011) reported that a post-N170 negativity varied in amplitude with changes in the type of stimuli. Contrasting English words, pictures of common objects and

Chinese characters they found that a posterior negativity following the N170 (accompanied by an anterior positivity) was differentially sensitive to these three types of stimuli. English words produced a larger negativity than either pictures of objects or Chinese characters (that latter in native Chinese speakers) in the epoch between 250 and 300 ms.

1.3. The current study

In this study, following Chanceaux et al. (2013) and Vejnović and Zdravković (2015) we examined the influence of crowding in the parafovea by presenting participants with a brief target stimulus centered either 1.8° to the left or right of a central fixation point and followed by a pattern mask (see Fig. 1).¹ The side of the target presentation was referred to as visual Field (LVF vs. RVF) variable. Targets were either letters or symbols which was referred to as Type of stimulus (letters vs. symbols). Targets could be single *isolated* characters (e.g., F or %) or *flanked* arrays formed from three adjacent letters or symbols arranged either horizontally or vertically (see Fig. 1). This variable, referred to as the kind of Flanker (isolated vs. vertical flankers vs. horizontal flankers), contained the critical crowding manipulation. Participants made two-alternative forced choice (2-AFC) directional responses on a gamepad to a central response prompt containing both the center character from the previous target stimulus and a same category foil. A correct response was indicated by pressing a button that indicated the location of the correct target letter or symbol stimulus (see Fig. 1). ERP recording was time-locked to the onset of the target stimulus and 2-AFC performance was measured to the prompt stimulus that followed the mask.

Here we sought to determine whether ERPs might be sensitive to differences in visual crowding between letters and symbols as has been seen in previous studies using performance measures of perception. It is still unknown at what visual processing level crowding operates, however there is growing evidence (e.g., perceptual grouping effects: Herzog et al., 2015) that suggests crowding cannot only be due to pooling in early visual cortex, but rather that some object-level information survives crowding – indicating that crowding must operate at least in part at this stage of visual processing (Manassi and Whitney, 2018). Given this, and the behavioral evidence for differential effects of crowding on the identification of letters and symbols, we predicted that the ERP correlate of letter-specific crowding would first emerge in a time-window known to capture the mapping of visual features onto letter identities and the activation of sublexical orthographic representations (i.e., position-coded letter identities and letter combinations). That time-window encompasses the N170 component (Maurer et al., 2008) and the subsequent but temporally overlapping post-N170 negativity. To our knowledge, no one has compared single character to multicharacter stimuli in studies focusing on the N170 and the following post-N170 negativity.² Here we predicted that differences between isolated and flanked targets (i.e., crowding effects) should

differ for letter stimuli compared to symbol stimuli, and that these differences should be visible on the N170 component and continue on to impact the subsequent negativity reported by Yum et al. (2011). Moreover, we predicted even earlier differences between isolated and flanked targets on the P1 component given differences in retinal size and/or featural complexity, with isolated letters and symbols producing a smaller P1 component than comparable 3-character stimuli. Crucially, we predicted that this early effect would not differ for letters and symbols given that previous studies have failed to show the P1 being sensitive to category-level properties of the stimulus (e.g., Emmorey et al., 2017).

2. Methods

2.1. Participants

Thirty-one young adults participated in this study, however two were rejected from analysis due to excessive EEG artifacts (>30% of trials rejected after ICA correction) and three for experimenter error/equipment malfunction. The behavioral and EEG data from the remaining 26 (mean age 22.7 years, SD = 2.9, 14 male) were used for the behavioral and ERP analyses. All participants reported being right-handed, native readers of a Latin script (e.g., English or Spanish), had normal or corrected-to-normal vision, and no history of neurological impairment. Participants were compensated \$15 per hour for their participation, and informed consent was obtained from each.

2.2. Stimuli

To keep our paradigm parallel to the prior behavioral crowding studies that motivated the current experiment, we used the same ASCII characters and general presentation parameters used in those prior studies (Vejnović & Zdravković, 2015; Grainger et al., 2010). Upper case consonants were selected as is typical in studies of letter crowding and vowels were not used so that the multi-letter stimuli would not be easily pronounceable. Target stimuli were presented on the horizontal meridian with a center eccentricity (the mid-point of stimulus) 1.8° to the left or right of a central fixation cross. Targets were the same ones used in the prior behavioral study of Vejnović & Zdravković (2015) and consisted of eight letters (B, D, F, G, K, L, N, S, T) or symbols (%/, ? @, <, }, £, §, µ), presented in white nonproportional Courier New font, on a black background. The cell sizes for all letter and symbol characters (including blank pixels surrounding each character) were the same at 0.4° × 0.6°. There was no additional spacing between characters in multi-character stimuli. Targets could be presented alone (isolated) or flanked either horizontally or vertically by two different characters from the same set (e.g., a letter trial could only be made up of three different letters). Horizontal flankers were presented 0.4° (0.22φ) degrees away from the target (center-to-center spacing) and vertical flankers 0.6° (0.33 φ) from the target. There were 324 total trials, meaning there were 27 trials per cell in the design, which included 2 stimulus Type conditions (letters or symbols), 2 visual Field conditions (left vs right), and 3 types of Flankers conditions (isolated, horizontal, vertical). The characters used in each condition were balanced so that every character appeared in each position an equal number of times (e.g., in the right horizontally-flanked letter condition, the letter “B” appears 3 times each as a target, left flanker, and right flanker).

2.3. Procedure

After giving informed consent, subjects were seated in a comfortable chair, 140 cm from a stimulus monitor, in a dimly lit room. Each subject completed 324 trials of a two-alternative forced-choice (2AFC) task in one of two order-counterbalanced lists. A schematic of two example trials can be seen in Fig. 1. Targets (and in flanked conditions, their flankers) were presented along with a central fixation cross for 100 ms.

¹ Pattern masking was used because the prior behavioral studies upon which the current study is modeled used this manipulation. This approach is frequently used in behavioral studies seeking to examine differences in accuracy between conditions where without masking accuracy might approach ceiling and therefore make finding condition differences more difficult. We kept this methodological feature in our design so as to make comparison of results between our study and the previous behavioral studies possible.

² We refer to this post-N170 negativity as the N250 even though it does not manifest as an exogenous peak as in Yum et al. (2011). However, readers can see what are clear negative peaks near 170 and 250 ms in the data from the current study by examining Supplementary Fig. S1 which shows the difference (subtraction) ERPs of the word minus symbol stimuli. Similar negativities that do not necessarily produce an exogenous peak have been reported in prior studies. For example, the ND (negative difference) is a well known auditory attention effect that requires a difference wave for it to be isolated from the surrounding N1 and P2 (e.g., Hansen and Hillyard, 1980).

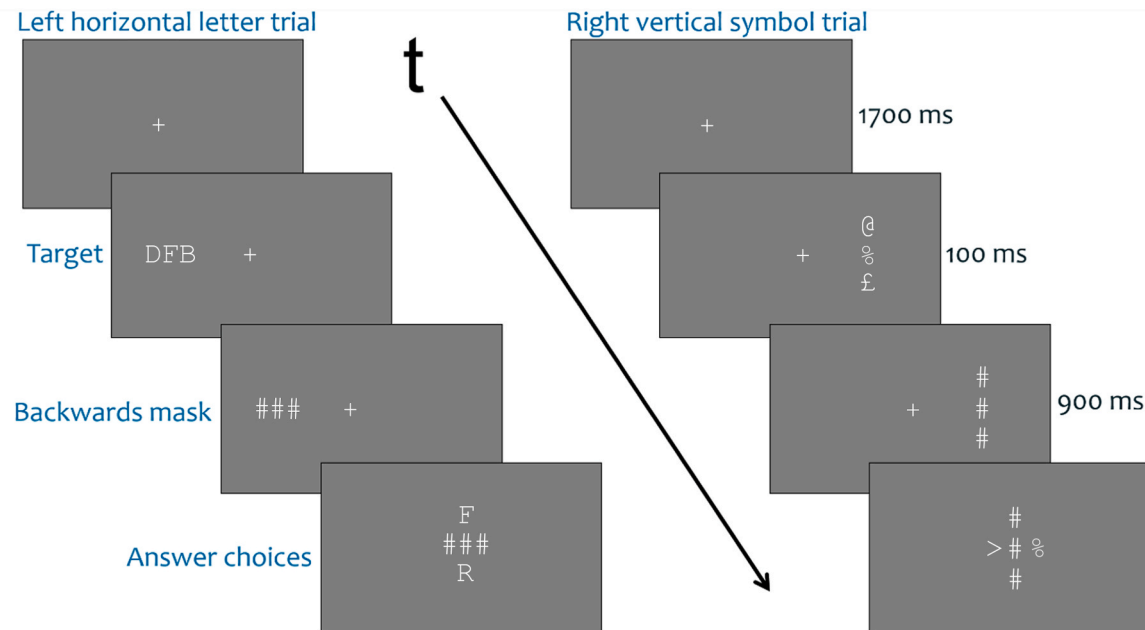


Fig. 1. Examples of stimuli tested in the flanked character conditions.

Afterwards there was a 900 ms backwards mask made up of hash marks (#) at each location a character had previously been presented, followed by two answer choices. Answer choices consisted of the target and one distractor of the same stimulus type that was not presented as the target or flanker on the immediately preceding trial. Participants responded using a gamepad, indicating which of the two answer choices was the target. Participants were told to be as accurate as possible. After a response was made, there was an inter-trial-interval for 1700 ms during which a fixation cross was presented before the next trial began.

2.4. EEG recording and processing

EEGs were recorded from 29 passive tin electrodes (Electro-Cap) arranged in standard locations across the scalp (see Fig. 2). An electrode

placed on the left mastoid served as a reference during recording. An electrode was placed under the left eye to help in identifying blinks. Electrodes were placed on the outer canthus of each eye to monitor horizontal eye movements. The impedances of scalp and mastoid electrodes were kept below 2.5 kOhms, and all eye channels were kept below 5 kOhms. The EEGs were continuously sampled at 500 Hz and amplified with a SynAmpsRT amplifier (Neuroscan) with a bandpass of DC to 00 Hz. Offline, ICAs were run on each participant's EEG and blink and horizontal eye movement artifact components were removed from the data (Makeig et al., 2004; Delorme et al., 2007). The data were low-pass filtered at 20 Hz, and re-referenced to an average reference of all scalp electrode channels as is standard in N170 studies (Rossion et al., 2003). ERPs were time-locked to targets and averaged in 400 ms epochs, with a 100 ms pre-stimulus baseline. Trials which contained remaining artifacts were excluded from analysis (less than 1% of trials after ICA correction).

2.5. Data analysis

Behavioral data (proportion correct) were analyzed using a within-subjects omnibus ANOVA contrasting the three kinds of Flanker stimuli (isolated vs. vertical flanked vs. horizontal flanked), the two Types of stimuli (letters vs. symbols) and the Visual Field of presentation (left vs. right). In the presence of interactions, separate follow-up ANOVAs were run comparing symbols and letters in just the isolated condition, and in just the flanked conditions.

ERP data were measured as the mean amplitude in three different time windows consistent with prior studies using similar stimuli corresponding to the P1 (80–120 ms; Emmorey et al., 2017), the N170 (140–200 ms; Yum et al., 2011) and the N250 (200–300 ms; Yum et al., 2011). Analyses were limited to four temporo-parietal and occipital electrodes (T5/6 and O1/2) as is standard in N170 studies of letter processing (e.g., Emmorey et al., 2017). The analysis used was similar to the one used for the accuracy data but with the addition of two scalp site variables to capture distributional differences. This resulted in factors of stimulus Type (Letters vs. Symbols), kind of Flanker (Isolated non-flanked vs. Vertical flanked vs. horizontal flanked), presentation visual Field (LVF vs. RVF), scalp Laterality (LH vs. RH) and scalp Temporo-Occipital location (T vs. O). Given that the hypotheses of the study were focused on crowding (flanked vs. isolated) and stimulus type

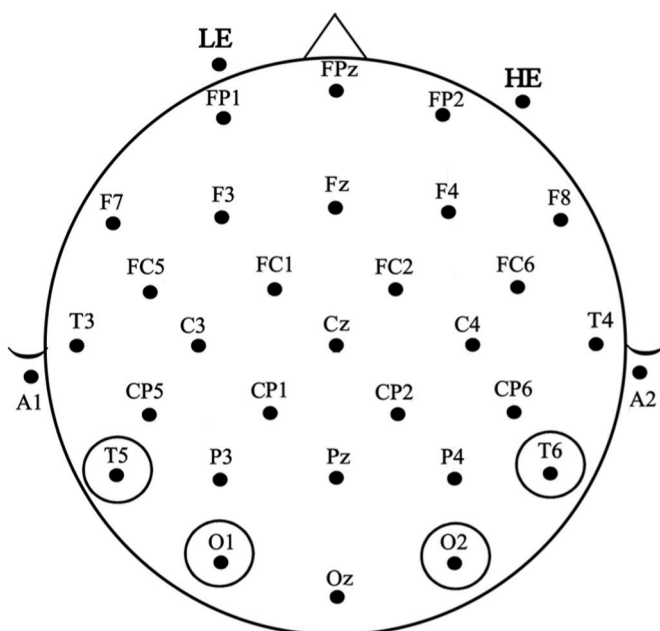


Fig. 2. ERP montage with the 4 analysis sites circled.

(letter vs. symbol), only main effects and interactions with the factors of stimulus Type and kind of Flanker are interpreted or followed up on. Significant interactions of the stimulus Type by kind of Flanker variables were followed up with two sets of a-priori specified analyses; in one set we compared isolated and flanked stimuli for the effects of stimulus Type (letters vs. symbols), and in a second we compared letters and symbols in isolated vs. flanked displays (i.e., collapsing the horizontal and vertical flanked conditions). Geisser-Greenhouse correction was applied to all effects with more than one degree of freedom in the numerator (Greenhouse and Geisser, 1959).

3. Results

3.1. Behavioral results

We analyzed the accuracy data from the 2AFC task in within-subjects omnibus ANOVA contrasting the three kinds of Flanker stimuli (isolated vs. vertical vs. horizontal), the two Types of stimuli (letters vs. symbols), and the Visual Field of presentation (LVF vs. RVF). There was a main effect of stimulus Type ($F(1,25) = 45.34$, $p < .0001$) indicating that letters were responded to more accurately than symbols (0.89 vs. 0.80), while a main effect of kind of Flanker ($F(2,50) = 102.32$, $p < .0001$) indicated that isolated non-flanked stimuli produced more accurate responding than both kinds of flanked stimuli (isolated = 0.95 vs. vertical = 0.80 vs. horizontal = 0.77). Finally, the main effect of visual Field ($F(1,25) = 25.98$, $p < .0001$) revealed that RVF stimuli were responded to more accurately than LVF stimuli (0.87 vs. 0.82). There was also a stimulus Type \times kind of Flanker interaction ($F(2,50) = 17.0$, $p < .0001$ – see Fig. 3). Two follow-up ANOVAs were run to better understand this interaction. In one analysis we contrasted the two kinds of flanked stimuli (horizontal vs. vertical) and in the other we examined accuracy only for the isolated non-flanked characters. In the analysis of isolated characters there were no main effects or interactions involving stimulus Type ($ps > .13$). However, in the analysis of flanked stimuli there were main effects of stimulus Type ($F(1,25) = 46.17$, $p < .0001$) and kind of Flanker (horizontal vs. vertical: $F(1,25) = 9.3$, $p = .0054$). Participants were more accurate for letters than symbols (0.85 vs. 0.73) and for central targets in vertical than horizontal displays (0.80 vs. 0.77). There was also an interaction between stimulus Type and kind of Flanker ($F(1,25) = 4.8$, $p = .038$ – see the center and right side of Fig. 3). Further follow-up analyses breaking down this interaction revealed that the effect of kind of Flanker was significant only for symbols ($F(1,25) = 13.92$, $p = .001$) with horizontal symbols producing the least accurate responses (0.70 vs. 0.75). Response accuracy for letters was almost identical for horizontal and vertically flanked targets (0.845 vs. 0.854 – all $ps > .58$).

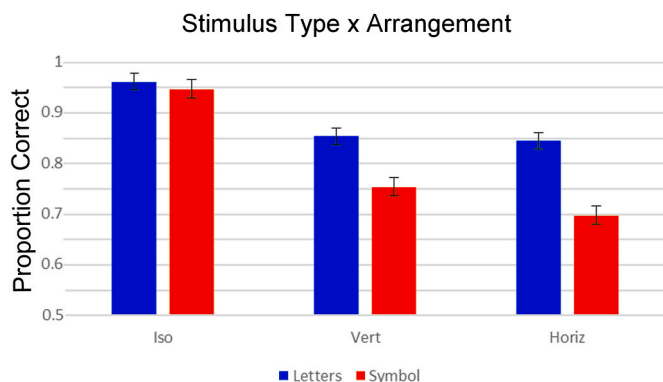


Fig. 3. Mean probability correct (SEM) for isolated, vertical and horizontal (the stimulus Arrangement variable) letters and symbols (stimulus Type variable) in 26 participants.

3.2. ERPs

Plotted in Fig. 4 are the ERPs time-locked to the onset of laterally presented target characters at the two temporal and two occipital scalp sites contrasting isolated (i.e., non-flanked stimuli) with the two orientations of flanked target stimuli. The left panel shows ERPs to letter stimuli and the right panel ERPs for symbols. As can be seen ERPs at all sites start with an early occipital maximum positivity that peaks just after 100 ms (P1) and is followed by a temporally broad negativity peaking around 200 ms. This negativity tends to be larger over left hemisphere sites. At some sites (e.g., T5) the negativity appears to extend to almost 300 ms while at other sites (O1/2) the negativity is followed by a large positivity (P2) peaking between 225 and 275 ms. Following prior similar ERP studies (Emmorey et al., 2017; Yum et al., 2011) we refer to the earlier occipital maximum negativity as the N170 and later T5 peaking negativity as the N250.

3.3. P1 (80–120 ms)

In this epoch there were two main effects in the ANOVA. The first was kind of Flanker ($F(2,50) = 11.51$, $p = .0001$) with isolated non-flanked stimuli producing the smallest P1 and targets flanked by similar characters producing the largest P1 (0.68 vs. 1.23 μ volts). The second effect was for visual Field ($F(1,25) = 12.41$, $p = .0017$) with RVF stimuli generating a larger P1 than LVF stimuli (1.33 vs. 0.77 μ volts). The only interaction in this epoch was between visual Field and Laterality ($F(1,25) = 7.02$, $p = .014$) with larger P1s recorded from electrode sites contralateral to the visual field of presentation (see Fig. 5 left). Importantly, there were no significant effects of stimulus Type or kind of Flanker during this epoch.

3.4. N170 (140–200 ms)

As in the P1 epoch there was a significant visual Field by scalp Laterality interaction ($F(1,25) = 67.87$, $p < .0001$), although here this effect was due to a larger negativity over scalp sites contralateral to the visual field of stimulus presentation (see Fig. 5 middle). Unlike for the P1, there was a main effect of stimulus Type ($F(1,25) = 22.6$, $p = .0001$), with letters producing significantly more negative-going ERPs than symbols (-0.09 vs. 0.43 μ volts). Moreover, the stimulus Type variable also interacted with the kind of Flanker variable ($F(2,50) = 4.54$, $p = .016$). This interaction suggested that there was a difference in the size of the N170 for letters compared to symbols as a function of kind of flanker. To better understand this interaction, we conducted two sets of follow-up analyses.

In the first set of follow-up analyses we used one ANOVA to zero in on differences between letters and symbols on trials with central target characters that were flanked by distractor characters and a separate ANOVA contrasted letters and symbols in isolated displays. There were no significant differences between letters and symbols in isolated character displays, (all ps including the stimulus Type variable $> .21$). However, for stimuli with flanking characters, letters had significantly more negative-going ERPs than symbols (-0.23 vs. 0.51 μ volts; $F(1,25) = 25.0$, $p < .0001$). These effects can be seen in the voltage maps in Fig. 6 (top and bottom left). In the latter analysis the interaction between stimulus Type and kind of Flanker (i.e., vertical vs. horizontal) was not significant ($p > .11$).

In a second set of follow-up analyses we directly assessed flanker effects separately for letters and symbols by comparing N170 activity for isolated stimuli to the average of the two types of flanked stimuli (see Fig. 7). In these analyses there were differences between isolated letters and flanked letters (main effect of kind of Flanker, $F(1,25) = 4.68$, $p = .04$) with flanked letter stimuli producing -0.43 μ volt more negative-going activity than isolated letters (see Fig. 7 left top). For symbol stimuli the trend was in the opposite direction with flanked symbol stimuli showing slightly less negativity compared to isolated symbol

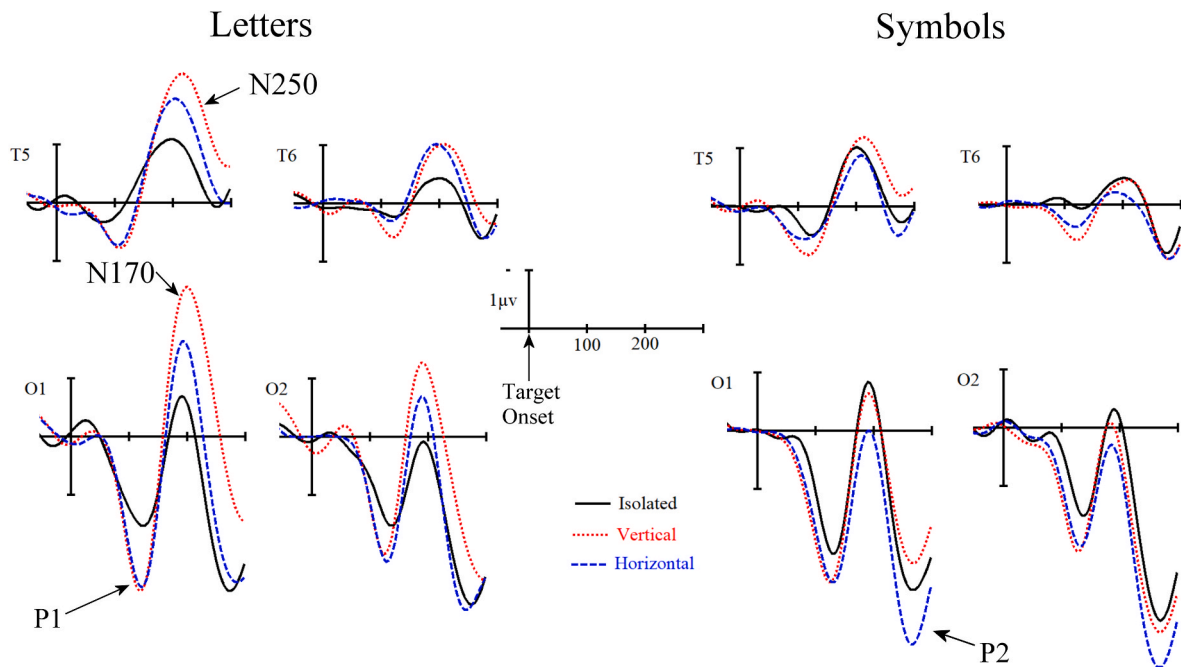


Fig. 4. ERPs time-locked to target character stimuli averaged across visual field of presentation (RVF + LVF/2) in the three stimulus arrangements (isolated, vertical and horizontal). On the left side of the figure are ERPs to letter stimuli and on the right side of the figure are ERPs to symbol stimuli. Negative voltages are plotted up.

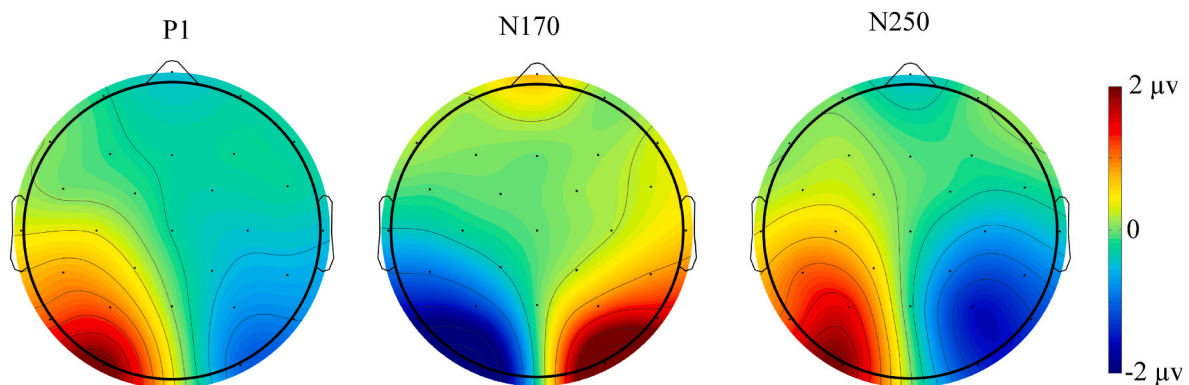


Fig. 5. Visual Field (RVF - LVF) ERP effects in three temporal windows corresponding to the P1, N170, and N250.

stimuli. However, this difference was not significant ($p > .15$ – see Fig. 7, bottom left).

3.5. N250 (200–300 ms)

As in the previous two temporal windows there was an interaction between the visual Field of presentation and electrode Laterality ($F(1,25) = 24.97$, $p < .0001$) with greater positivity over scalp sites contralateral to the visual field of stimulus presentation (see Fig. 5 right side). Also as in the previous epochs, visual field of presentation did not interact with the stimulus Type or kind of Flanker variables. There was also a main effect of stimulus Type ($F(1,25) = 34.61$, $p < .0001$) with greater negativity for letters than symbols (0.80 vs. 1.50 μ volts), and a main effect of kind of Flanker ($F(2,50) = 18.38$, $p < .0001$). There were also interactions between stimulus Type and kind of Flanker ($F(2,50) = 12.86$, $p < .0001$), and stimulus Type, kind of Flanker and Temporo-occipital scalp distribution ($F(2,50) = 9.18$, $p = .0004$) suggesting a difference in the amplitude of ERPs in this epoch between letters and symbols as a function of kind of Flanker. In order to decompose these interactions, we used the same strategy of follow-up analyses as in the prior epoch.

As in the N170 epoch, the stimulus Type variable was not significant for isolated characters (all p s $> .22$ – see Fig. 6 top right). However, for the flanked conditions there was a main effect of stimulus Type ($F(1,25) = 44.94$, $p < .0001$) with greater negative-going activity for letters than symbols (0.61 vs. 1.58 μ volts – see Fig. 6 bottom right). There was also a main effect of kind of Flanker ($F(1,25) = 32.58$, $p < .0001$) and a stimulus Type by kind of Flanker by Temporo-occipital scalp site interaction ($F(1,25) = 6.55$, $p = .017$). Separate follow-up analyses run at the temporal and occipital sites revealed that at both locations letters produced more negative-going ERPs than symbols (main effect of stimulus Type) but only occipital sites produced a stimulus Type by kind of Flanker interaction (occipital: $F(1,25) = 5.97$, $p = .022$; temporal $p = .40$) indicating that the N250 was significantly larger for vertical letters than horizontal letters over occipital sites. The larger occipital focus of the flanker direction can be seen in Fig. 8.

Finally, in the analyses comparing the pooled horizontal and vertical flanked targets with the isolated targets separately for letters and symbols, there were clear differences between isolated and flanked letters (main effect of kind of Flanker, $F(1,25) = 22.15$, $p < .0001$) with flanked letter stimuli producing more negative-going N250 activity than isolated letters (a -0.75 μ volt difference). Moreover, the difference between

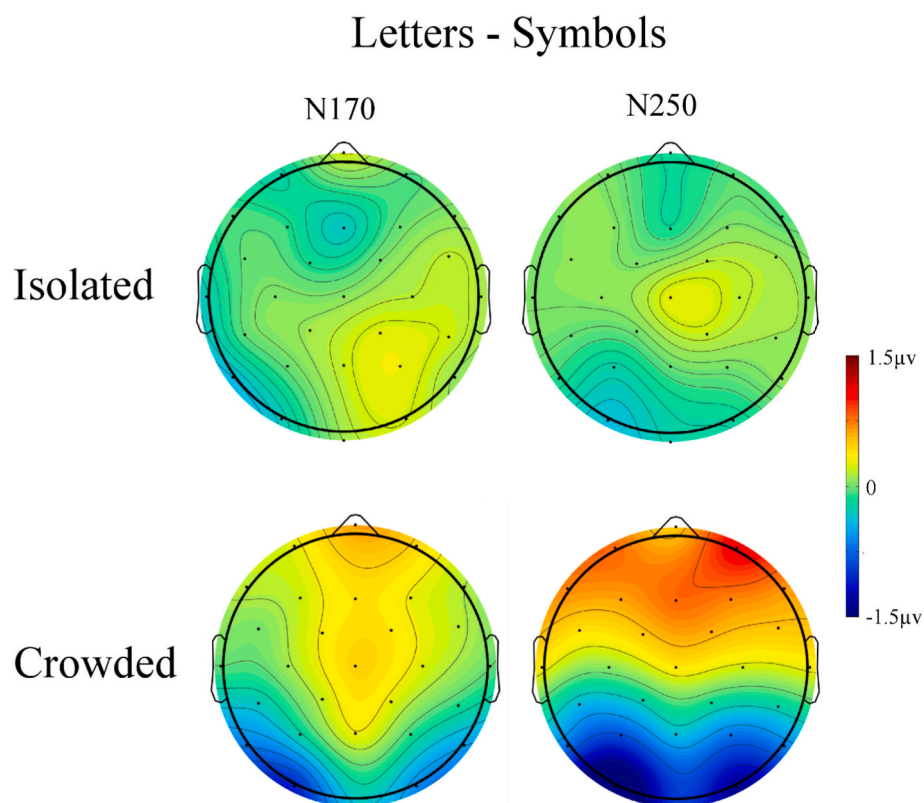


Fig. 6. Letter minus Symbol effects for isolated stimuli (top) and flanked (crowded) stimuli (bottom) in the N170 (left) and N250 (right) epochs.

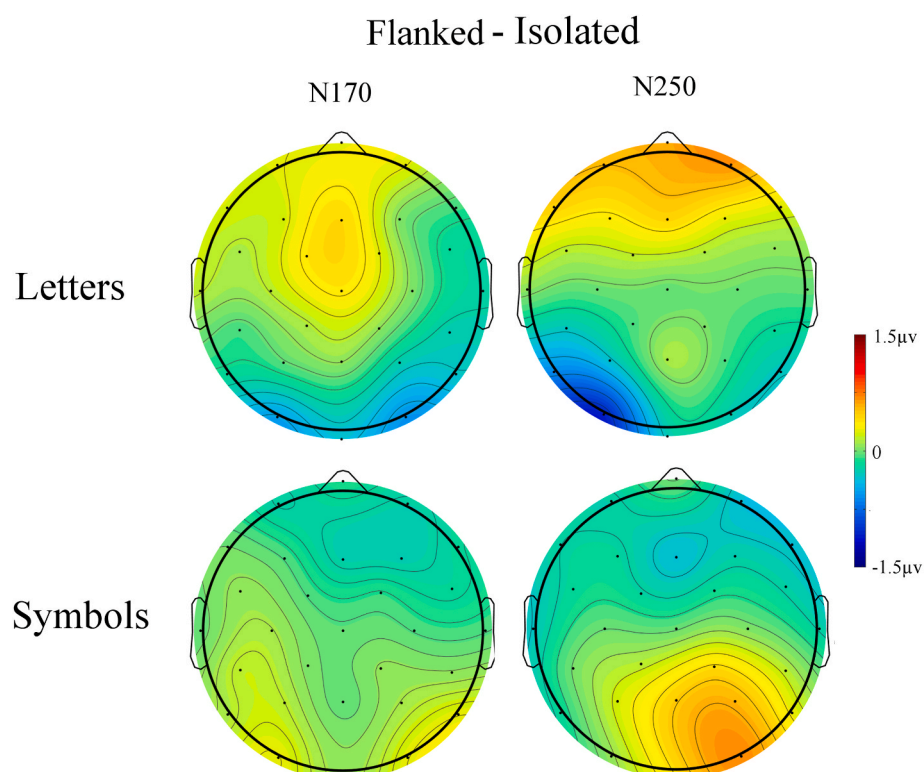


Fig. 7. Flanked minus Isolated ERP effects for letters (top) and symbols (bottom) for the N170 (left) and N250 (right) epochs.

flanked and single letter stimuli was larger over the left hemisphere ($-1.1 \mu\text{V}$) than the right hemisphere ($-0.4 \mu\text{V}$ – kind of Flanker \times Laterality interaction, $F(1,25) = 9.39$, $p = .0052$ – see Fig. 7 top right).

For symbol stimuli the pattern was again in the opposite direction with isolated non-flanked symbols producing significantly more negative-going activity than flanked symbol stimuli especially over the right

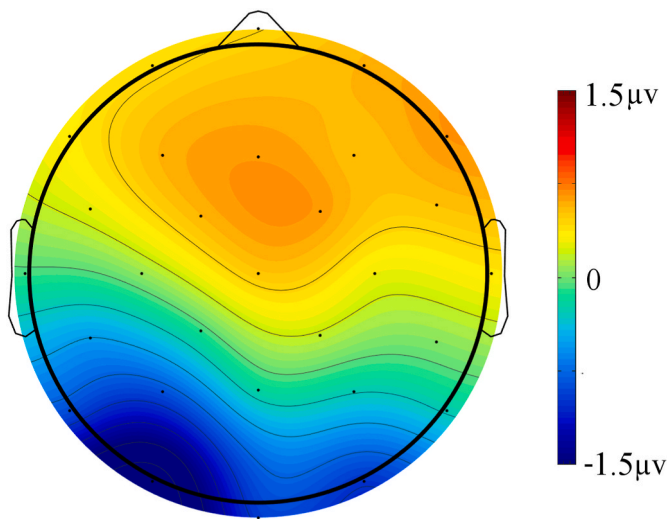


Fig. 8. Vertical minus horizontal N250 effect for flanked letters.

hemisphere ($F(1,25) = 5.17$, $p = .032$ – see Fig. 7 bottom right).³

4. Discussion

In the present study we sought evidence for differences in the processing of letters and symbols when presented as 3-character arrays (3 letters or 3 symbols) accompanied by no difference in the processing of isolated letters and symbols. This was motivated by the hypothesis that in order to optimize letter-based word recognition, letter arrays are less affected by crowding (i.e., the presence of flanking stimuli) than arrays of symbols in skilled readers. Our results provide support for this hypothesis and provide crucial information with respect to the timing of the hypothesized differences in crowding for letters and symbols as predicted by prior ERP studies investigating differences in the processing of letter strings and other types of stimuli.

Firstly, the behavioral results replicate prior findings showing greater effects of crowding for letters than symbols. When presented in isolation, letters and symbols were identified with similar accuracies. However, when participants had to identify the central character in a 3-character array formed of the same stimulus category (letters vs. symbols), then accuracy was found to be significantly greater for letters than symbols. Moreover, this advantage for letters over symbols when presented in arrays was significantly greater when the arrays were aligned horizontally compared with a vertical orientation. This effect of stimulus orientation can be accounted for by the modified receptive field hypothesis (Grainger et al., 2010), according to which the reduced effects of crowding for letter arrays should mainly arise with horizontally arranged stimuli when that is the orientation adopted by the written language known to participants. Note that the overall higher accuracy for vertically arranged arrays over horizontal arrays is predicted by the radial-tangential anisotropy exhibited by crowding (Toet and Levi, 1992), where flankers arranged radially relative to fixation (i.e.,

horizontal flankers if the target is on horizontal meridian, as was the case in the present study) produce more crowding than flankers arranged tangentially (the vertical flankers in the present study). That is, the orientation of the elliptical shape of the region of uncrowded identification (Pelli and Tillman, 2008) depends on the location of the target relative to central fixation. When targets are placed on the horizontal meridian, then the critical spacing required for uncrowded identification has a greater horizontal extent than vertical extent (hence the stronger interference of horizontal flankers seen with symbol stimuli). It is the combination of this radial-tangential anisotropy and the hypothesized greater extent of the uncrowded region for horizontally arranged letters compared with horizontally arranged symbols (the modified receptive field hypothesis) that explains the pattern of behavioral effects shown in Fig. 3 for flanked letters and symbols. Flanker interference (i.e., lower levels of target identification accuracy) is overall greater for horizontally arranged flankers due to the radial-tangential anisotropy, but this impact of stimulus orientation is reduced for letter stimuli because horizontally arranged letters are less impacted by crowding than horizontally arranged symbols.

Most important, however, is the fact that these differences in the processing of letter and symbol arrays were first seen on the N170 ERP component. Prior to that, differences between isolated and flanked stimuli were found on the P1 component, but these did not vary as a function of stimulus type. These early differences between isolated and flanked stimuli likely reflect the increase in retinal size of the flanked stimuli relative to the isolated stimuli as the P1 is known to be sensitive to such exogenous properties of stimuli (Pratt, 2011). The lack of the effect of stimulus type on the P1 agrees with another similar N170 study using symbols and letter stimuli (Emmorey et al., 2017), and suggests that letter specific processing is not occurring in the P1 epoch. As predicted, we found the first impact of stimulus type (letters vs. symbols) and its interaction with the presence or absence of flankers on the N170 component. Here, flanked letters showed greater N170 amplitudes than isolated letters, whereas there was no effect for symbols, with a weak trend in the opposite direction. We argue that a larger N170 is indicative of relatively unimpaired parallel processing of the individual abstract units of complex displays. That is, in an uncrowded display the letter and symbol stimuli both activated their respective representations generating roughly similar N170 activity. However, when more elements were added to the stimulus display, only letters showed an increase in N170 amplitude, suggesting crowded arrays of letters are still able to activate individual letter representations and leading to a larger N170 to letter arrays. On the other hand, symbols actually showed evidence of a slight decrease in early-N170 amplitude presumably because crowded symbols are less able to activate their representations, leading to a relatively smaller or even suppressed N170. This fits well with the existing research on crowding and ERPs in similar time windows which shows that for other visual stimuli (e.g., vernier lines) crowding suppresses the N1 component (Chicherov et al., 2014). We speculate that the extensive experience readers have recognizing letters in crowded conditions is the likely reason that letters are more able to escape the typical pattern crowding has of obstructing the visual feature mapping or binding indexed by the N170 family of ERP components.

The pattern of letter-specific crowding effects seen on the N170 continued into a post-N170 period referred to here as N250 epoch, with greater negativity in the presence of flankers for letters, but not for symbols. Moreover, flanker orientation (horizontal vs. vertical) had a significant impact on the post-N170 amplitudes to letter arrays. One somewhat speculative possibility for activity in the N250 epoch is the possibility that letter processing immediately following the N170 reflects the mapping of location-specific letter identities onto a location-invariant sublexical orthographic code (see Grainger and Holcomb, 2009). Following from this, one possible explanation to why horizontally flanked letters have smaller N250s than vertically flanked letters may be related to how the word recognition system is optimized to be able to combine and represent horizontally oriented letter strings as

³ As suggested by an anonymous reviewer we randomly sorted half of the trials in each of the two flanked conditions into two separate smaller bins which were roughly equal to the number of items in the isolated condition. This allowed us to do two separate contrasts between flanked and isolated conditions testing the possibility that differential noise between bins with more and less items might have distorted the pattern of effects. When we re-ran the two parallel follow-up ANOVAs contrasting the two samples of flanked and isolated conditions there was no evidence of a difference in the pattern of effects from what is reported in Results section – all three sets of analyses (the two new supplemental and the original) were virtually identical in terms of size and direction of effects.

higher order abstract word representations, but not vertically oriented letter strings. Thus, for vertical strings, letter-level activation may continue to accumulate for longer, or fail to transition to a more abstract representation, leading to persistent N170 activity.

Overall, this study replicates the behavioral finding that letters are more resilient to crowding than letter-like symbols, and suggests this effect is due to differences in neural activity during N170, fitting with other ERP studies of crowding showing effects on the N1 (e.g., Chicherov et al., 2014; Ronconi et al., 2016). We argue this pattern is due to extensive experience reading crowded letters, which modifies the way letters are represented in order to reduce interference from other letters (Grainger et al., 2010). With regard to models of crowding, these results add to other findings (e.g., grouping effects – Manassi et al., 2012) that are insufficiently explained by simple pooling models, and suggest that crowding is at least partially due to interactions at later perceptual stages of processing.

4.1. Limitations and future directions

Moving forward there are still a number of unanswered questions that could be addressed in future ERP studies of crowding. In particular, the somewhat larger N170 effects of crowded vertical as compared to horizontal letter arrays needs further exploration. Because our vertical strings were crowded along their narrower axis while the horizontal arrays were crowded along their longer axis is one possibility and by using characters that are equal (square) in the horizontal and vertical directions would address this possibility. Another issue that merits further investigation is overall familiarity since there is a large difference in the familiarity of letter combinations compared to combinations of symbols. Contrasting ERP crowding effects for letter strings with other more familiar stimuli such as strings of numbers or possibly strings of musical notes (in expert musicians) could provide further clarity on the specificity of the effects reported here. Also interesting would be to include a combination of vowels and consonants as well as upper and lower case letters. As it stands the results of the current study cannot be generalized to these other kinds of letter stimuli. It is probably also important to examine crowded letter strings in more ecologically realistic contexts, for example, without masking or in a sentence context.

Credit author statement

Conceptualization Grainger, Holcomb, Winsler, Methodology Grainger, Holcomb, Winsler, Analysis Holcomb & Winsler, Investigation Winsler, Writing Winsler, Holcomb & Grainger, Review & Editing Holcomb & Grainger, Funding acquisition Holcomb & Grainger.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2022.108396>.

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