Representational Levels of Bilateral N170 for Japanese Hiragana Strings during Focal Spatial Attention to Letters

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Fluent reading requires the rapid integration of letters into a unified letter-string percept. Previous studies have shown that this process is related to specific enhancement of the left-lateralized event-related potential (ERP) called N170. However, our previous studies found bilateral N170, rather than left-lateralized N170, enhancement for rapidly-presented Japanese Hiragana strings that were either unattended or had wide interletter spacing (Okumura et al., 2014, 2015). To explore the possibility that bilateral N170 reflects the processing of separate letters, the present study examined lateralized ERP attention effects for widely-spaced Hiragana words, nonwords, and alphanumeric symbol strings. Twelve participants were required to attend to the left or right end of strings, and to respond to a target letter/symbol at the attended location. We found bilateral N170 enhancement for
Hiragana strings (130-210 ms poststimulus), while a spatial attention effect was seen in the 160—210 ms interval regardless of Hiragana or symbol strings. These results suggest that N170 specialization involves processing of letter strings at the level of separate constituent-letters when they are widely spaced or when attention does not cover letter strings.

Key words: letter-string processing, perceptual integration, spatial attention, event-related potentials, N170

Extensive practice and experience with reading leads to remarkable speed and efficiency in processing visually presented letters, words, and word-like strings of letters. Such fluent reading has been considered to depend on a process that integrates the letters of a word into a unified percept. This has been evidenced by the absence of a word-length effect, in that the speed of word recognition remains constant regardless of the number of letters in a word (e.g., Frederiksen & Kroll, 1976). The word/pseudoword superiority effect, which refers to the more accurate identification of letters embedded in briefly presented words (e.g., Reicher, 1969; Wheeler, 1970) and pseudowords (e.g., Chase & Tallal, 1990) than those in unpronounceable letter strings or those presented in isolation, also supports the above notion. These effects indicate that the constituent letters of a letter string are integrated into a unitary object and processed efficiently in parallel.

Neuroimaging studies with functional magnetic resonance imaging (fMRI) have also demonstrated that the perceptual integration of letters into a unified percept is important for understanding reading-related neural specialization. In expert adult readers, a portion of the left fusiform gyrus, known as the visual word form area (VWFA), is activated preferably in response to learned letter stimuli (for a review, see McCandliss et al., 2003). While the VWFA is generally insensitive to lexical attributes, such as lexicality (Dehaene et al., 2002) and word frequency (Fiebach et al., 2002), it distinguishes poorly-structured letter strings (i.e., consonant strings) from well-structured words (Cohen et al., 2002). These results show that the functional specialization of the VWFA is linked to the level of an integrated letter-string percept in print processing.

The temporal aspects of such neural specialization have been explored in studies using event-related potentials (ERPs), which reflect brain activities that occur on the order of milliseconds. A large body of evidence has shown that letter strings elicit enhanced N170 relative to non-linguistic visual control stimuli, such as strings of symbols and forms, typically between 140-200 ms poststimulus at occipito-temporal electrodes (Bentin et al., 1999; Mahé et al., 2012; Maurer et al., 2005; Simon et al., 2004). The amplitude and/or enhancement of N170 in response to letter strings is characterized by a left-lateralized
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topography that is distinct from N170 in response to non-linguistic objects (Bentin et al., 1996; Gauthier et al., 2003; Rossion et al., 2003; Tanaka & Curran, 2001). This letter-string-specific N170 is most likely to originate from the VWFA (Brem et al., 2006, 2009). Therefore, the left-lateralized N170 for letter strings is widely recognized to reflect reading-related expertise based on unitary letter-string percepts in the early stages of visual processing.

However, these previous studies identified N170 specialization for letter strings under very slow stimulus presentation (i.e., one stimulus every few seconds), in contrast to the input rate in normal reading. Under such conditions, the availability of ample processing resources for each stimulus may favor unintentional or even deliberate linguistic processing (Kronschnabel et al., 2013). Thus, it was unclear whether this N170 specialization truly reflects expertise in perceptual processing. To solve this problem, our previous studies tested N170 specialization for Hiragana strings under a condition in which the attentional resources allocated to linguistic processing were restricted through the use of rapid stimulus presentation (i.e., 2–3 stimuli every second) and a task that requires attention to a fixation cross rather than the letters themselves (Okumura et al., 2014). As a result, we found bilateral N170 enhancements in response to Hiragana strings versus symbol strings, both when interletter spacing was normal and wide (Okumura et al., 2014). In our subsequent study, the N170 for task-relevant letters was left-lateralized with normal interletter spacing, but was bilateral with wide spacing (Okumura et al., 2015). These studies indicated that there are two types of N170 specialization for Hiragana strings, and that the deployment of attention toward print and interletter spacing are both critical in determining which of these types occurs.

Given that bilateral N170 specialization was observed for unattended and/or widely-spaced Hiragana strings, it may occur when the constituent letters can not be readily integrated. More specifically, focal spatial attention may be crucial for the integration of features (Treisman & Gelade, 1980), and wide interletter spacing may reduce the physical integrity of letter strings and lead to letter-by-letter processing (Cohen et al., 2008; Risko et al., 2011). Therefore, the bilateral N170 could be associated with the processing of separate letters within letter strings, instead of integrated letter-string percepts reflected by the left-lateralized N170.

The present study explored this possibility by using a sustained spatial attention paradigm that can examine the perceptual integrity of visual objects by indexing lateralized attention effects in posterior ERPs. When subjects direct their attention to the left or right visual field, early occipito-temporal ERPs, such as P1 (around 100–140 ms poststimulus) and N1 (around 140–220 ms), in response to bilateral stimulus arrays are enhanced over the hemisphere contralateral to the attended location (Heinze et al., 1990, 1994; Kasai, 2010; Kasai & Takeya, 2012). This lateralized spatial attention effect of N1 decreased, as were the speed and/or accuracy of discriminating stimuli at the attended locations, when bilateral stimuli were grouped or connected, which suggests that attention spreads over the entire representation of grouped stimuli or a unitary object (Kasai, 2010; Kasai & Takeya, 2012). Thus, this paradigm should be useful for clarifying whether bilaterally presented stimuli are integrated, and the underlying neural processes.

In the present study, Hiragana words, nonwords, and alphanumeric symbol strings were presented with wide interletter spacing over the left and right visual fields, which was expected to elicit bilateral N170 enhancement for Hiragana strings (Okumura et al., 2014, 2015). Participants were instructed to attend to either the left or right end of the stimuli and to press a button when a letter or symbol with a designated local visual feature (i.e., two parallel horizontal strokes) appeared at the attended location. If widely-spaced Hiragana letters are integrated into a unified percept by the N170 latency range, lateralized spatial attention

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effects for words and nonwords should be smaller than those for symbol strings, concomitantly with N170 print-specialization. Moreover, the ability to discriminate targets at the left or right ends of strings should be worse for words and nonwords.

Methods

Participants

Twelve volunteers (6 males; age 19–38 years, mean 22.7 years) participated in the experiment. All participants were right-handed monolingual native Japanese speakers and had normal or corrected-to-normal vision. They all gave their written informed consent as required by the Declaration of Helsinki, and were paid for their participation. The study was approved by the local ethics committee.

Stimuli

The stimuli consisted of 100 familiar Japanese Hiragana words (mean rated familiarity of 6.01, SD = 0.22, according to the NTT database; Amano & Kondo, 1999), nonwords, and alphanumeric symbol strings that consisted of four letters or symbols. Nonwords were constructed by shuffling the letters of the words at each position (i.e., the first letter of a word was replaced by that of another word, and so on), so that the letters used and frequencies of each letter were controlled between the word and nonword sets. All nonwords were pronounceable. Alphanumeric symbols were chosen as visual controls because they are non-linguistic but familiar to Japanese readers. Seventeen different symbols were used to construct symbol strings. Hiragana letters and symbols used in the experiment were classified into two types; those with two parallel horizontal strokes (i.e., targets, Figure 1A) and those with no such visual feature. Sets of words, nonwords and symbol strings each consisted of 76 stimuli with no targets, 12 with a target at the left end, and 12 with a target at the right end.

Stimuli were presented in black against a gray background at the center of a computer monitor situated 70 cm in front of the participants (Figure 1B). The four constituents were aligned horizontally across the left and right hemifields, which extended 3.93° to the left and right of a central fixation cross (0.57° by 0.57°, presented 1.23° below the stimulus). Each letter/symbol extended roughly 1.06° horizontally and vertically. Each stimulus was presented for 100 ms with a random interstimulus interval (ISI) of 300 to 600 ms (50 ms per step), and the central fixation cross remained on the monitor throughout the experiment. Under such rapid presentation, ERPs in response to a successive stimuli overlap. However, this overlap should not have systematic effects because of the randomized stimulus order and the sufficient number of epochs to be averaged.
Procedure
Participants were seated in a sound-proof and electrically shielded room and maintained their fixation on a central fixation cross during the experimental blocks. At the beginning of each block, they were asked to direct their attention to a letter/symbol at either the left or right end of the stimuli and to press a button as accurately and quickly as possible when a target appeared at the attended location (attended target). The button was pressed with their right thumb. Stimuli with no target (standards) and with a target at the ignored end (unattended targets) did not require a response.

Four attend-left and four attend-right blocks were presented in an alternating and counterbalanced order. Each block consisted of 300 stimuli (76 standards, 12 attended targets, and 12 unattended targets for each kind of stimulus) with a short break after every 100 stimuli. Therefore, participants received a total of 304 standards, 48 attended targets, and 48 unattended targets in each attention condition.

Stimulus presentation and response collection were controlled by E-prime software (version 2.0, Psychology Software Tools, Sharpsburg, PA, USA). At the beginning of the experiment, participants received one block of practice with half of the trials in the attend-left condition and the other half in the attend-right condition to stabilize task performance and eye movement. The stimuli used in the practice were the same as those in the main experiment.

Recordings and analysis
Button presses were classified as hits or false alarms. Hits were defined as the first response between 230 to 1000 ms after the presentation of attended targets, and any other responses were classified as false alarms. The mean reaction time (RT) for hits, hit rate, and false alarm rates were calculated and subjected to two-way repeated measures analyses of variance (ANOVA) with the attended hemifield (attend-left, attend-right) and stimulus (word, nonword, symbol) as factors. For false alarms, a type factor (standard, unattended) was also included. The Tukey correction was used for pairwise comparisons among stimulus types to avoid multi-comparison errors.

The electroencephalogram (EEG) was recorded using an electrode cap (Easycap GmbH, Herrsching, Germany) with 28 Ag/AgCl electrodes aligned according to the extended International 10–20 system (F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8, O1, Oz, O2). All channels were referenced to the nose tip. Blinks and eye movements (electrooculogram, EOG) were recorded bipolarly through electrodes placed at Fp1 and below the left eye (vertical) and at the outer canthi of both eyes (horizontal). The EEGs and EOGs were amplified by a SynAmps amplifier (NeuroScan, Sterling, USA), filtered with a band-pass of 0.1–30 Hz, and sampled at 500 Hz. Electrode impedance was kept below 10 kΩ. The continuously recorded EEG signals were divided into epochs starting at 200 ms before and ending at 800 ms after stimulus onset. Epochs with artifacts above 85 µV at any EEG or EOG channel were automatically rejected. Epochs with false alarms, misses, and those immediately after a response were also excluded before averaging. ERPs were averaged separately for the type (standard, attended target, unattended target), attended hemifield, and stimulus. Baseline correction was applied to all time-points by subtracting the mean amplitude during the 200 ms prestimulus interval. The mean numbers of epochs averaged for standard words (attend-left: 232, attend-right: 227), nonwords (attend-left: 232, attend-right: 228), and symbols (attend-left: 234, attend-right: 230) were comparable, and the minimum was 185 per condition for all participants included in the analysis.

Analyses of ERP data were conducted on those for standards and focused on early visual components at posterior electrode sites. Based on the visual inspection of grand-average waveforms and difference waves for attention and stimulus effects (Figure 3), ERPs were quantified as mean amplitudes during 100–130 ms (P1) at PO7/8, 130–160 ms (early N170) at P7/8, and 160–210 ms (late N170) at P7/8.
Although print-symbol differences in ERPs typically continue after 200 ms, they should increasingly involve language-related processes rather than print-specialization in visual processing (Bentin et al., 1999), which go beyond the scope of this study. Mean amplitudes were subjected to three-way repeated measures ANOVA with attended hemifield, stimulus, and hemisphere (left, right) factors. The Greenhouse-Geisser correction was applied to contrasts with more than 1 degree of freedom. Pairwise comparisons among the three kinds of stimuli were Tukey-corrected, as with behavioral measures.

**Results**

**Behavioral Results**

Figure 2. shows the behavioral results. With regard to RTs (Figure 2A), faster responses in the attend-right than in the attend-left condition were reflected by a main effect of attended hemifield \((F(1, 11) = 26.48, p<.001)\). There was also an attended hemifield by stimulus interaction \((F(2, 22) = 5.74, p<.01)\), which was due to longer RTs for nonwords than for symbols only in the attend-left condition \((p<.004)\). Similarly, hit rates (Figure 2A) were overall higher in the attend-right condition \((F(1, 11) = 6.48, p<.03)\), and there was also a significant attended hemifield by stimulus interaction \((F(2, 22) = 4.63, p<.03)\). Post hoc analyses revealed a simple main effect of stimulus only in the attend-left condition \((F(2, 22) = 4.78, p<.02)\), which was due to lower hit rates for words and nonwords than for symbols \((\text{word vs. symbol: } p<.04, \text{nonword vs. symbol: } p<.05)\). With regard to FAs (Figure 2B), only a main effect of stimulus was significant \((F(2, 22) = 3.53, p<.05)\), which was due
to lower FAs for symbols than for nonwords ($p<.04$).

**ERP data**

In grand-averaged ERPs for standard stimuli, spatial attention effects were revealed as differences in amplitudes between the attend-left and attend-right condition during P1 and N170 latency ranges, which were predominant at occipito-temporal scalp regions (Figure 3A). Enhancements of N170 for words and nonwords against symbol strings were also predominant at occipito-temporal sites (Figure 3A). Table 1 summarizes the $p$ values of overall ANOVAs.

In the 100-130 ms interval (P1), ERPs at PO8 were more positive in the attend-left than in the attend-right condition, while no such difference was observed at PO7 (Figure 3). These were reflected by a significant attended hemifield by hemisphere interaction ($F(1, 11) = 5.62$, $p<.04$) with a significant simple main effect of the attended hemifield only at PO8 ($F(1, 11) = 12.18$, $p<.006$), as shown in Figure 4A. No contrast involving stimulus factor was significant in this latency range (all $ps>.2$).

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![Figure 3](image.png)

**Figure 3.** (A) Grand-average ERPs at occipito-temporal sites (P7/8, PO7/8) for standard stimuli. ERPs for each stimulus overlapped. (B) Top: Attention effect for each type of stimulus (L−R: attend-left minus attend-right). Bottom: Difference waves for the effect of stimulus. Attend-left and attend-right conditions were collapsed. Lines with ticks indicate intervals of the mean amplitude.
As shown in Figure 3B, ERPs for words and nonwords started to diverge from that for symbols in a negative direction around 120 ms poststimulus, which affected the overall N170 amplitude. Meanwhile, N170 at P7 had greater amplitude when participants attended to the contralateral hemifield, but such an amplitude difference was not observed at P8. Interestingly, the onset of the N170 enhancement for Hiragana strings was approximately 30 ms earlier than that of the lateralized spatial attention effect (see P7 in Figure 3B). Therefore, the N170 latency range was divided into early (130–160 ms) and late (160–210 ms) phases for further analyses.

In the 130–160 ms interval (early N170, Figure 4B), there was a significant main effect of stimulus \(F(2, 22) = 6.44, p < .02\). Pairwise comparisons showed more negative ERPs for words and nonwords than for symbols (both \(ps < .02\)), but no significant difference between words and nonwords (\(p > .9\)). No effects involving hemisphere were significant (all \(ps > .3\)), which indicated a bilateral distribution of this print-tuning effect in this latency range.

In the 160–210 ms interval (late N170, Figure 4C), a main effect of stimulus was also significant \(F(2, 22) = 5.10, p < .03\), which involved the same contrasts among stimuli as the early N1 (word vs. symbol: \(p < .03\), nonword vs. symbol: \(p < .04\), word vs. nonword: \(p > .9\)). This print-tuning effect, again, did not interact with hemisphere (all \(ps > .3\)). Moreover, there was a significant attended hemifield by hemisphere interaction \(F(1, 11) = 8.19, p < .02\).

As shown in the Figure 4C, it was due to more negative ERPs in the attend-right than in the attend-left condition at P7 \(F(1, 11) = 14.63, p < .003\), while an effect of attended hemifield was not significant at P8 \(F(1, 11) = 0.78, p > .3\).

**Discussion**

The present study explored whether the bilateral print-tuned N170 in response to Hiragana strings reflects the processing of separate letters or unified letter-string percepts, by indexing lateralized spatial attention effects in early visual ERPs. As a result, a bilateral N170 enhancement for Hiragana strings was observed in the 130–160 ms and 160–210 ms intervals, consistent with Okumura et al. (2014) and with the widely-spaced condition in Okumura et al. (2015). Spatial attention effects were observed as amplitude enhancements during the 100–130 ms interval (P1) at the right occipito-temporal site and during the 160–210 ms interval (late N170) at the left occipito-temporal site contralateral to the attended hemifield. These attention effects were seen regardless of stimulus type, namely Hiragana or symbol strings. Since they do not indicate integrated Hiragana-string percepts in the N170 latency range, they lend support to the view that bilateral N170 specialization is associated with the level of processing of separate Hiragana letters.

While previous studies found P1 and N1 spatial attention effects equally in both hemispheres (Kasai,
Figure 4. (A) Mean amplitude of the 100–130 ms interval (P1) at occipito temporal electrodes (PO7/8). (B) Mean amplitude of the 130–160 ms interval (early N170) at P7/8. (C) Mean amplitude of the 160–210 ms interval (late N170) at P7/8. Error bars indicate the standard errors of the mean.

2010; Kasai et al., 2011; Kasai & Takeya, 2012), such effects in the present study were asymmetric across the left and right hemispheres. This could partly be due to the use of linguistic materials. It is well known that the processing of letter strings exhibits right visual field superiority; i.e., more accurate and quicker responses for letter strings presented in the right visual field than in the left visual field (for a review, see Brysbaert et al., 2012). This effect may exist because the presentation of linguistic materials preferentially activates the left hemisphere and leads to the increased deployment of attentional resources to the contralateral (i.e., right) visual field (Kinsbourne, 1970; Perez et al., 2012). In the present
study, presentation of letter strings may have caused a rightward bias and an attention effect in the left hemisphere during the late N170 latency range (160–210 ms). However, further investigations will be needed to explain how early spatial selection processes indexed by early occipito-temporal ERPs are modulated by the presentation of linguistic stimuli.

In our studies, widely-spaced Hiragana strings consistently elicited bilateral N170 enhancement irrespective of whether or how attention was directed to them (Okumura et al., 2014, 2015, this study). Previous studies have shown that the insertion of more than two letter spaces induces the serial application of attention to letters within a letter string, which was evidenced by the appearance of a word-length effect in behavioral reading measures (Cohen et al., 2008; Risko et al., 2011). Moreover, Cohen et al. (2008) showed that such serial letter processing is associated with increased activations in the posterior portion of the VWFA that may be devoted to the encoding of single letters (Vinckier et al., 2007). In the present result, the attention effect in the late N170 latency range indicated that attention selected a letter within letter strings with wide interletter spacing, consistent with previous studies. In addition, the task, which required the participant to discriminate a local feature within single letters, may have also facilitated such selection in the present study.

Although the results regarding early ERPs did not indicate the generation of integrated Hiragana-string representations, the behavioral results did. The hit rate was lower for words and nonwords than for symbols in the attend-left condition, which may reflect that attentional resources to discriminate the target feature (i.e., two parallel horizontal strokes) were decreased at the attended location due to attention-spreading (Kasai, 2010; Kasai & Takeya, 2012; Richard et al., 2008). Thus, wildly-spaced Hiragana letters may have been integrated into unitary percepts in later stages of processing. The lack of this behavioral object-based attention effect in the attend-right condition may be associated with the attention effect in the late N170 latency range that was limited in the left hemisphere. Since target feature selection may depend on earlier spatial selection (Anllo-Vento & Hillyard, 1996; Hillyard & Anllo-Vento, 1998; Hillyard & Münte, 1984), the successful early spatial selection in the attend-right condition may have facilitated target feature discrimination, as reflected by faster RTs than in the attend-left condition, and negated the object-based attention effect.

**Conclusion**

The present study showed that the directing of attention to a part of widely-spaced Hiragana strings leads to the processing of separate letters in early stages of processing, while the processing of integrated letter-string percepts can occur in later stages. Thus, it was suggested that the bilateral N170 specialization for Hiragana strings is associated with the processing of separate letters. However, this conclusion must be accepted with caution, since mutual relationships between spatial attention and print-specialization, and their ERP manifestations, must be clarified further. Interestingly, the bilateral print-specialization effect preceded the attention effect during the N170 latency range; thus, the processing of individual Hiragana letters may start regardless of spatial attention. Individual letters may be coded via a base grouping mechanism, in which neurons are tuned directly to feature conjunctions, while the integrated Hiragana-string percepts may involve an incremental grouping mechanism that requires attention and causes the gradual spreading of enhanced neuronal activities over representations of an object (Roelfsema, 2006; Roelfsema & Houtkamp, 2011). Since the N170 component is a potential index for neural mechanisms that underlie fluent reading (Mahé et al., 2012; Maurer et al., 2006), clarification of its nature should be important for understanding both expert and impaired reading.
Note

1) More specifically, stimuli were presented for 100 ms with an interstimulus interval (ISI) of 300–600 ms (50 ms per step). This ISI range was set to avoid overlap between early visual ERP components, while sustaining the participants’ attention by reducing the predictability of stimulus onset. Although this input rate is still slower than that in normal reading, it is much faster than those in previous N170 studies and the allocation of attentional resources to letters or letter strings should have been considerably limited.

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