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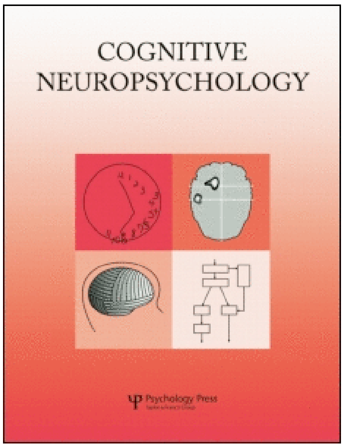

Cognitive Neuropsychology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713659042

Expertise with characters in alphabetic and nonalphabetic writing systems engage overlapping occipito-temporal areas

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First Published:February2009

To cite this Article Wong, Alan C. -N., Jobard, Gael, James, Karin H., James, Thomas W. and Gauthier, Isabel(2009)'Expertise with characters in alphabetic and nonalphabetic writing systems engage overlapping occipito-temporal areas',Cognitive Neuropsychology,26:1,111 — 127

To link to this Article: DOI: 10.1080/02643290802340972

URL: http://dx.doi.org/10.1080/02643290802340972

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COGNITIVE NEUROPSYCHOLOGY, 2009, 26 (1), 111–127

Psychology Press
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Expertise with characters in alphabetic and nonalphabetic writing systems engage overlapping occipito-temporal areas

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Parts of the left ventral visual pathway are engaged selectively during the perception of words, letter strings, and even single letters. While studies have shown overlap between activations for letters and characters across writing systems, they adopted group analyses with very limited spatial resolution, or used words and letter strings that have been shown to activate different regions from those activated by single characters. The current study compared activity within individual participants for the perception of single characters from different writing systems. Roman letters, Chinese characters, objects, and faces were presented to Chinese–English bilinguals and English readers with no Chinese reading experience. Individual subject analyses revealed a large overlap between Roman- and Chinese-selective areas in the bilinguals. In general, the activity in the Roman-selective area of the left hemisphere is associated with experience with the script, as non-Chinese readers showed lower activations to Chinese characters than to Roman letters. Further analyses found considerable variation within non-Chinese readers in the activation for Chinese characters: While the majority had no selectivity for Chinese characters at all, some showed activations for Chinese characters at locations similar to those selective for Roman letters. The results suggest that both stimulus properties and experience are important factors in determining the response to single characters across writing systems.

Keywords: Chinese; Functional magnetic resonance imaging; Letters; Object recognition; Reading; Expertise.

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This research was supported by grants from the James S. McDonnell Foundation, the National Eye Institute (EV13441–01), and the Temporal Dynamics of Learning Center (NSF Science of Learning Center SBE-0542013) to I.G. The authors would like to thank the members of the Perceptual Expertise Network for helpful discussions.

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http://www.psypress.com/cogneuropsychology DOI:10.1080/02643290802340972

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Letter perception is a common example of perceptual expertise. Our extensive experience with reading is likely to have a deep influence on the way our visual system processes letters. Recent studies have demonstrated behavioural markers common to different writing systems for expertise in processing single characters. For example, experience with characters in a writing system is associated with a larger "basic-level advantage" when recognizing those characters. In general, characters are recognized at the basic level (e.g., as a "B") more efficiently than at a subordinate level (as a "B in Courier"), and basic-level categorization of characters is even better for those who are familiar with the writing system (Wong & Gauthier, 2007). In addition, observers are capable of utilizing the regularity of fonts within a text to facilitate letter perception when they are familiar with a writing system (Sanocki, 1987, 1988). Interestingly, these results apply to stimuli as different as Roman alphabets and Chinese characters (Gauthier, Wong, Hayward, & Cheung, 2006), which belong to language systems with drastically different linguistic properties, suggesting a perceptual (rather than linguistic) origin for the common phenomena.

According to the process-map account of specialization for categories in the visual system (Gauthier, 2000), stimuli with different geometries that engage similar processing strategies are expected to recruit common areas. Is this the case for characters of different writing systems? On the one hand, several neuroimaging studies have indeed hinted at common neural regions supporting specialized perception of characters across very different writing systems. For instance, a meta-analysis of brain imaging studies of word recognition described considerable overlap in the cortical regions recruited by perception of printed words for several alphabetic and nonalphabetic writing systems (Bolger, Perfetti, & Schneider, 2005). A similar network of brain areas was observed regardless of writing system, including regions in the ventral inferior frontal lobe and the superior temporal/inferior parietal area, as well as occipito-temporal areas including part of the left fusiform gyrus. This last region, often called the visual word form area (VWFA; Cohen et al., 2000; Cohen et al., 2002), has been proposed to support expert perception of orthographic forms (McCandliss, Cohen, & Dehaene, 2003). On the other hand, despite evidence of impressive correspondence across different writing systems, it should be noted that there is considerable variability across individuals in the exact location of the areas that demonstrate visual selectivity for letters and words (see in Table 1). Group comparisons or meta-analyses probably lack adequate spatial resolution to precisely address issues of segregation and overlap (Bolger et al., 2005; Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2005). Therefore, it may be premature to draw conclusions concerning the overlap for different types of characters in the absence of within-subject comparisons.

A recent functional magnetic resonance imaging (fMRI) study examined the overlap between Roman and Hebrew letter strings at the level of individual participants (Baker et al., 2007). An area in the extrastriate region was found to respond to both English and Hebrew words more than the visual control in Hebrew readers. Importantly, the area showed higher activations to Hebrew words in Hebrew readers than in non-Hebrew readers, suggesting a dependence on expertise. The selectivity was also found for both words and consonant strings, which led the authors to conclude that the region is selective for individual characters rather than for words per se. This is based on the (often implicit) assumption that contrasting unpronounceable letter strings with a visual control (e.g., in Baker et al., 2007) should reflect the sum of the selectivity for individual characters, since unpronounceable letter strings lack orthographic, phonological, or semantic content (Polk & Farah, 1998; Polk et al., 2002).

However, there may be fundamental differences between the processing of letters and letter strings. In recent years, evidence has been growing supporting specialization for single letters within the occipito-temporal cortex (Flowers et al., 2004; James & Gauthier, 2006; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Gathers, & Piper, 2003). Moreover, an area in the left

Table 1. *The Talairach coordinates of the single-character-selective areas in different studies*

	Study	*Comparison*	*Talairach coordinates (x, y, z)*
Roman letters	Flowers et al., 2004	(Letter task−fixation) > (colour task−fixation) & (Letter task−fixation) > (symbol task−fixation)	−62, −57, −6
	Garrett et al., 2000	Activation correlated with letter recognition accuracy	−46, −68, −11
	Gauthier et al., 2000	Letter > face	−53, −62, 3 (left) 50, −59, 3 (right)
	James et al., 2005	Letter > digit	x = −33 to −45 y = −29 to −47 z = −5 to −9
	Joseph et al., 2003	(Letter > noise) & (Letter > object) & (Letter > fixation	−41, −48, −6
	Longcamp et al., 2003	Letter > oblique lines	−30, −88, −6 (left) 32, −93, 1 (right) 40, −49, −14 (right)
Chinese characters/kanji	Peng et al., 2003	High-frequency character > noncharacter (long exposure 151 ms)	−31, −65, −16 (left) −30, −69, −11 (left) 48, −56, −6 (right)
		Low-frequency character > noncharacter (long exposure 151 ms)	−41, −62, −10 (left) −37, −66, −10 (left) 49, −50, −17 (right)
	Tan et al., 2000	Vague-meaning character > fixation	−42, −61, −12 (left) −44, −43, −10 (left) 42, −59, −11 (right)
		Precise−meaning character > fixation	−48, −56, −14
	Chee et al., 2000	Two-character words > pictures	(BA37) $x = -43$ to -50 $y = -45$ to -63 $z = -8$ to -11 (BA21) $x = -40$ to -56 $y = -45$ to -50 $z = 3$ to 8
	Ding et al., 2003	Character > fixation (orthographic search task)	−48, −53, −12
	Uchida et al., 1999	Kanji > scrambled kanji	$x = -27$ to -44 $y = -75$ to -81 $z = 4$ to -16
Current study	Bilinguals	(Roman > object) & (Roman > face) & (Roman > fixation) & (Chinese > object) & (Chinese > face) & (Chinese > fixation)	$x = -42$ to -54 $y = -43$ to -61 $z = -20$ to 1
	Non-Chinese readers	(Roman > object) & (Roman > face) & (Roman > Chinese) & (Roman > fixation)	$x = -44$ to -64, $y = -46$ to -61 $z = -14$ to 4

Note: Only areas close to occipital and temporal areas are included. Ranges are provided for studies with individual-subject coordinates provided and single coordinates for other studies. As seen, the locations of the character-selective areas highly vary across participants and studies.

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fusiform of individual subjects, anterior to the VWFA, showed responses that could reflect experience for single letters. It is selective for single letters compared with single digits or simple Chinese characters (in non-Chinese readers) but, surprisingly, shows no such selectivity for letter strings. A separate, more posterior area, in contrast, showed selectivity for letter strings but not single letters (James et al., 2005). Along similar lines, Dehaene, Cohen, Sigman, and Vinckier (2005) have proposed a hierarchical organization of neural word processing, with different regions along the ventral stream responsible for processing at different levels, including features, letter shapes, abstract letter identities, bigrams, and word forms. These studies suggest that specialization can occur at levels lower than that for word forms, and whether it occurs at the level of character shapes across character types remains a question.

Notably, in a recent event-related potential (ERP) study, Chinese–English bilinguals demonstrated an enhanced N170 component for both single Roman letters and Chinese characters compared with pseudoletters, suggesting the existence of early visual processes recruited by single characters across alphabetic and nonalphabetic writing systems (Wong, Gauthier, Woroch, Debuse, & Curran, 2005). The spatial resolution of the ERP technique is, however, too limited to determine whether the two types of characters recruit similar visual areas.

The current study directly examines selectivity for single characters and its relationship with expertise. We examined selectivity for Roman letters and Chinese characters in a group of Chinese–English bilinguals, with objects and faces as contrast categories (Figure 1A). Participants performed a one-back repetition judgement task in which they reported by key press whenever they saw two identical consecutive images. If different writing systems engage shared processing not only at the word and letter string levels but also at the single-character level, then characters from different writing systems should recruit the same areas. Keeping in mind that this question can only be addressed within the limits

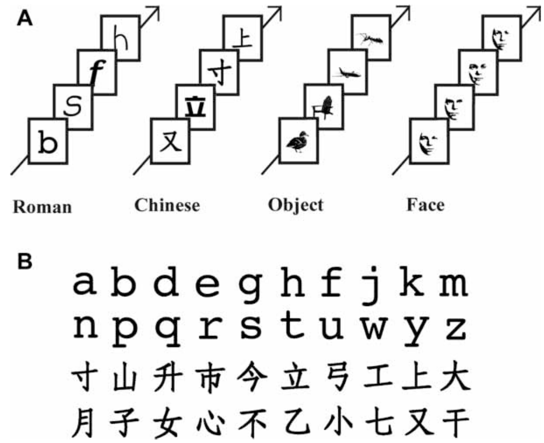

Figure 1. *Examples of stimuli used. (A). Participants underwent a one-back repetition judgement task with images of a certain object category presented sequentially and made a key response when two consecutive images were identical to each other. (B). The 20 Roman letters and 20 Chinese characters in one of the font types used.*

of the spatial resolution of the fMRI technique used in our study, we attempted to avoid any spurious overlap between categories by conducting within-subject comparisons between the locations of Roman- and Chinese-selective areas.

Chinese is written with characters called hanzi, each made out of 1 to 64 strokes and each associated with one or more syllables as well as meanings. The Chinese writing system is open-ended, although knowledge of about 4,500 characters is sufficient to read Modern Standard Chinese. These (and other) characteristics, drastically different from those of the Roman alphabets, are clearly likely to influence the organization of neural systems supporting reading with each of these writing systems, and many differences in the neural networks engaged are expected. However, here we are specifically concerned with the possible overlap in the processing of single characters in the extrastriate cortex, which may arise because of common perceptual strategies (Gauthier et al., 2006) despite the many differences between the two writing systems.

To study the association between experience and character selectivity, we also recruited a group of non-Chinese readers who read English fluently but had no prior Chinese-learning experience. If experience has a role in determining selectivity for characters, then Chinese characters should elicit different levels of activity depending on experience. In other words, while non-Chinese readers were expected to show higher activity for Roman letters than for Chinese characters, this difference should be smaller or nonexistent for Chinese–English bilinguals. Alternatively, if character selectivity occurs because of nonexpertise factors, such as the stimulus properties of characters (two-dimensional simple patterns) as opposed to other object categories, then Roman letters and Chinese characters should cause similar levels of activations in both bilinguals and non-Chinese readers.

Materials and methods

Participants

A total of 8 Chinese–English bilinguals (mean age = 24 years, range = 21–28; 3 females) and 9 non-Chinese readers (mean age = 27.2 years, range = 23–32; 3 females) participated in the experiment. Because the behavioural data during the fMRI study were unavailable, an additional group of 10 bilinguals (mean age = 21.9 years, range = 19–28; 7 females) and 10 non-Chinese readers (mean age = 19.4 years, range = 18–22; 4 females), who had not participated in the fMRI experiments, were tested outside the scanner with the identical task and stimuli for measures of behavioural performance. The imaging and behavioural participants were faculty members, graduate students, or research staff at Vanderbilt University. The bilinguals all had Chinese as their first language and had studied English for more than 15 years. All gave informed consent according to the guidelines of the institutional review board of the Vanderbilt University Medical Center and were paid for their participation. All participants reported normal or corrected-to-normal visual acuity, had no history of neurological disorders, and were right-handed.

Stimuli and tasks

All testing was conducted using Macintosh computers and RSVP software (Williams & Tarr, 1998). The stimuli were presented on a projection screen through a mirror mounted on top of a radio frequency (RF) coil above the participant's head. Stimuli were projected onto the screen by means of an LCD projector located outside the scanner room. The screens were 76.2 × 57.2 cm large and were viewed from a distance of about 150 cm. Sizes for each stimulus type are provided below. All stimuli were presented in the centre of the screen with their exact location varying from trial to trial about one half of a degree of visual angle around the centre of the screen.

There were 60 images for each of the four types of stimuli (Figure 1): 20 lowercase Roman letters in three font types (except for c, i, l, o, v, and x), 20 Chinese characters in three font types, 60 greyscale objects (30 living and 30 nonliving), and 60 two-tone thresholded face images (30 males and 30 females). In separate runs for expertise effect analyses, a different set of 20 lowercase Roman letters and 20 Chinese characters in six font types was used. Each image was about 80 × 80 pixels (4.5 × 4.5 cm) large and spanned a visual angle of 1.8°. The Chinese characters were simple ones, each with five strokes or fewer, to match with the complexity of Roman letters.

Participants were required to perform a one-back repetition judgement task throughout the experiment. They had to press a button with their right index finger on a response box attached to their hand when they saw two identical images presented consecutively. No response was required on a nonmatch trial. The ratio of match to nonmatch trials was 1:11. Each trial began with a blank for 275 ms followed by the stimulus for 725 ms. Each block contained 16 trials of only one type of stimulus and was 16 s long. There were three runs, each containing 12 blocks (3 for each stimulus type), with blocks separated by a 6- or 10-s fixation cross. We also included one to three separate runs in the end to examine the effect of expertise in the regions of interests located in former runs. Each run contained 12 blocks, with 6 showing Roman letters and 6

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showing Chinese characters. For each character type there were blocks where all characters were presented in the same font and blocks where characters were presented in different fonts. The same- and different-font blocks showed similar results and were thus collapsed in later data analyses. The order of trials was randomized within blocks, and the order of block presentation was counterbalanced across runs and participants. Each run was about 5 minutes long.

Imaging parameters and analysis

Imaging was performed using a 3-Tesla, whole body gradient echo (GE) MRI system and a birdcage head coil located at the Vanderbilt Medical Center (Nashville, USA). The field of view was $24 \times 24 \times 13.0$ cm, with an in-plane resolution of 64×64 pixels and 26 contiguous oblique coronal scan planes per volume (whole brain), resulting in a voxel size of $3.75 \times 3.75 \times 5.0$ mm. Images were collected using a T2*-weighted echo planar imaging (EPI) acquisition (echo time, TE = 25 ms; time to repetition, TR = 2,000 ms; flip angle, FA = 60°) for blood-oxygen-level-dependent (BOLD)-based imaging (Ogawa et al., 1993). High-resolution T1-weighted anatomical volumes were also acquired using a 3-D fast spoiled grass (FSPGR) acquisition (inversion time, TI = 400 ms; TE = 4.18 ms; TR = 10 ms; FA = 20°). The functional data were analysed using the BrainVoyager™ (Goebel, Esposito, & Formisano, 2006, http://www.brainvoyager.com) multistudy GLM (general linear model) procedure and in-house programs written in Matlab™ (2005, The MathWorks, Natick, MA, http://www.themathworks.com). The data were motion corrected and spatially smoothed with a Gaussian kernel of 6-mm full width at half maximum (FWHM). A GLM analysis computed the correlation of predictor variables or functions with the recorded activation data (criterion variables) across scanning sessions. The predictor functions were based on the blocked stimulus presentation paradigm of the particular run being analysed and represented an estimate of the predicted haemodynamic response during that run. To properly model the haemodynamic response, the predictors were represented as the stimulus protocol boxcar functions convolved with the appropriate gamma function ($\Delta = 2.5$, $\tau = 1.25$) estimate of a typical haemodynamic response (Boynton, Engel, Glover, & Heeger, 1996). To increase power, statistical parametric maps were computed within a preset search region—Talairach coordinates: $x = -69 \sim 69$, $y = -15 \sim (-101)$, $z = -30 \sim 32$—in order to focus on the occipital and posterior temporal regions in both hemispheres. Also, corrections for multiple comparisons were conducted with the false discovery rate (FDR) method, which controls for the expected proportion of false positive voxels among those that are above threshold (Genovese, Lazar, & Nichols, 2002). For the overlap analyses, overlap indices were computed to evaluate the overlap of pairs of areas, using the overlap index advocated by Kung, Peissig, and Tarr (2007):

$$\text{Overlap index} = [(\text{ROI}_1 \cap \text{ROI}_2)/\text{ROI}_1 + (\text{ROI}_1 \cap \text{ROI}_2)/\text{ROI}_1)]/2$$

Results

Behavioural results

For both Chinese–English bilinguals and non-Chinese readers tested outside of the scanner in the same task as that used in the fMRI experiment, performance was similar among Roman letters, Chinese characters, and objects and was the worst for faces, presumably because only faces require subordinate-level discrimination (Table 2). A 2×4 (Group × Stimulus Type) analysis of variance (ANOVA) was conducted on percentage correct for matching trials where a response was required, response time on those trials, and false-positive rate. There was no main effect of group (Fs < 1) or interaction between group and stimulus type (ps > .16). The main effect of stimulus type was significant—accuracy: $F(3, 54) = 22.79$, $p < .0001$; reaction time (RT): $F(3, 54) = 40.57$, $p < .0001$; false positive: $F(3, 54) = 19.85$, $p < .0001$. Scheffé tests ($p < .05$) showed that accuracy and response time were similar among Roman letters, Chinese characters, and objects. Again, responses were less accurate

Table 2. *Behavioural performance for the one-back repetition judgement task*

	Chinese–English bilinguals			*Non-Chinese readers*		
	% correct	*RT (ms)*	*% false positive*	*% correct*	*RT (ms)*	*% false positive*
Roman	94.2	499	1.06	93.3	468	1.67
Chinese	95.0	468	1.06	92.5	479	0.53
Face	61.7	563	3.33	70.8	559	3.86
Object	95.0	479	0.23	95.0	471	0.38

and slower for faces than for the other three stimulus types. For the nonmatch trials with no response required, a significantly higher false positive rate was observed for faces than for the other stimulus types. Therefore the one-back matching task was more difficult for the face stimuli but, more importantly, comparable in difficulty for Roman letters, Chinese characters, and common objects.

Imaging results

Overlap between Roman- and Chinese-selective areas. We localized, in each Chinese–English bilingual, cortical areas selective for Roman letters, Chinese characters, or faces relative to both objects and fixation (Tables 3 and 4). All but one bilingual showed selectivity for both Roman and Chinese characters (Figure 2A). The most remarkable finding was that the bilinguals consistently revealed overlapping Roman- and Chinese-selective areas in the left hemisphere. Region overlap and comparisons of peaks of activation were conducted in the 6 bilinguals who showed selectivity for Roman letters, Chinese characters, and faces in the left hemisphere. Pairwise overlap indices ($0 \leq$ overlap index ≤ 1) were calculated (Figure 2B) based on the formula suggested to be relatively reliable among other measures (Kung et al., 2007). Results of t tests showed that the overlap between Roman- and Chinese-selective areas (0.54) was significantly larger than the overlap between Roman- and face-selective areas (0.034) as well as Chinese- and face-selective areas (0.083; ps $< .01$).

Peak-distance measures were also used to complement the overlap index (Kung et al., 2007). The peak coordinates were defined as the selectivity peak (i.e., the point with the highest statistical value in the contrast between activations of letters/characters/faces relative to objects) in the Talairach space. The peaks of the Roman- and Chinese-selective areas were remarkably close—mean peak coordinates (x, y, z): Roman (−51, −52, −13), Chinese (−51, −54, −13)—and were lateral to the peak of the left face-selective area in the fusiform gyrus—mean peak coordinates = (−40, −54, −15). We computed the Euclidean distance as well as distance along each dimension between the peaks of these areas for the 6 bilingual participants who showed selectivity for all three stimulus types (Figure 2B). Results of t tests showed that the Euclidean distance between the peaks for the Roman- and Chinese-selective areas (5.6 mm) was significantly less (both ps $< .005$) than that between the peaks of Roman- and face-selective areas (16.4 mm) as well as that between Chinese- and face-selective areas (14.6 mm). When the distance was broken down into the three dimensions (anterior–posterior, dorsal–ventral, medial–lateral), this pattern was found to be reflected only along the medial–lateral dimension (ps $< .005$). Although the distance between the Roman and Chinese peaks was significantly over zero, in all 6 participants there was considerable overlap of activity over the range of thresholds for which selectivity for both categories was observed (see Figure 2A). Both Roman- and Chinese-selective activations were more lateral than the face-selective activations.

In the right hemisphere (Table 4), letter selectivity was less robust, with only 5/8 bilinguals showing selectivity for both Roman and Chinese characters (compared with 7 in the left hemisphere. However, there was still notable overlap

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Table 3. *The peak coordinates and the region sizes of the Roman-selective, Chinese-selective, and face-selective areas in the left hemisphere for individual participants*

		Roman-selective area (lLA)		Chinese-selective area		Face-selective area (lFFA)	
Group	Participant	Peak coordinates	Region size (mm^3)	Peak coordinates	Region size (mm^3)	Peak coordinates	Region size (mm^3)
Bilingual	C1	−42, −58, −9	238	−42, −57, −8	1,668	−35, −52, −4	164
	C2	−57, −46, −8	2,710	−54, −46, −8	3,674	−45, −46, −20	67
	C3	−48, −49, 1	521	−48, −55, −8	652	−30, −64, −5	3,033
	C4	−51, −40, −20	519	−51, −43, −20	48	—	—
	C5	−54, −48, −18	239	−54, −61, −18	1,452	−39, −58, −14	774
	C6	−53, −58, −17	761	−54, −57, −17	294	−48, −52, −17	988
	C7	−52, −58, −17	492	−51, −58, −14	55	−37, −45, −17	515
	C8	—	—	—	—	−45, −58, −14	675
	Average (±*SD*)	−51 ± 4.8, −52 ± 7.1, −13 ± 7.5	783 (±869)	−51 ± 4.4, −54 ± 6.7, −13 ± 5.3	1,113 (±1,306)	−40 ± 6.4, −54 ± 6.9, −13 ± 6.2	888 (±1,001)
Non-Chinese	N1	−64, −49, −11	514	—	—	−42, −55, −14	537
	N2	−51, −61, 4	1,049	—	—	−40, −43, −8	1,338
	N3	−63, −52, 1	1,216	−57, −55, −1	265	−48, −43, −11	66
	N4	−48, −55, −14	366	—	—	—	—
	N5	−48, −52, −5	914	−54, −43, −8	2,605	−42, −61, −15	986
	N6	−45, −42, −2	1,568	−48, −43, −3	1,189	−42, −43, −14	2,815
	N7	−42, −46, −11	106	−42, −46, −12	1,248	—	—
	N8	—	—	—	—	−39, −67, −14	743
	N9	—	—	—	—	—	—
	Average (±*SD*)	−52 ± 8.6, −51 ± 6.2, −5.4 ± 6.8	819 (±514)	−51 ± 6.7, −47 ± 5.7, −6 ± 5.0	1,327 (±964)	−42 ± 3.1, −52 ± 10.6, −13 ± 2.7	1,081 (±951)

Note: The peaks for the Chinese-selective areas were also included. There was a remarkable proximity of the Roman- and Chinese-selective areas, which are both more lateral than the lFFA. There was also an expertise effect in that more bilinguals showed selectivity for Chinese characters than non-Chinese readers. lLA = left Roman-letter-selective area; lFFA = left fusiform face area.

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between the Roman and Chinese peaks of activity for those bilinguals showing selectivity for both categories (4 out of 5 bilinguals showed similar peak coordinates for the two areas).

The role of expertise. In a subsequent analysis, we compared the selectivity for Roman and Chinese characters in Chinese–English bilinguals and non-Chinese readers. To test the role of expertise, for each participant we used as regions of interest the Roman-selective and face-selective areas defined in the overlap analyses. The same criteria were used for both groups (Roman-selective areas: Roman > object and Roman > fixation; face-selective areas: face > object and face > fixation). Within these areas, we compared the responses for Roman letters and Chinese characters in each group of participants using independent data from different runs (Figure 3).

In the left Roman-letter-selective area (lLA), there was a significant interaction between group and stimulus type, $F(1, 12) = 4.76$, $p < .05$. Scheffé tests ($p < .05$) showed more activity for Roman than Chinese characters in non-Chinese readers but no difference between the two character types in bilinguals. In other words, the response in the lLA was a function of one's expertise with a specific writing system. In the left fusiform face area (lFFA), the Group × Stimulus Type interaction was not significant, $F(1, 11) = 1.29$, $p = .28$.

The degree of selectivity was much lower in the right hemisphere. Only 5 out of 9 non-Chinese

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Table 4. *The peak coordinates and the region sizes of the Roman-letter-selective, Chinese-selective, and face-selective areas in the right hemisphere for individual participants*

		Roman-selective area (rLA)		*Chinese-selective area*		*Face-selective area (rFFA)*	
Group	*Participant*	*Peak coordinates*	*Region size (mm^3)*	*Peak coordinates*	*Region size (mm^3)*	*Peak coordinates*	*Region size (mm^3)*
Chinese	C1	42, −55, −11	564	42, −55, −10	1,601	39, −55, −8	2,423
	C2	59, −40, −5	3,168	54, −40, −5	2,391	—	—
	C3	54, −55, −8	44	54, −55, −8	443	39, −64, −11	2,592
	C4	54, −49, −2	1,468	—	—	37, −52, −9	18
	C5	—	—	45, −64, −14	1,897	36, −58, −11	1,597
	C6	57, −60, −2	1,976	36, −54, −11	2,358	36, −61, −2	3,499
	C7	—	—	—	—	39, −55, −14	568
	C8	50, −55, 2	172	51, −55,7	916	36, −40, −17	2,229
	Average (±*SD*)	53 ± 6.1, −52 ± 7.0, −4.3 ± 4.7	1,232 (±1,211)	47 ± 7.3, −54 ± 7.7, −6.8 ± 7.4	1,601 (±787)	38 ± 1.4, −55 ± 7.7, −10 ± 4.8	1,847 (±1,211)
Non-Chinese	N1	—	—	—	—	—	—
	N2	42, −43, −6	867	—	—	39, −40, −11	1,298
	N3	45, −49,1	290	45, −49,1	409	36, −48, −5	13
	N4	60, −52,2	81	42, −61,11	90	39, −58, −9	3,036
	N5	51, −52, −5	905	40, −59, −17	2,236	—	—
	N6	44, −43, −11	1,544	42, −46, −11	1,576	41, −46, −8	3,809
	N7	—	—	—	—	39, −64, −8	742
	N8	—	—	54, −58, −11	128	—	—
	N9	—	—	—	—	—	—
	Average (±*SD*)	48 ± 7.3, −48 ± 4.5, −3.8 ± 5.4	737 (±576)	45 ± 5.5, −55 ± 6.7, −5.4 ± 11.3	888 (±966)	39 ± 1.8, −51 ± 9.7, −8.2 ± 2.2	1,780 (±1,591)

Note: rLA = right Roman-letter-selective area; rFFA = right fusiform face area.

readers showed selectivity for Roman letters in the right hemisphere. Although there was insufficient power to observe a Group × Stimulus Type interaction, the effect of expertise on the response to Chinese characters was qualitatively similar in both the right and left letter-selective areas. The activation difference between Roman letters and Chinese characters was numerically larger for the non-Chinese readers than for the bilinguals. The right fusiform face area (rFFA) did not show any difference between activations for the two character types (*p*s $>$ .13). Bolger et al. (2005) reported that Chinese characters recruited more right occipito-temporal regions than did other languages. It has been suggested that each component (radical) of a Chinese character could be regarded as a word form, which would therefore be processed in the left hemisphere, while the spatial arrangement of the components would require right-hemisphere involvement (Bolger et al., 2005; Liu, Perfetti, & Hart, 2003; Perfetti, Liu, & Tan, 2005). This may explain why our Chinese characters, which were all composed of only single components, did not lead to more robust selectivity in the right hemisphere.

The role of stimulus property. Although our results reveal an expertise effect with Chinese characters, it should be noted that there is considerable variability within the non-Chinese readers in terms of the response to the Chinese characters. Out of the 9 non-Chinese readers, 5 did not show any selectivity for Chinese characters compared to both objects and fixation (Figure 4A). However, 4 of them showed some activity for Chinese

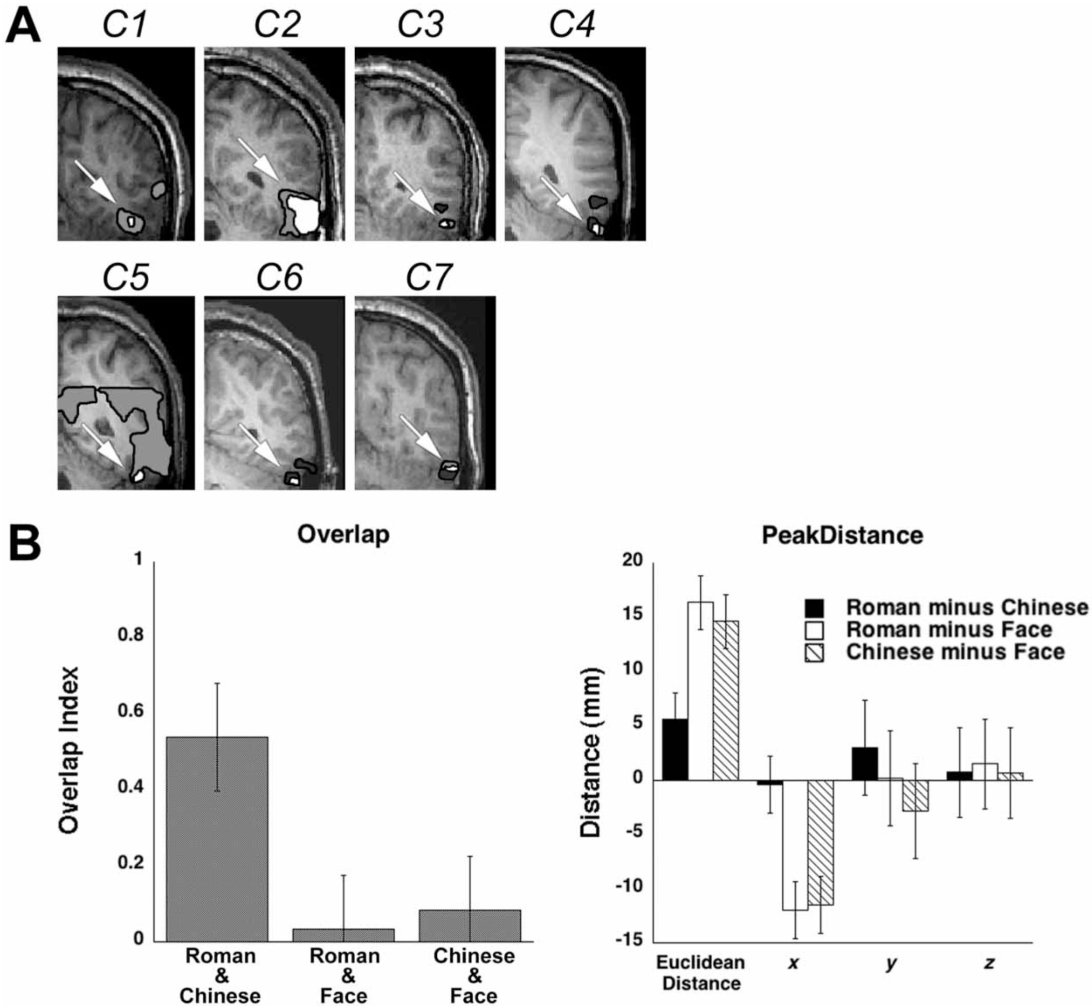

Figure 2. *(A). The overlap of activations for bilinguals. The activations for Roman characters (dark grey regions) were defined by (Roman−object) and (Roman−fixation) contrasts. The activations for Chinese characters (grey regions) were defined by (Chinese−object) and (Chinese−fixation) contrast. Their overlap are indicated by white regions and are pinpointed with arrows. The Roman−Chinese overlap was observed constantly in the left occipito-temporal region. All contrasts had a threshold of q(FDR) < .05. Coronal slides are shown at y = −45 for C2, C3, C4, and C5 and at y = −55 for C1, C6, and C7. The left hemispheres are shown on the right. (B). Average pairwise overlap indices and peak distances between Roman-, Chinese-, and face-selective areas in bilinguals. The overlap between Roman and Chinese activations was larger than those between Roman and face as well as those between Chinese and face activations. The Euclidean distances between Roman and Chinese activation peaks were shorter than those between Roman and face activation peaks as well as those between Chinese and face activation peaks. The distances were further broken into those along the x-, y-, and z-axes. The distances between the Roman- and face-selective areas and those between the Chinese- and face-selective areas were mainly along the x-axis—that is, both Roman-selective and Chinese-selective areas were more lateral than the face-selective areas. The error bars represent the 95% confidence interval for the effect of different pairwise contrasts.*

characters, with considerable overlap with the Roman activations (Figure 4B). One reason for this result may be that the low-level visual features (i.e., spatial frequency components, visual complexity) are more similar between the two types of characters than between the characters and

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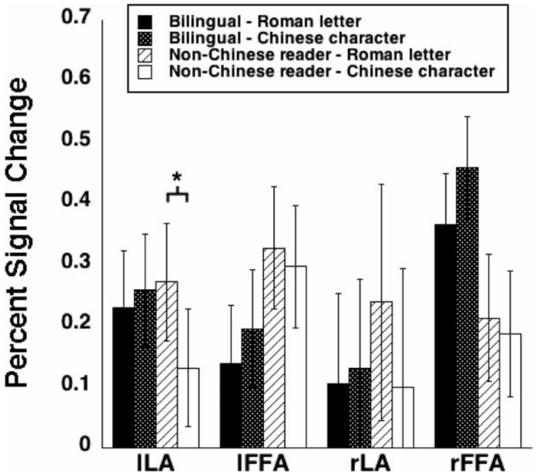

Figure 3. *Average activations of the left letter-selective area (lLA), the right letter-selective area (rLA), the left fusiform face-selective area (lFFA), and the right fusiform face-selective area (rFFA) in separate runs for expertise effect analyses. The bilinguals showed in their lLA similar level of activations for Roman and Chinese characters, whereas the non-Chinese readers revealed a higher lLA activations to Roman than Chinese characters. The rLA showed a similar pattern of results though it was not significant. No difference between activations to the two character types was found for either group in lFFA and rFFA. Error bars represent the 95% confidence interval of the Roman–Chinese differences.*

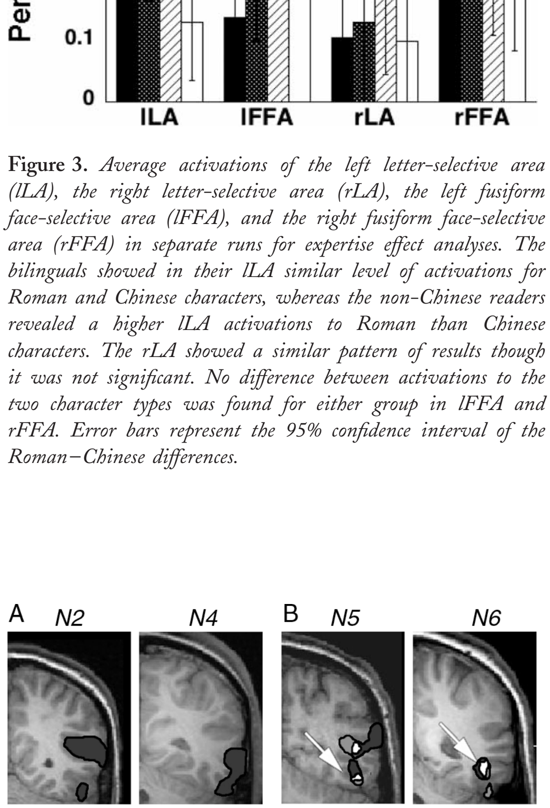

Figure 4. *The activation patterns for non-Chinese readers. The activations for Roman characters (dark grey regions) were defined by (Roman–object) and (Roman–fixation) contrasts. The activations for Chinese characters (grey regions) were defined by (Chinese–object) and (Chinese–fixation) contrast. Their overlap are indicated by white regions and are pinpointed with arrows. (A). Two examples of non-Chinese readers with no selectivity observed for Chinese characters. (B). Two examples of non-Chinese readers with some selective activations for Chinese characters that overlap considerably with Roman letter activations. Coronal slides are shown at $y = -45$ for N4 and N6 and at $y = -55$ for N2 and N5.*

faces. Non-Chinese readers may therefore have recruited the Roman-selective areas when viewing the Chinese characters. The fact that this did not happen for a majority of participants suggests a possible influence of strategy (some participants may have relied on similarity of simple Chinese characters with Roman letters)—such top-down effects have been obtained before for faces and could be tested directly in future work (Bentin, Sagiv, Mecklinger, Friederici, & Cramon, 2002; Cox, Meyers, & Sinha, 2004; Ge, Wang, McCleery, & Lee, 2006).

Discussion

Overlap of character selectivity across writing systems

This study investigated the overlap in selectivity for characters of two very different writing systems within the occipito-temporal cortex. In the left occipito-temporal cortex, the peaks of activity for Roman and Chinese characters in Chinese–English bilinguals were very close, leading to considerable overlap in the regions activated. This overlap was observed consistently in individual participants, rather than in group-averaged statistical maps or in meta-analyses (Bolger et al., 2005; Nakamura et al., 2005), thus providing stronger support for functional convergence of processing of the two character types. Also, overlap was observed in bilinguals at a resolution that is at least sufficient to dissociate selectivity for faces and letters. The activations for Roman and Chinese characters had a higher overlap index and a shorter peak distance than did activations for either type of characters and faces. Further, with the same spatial resolution, we have in other studies dissociated in individual participants areas that are selective for single letters and consonant strings, both distinct from the VWFA (James et al., 2005). Our results are consistent with the finding of common regions activated by English and Hebrew words and letter strings in Hebrew readers (Baker et al., 2007) and extend this finding to single characters.

Interestingly, one line of research suggests that Roman letters and Chinese characters should not be specialized for the same visual areas. According to the co-occurrence hypothesis, specialization depends on spatio-temporal correlations (Polk & Farah, 1998; Polk et al., 2002). Letters generally co-occur in time and space, while they are rarely seen amongst other alphanumeric stimuli, such as digits (or Chinese characters, even in the experience of bilingual readers). Correlation-based learning mechanisms that depend on such temporal and spatial co-occurrence patterns are thought to be able to produce a letter-selective area segregated from areas selective for other stimuli (Polk & Farah, 1998). However, support for segregated letter and digit areas is inconclusive. For instance, a high degree of overlap was observed between letter- and digit-selective areas when either a fixation (Polk & Farah, 1998) or characters that observers were unfamiliar with (James et al., 2005) were used as the baseline for subtraction. Such findings challenge the predictions of the co-occurrence model. One problem with the use of digits is that they co-occur with letters at least to some extent (as can be noted on most pages of this journal). The present finding of overlap between Roman letters and Chinese characters, which seldom co-occur, provides further evidence against the co-occurrence theory. Therefore, the co-occurrence principle does not appear to be a main factor determining organization of the ventral occipito-temporal cortex, at least at the scale sufficient for separating regions selective for faces, single characters, and letter strings. Certainly, it remains possible that co-occurrence could account for patterns of specialization at a finer scale.

While the present study focuses on whether there is overlap of selectivity for different writing systems, it is also clear that the processing of different scripts may also rely on differentiated neural substrates. Nakamura et al. (2005), for example, found that kanji activates bilateral medial fusiform more than does kana. Two explanations were suggested for this difference. First, kanji may require more foveal processing and thus may recruit neurons biased towards a more medial part of the fusiform gyrus; second, kanji may activate more regions associated with semantic processing than does kana. We did not see any reliable difference in bilinguals between Chinese and Roman characters in the left Roman-selective areas. Because our Chinese characters were relatively simple (fewer than five strokes), we would not expect as much of a difference in the need to foveate between these characters and Roman letters. In addition, our use of single simple Chinese characters in a perceptual matching task is likely to recruit less semantic processing than the two-character kanji words used by Nakamura et al. (2005) in a semantic categorization task (natural object/artifact). In sum, potential differences in the neural substrates of two writing systems is likely to be affected by several factors, which include properties of the stimuli that interact with requirements of the task performed. Therefore, we do not make any claims about the absolute amount of spatial overlap between letters and Chinese characters. On the one hand, the absolute values of overlap indices are not especially meaningful (Kung et al., 2007), and on the other hand, any account would predict some degree of differentiation. Importantly, however, our results suggest that the overlap between the two character types is larger than that between characters and faces (or between letters and consonant strings in our previous work) and that it is considerable despite important linguistic and geometric differences.

One question concerns whether the selectivity found here is primarily driven by visual processes. Converging evidence can be found in our recent ERP study showing higher amplitudes of the N170 component for Roman and Chinese characters than for pseudoletters in Chinese–English bilinguals and higher N170 amplitudes for Roman than Chinese characters and pseudoletters in non-Chinese readers (Wong et al., 2005). The N170 effect has been typically associated with visual processing, and higher level effects, such as phonological and semantic effects, are usually seen in later ERP components (Liu et al., 2003). Since our task and conditions are quite similar between the ERP and fMRI experiments, there is also probably a visual component in the selectivity for characters in the current study. However,

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one may still ask to what extent the character-selective areas found in bilinguals could be engaged by nonvisual processes associated with naming the characters and accessing semantic information. Indeed, Cohen and colleagues (Cohen, Jobert, Le Bihan, & Dehaene, 2004) report an area that responds to both auditory and visual presentation of words in both auditory and visual tasks. This region, termed the lateral inferotemporal multimodal area (LIMA), is lateral and anterior (average coordinates: −48, −60, − 16) to the VWFA (−44, −68, −4) localized in their study. It remains a question of how the character-selective areas found in the current study are related to the LIMA. Note that the location of the VWFA in Cohen et al. (2004) is much more posterior than that found in other studies (e.g., −42, −54, −6; Cohen et al., 2000). While this may occur given the large individual differences observed in the literature (see Table 1), it demonstrates the importance of within−subject comparisons. It would be interesting to localize the LIMA, VWFA, and the single-character-selective areas in the same participants and to examine their overlap. However, the concern about naming and semantics motivated our inclusion of easily nameable common objects in the present study, and our results suggest that any automatic naming and semantic processing elicited by these stimuli do not engage the lLA to the same extent as do letters and characters. In addition, single Roman letters have little associated semantic content (much less than words or objects) so that an area selective for both single Roman letters and Chinese characters is unlikely to be driven by semantic access.

The role of expertise and stimulus properties

While the co-occurrence account may not explain the organization of selectivity for single-character processing in different scripts, experience could. A study of fMRI activity in monozygotic and dizygotic twins showed that cortical responses to words develop mainly as a result of experience, not genetics, in contrast to cortical responses to faces and places (Polk, Park, Smith, & Park, 2007). The current study also showed that character selectivity across writing systems in Chinese−English bilinguals was associated with experience with the writing system. Whereas no difference was found in bilinguals between the character types, non-Chinese readers showed higher activations in the left character-selective area for Roman than for Chinese characters. One account is that the areas engaged by both Roman and Chinese characters are responsible for common processes that are recruited through similar experience with these characters. Indeed, expertise with both scripts is associated with similar perceptual hallmarks—for instance, increased sensitivity to regularity in font (Gauthier et al., 2006). An alternative that we cannot rule out is that the crucial aspect of experience in expert readers is simply exposure to a pool of characters. Indeed, there is growing evidence that exposure can drive not only neural responses that are stimulus specific (Peissig, Singer, Kawasaki, & Sheinberg, 2007) but also responses that generalize to new exemplars of a category (Scott, Tanaka, Sheinberg, & Curran, 2006). This issue may be best explored in a design where two groups receive equivalent exposure but qualitatively different experience with the same stimulus set. It is notable that controls for exposure effects have been absent from prior fMRI training studies (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Jiang et al., 2007; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Yue, Tjan, & Biederman, 2006). But crucially, exposure alone cannot explain why Roman letters and Chinese characters are specialized for similar areas whereas faces are specialized for another.

While our results uncover an expertise effect in the response to Chinese characters, the consideration of individual activation profiles also reveals selectivity for these shapes in novices. That is, consistent with the group expertise effect, several non-Chinese readers show selectivity for Roman letters only, with no selectivity at all to Chinese characters. However, a few non-Chinese readers unexpectedly showed selective responses to Chinese characters in regions overlapping with the Roman-selective areas. Our

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results suggest that the manner in which characters are processed is more variable in novices than in experts, consistent with prior findings in the FFA that task manipulations have a larger effect in novice than expert observers (Gauthier, Skudlarski, Gore, & Anderson, 2000). Future studies could explore this question by assessing responses to characters in tasks that are more or less constraining: We would predict an interaction between expertise and task constraints, such that novices would show stronger task effects, and more individual differences with a less constraining task.

Nonetheless, the response to Chinese characters in novice participants is surprising. This may be because of similar low-level visual features involved and/or because the non-Chinese readers knew the characters were linguistic stimuli. An intriguing possibility, however, is that the recruitment of Roman-selective areas for Chinese characters in some non-Chinese readers reflects cortical biases that are independent from experience. The responses in novices may reflect an underlying topography of selectivity to shape (Op de Beeck, Deutsch, Vanduffel, Kanwisher, & DiCarlo, 2008). It has been suggested that while experience can change the spatial distribution of responses to object categories, the distribution of pretrained selectivity does not predict training effects (Op de Beeck et al., 2006). However, while this may not be the case at the scale of the distributed map that spans extrastriate cortex, there may be localized regions of shape selectivity that can act as attractors to influence learning effects. To some extent, this may even be necessary to explain why expertise can lead to similar category specialization in different brains. The "process-map" hypothesis suggests that category selectivity observed in the ventral pathway is due to automatic recruitment of cortical regions that support computations associated through experience with a specific object category (Bukach, Gauthier, & James, 2006; Gauthier, 2000). For example, for faces this hypothesis translates into the following logic. Faces are more often recognized at the subordinate level than other objects and are processed more holistically. In face experts, these computations are engaged upon presentation of a face regardless of the task, and the FFA may simply be the area that best supports these computations. However, for such a process to recruit similar areas in different brains for a given category, it is necessary to postulate preexisting biases in the cortical sheet, biases that essentially account for why a specific cortical region would be the best suited for a given computation. Recent work suggests that some of these biases are driven by eccentricity preferences found in higher order areas (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001) and also to some extent by a map of image-based attributes (Haxby et al., 2001). Thus, the selectivity for characters relative to faces and objects may be partly caused by processing biases determined by the properties of the stimuli—those common to both types of characters and distinguishing them from faces and objects. Indeed, the same explanation could account for the overlap of activity for digits and letters in prior studies (James et al., 2005; Polk & Farah, 1998; Polk et al., 2002). Such selectivity would then represent the scaffolding onto which selectivity due to experience can develop. A prediction based on this hypothesis is that such expertise-unrelated selectivity should be observed early in development and regardless of the level of literacy of a participant.

To conclude, our findings suggest that experience, through exposure and/or the specific processes engaged during our encounters with objects, constrain how different categories come to be specialized in the cortex. In addition, preexisting cortical biases possibly dependent on visual appearance may influence what part of the cortex will come to be recruited for skilled perception of a given category. Beyond their relevance for the origins of category specificity in the visual system, these results have implications for our understanding of the neural basis of reading by demonstrating that skilled reading in alphabetical and nonalphabetical writing systems share common neural substrates at an early stage, that of the perception of single characters.

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