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An early electrophysiological response associated with expertise in letter perception

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Expertise with print is likely to optimize visual processes for recognizing characters of a familiar writing system. Although brain activations have been identified for words and letter strings in contrast with other stimuli, relatively little work has focused on the neural basis of single-letter perception. English readers and Chinese–English bilinguals participated in an ERP study and performed a 1-back identity judgment on Roman letters, Chinese characters, pseudofonts, and their string versions. The Chinese–English bilinguals showed an enhanced N170 for both Roman letters and Chinese characters relative to pseudofonts. For the non-Chinese readers, the N170 amplitude was larger for Roman letters relative to Chinese characters and pseudofonts. Our results suggest that changes in relatively early visual processes underlie expert letter perception.

Perceptual expertise with letters is a result of prolonged experience with print. The extensive reading experience taking place over the years after we become literate likely modifies the way we process and perceive individual letters. For instance, as expert readers we are used to seeing print in a coherent style and can thus extract font information to aid letter recognition. We perform a letter identification task better with letter strings in the same font rather than in mixed fonts (Sanocki, 1987, 1988). Novice readers (e.g., English readers viewing Chinese characters), however, are much less sensitive to variations in font information (Gauthier, Wong, Hayward, & Cheung, in press). Likewise, expert readers are accustomed to seeing letters in the context of words. When we fixate on part of a word, we obtain not only high-resolution information about the letters in the fovea but also low-resolution information about the parafoveal letters. With experience in reading, we develop a strong tendency to use the low-resolution information about the parafoveal letters, to such an extent that even when high-resolution information about them is artificially made available (by magnifying the parafoveal letters), we are unable to utilize this extra information (Nazir, Jacobs, & O'Regan, 1998). Such behavioral phenomena demonstrate that our perception of letters is influenced by our reading experience.

Neural selectivity can develop as a result of perceptual expertise with certain categories of objects (Gauthier, 2000). There are at least two neural hallmarks of the kind of expertise we acquire for identifying objects within homogeneous classes (e.g., faces, cars, dogs, birds, or computer-generated novel objects). In comparison with common objects, objects with which we have expertise elicit a larger event-related potential (ERP) component—N170—in posterior brain regions (Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Tanaka & Curran, 2001) and greater recruitment of a small region in the fusiform gyrus, mainly on the right (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Because the kind of expertise we have with letters differs in several respects from our expertise with faces, cars, or dogs, letters should recruit a different part of the extrastriate cortex. Indeed, as we will describe below, words and letter strings (Cohen et al., 2002; Polk & Farah, 1998), and more recently single letters (James, James, Jobard, Wong, & Gauthier, in press), have been shown to elicit greater activity in parts of the left fusiform gyrus than do control stimuli, including digits and unfamiliar characters.

The majority of studies concerning the neural bases of print perception have focused on selectivity for words and pronounceable strings (Assadollahi & Pulvermüller, 2003;

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Bookheimer, 2002; Cohen et al., 2000; Cohen et al., 2002; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002; Hauk & Pulvermüller, 2004; McCandliss, Posner, & Givón, 1997; Petersen, Fox, Snyder, & Raichle, 1990; Proverbio, Vecchi, & Zani, 2004). These studies therefore have addressed the linguistic (orthographic, phonological, or semantic) more than the perceptual aspects of reading. More relevant to the question of neural selectivity for letter perception per se are studies showing more activity for unpronounceable letter strings than for control stimuli. For example, the amplitude of the N170 is greater for words, pseudowords, and unpronounceable consonant strings than for strings formed by alphanumeric symbols and forms (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999). A greater P150 component has also been found not only for words and letter strings, but also for strings of letterlike stimuli, in comparison with object icon strings (Schendan, Ganis, & Kutas, 1998). The P150, maximal at the central top electrode (Cz) when recorded with respect to a mastoid reference, may be the positive counterpart of the N170, which is maximal at occipito-temporal electrodes. A larger intracranial N200 has also been found bilaterally in the posterior fusiform gyrus for words and nonwords (pronounceable or not) relative to objects like cars and butterflies (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Nobre, Allison, & McCarthy, 1994). In addition to these electrophysiological findings, fMRI has revealed more activity in the left occipito-temporal junction for letter strings relative to textures and faces (Puce, Allison, Asgari, Gore, & McCarthy, 1996). Letter strings have also been found to elicit more activity than do digit strings with fMRI in a widespread area around the left fusiform gyrus (Polk et al., 2002). These results suggest neural selectivity for strings of letters and letterlike stimuli that do not readily contain linguistic information at a word level, although it has been argued that letter strings are more wordlike and may evoke more word-level processes involving orthography, phonology, and so forth, than do single letters (Price, 2000).

A few other studies suggest selectivity for individual letters. For example, fMRI activity in bilateral occipito-temporal areas habituates to the same letter in the same font (vs. the letter in different fonts) but not to the same human face (vs. different faces) (Gauthier, Tarr, et al., 2000). Also, there is more fusiform gyrus activity for single letters than for oblique lines (Longcamp, Anton, Roth, & Velay, 2003). An anterior region in the left fusiform region has been shown to be selective for Roman letters and a more posterior region for Roman strings, with digits and Chinese characters as controls (James et al., in press). More left middle occipital activations have also been shown for single letters than for symbols and colors (Flowers et al., 2004; Garrett et al., 2000). A concern is that these fMRI activations may be caused by feedback from higher level processing—for example, from letter naming. However, a number of MEG studies conducted by Tarkiainen and colleagues have cast doubt on this alternative account (Tarkiainen, Cornelissen, & Salmelin, 2002; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). These authors identified a left inferior occipito-temporal region that showed more activity at about 150 msec for pronounceable letter strings than for strings of geometric shapes. Despite their emphasis on strings, these studies revealed that this region also shows more activity for single upright letters than for geometric shapes. The early latency of these MEG responses makes feedback from higher level processes a less likely explanation for the selectivity found in the above-mentioned fMRI studies.

The present study examines the early neural selectivity associated with letter expertise. Two groups of subjects (English readers who cannot read Chinese and Chinese–English bilinguals) took part in an ERP experiment in which they saw three types of characters (Roman, Chinese, and pseudofont). The group × stimulus design featured expert (non-Chinese readers viewing Roman characters, bilinguals viewing Roman or Chinese characters) and novice (non-Chinese readers viewing Chinese or pseudofont characters, bilinguals viewing pseudofont characters) situations, allowing for a more direct test of the association between expertise and neural selectivity for letters. For example, the same stimuli (Chinese characters) were expected to elicit different levels of activity depending on amount of expertise—that is, bilinguals were expected to show comparable activity for Roman letters and Chinese characters, but non-Chinese readers were expected to show more activity for Roman letters than for Chinese characters. Such results would not be explained by the feature differences between the stimuli, which are difficult to control perfectly. The use of characters from very different writing systems will also improve the generalizability of the results.

We adopted ERPs as a means to tap into early visual letter processing in relative isolation from most linguistic processes. Past research has shown that the earliest potential to reflect high-level visual differences among object categories appears as a posterior negative component peaking at about 170 msec after stimulus presentation (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Curran, Tanaka, & Weiskopf, 2002; Rossion, Gauthier, et al., 2002; Tanaka & Curran, 2001). This N1/N170 potential is associated with expertise with a visual category (Busey & Vanderkolk, 2005; Gauthier, Curran, Curby, & Collins, 2003; Rossion, Gauthier, et al., 2002; Tanaka & Curran, 2001). Therefore, we expected a larger N170 (relative to a pseudofont control) at posterior channels for letters with which subjects have expertise—that is, for Roman letters with non-Chinese readers and for both Roman letters and Chinese characters with bilinguals. It is important to note that the finding of an N170 effect for letter expertise does not necessarily reflect the same processes that an N170 effect found for object and face expertise would. Since various spatiotemporally overlapping visual processes are likely to contribute to the scalp-recorded N170 (Rossion, Curran, & Gauthier, 2002), it is a reasonable postulate that the N170 can be modulated by different types of perceptual expertise with objects. Our primary aim here is not to equate letter expertise with or dissociate it from face expertise but to describe properties of the selectivity associated with expertise for letters and letter strings.

METHOD

Subjects

Thirty-seven undergraduates from the University of Colorado at Boulder participated for course credit. Twenty-two Chinese–English bilinguals participated for payment of $15/h. Because we were unable to recruit as many bilingual as non-Chinese subjects, the present results include only 18 non-Chinese readers and 18 Chinese–English bilinguals. Subject selection was based upon absence of EEG artifact (6 monolingual subjects and 1 bilingual subject were excluded for excessive artifact); maintaining high accuracy levels and minimizing group differences in accuracy (subjects with less than 90% accuracy, 6 from the non-Chinese and 3 from the Chinese–English group, were excluded); maintaining counterbalancing; and equating the sex distributions of the two groups (9 males and 9 females per group). The Chinese–English bilinguals, who were mostly graduate students, were older (mean age = 24, range = 19–29) than the undergraduate non-Chinese readers (mean age = 19, range = 18–22). All of the Chinese–English bilinguals were born in China, learned English in China (mean starting age = 11, range = 4–15), had known English for a long time (mean = 13 years, range = 5–21 years), and had recently moved to the United States (mean = 3 years in U.S., range = 1–10 years). The bilinguals were either graduate students or teaching/research staff at the university. Although we did not quantify their proficiency, the fact that they all study or work in the United States makes it clear that they are very familiar with the Roman alphabet. Also, the bilinguals had no problems with reading consent forms, communicating, or comprehending the experimental instructions in English.

Stimuli, Design, and Procedure

There were six types of stimuli (Roman, Chinese, and pseudofont characters, and their string versions). Figure 1 shows the eight Roman consonants, eight Chinese characters, and eight pseudofont characters used and one example of each type of trial. Each character measured about 1 × 1 cm onscreen (0.57° at a viewing distance of 100 cm). Each string consisted of five characters and was about 7 cm wide (4° at a viewing distance of 100 cm). The Roman strings were formed by randomly picking and assembling Roman letters to form 100 different five-character strings and then replacing characters in certain strings according to the following rules: (1) No repetition of letters was permitted within a string. (2) All letters occurred at approximately the same frequency in the 100 strings (mean = 62, range = 58–65). (3) All letters occurred at approximately the same frequency (12 or 13) in the central, underlined position. (4) No familiar or potentially meaningful two-letter combinations were permitted (e.g., *HP*, *HB*, *BP*, *HK*). (5) No valid graphemes were permitted (e.g., *BL*, *PH*). (6) All two-letter combinations (e.g., *DF*), except for the removed ones, occurred at similar frequencies (mean = 7.96, range = 6–12). The Chinese and pseudofont strings were formed by taking the 100 Roman strings and replacing them with corresponding Chinese or pseudofont characters.

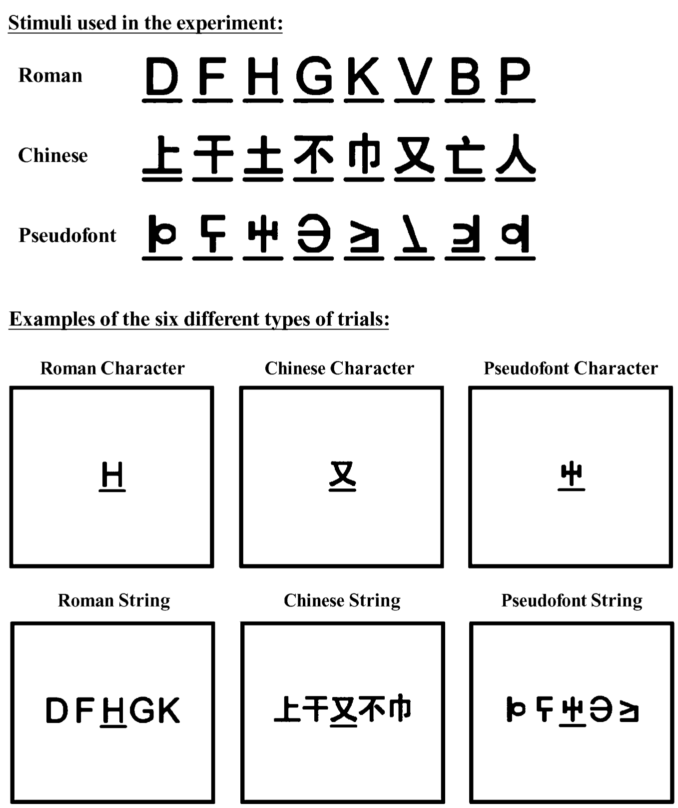

Figure 1. All of the stimuli used in the experiment, as well as examples of each type of trial.

We also checked to ensure that there were no meaningful character combinations in the Chinese strings (e.g., 干土, which means "dry soil").

There were 100 trials for each of the six types of stimuli, separated into 5 blocks containing 20 trials each. The subjects performed a 1-back identity-matching task. Each trial started with a fixation cross at the center of the screen for a random period between 250 and 750 msec. A stimulus (a character or string) then appeared for 750 msec, followed by a 500-msec blank screen and the fixation cross for the next trial. The subjects were instructed to press "1" on the number keypad when the character shown was identical to the previous one or when the central, underlined character of the current string repeated that of the previous string (flanking characters were always different in consecutive trials). *Same* trials amounted to 10% of all trials for each stimulus (i.e., 10 out of 100). In other, nontarget trials, no response was required. The numbers of *same* trials in the 5 blocks were 1, 2, 2, 2, and 3. The six types of stimuli resulted in a total of 600 trials presented in 30 blocks. Each block only contained one type of stimulus. The different stimulus blocks alternated with each other, such that the six types of stimulus blocks were each presented once before any of them was presented a second time, and so forth in later blocks. The order of block presentation was counterbalanced across subjects. Forty trials (20 for Roman letters, 20 for Roman strings) were introduced at the beginning as practice.

EEG/ERP Methods

Scalp voltages were collected with a 128-channel Geodesic Sensor Net (Tucker, 1993) connected to an AC-coupled, 128-channel, high-input impedance amplifier (200-MΩ Net Amps; Electrical Geodesics, Inc., Eugene, OR). Amplified analog voltages (0.1–100 Hz bandpass, −3 dB) were digitized at 250 Hz. Individual sensors were adjusted until impedances were less than 50 kΩ. The EEG was digitally low-pass filtered at 40 Hz. Trials were discarded from analyses if they contained incorrect responses or eye movements (EOG over 70 μV) or if more than 20% of the channels were bad (average amplitude over 100 μV or transit amplitude over 50 μV). Target (*same* judgment) trials were also excluded from analyses. The mean number of trials per subject per condition was 81 (range = 56–90). Individual bad channels were replaced on a trial-by-trial basis according to a spherical spline algorithm (Srinivasan, Nunez, Silberstein, Tucker, & Cadusch, 1996). EEG was measured with respect to a vertex reference (Cz), but an average-reference transformation was used to minimize the effects of reference-site activity and to estimate accurately the scalp topography of the measured electrical fields (Bertrand, Perin, & Pernier, 1985; Curran, Tucker, Kutas, & Posner, 1993; Dien, 1998; Lehman & Skrandies, 1985; Picton, Lins, & Scherg, 1995; Tucker, Liotti, Potts, Russell, & Posner, 1994). Average-reference ERPs were computed for each channel as the voltage difference between that channel and the average of all channels. The average reference was corrected for the polar average reference effect (Junghöfer, Elbert, Tucker, & Braun, 1999). ERPs were baseline corrected with respect to a 100-msec prestimulus recording interval.

RESULTS

Behavioral Results

The two groups of subjects maintained a similarly high level of accuracy [non-Chinese readers, 96%; Chinese–English bilinguals, 97%; $t(34) = 1.44$, $SE = 0.81$, $p > .10$]. Analyses of variance (ANOVAs) were conducted on both accuracy and response time data with group (non-Chinese reader or Chinese–English bilingual), stimulus (Chinese, Roman, or pseudofont), and character/string as factors. When necessary in this and all subsequently reported ANOVAs, degrees of freedom were adjusted according to the conservative Greenhouse–Geisser procedure for sphericity violations (Winer, 1971).

There was a correspondence between accuracy and level of expertise, as revealed by a significant group × stimulus interaction [$F(2,68) = 8.13$, $p < .01$]. For non-Chinese readers, accuracy was ordered from Roman (98.6%) to pseudofont (96.7%) to Chinese (93.3%) stimuli, with both the Roman–pseudofont [$t(17) = 4.49$, $p < .01$] and pseudofont–Chinese [$t(17) = 2.61$, $p < .05$] differences being significant. The Chinese–English bilinguals performed best with Chinese stimuli (98.3%), followed by Roman (98.1%) and pseudofont (96.1%) stimuli, and only the Roman–pseudofont difference was significant [$t(17) = 2.36$, $p < .03$]. In terms of response time, only the group × character/string interaction was significant [$F(1,34) = 7.78$, $p < .05$]: Whereas the non-Chinese readers responded faster for characters than for strings [485 vs. 515 msec; $t(17) = 2.94$, $p < .05$], no significant difference was observed between characters and strings for bilinguals (482 vs. 460 msec, $p > .20$).

When the data for the 11 non-Chinese readers excluded on the basis of lower accuracy or the sex composition of the two groups were also included, similar results were obtained, with an additional effect of group. Not surprisingly, the inclusion of the previously excluded non-Chinese readers caused the performance of non-Chinese readers to become worse than that of bilinguals [accuracy, $F(1,45) = 7.26$, $p < .01$; response time, $F(1,45) = 3.97$, $p = .052$].

ERP Results

ERPs from selected 10–20 locations are shown in Figures 2 (non-Chinese readers viewing characters), 3 (non-Chinese readers viewing strings), 4 (Chinese–English bilinguals viewing characters), and 5 (Chinese–English bilinguals viewing strings). Overall, the most outstanding feature is the P300 difference related to expertise (e.g., channel Pz between about 300 and 600 msec). P300 amplitude was smaller when subjects viewed stimuli with which they had experience (non-Chinese readers viewing Roman stimuli, bilinguals viewing Roman or Chinese stimuli) than when they viewed unfamiliar stimuli (non-Chinese readers viewing Chinese or pseudofont stimuli, bilinguals viewing pseudofont stimuli). Presumably, unfamiliar characters and strings were perceptually more complex, and P300 amplitude is known to increase with stimulus complexity (Johnson, 1986, 1993). Although our interest was in early visual processes, formal analyses were conducted on both the N170 and P300 effects.

Subsequent analyses were conducted on ERPs averaged across all artifact-free, nontarget trials (those to which no response was required). For both the N170 and P300 analyses, peak ERP amplitude was the primary independent measure. Previous studies have used mean amplitude as the primary dependent measure, but peak

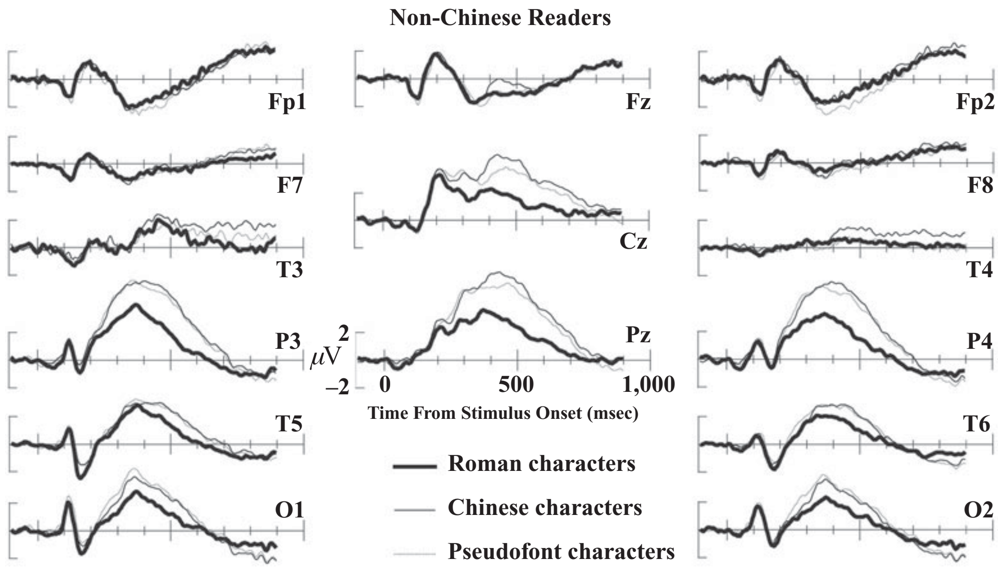

Figure 2. ERPs from selected 10–20 locations for non-Chinese readers viewing characters.

amplitude (i.e., minimum for N170 and maximum for P300) was used for the present analysis for two reasons: First, latency differences among conditions (as will appear later) may bias the results if a fixed window is used for calculating mean amplitude. Second, inspection of the ERPs suggested that expertise-related group × stimulus interactions in both the N170 and P300 components overlapped in time with each other, so that at least in some conditions, we were unable to select a N170 mean amplitude window that did not overlap with P300, and vice versa.

N170 results. The first step in our analysis was the identification of the locations where the N170 component was maximal so that further analyses could focus on these channels. For each subject, we computed the amplitude of the greatest negative deflection occurring over all posterior electrode sites between 120 and 250 msec after stimulus onset. Averaged across all subjects and conditions, the N170 was most negative for left-hemisphere channel 65 (falling between standard 10–20 locations T5 and O1; see Figure 6). To allow for spatial variability across subjects and conditions, we selected a group of

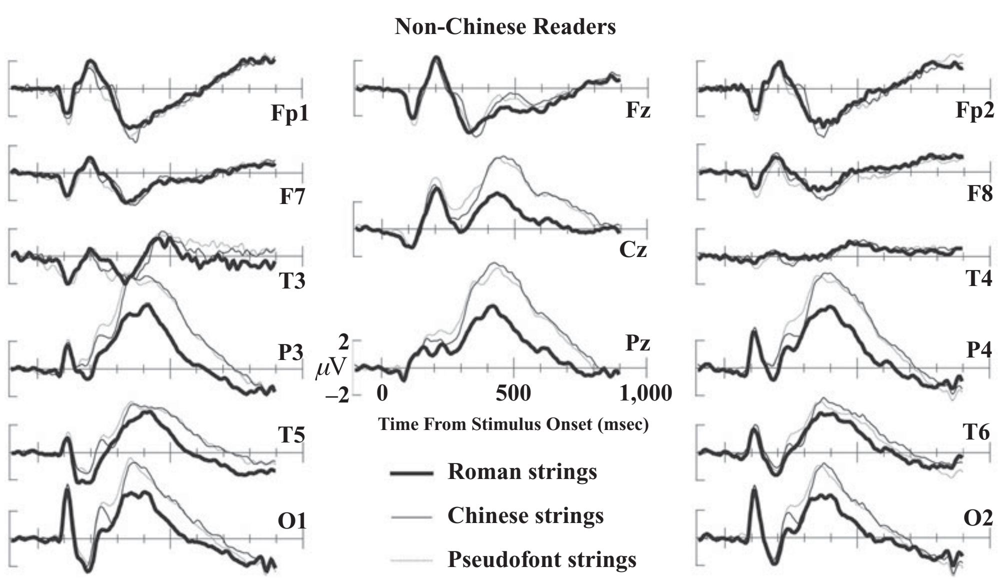

Figure 3. ERPs from selected 10–20 locations for non-Chinese readers viewing strings.

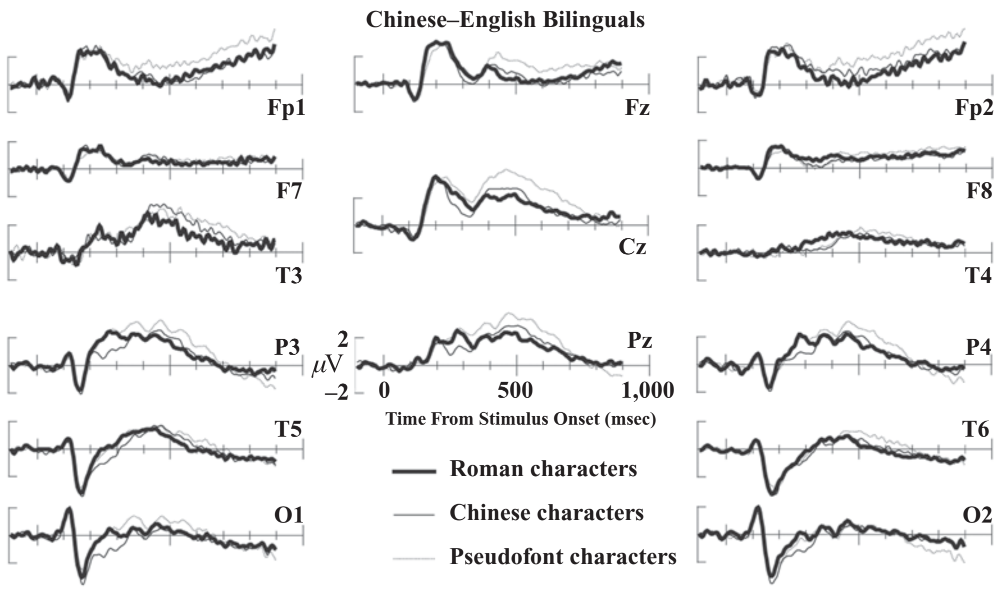

Figure 4. ERPs from selected 10–20 locations for Chinese–English bilinguals viewing characters.

channels surrounding 65 for further analysis (T5, 59, 64, 65, 66, 70, O1) along with their right-hemisphere counterparts (O2, 85, 90, 91, 92, 96, T6). The ERPs obtained by averaging the channels within each region are shown in Figures 7 (non-Chinese readers) and 8 (Chinese–English bilinguals).

Minimum amplitude was entered into a group (non-Chinese readers or Chinese–English bilinguals) × stimulus (Chinese, Roman, or pseudofont) × character/string × hemisphere ANOVA. All significant ($p < .05$) results and their statistics are reported in Table 1. Overall N170 amplitudes were more negative for the bilingual than for the non-Chinese subjects. The key result was the significant group × stimulus interaction (Figure 9). A significant group × character/string interaction was also observed. Separate ANOVAs were conducted for the two groups to better interpret the results.

The non-Chinese subjects were considered alone in a stimulus (Chinese, Roman, or pseudofont) × character/string × hemisphere ANOVA. Only the stimulus con-

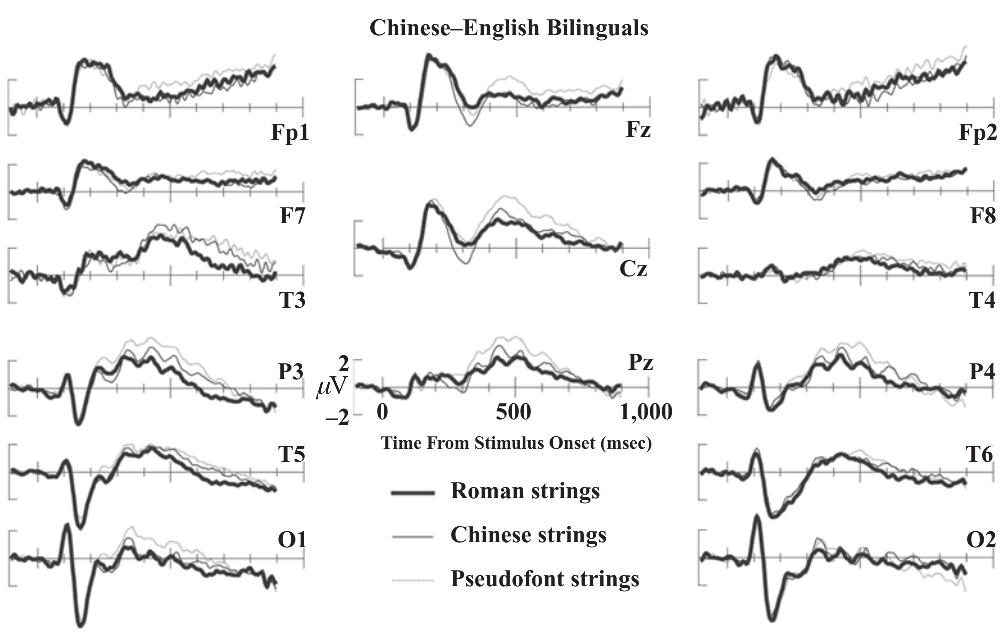

Figure 5. ERPs from selected 10–20 locations for Chinese–English bilinguals viewing strings.

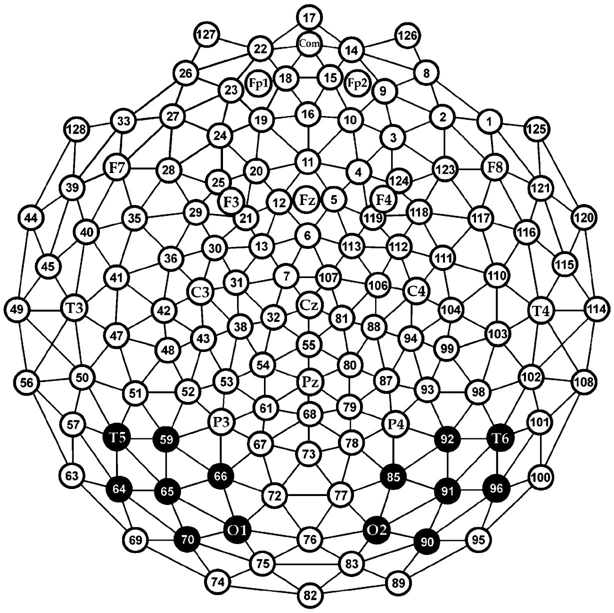

Figure 6. Channels selected for analyses (black).

dition effect described previously was significant (see Table 1): Roman stimuli led to greater N170 amplitudes than did Chinese [$t(17) = 2.96$, $p < .01$] or pseudofont [$t(17) = 3.76$, $p < .01$] stimuli. When the Chinese–English bilinguals were considered alone, the stimulus condition effect was again significant: Whereas Roman and Chinese stimuli did not differ from each other ($t < 1$), they both led to larger N170 amplitudes than did pseudofonts [Roman vs. pseudofonts, $t(17) = 2.25$, $p < .05$; Chinese vs. pseudofonts, $t(17) = 3.88$, $p < .001$]. The stimulus × hemisphere interaction suggested that these condition effects were more pronounced over the left hemisphere. Also, N170s were significantly more negative for strings than for characters.

Other significant effects for both groups include the main effects of stimulus and character/string and the stimulus × hemisphere and stimulus × character/string × hemisphere interactions. The interactions were caused by N170s being more negative for Roman and Chinese than for pseudofont stimuli in the left hemisphere, whereas in the right hemisphere such differences only occurred for characters but for not strings (all ps < .05 for significant differences).

The latency of the minimum N170 was entered into a group × stimulus × character/string × hemisphere ANOVA (Table 2). The N170 was faster for the left (176 msec) than for the right (185 msec) hemisphere and for strings (178 msec) than for characters (183 msec), and these factors interacted in such a way that the latency difference between characters and strings was only significant for the left hemisphere. A significant group × character/string interaction was also found. Whereas characters and strings did not differ from each other for non-Chinese readers ($t < 1$), longer latencies were observed for characters (164 msec) than for strings (152 msec) among bilinguals [$t(17) = 3.32$, $p < .01$]. The group × stimulus × hemisphere interaction was also significant. Subsequent comparisons, however,

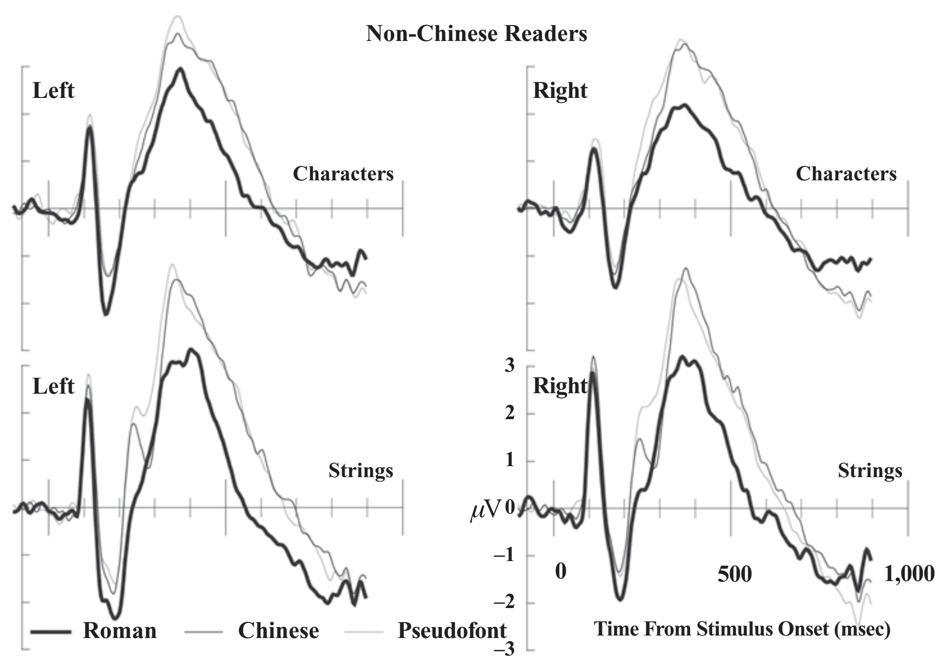

Figure 7. ERPs from averaging the selected channels for non-Chinese readers.

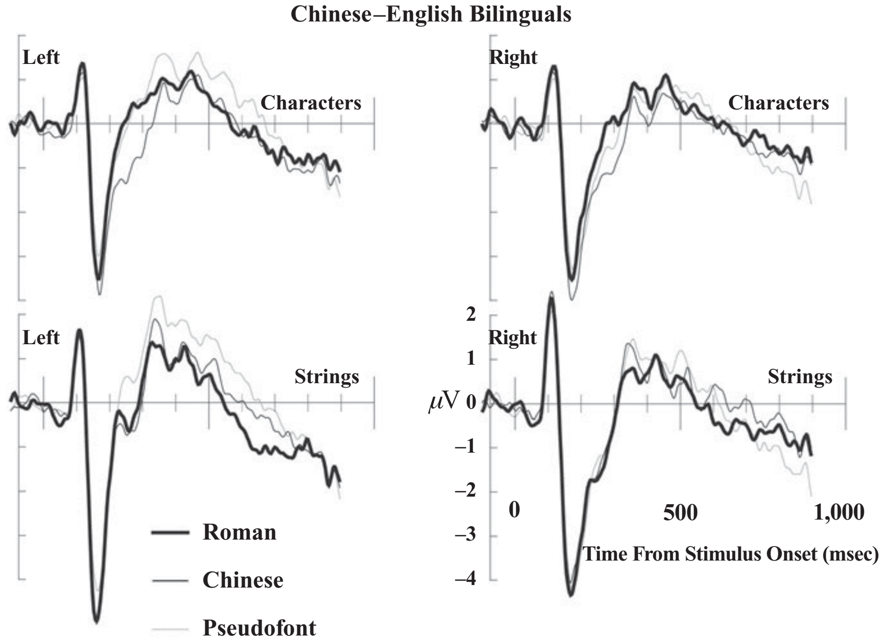

Figure 8. ERPs from averaging the selected channels for Chinese–English bilinguals.

showed only a significant difference between Roman and pseudofont stimuli in the right hemisphere for bilinguals [182 vs. 188 msec; $t(17) = 2.73, p < .05$]. Across the 24 conditions, the mean latencies ranged from 168–191 msec.

Results were similar when the data from the 11 previously excluded non-Chinese readers were included: All effects reported above remained significant except for the effect of character/string in N170 latency.

P300 results. The P300 analyses focused on channels Fz, Cz, and Pz. Figures 2–5 show the ERPs for these channels. Maximum amplitude was entered into a group (non-Chinese readers or Chinese–English bilinguals) × stimulus (Chinese, Roman, or pseudofont) × character/string × channel (Fz, Cz, or Pz) ANOVA (Table 3). There were significant interactions between group and stimulus and between group and channel. There were also significant group × stimulus × channel and group × character/string × channel interactions. Separate analyses were thus performed for each group.

The non-Chinese subjects were considered alone in a stimulus × character/string × channel ANOVA (see Table 3). There was a stimulus × channel interaction: P300 amplitude was smaller for Roman than for Chinese and pseudofont stimuli in both the Cz and Fz channels [all ts$(17) > 5.00$, ps $< .01$]. The character/string × channel interaction was also significant: P300 amplitude was smaller for characters than for strings at Pz [$t(17) =$

Table 1
ANOVA Results on N170 Amplitude

Effect	*df*	*F*	MS_e	*p*
Both Groups				
Group	1,34	10.11	14.27	<.01
Stimulus	2,68	9.98	1.27	<.001
Group × stimulus	2,68	5.93	1.27	<.01
Character/string (CR/ST)	1,34	19.50	2.86	<.001
Group × CR/ST	1,34	4.81	2.86	<.05
Stimulus × hemisphere	2,68	4.73	0.38	<.05
Stimulus × CR/ST × hemisphere	2,68	4.28	0.19	<.05
Non-Chinese Readers				
Stimulus	2,34	9.57	1.51	<.01
Chinese–English Bilinguals				
Stimulus	2,34	5.60	1.03	<.01
CR/ST	1,17	22.25	2.81	<.001
Stimulus × hemisphere	2,34	5.71	0.32	<.01

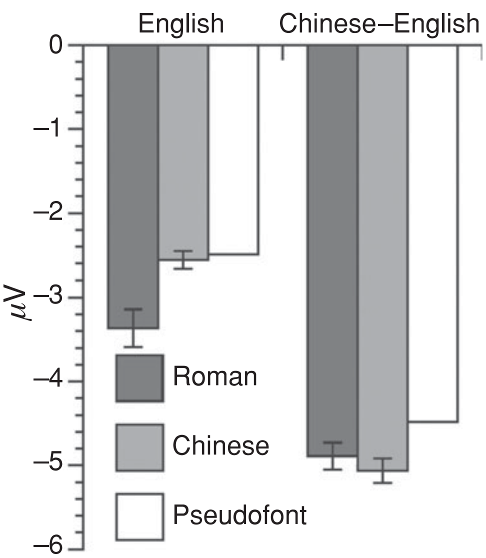

Figure 9. Averages of minimum N170 amplitudes. Error bars show standard errors of the Chinese–pseudofont and Roman–pseudofont differences.

2.63, $p < .05$] but higher for characters than for strings at Fz [$t(17) = 3.41, p < .01$]. When the Chinese–English bilinguals were considered alone, an effect of stimulus emerged, with P300 amplitudes being smaller for Chinese than for pseudofont stimuli [$t(17) = 4.29, p < .05$] and for Roman than for pseudofont stimuli [$t(17) = 4.58, p < .05$]. The effect of character/string was also significant, with greater amplitude for characters than for strings.

P300 peak latency was also entered into a group × stimulus × character/string × channel ANOVA (Table 4). The effect of stimulus was significant: Latencies for Roman stimuli were shorter than those for Chinese [$t(17) = 4.23, p < .05$] and for pseudofont [$t(17) = 2.91, p < .05$] stimuli. The effect of character/string was also significant, with characters having shorter latencies than strings did. There was also a group × channel interaction, with latencies at Pz being shorter than those at Cz for non-Chinese readers, and latencies at Fz being shorter than those at Cz for bilinguals.

Summary of main results. The effects of primary interest consist of the differences in N170 amplitude among stimuli as a function of expertise level—that is, the group × stimulus interaction. Figure 10 shows topographic distributions of N170 amplitude differences between Roman, Chinese, and pseudofont stimuli at 168 and 192 msec, the shortest and longest N170 peak latencies, across all conditions (and rounded to the nearest 4-msec time samples). In keeping with the N170 analyses, more negative amplitudes were observed at 168 msec in situations involving expertise (non-Chinese readers viewing Roman stimuli, bilinguals viewing Roman and Chinese stimuli) at posterior and inferior channels. These expertise effects are especially evident over the left hemisphere, although the hemisphere × stimulus interaction only reached significance for bilinguals. The differences among stimuli have started to extend to the superior channels for non-Chinese readers at 192 msec.

Both the N170 and P300 peak amplitudes revealed an expertise effect. We are mainly interested in the earlier N170 effect, and a potential concern is that a P300 effect with an early onset could cause early differences among stimuli that would be mistaken for an N170 effect. This is unlikely, however, for two reasons: First, in the ERP plots for the channels selected for N170 analyses (Figures 7 and 8), the curves for different stimuli converged between the N170 and P300 peaks. If P300 were driving the effects, we would expect the differences among stimuli to grow larger from 150 msec onward. Second, correlation analyses across subjects were conducted between the N170 (left or right hemisphere) and P300 (Fz, Cz, or Pz) peak latencies across the six stimulus types (Chinese, Roman, and pseudofont characters or strings). Only 4 of the 36 correlations were significant ($p < .05$, uncorrected), suggesting that the N170 and P300 effects were separate from each other.

Another result worth mentioning is the group × character/string interaction. Whereas an N170 with a larger amplitude and shorter latency was found with strings than with characters for bilinguals, there was no such difference for non-Chinese readers. Interestingly, this interaction did not depend on the type of stimulus presented (Roman, Chinese, or pseudofont). Although Tarkiainen and colleagues (Tarkiainen et al., 1999) obtained greater early MEG activity as the number of letters in a string increased, this does not explain why in our experiment string/character differences only occurred for bilinguals. Past studies have suggested that bilingualism causes changes in orthographic processing, such as an increase in lateralization

Table 2
ANOVA Results on N170 Latency for Both Groups

Effect	*df*	*F*	MS_e	*p*
Character/string (CR/ST)	1,34	7.76	419.68	<.01
Group × CR/ST	1,34	4.69	419.68	<.05
Hemisphere	1,34	15.60	538.97	<.001
Hemisphere × CR/ST	1,34	7.17	94.28	<.05
Group × stimulus × hemisphere	2,68	4.33	86.64	<.05

Table 3
ANOVA Results on P300 Amplitude

Effect	*df*	*F*	MS_e	*p*
Both Groups				
Stimulus	2,68	37.39	2.78	<.001
Group × stimulus	2,68	16.17	2.78	<.001
Channel	2,68	103.93	7.95	<.001
Group × channel	2,68	36.04	7.95	<.001
Stimulus × channel	4,136	18.83	0.71	<.001
Group × stimulus × channel	4,136	8.01	0.71	<.001
Channel × character/string (CR/ST)	2,68	7.05	0.64	<.01
Group × channel × CR/ST	2,68	11.32	0.64	<.001
Non-Chinese Readers				
Stimulus	2,34	34.99	3.20	<.001
Channel	2,34	101.54	10.25	<.001
Stimulus × channel	4,68	22.26	0.81	<.001
CR/ST × channel	2,34	12.70	0.87	<.001
Chinese–English Bilinguals				
Stimulus	2,34	15.67	2.37	<.001
CR/ST	1,17	1.95	5.69	<.05
Channel	2,34	12.80	5.66	<.001

(Ding et al., 2003; Hoosain, 1992). To understand whether experience with a second language, and with Chinese in particular, may lead to general changes in visual processing will require further experimentation.

DISCUSSION

To our knowledge, this is the first study showing selectivity of the N170 component to individual letters associated with expertise. The present results are consistent with and complement previous findings in several ways: First, a larger N170 was shown with Roman letters than with pseudofont characters for all subjects. This early component, selective for individual letters and letter strings, suggests that the selectivity found in other fMRI studies (Flowers et al., 2004; James et al., in press; Longcamp et al., 2003) was not solely caused by feedback from higher level areas related to linguistic processing or letter name knowledge. Second, the group × stimulus design of our study bypassed the problem of choosing a well-designed control stimulus. The same Chinese characters resulted in either a smaller N170 amplitude than with Roman letters (in non-Chinese readers) or a comparable amplitude (in Chinese–English bilinguals), depending on whether subjects were experienced with the Chinese characters or not. This expertise-associated letter selectivity cannot be explained by stimulus differences. Third, the use of Chinese characters enables us to generalize our results to characters in a very different writing system. Fourth, the present results with letters demonstrate expertise effects on the N170 that are similar to expertise effects previously demonstrated with objects (Gauthier et al., 2003; Rossion, Gauthier, et al., 2002; Tanaka & Curran, 2001). Finally, the stronger expertise effect in the left hemisphere, as suggested by the stimulus × hemisphere interaction on N170 amplitude in the Chinese–English bilinguals and the topographic distributions (Figure 10), is consistent with Tarkiainen and colleagues' (Tarkiainen et al., 2002; Tarkiainen et al., 1999) finding of a left-hemisphere preponderance for letter and letter string selectivity.

Table 4
ANOVA Results on P300 Latency for Both Groups

Effect	*df*	*F*	MS_e	*p*
Stimulus	2,68	8.48	5,285.66	<.001
Character/string	1,34	8.47	5,978.80	<.01
Channel	2,68	4.16	8,362.62	<.05
Group × channel	2,68	11.47	8,362.62	<.001

Letter Expertise and Linguistic Effects

The neural selectivity that we found for individual letters is unlikely to reflect, in a direct fashion, language-related processes, such as those invoked by words and potentially also by nonword strings. ERP components other than the N170 are generally found to be sensitive to information at the word level, such as orthography (Proverbio et al., 2004), phonology (Bentin et al., 1999), and semantics (Bentin et al., 1999; McLaughlin, Osterhout, & Kim, 2004). The early N170 selectivity for individual letters is likely to be free from these linguistic effects, because (1) these linguistic factors typically have a late effect, occurring after 300 msec (except for the lexical frequency and orthography effects discussed below); and (2) we have shown selectivity with single Roman letters, which do not contain the linguistic information involved with a word or multiple letters. There does remain a possibility that the selectivity we found, at least for Chinese characters, reflects linguistic processing at a character level. For example, Perfetti and colleagues (e.g., Perfetti & Tan, 1998) have found that orthographic and phonological processing started with individual Chi-

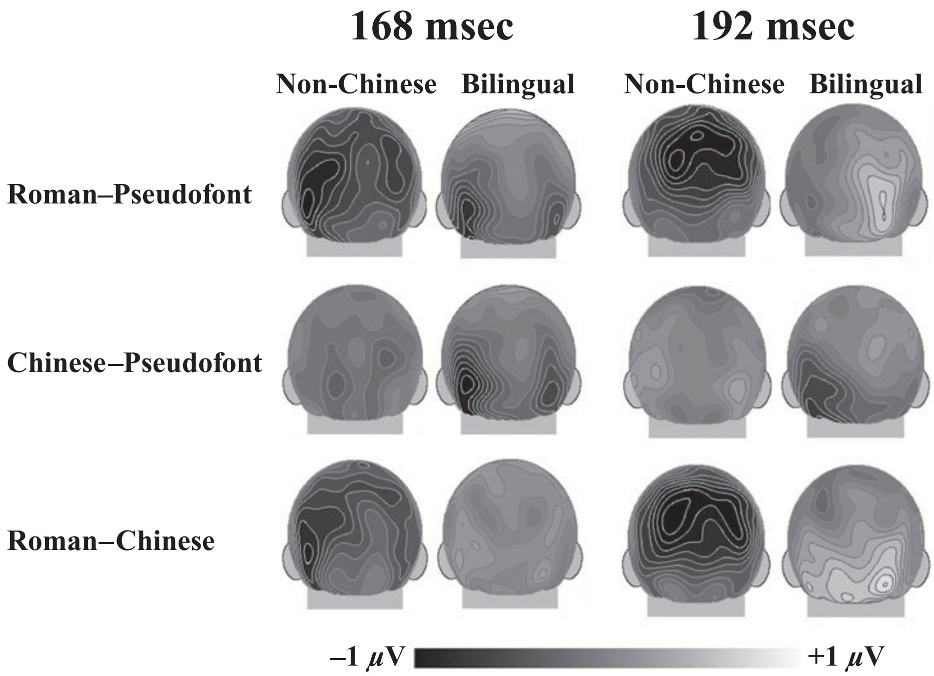

Figure 10. Topographic distributions of ERP differences between stimuli for non-Chinese readers and Chinese–English bilingual readers at 168 and 192 msec, which represent the range of N170 latencies for different conditions.

nese characters within 100 msec after stimulus presentation. However, in their recent ERP study (Liu & Perfetti, 2003), the phonological processing component found for Chinese characters did not appear until 400 msec after stimulus onset.

It is worth mentioning that some linguistic factors, such as lexical frequency and orthography, do have an effect on early ERP components (Hauk & Pulvermüller, 2004; McCandliss et al., 1997; Proverbio et al., 2004; Sereno, Brewer, & O'Donnell, 2003; Sereno, Rayner, & Posner, 1998). The effect of lexical frequency is particularly interesting, since it apparently contradicts our expertise effect. Studies have found a larger N1/N170 for low- than for high-frequency words (Hauk & Pulvermüller, 2004; McCandliss et al., 1997; Proverbio et al., 2004; Sereno et al., 2003; Sereno et al., 1998). In contrast, our results show a larger N170 for more familiar, expert characters than for nonexpert characters. It has been suggested that the greater difficulty of processing low- rather than high-frequency words may lead to a larger N1 for the low-frequency words (Sereno et al., 2003). In that case, words of different frequencies utilize the same neural substrates. The situation may be different in this study, in that expert and nonexpert characters may be treated as different types of stimuli, potentially by partly dissociable neuronal ensembles. The larger N170 for characters with which subjects have expertise may indicate that additional substrates are recruited for them.

Letter Expertise and Object Expertise

Past studies have shown a greater N170 for faces than for other common objects (Bentin et al., 1996; Rossion et al., 2000). Enhanced N170 components have also been observed when people develop expertise with cars, dogs, birds, and even novel objects (Curran et al., 2002; Rossion, Gauthier, et al., 2002; Tanaka & Curran, 2001). The present results generalize this effect to another stimulus domain—individual letters. One question is whether the same processes underlie expertise with letters and with other categories of objects. The process map hypothesis of cortical organization provides a framework for considering this question (Gauthier, 2000). According to this hypothesis, one develops neural selectivity to an object class after prolonged experience of processing the objects in a specific manner. In other words, the specific neural selectivity is related to the specific constraints of the task associated with the category. Following this logic, letter expertise may be regarded as different from object expertise, because different computational demands are involved. In order to perceive letters during reading, readers need to perceive a particular letter as, for instance, a *g* and not an *f*, irrespective of any physical differences like font, size, color, and so on. For expertise with faces and many other categories of objects, however, people usually gain experience in discriminating among very similar objects of a homogeneous class (e.g., telling one face from another or distinguishing between two different bird species), and it is thought that the resulting expertise relies on holistic and configural processes (Diamond & Carey, 1986). The N170 component has recently been associated with holistic processing in car experts (Gauthier et al., 2003) and fingerprint experts (Busey & Vanderkolk, 2005). The differences in task demands between objects and letters suggest that different neural and behavioral phenomena may be found for these two types of expertise. Indeed, the two types of expertise seem to be supported by different neural substrates, as shown in an fMRI study (Gauthier, Tarr, et al., 2000).

Although the above question is worth examining, it should be noted that distinguishing expertise for letters from the expertise we have with faces or other objects was not the purpose of this study, especially given the limited spatial resolution of the ERP technique. In fact, we did not find any significant differences between experience-associated selectivity for individual letters and letter strings in terms of the topography of their activations, despite the different loci of letter- and string-selective regions shown in recent fMRI results (James et al., in press). We can only conclude that the visual processing associated with expertise for letters, letter strings, faces, and other objects as well (e.g., birds, dogs, or cars) appears to occur within the same time window.

Up to now, single-letter recognition has not been the focus of reading or object recognition studies, but our results suggest that it may be an important avenue for future exploration. Psychophysical studies have shown that performance in word recognition depends on how well individual letters are identified (Nazir et al., 1998; Pelli, Farell, & Moore, 2003). Some studies of pure alexia have linked that reading disorder to deficits in letter recognition (Arguin, Fiset, & Bub, 2002; Saffran & Coslett, 1998). Accordingly, understanding letter recognition is one important step in understanding the reading process. In addition, the perception of letters distinguishes itself from that of other shapes and objects, as indicated by some unique behavioral phenomena (Gauthier et al., in press; Sanocki, 1987, 1988). The present study provides another source of support for the existence of specialization for individual letter perception in the visual system by providing evidence of early neural selectivity for familiar individual letters. In the future, efforts to compare processes and neural substrates supporting the perception of common objects and objects of different types of expertise (e.g., letters or faces) should further our understanding of visual object recognition and how it changes when we acquire expertise in various domains.

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