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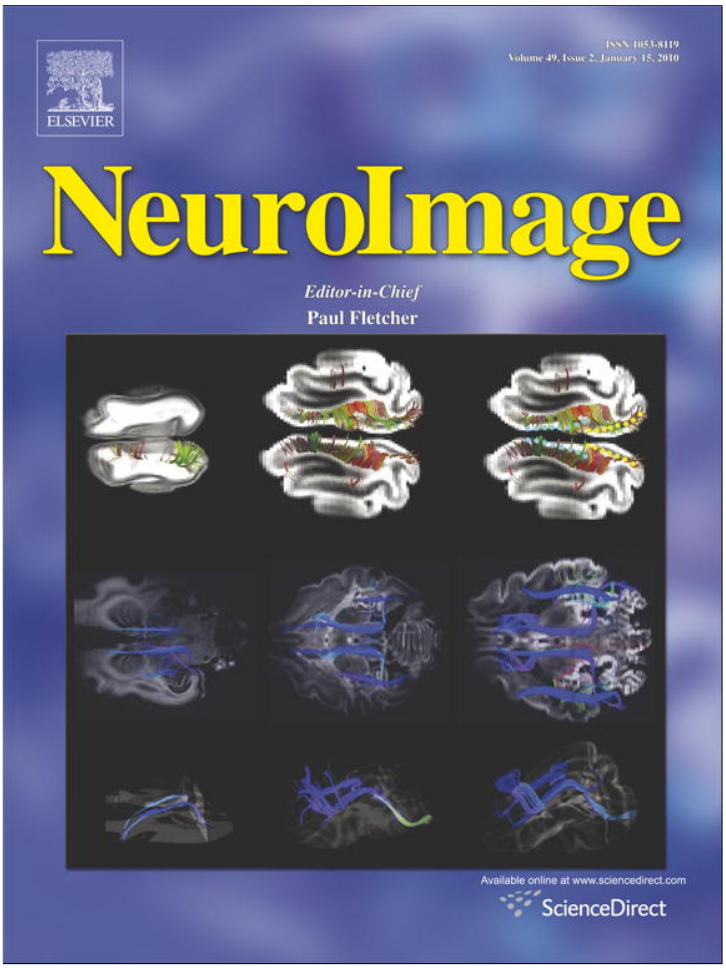

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Why do children make mirror errors in reading? Neural correlates of mirror invariance in the visual word form area

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ABSTRACT

Young children often make mirror errors when learning to read and write, for instance writing their first name from right to left in English. This competence vanishes in most adult readers, who typically cannot read mirror words but retain a strong competence for mirror recognition of images. We used fast behavioral and fMRI repetition priming to probe the brain mechanisms underlying mirror generalization and its absence for words in adult readers. In two groups of French and Japanese readers, we show that the left fusiform visual word form area, a major site of learning during reading acquisition, simultaneously shows a maximal effect of mirror priming for pictures and an absence of mirror priming for words. Thus, learning to read recruits an area which possesses a property of mirror invariance, seemingly present in all primates, which is deleterious for letter recognition and may explain children's transient mirror errors.

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Introduction

Many parents have made the surprising observation that their child, when learning to read and write, occasionally reverses left and right—whole words are occasionally written from right to left, and letters b, d, p, q are often confounded (Fig. 1). Although longitudinal data are lacking, the scarce evidence to date suggests that mirror reading and writing may be normal behaviors, distinct from dyslexia (Cornell, 1985; Schott, 2007). For instance, using a simple task which required subjects to write their name next to the right-hand margin of a page, Cornell (1985) found that essentially all 5- to 6-year-olds spontaneously wrote from right to left, while this behavior disappeared by age 8. Indeed, with the notable exception of Leonardo da Vinci, very few adults remain fluent in mirror reading and writing, although these abilities occasionally reappear following brain lesions (Pflugshaupt et al., 2007; Schott, 2007). It is therefore intriguing to ask why such a sophisticated behavior might be spontaneously present in young children, without having been trained, and why this competence seems to be lost in adults, although their ventral visual system remains able to recognize mirror images of objects (Eger et al., 2004; Vuilleumier et al., 2005). Understanding what neural mechanisms underlie this putative difference in mirror generalization between words and pictures in adults is an especially important goal since it has been claimed that the recognition of these two categories relies on shared visual mechanisms (Price and Devlin, 2003; Price et al., 2006). In the present paper, we address the latter question by probing mirror invariance for pictures and words in adults using behavioral and fMRI priming.

Our experiment is predicated upon a recent evolutionary and neurological perspective on reading, based on the concept of "neuronal recycling" (Dehaene, 2009; Dehaene and Cohen, 2007). Cultural inventions such as reading and mathematics are too recent to have influenced the human genome. Therefore, they must be acquired through the recycling of neuronal networks evolved for other purposes, but whose initial properties are sufficiently similar to the target function and which possess enough plasticity, particularly during childhood, for their functionality to be partially converted to this novel task (Dehaene, 2009; Dehaene and Cohen, 2007). In the case of reading, there is ample evidence that the acquisition of visual word recognition proceeds by progressively specializing a subpart of the left ventral visual system which has been termed the visual word form area (Baker et al., 2007; Ben-Shachar et al., 2007; Cohen et al., 2000; Gaillard et al., 2006). This region is reproducibly localized within a few millimeters in readers of all cultures (Bolger et al., 2005; Nakamura et al., 2005), suggesting that it may possess intrinsic biases in its retinotopic inputs (Hasson et al., 2002), preferred features

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Fig. 1. Example of mirror writing in a young Italian child named Leone (courtesy of Manuela Piazza).

(Changizi et al., 2006; Szwed et al., 2009), or connectivity (Epelbaum et al., 2008) that make it most appropriate for learning the visual shapes of letters and words. These biases, together with the general architectural properties of the ventral visual pathway for invariant object recognition (Serre et al., 2007; Ullman, 2007), seem to be co-opted for efficient visual word recognition in expert readers (Dehaene et al., 2005).

The recycling hypothesis holds that cultural learning is generally facilitated by the pre-existing properties of cortical tissue (e.g. size and location-invariant recognition). Occasionally, however, cultural learning may require the overcoming of biases that were useful in a prior environment, but are now counterproductive. Mirror errors fit in this framework. Monkey electrophysiological evidence indicates that the responses of some infero-temporal neurons show a property of mirror-image generalization, particularly across inversions of left and right (Baylis and Driver, 2001; Logothetis and Pauls, 1995; Rollenhagen and Olson, 2000). This feature presumably arose in the course of evolution because most natural visual categories are invariant across left–right changes (Corballis and Beale, 1976). It is deleterious for reading, however, where minimal mirror pairs such as p and q exist, and it may therefore impede reading acquisition, giving rise to transient mirror errors. Under this admittedly speculative hypothesis, mirror generalization would be an intrinsic property of some subpart of the visual cortex that would have to be "unlearned" as we become efficient readers.

At the behavioral level, there is considerable evidence for a progressive unlearning of symmetry generalization for letters and words. Even infants generalize across mirror views of simple objects (Bornstein et al., 1978), and this ability seems to persist into preschool years, even for letters, but to disappear when reading is acquired (Cornell, 1985; Schott, 2007). The causal role of reading acquisition in this loss is suggested by the observation that dyslexic children transiently perform better than normal in same-different judgments with mirror letters (Lachmann and van Leeuwen, 2007; see also Schneps et al., 2007), and that illiterate subjects and readers of a curvilinear language (Tamil) without mirror-image letters such as p and q continue to generalize across mirror figures, contrary to other readers (Danziger and Pederson, 1998; Kolinsky et al., 1987; Pederson, 2003).

The underlying brain mechanisms, however, remain to be studied. Obtaining direct evidence for our theoretical framework would ultimately require the longitudinal testing of mirror-image generalization in children, or alternatively the scanning of adult illiterates. Prior to conducting such complex studies, however, the present work aimed at testing a simpler prediction in normal adult readers. Our framework predicts that the visual word form area should be the site of the major difference in mirror invariance for pictures and words—it should show mirror priming for pictures, but not for words. This prediction is of general interest inasmuch as it contrasts sharply with other researchers' claim that this cortical site implements a domain-general function which is shared by words and pictures (Price and Devlin, 2003; Price et al., 2006; Wright et al., 2008). Here, using fMRI repetition priming, we show in adult readers of two different cultures (French and Japanese), that at the very same fusiform location, mirror-image generalization exists for pictures but not for written words.

Results

Behavioral priming during semantic categorization

During fMRI, participants performed a primed semantic task on target words and line drawings (size comparison, Fig. 2). Each target was preceded by either the same or a different prime, which appeared either in the same orientation or in mirror image. We first examined whether behavioral priming was present—our prediction being that mirror priming should be observed for pictures but not words.

Median correct response times were entered into an ANOVA with group (French or Japanese) as a between-subjects factor and stimulus category (words or pictures), repetition (same or different prime) and orientation of the first stimulus (normal or mirror) as within-subject factors. A main effect of category was found ($p<0.001$), all participants being faster with pictures than with words. There was also an overall repetition effect, with faster response on repeated trials than on different trials (overall priming effect = 67 ms, $p<0.001$). This effect was qualified by several interactions. First, the repetition effect was stronger for physically identical primes than for mirror primes ($p<0.001$). Second, the effect was larger for line drawings than for written words ($p<0.001$). Third, there was a triple interaction of repetition, orientation and stimulus category ($p<0.001$). Priming was significant in all cells of the design (all $p<0.001$), but with pictures targets, the difference between mirror priming and physical priming was relatively small (66 ms versus 93 ms priming effect, $p<0.001$), whereas with words it was much larger (25 versus 85 ms priming effect, $p<0.001$). Thus, pictures were accelerated by mirror primes much more than words were (repetition × category interaction restricted to mirror primes, $p<0.001$).

An interesting cultural difference also emerged. Although there was no overall group difference in RT ($F<1$), differences between the Japanese and French participants were revealed by significant interactions of group × repetition × orientation ($p<0.001$), group × repetition × stimulus category ($p<0.001$) and the quadruple interaction ($p=0.048$). As seen in Fig. 2, these findings essentially reflect that the difference in mirror priming between words and pictures was stronger in the French group than in the Japanese group. There was no mirror priming for alphabetic stimuli in French participants (4 ms priming effect, $p=0.25$), but significant mirror priming for Japanese characters in Japanese participants (44 ms priming effect, $p<0.001$).

The mean error rate was 10.7% for Japanese subjects, and 4.0% for French subjects, a significant difference ($p<0.001$). An ANOVA on error rates revealed effects essentially parallel to the RT analysis, indicating that there was no speed-accuracy trade-off. In particular, a significant triple interaction of repetition, orientation and stimulus category ($p=0.014$) was due to the fact that repetition priming did not differ across pictures and words (interaction $p=0.35$; priming effects, i.e. reductions in error rate on same compared to different-prime trials: pictures = 1.2%, words = 1.9%), while mirror priming was significantly stronger for pictures than for words (interaction $p=0.004$; priming effects: pictures = 2.7%, words = 0%). These effects did not differ significantly in French versus Japanese subjects.

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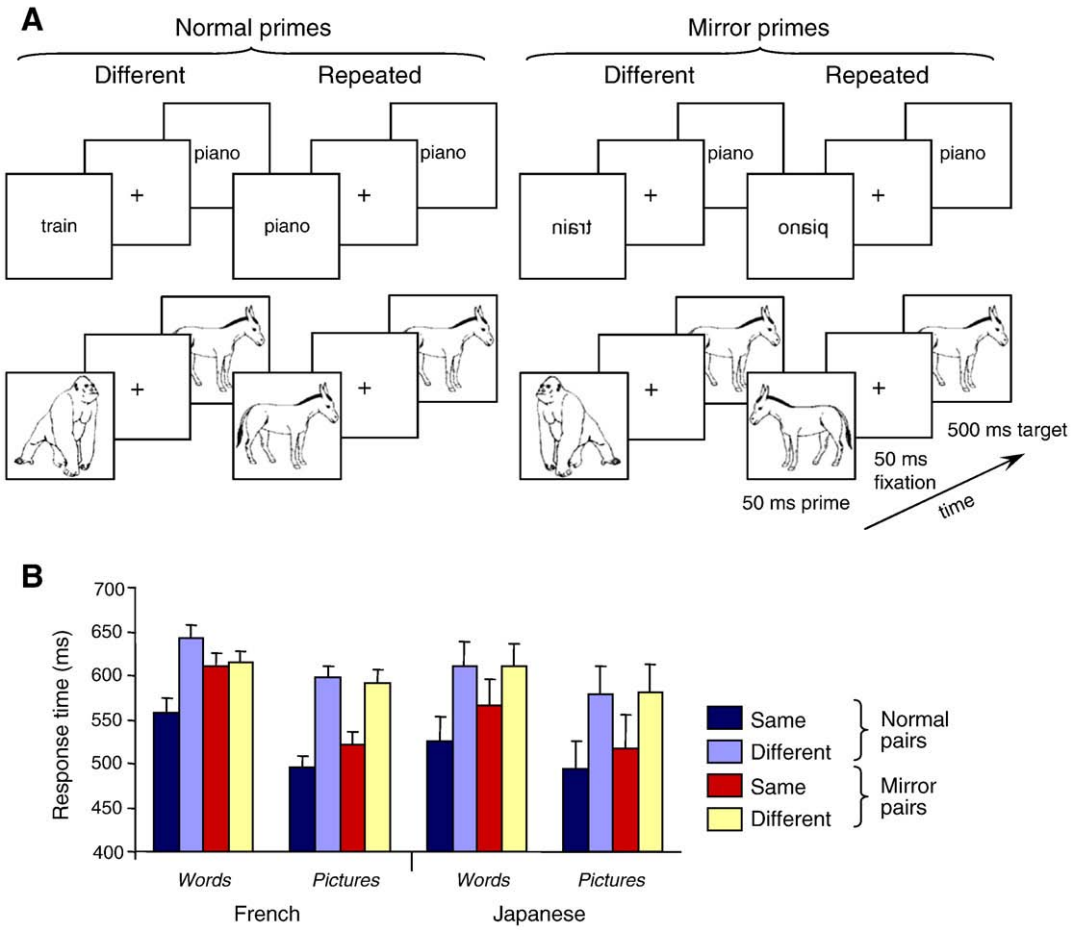

Fig. 2. fMRI design and behavioral results. (A) sample stimuli illustrating the 2×2×2 design with factors of stimulus type (word or picture), repetition (same or different), and orientation (normal or mirror). Participants judged whether the target, in real-life, is larger or smaller than a standard computer screen. (B) responses times collected during fMRI in both French and Japanese participants during the size judgment task.

Altogether, the behavioral results revealed that repetition priming was strong for both categories, but that mirror priming was strong for pictures and much weaker or downright absent for written words, especially in the French participants.

fMRI results

Differences in activation to words and pictures

Relative to rest, both words and pictures activated extended bilateral sectors of ventral occipito-temporal cortex, as well as bilateral intraparietal sulcus (IPS), frontal eye field (FEF), and midline and lateral prefrontal cortices (PFC). However, relative to pictures, the visual activation to words was focal and extended essentially only along the lateral occipito-temporal sulcus bordering the fusiform gyrus (VWFA), particularly in the left hemisphere, as previously described (Ben-Shachar et al., 2007; Cohen et al., 2000). Thus, extensive regions of greater activation to pictures than to words were seen in bilateral ventral occipito-temporal cortex (Fig. 3), except at the site of the VWFA where no significant difference was seen. In the converse direction (words>pictures), no significant regions were found. In summary, words activated a focal region which was a narrow subset of the large activation evoked by pictures.

Cultural differences on this word-picture contrast were seen in only one direction: French participants showed significantly greater activation than Japanese participants in the pictures>words contrast, outside the VWFA, but at two distinct bilateral posterior sites in lateral occipital cortex (LOC), a very posterior one (−27, −93, 3; $t=6.40$ and 30, −93, 6; $t=10.3$) and a more lateral and anterior region (−48, −81, −6; $t=9.75$ and 51, −81, 6; $t=11.9$). Because these regions may correspond to recently reported retinotopic areas LO1 and LO2 (Larsson and Heeger, 2006) and because the retinal extent of the stimuli differs for Japanese and French participants (Kanji characters versus alphabetic strings), interpretation must be cautious. However, the difference is unlikely to be due to solely to retinotopic factors, because it was also found for pictures, which were identical for the two groups. Indeed, in the right occipital cortex at least, a significant cross-over effect was seen, with significantly differences both for Japanese>French participants with words and for French>Japanese participants with pictures (peak at 30, −90, 6; both $p<0.001$; Fig. 4; similar trends were present in all four LOC regions). Thus, the activation difference between Kanji characters and pictures in the Japanese participants was smaller than the difference between alphabetic strings and pictures in the French participants.

In inter-hemispheric comparisons, a highly significant left-hemispheric dominance was found in occipitotemporal cortex for words relative to pictures. This large cluster extended from the posterior occipital cortex (−21, −81, −3; $t=5.87$) to more anterior inferior temporal regions in VWFA proper (subpeaks at −51, −57, −12, $t=8.93$; and −42, −42, −21, $t=9.19$; see Fig. 3F). Hemispheric differences in favour of words relative to pictures were also found in two smaller clusters in left occipito-parietal sulcus (−33, −72, 30, $t=5.89$) and right cerebellum (18, −75, −24, $t=4.79$). There was a marginally significant trend towards greater left-hemispheric lateralization for the French group relative to the Japanese group, at coordinates very close to the VWFA (−39, −60, −18, $t=3.77$, corrected $p_{cluster}=0.065$; see bar graphs in Figs. 3B and D).

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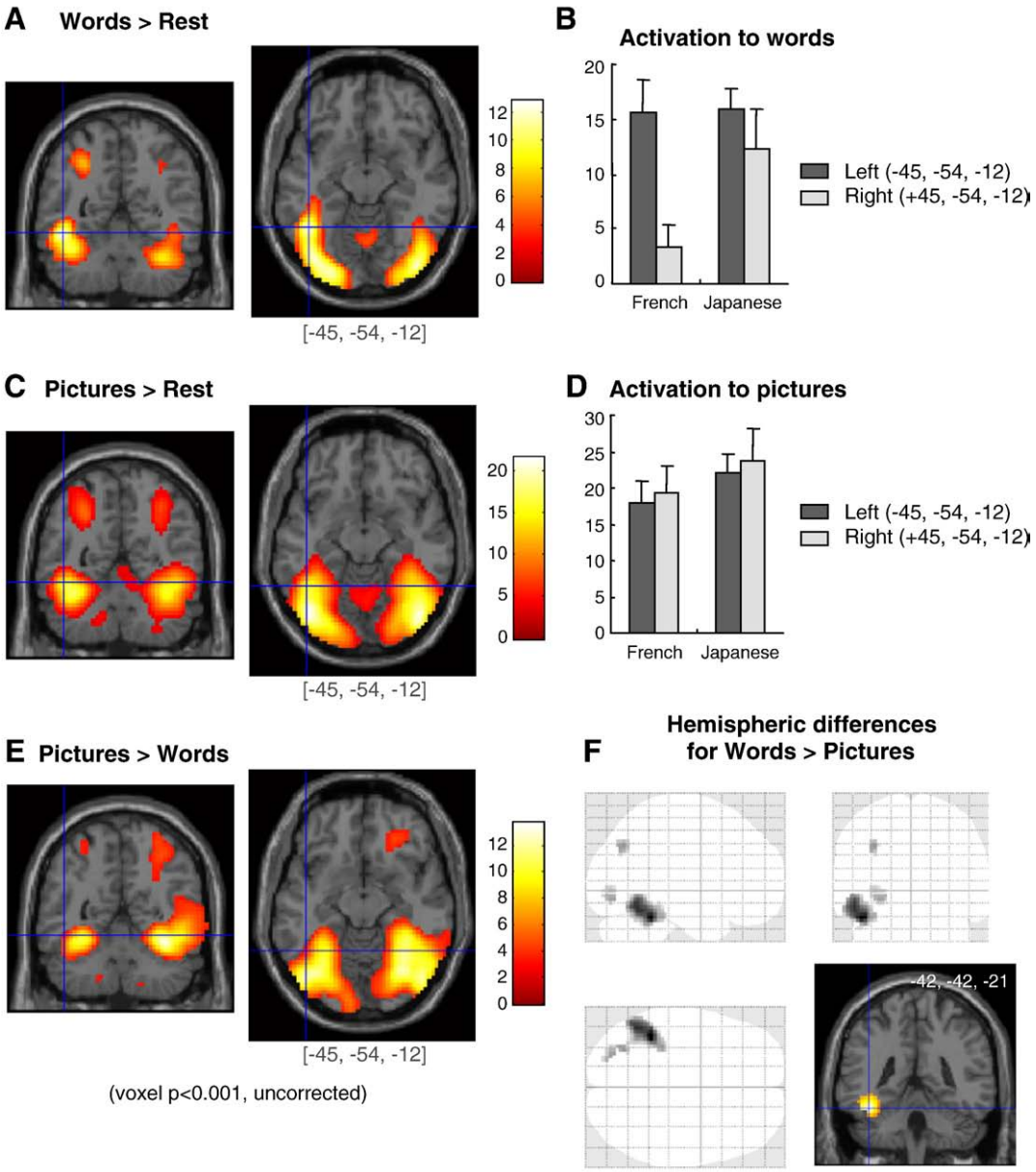

Fig. 3. Comparison of activations evoked by words and by pictures. Relative to rest, word stimuli evoked a left-lateralized ventral occipito-temporal activation, peaking at the usual coordinates of the VWFA (panel A). At this site, activation was more strongly left lateralized in French than in Japanese readers (panel B). Picture stimuli also activated this spot, but yielded a more distributed and overall symmetrical activation in both hemispheres (panels C and D). Thus, the direct comparison of word and pictures stimuli (panel E) yielded a greater activation for pictures throughout the occipito-temporal cortex, with the striking exception of the VWFA. At this site, words also yielded a significantly greater left-hemispheric advantage than pictures (panel F). For illustration purposes, all images are threshold at uncorrected $p_{voxel}<0.001$ (clusters with corrected $p_{cluster}<0.05$ are reported in the main text).

Brain regions associated with identity priming

We next examined brain regions showing sensitivity to stimulus repetition in the same orientation (identity priming). For words, repetition suppression (RS) was found in an extended antero-posterior section of the left occipito-temporal sulcus (Fig. 5, see coordinates in Table 1), with a peak at the classical VWFA coordinates (−45, −57, −12). For pictures, identity priming was extensive in the bilateral occipitotemporal regions, encompassing the region showing word identity priming, but with a peak picture priming effect located more laterally in the bilateral LOC. An intersection analysis showed that the occipitotemporal sites showing identity priming to words were, in fact, also sensitive to the repetition of pictures. In these overlapping regions, moreover, the magnitude of identity priming never differed between words and pictures.

For words, the magnitude of identity priming did not differ between the French and Japanese groups. Indeed, an intersection analysis confirmed that the VWFA and the rest of the occipitotemporal network exhibited identity priming for words commonly for alphabetic stimuli in French participants and for Kanji stimuli in Japanese participants (each at voxel-level $p<0.01$). This observation provides a further indication of cross-cultural convergence towards the same VWFA region sensitive to word repetition priming for alphabetic and non-alphabetic scripts (Bolger et al., 2005; Nakamura et al., 2005).

For pictures, the right LOC exhibited greater identity priming in the French group relative to the Japanese group (51,−81,−6; $t=5.10$). This same region is a part of the above bilateral lateral occipital region showing greater activation to pictures in French relative to Japanese. The magnitude of identity priming did not differ between two

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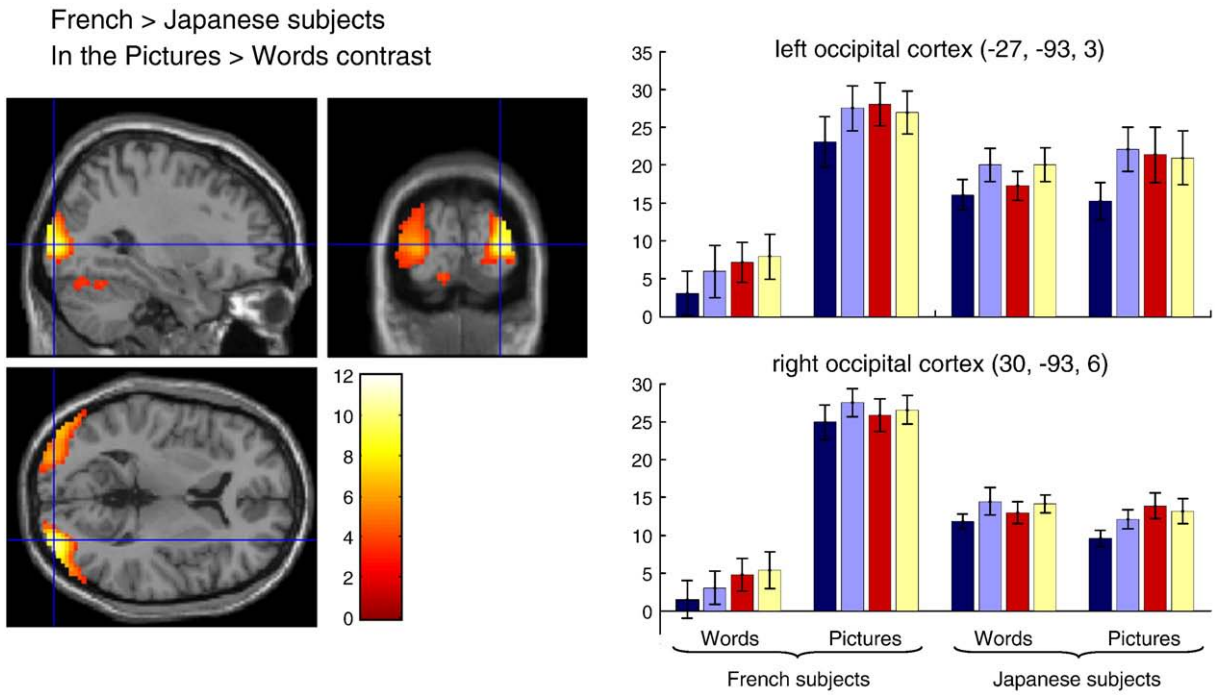

Fig. 4. A cultural effect in occipital cortex. Bilateral posterior and lateral occipital cortices exhibited a significant interaction between group and stimulus category, with more activation to pictures than to words in French participants, but no such difference in Japanese participants. Only a small identity repetition suppression effect was seen in this area (right graph).

hemispheres, either for words or for pictures. No repetition enhancement was found, either for words or for pictures.

Brain regions associated with mirror priming

Having characterized the brain regions sensitive to our stimuli and to identity priming, we then searched for repetition suppression induced by mirror primes. For pictures, mirror priming was found in a single region in the left occipitotemporal cortex, at coordinates very close to the VWFA (−39, −60, −21), with a trend towards a hemispheric asymmetry (peaking at −39,−63,−18; $t=2.77$, $p_{voxel}=0.003$, uncorrected). This region thus appears as a critical site for mirror-image invariance with pictures, since other occipitotemporal sites, shown earlier to be sensitive to identity priming, were not significantly affected by mirror priming for pictures. To show this more directly, we computed a contrast searching for regions with greater repetition suppression to identical pictures than to mirror pictures. This contrast identified bilateral occipital regions, the right LOC (54, −78, −3; $t=4.87$) and, at a lower threshold, the left LOC (−48, −72, 0; $t=4.06$, 55 voxels, uncorrected $p_{cluster}=0.046$). The activation profiles of the left and right LOCs were similar, as confirmed by a lack of between-hemisphere difference ($p>0.05$). The magnitude of this mirror priming for pictures did not differ between French and Japanese participants.

Crucially, when testing for mirror priming for words, no region emerged as significant, even at a very low threshold ($p_{voxel}<0.05$). Mirror priming for words did not approach significance, neither when masking by those regions showing identity priming, nor in the occipitotemporal cluster showing mirror priming for pictures. Fig. 6 shows the profile of response at the peak of the mirror priming effect for pictures, showing no trace of mirror priming for words in French participants, and only a small non-significant trend for Japanese participants ($p_{voxel}>0.05$).

We then computed a contrast searching for regions with greater repetition suppression to identical words than to mirror-reversed words. This comparison again pointed to the left occipitotemporal site close to VWFA (−45, −57, −12; $t=4.60$), though without a significant hemispheric difference. Surprisingly, an intersection analysis revealed that this cluster, defined by absence of mirror priming for words, overlapped largely with the left occipitotemporal site defined by presence of mirror priming for pictures (49 voxels in the intersection, both tests at $p<0.001$).

Concerning cultural differences, because behavioral results indicated that mirror priming was significantly greater for Kanji words than for French words, we searched for fMRI correlates of this effect. Between-group comparison revealed a trend for greater mirror-priming for words in the Japanese group relative to the French group in left medial frontal cortex (−9, −3, 57; $t=4.32$, 38 voxels; uncorrected $p_{cluster}=0.015$; see Fig. 6 for the corresponding plot). For pictures, the between-group difference in mirror priming was non-significant throughout the whole brain volume. More sophisticated analyses looking for triple- or quadruple-interactions of the stimulus category, orientation repetition and group factors did not add to these findings. No significant mirror-enhancement was found.

Additionally, we tested whether our mirror primes produced differential activation relative to normal primes, since some past studies showed extensive activations when subjects endeavour to decipher rotated or mirror-reversed words (Cohen et al., 2008; Goebel et al., 1998; Mochizuki-Kawai et al., 2006; Poldrack and Gabrieli, 2001). This main effect of mirror reversal was tested solely for non-repeated trials to avoid confounds with repetition priming. However, we found no difference in activation on trials where primes were normal versus mirror-reversed, whether the stimulus was a picture or, crucially, a word.

Behavioral same-different judgments: extension to other visual categories

Is the observed lack of mirror generalization for words unique to the learned script, or does it generalize to all symbols visually similar to writing? Although this issue will have to be further explored with fMRI, we obtained relevant data from an additional behavioral task, which probed the participants' ability to compare five different types of visual stimuli (faces, tools, Kanji, false font, and letter strings) in a mirror-invariant manner. Alphabetic strings and Japanese characters

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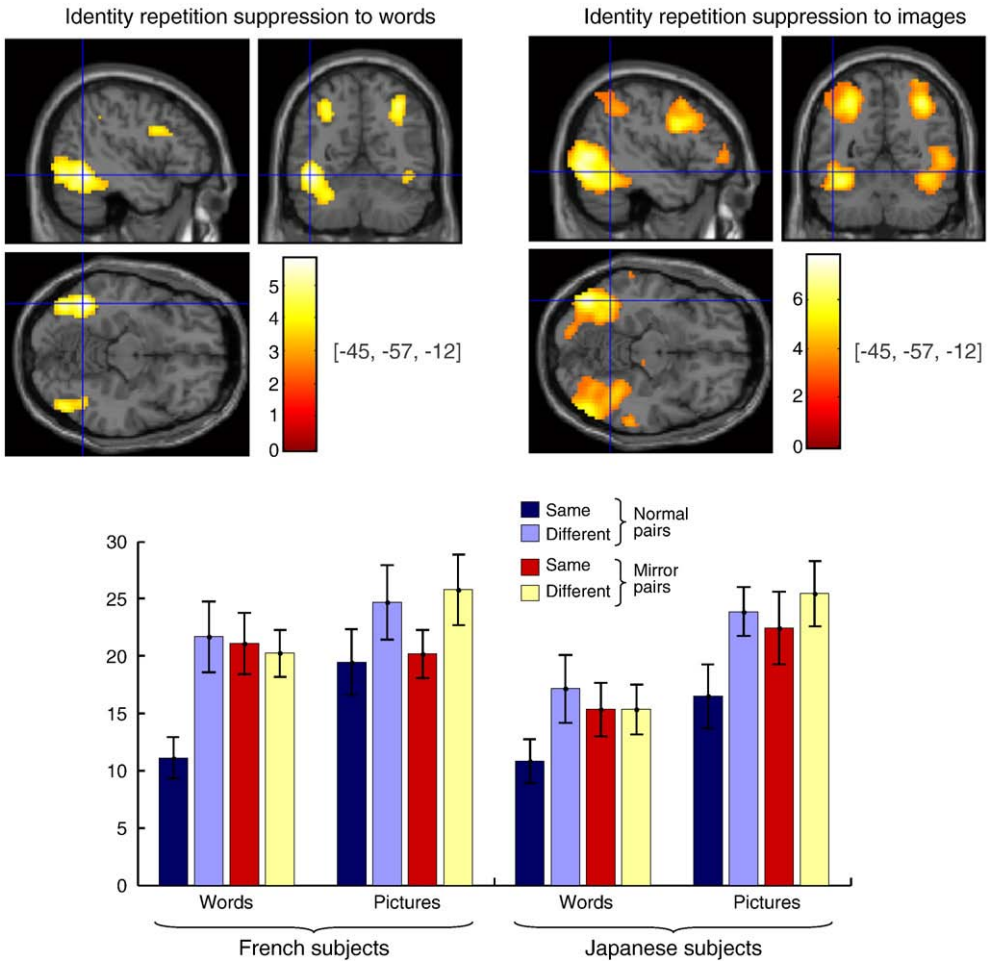

Fig. 5. Repetition effect in the VWFA differ for words and pictures. The top images show left occipito-temporal regions showing identity repetition suppression for words (top left) and images (top right). The images are centered at the peak of the identity repetition effect for words, which appears to coincide with the classical coordinates of the VWFA. The histogram illustrates the activation in the other conditions, for which this voxel was not selected. Statistical analyses confirmed an absence of mirror priming for words, but strong identity and mirror priming for images within the same voxel.

were presented to both French and Japanese participants, allowing us to investigate whether mirror invariance depended on script and familiarity.

Median correct response times were analyzed using an ANOVA with group as a between-subjects factor and stimulus category, repetition (same or different image) and orientation of the first image (normal or mirror; the second image was always in normal orientation) as within-subject factors. The results revealed a main effect of group ($p = 0.012$), Japanese participants responding significantly faster than French participants (respectively 563 and 711 ms). However, the group factor did not enter into any other interactions, indicating a similar profile in both groups. All other main effects and interactions, except the main effect of repetition, were significant ($p < 0.003$). Participants found it easy to judge that two mirror images of faces or tools were the same,

Table 1
Brain regions showing repetition suppression to words and pictures.

Brain regions	Identity priming						Mirror priming		
	Pictures			Words			Pictures		
	Number of voxels	Coordinates	*t*	Number of voxels	Coordinates	*t*	Number of voxels	Coordinates	*t*
L occipitotemporal cortex	2796	−48, −75, 0*	7.53	735	−45, −57, −12†	5.82	131	−39, −60, −21	4.44
					−42, −75, −12	5.03			
R occipitotemporal cortex	2381	51, −78, −6*	7.82	130	48, −72, −12	3.58			
					42, −57, −12				
L posterior parietal cortex	2796 #	−27, −63, 45	6.45	200	−27, −51, 42	4.66			
R posterior parietal cortex	2381#	36, −57, 48	6.69	239	33, −54, 48	4.92			
L prefrontal cortex	766	−42, 6, 30	6.22	113	−39, 21, 24	4.24			
R prefrontal cortex	746	51, 12, 33	4.77	136	39, 24, 24	4.61			
L medial frontal cortex	157	−3, 6, 51	3.91						

Identity priming yielded extensive clusters encompassing both parietal and occipito-temporal peaks (#). No brain region showed significant mirror priming for words. The bilateral LOC region (*) also showed (1) group × category interaction i.e., greater activation for French than Japanese participants in pictures > words contrast, and (2) greater identity priming than mirror priming for pictures. The VWFA (†) also showed (1) greater identity priming than mirror priming for words and (2) identity priming for words commonly for French and Japanese participants (see Results). All locations of local maxima are reported according the MNI coordinate system.

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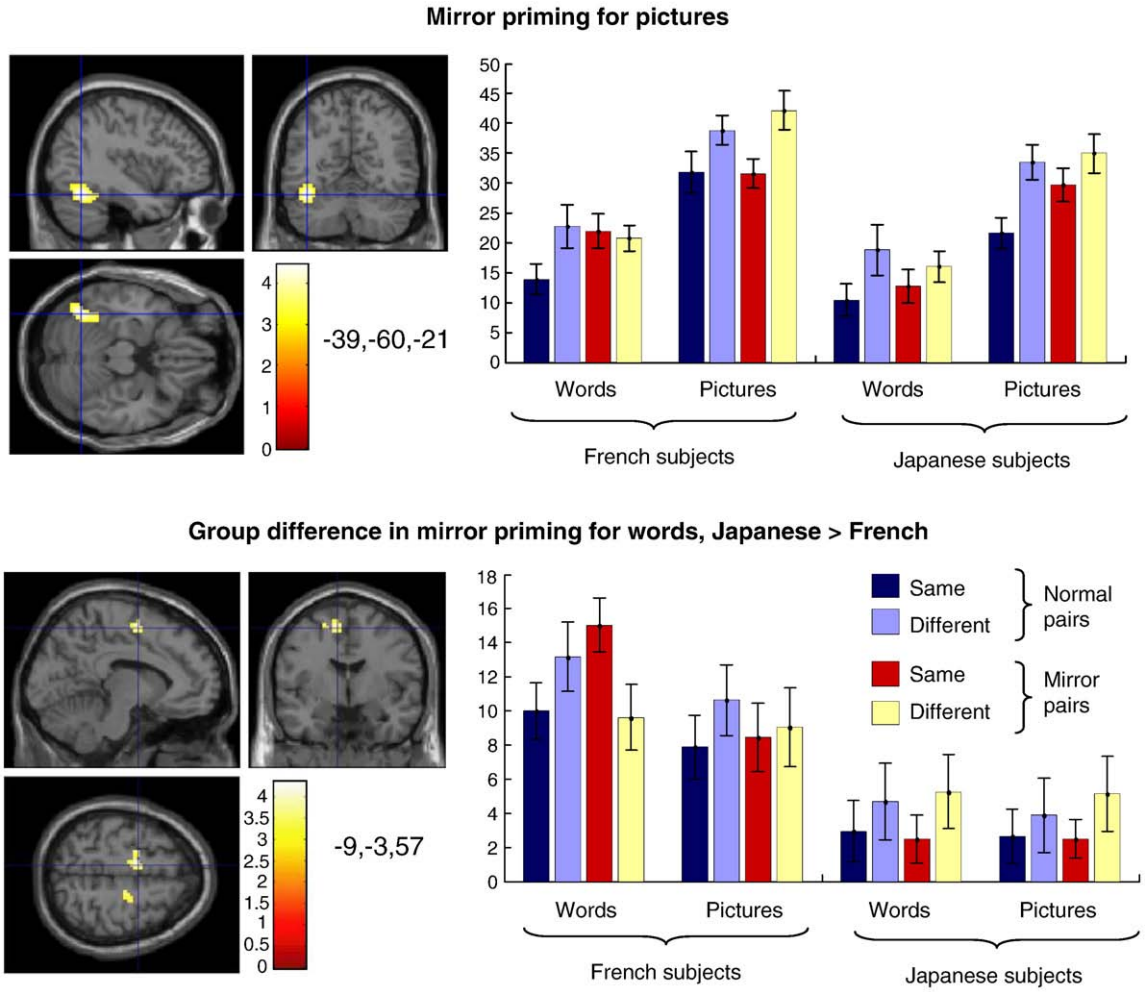

Fig. 6. fMRI correlates of mirror priming. For pictures (top), mirror priming was significant only in the left occipito-temporal cortex, at a site overlapping strongly with the classical VWFA. For words, although no overall mirror priming was found, a trend for greater mirror-priming for words in Japanese compared to French participants, congruent with behavioral findings, was observed in left medial frontal cortex (bottom).

and found it increasingly difficult to respond "same" to mirror images of written scripts (Fig. 7). Within the "same" responses, the added cost of mirror images relative to physically identical images was +76 ms for faces, +120 ms for tools, +166 ms for Japanese characters, +230 ms for pseudo-fonts, and as much as +252 ms for alphabetic stimuli. While all these difference scores were significantly different from zero (all $p<0.01$), indicating that mirror invariance exerted a cost even for face stimuli, they varied significantly across categories ($p<0.001$) and were significantly higher for written scripts than for pictures (faces and tools combined) ($p<0.001$).

Similar observations were made with error rates. Participants easily responded correctly in all situations, except when they had to respond "same" to mirrored written scripts. Within the "same" responses, the additional error rate induced by mirror images relative to physically identical images was only +1.7% for faces ($p=0.08$, n.s.) and +0.3% for tools ($p=0.26$, n.s.), but +7.0% for Japanese characters ($p=0.007$), +12.8% for alphabetic stimuli ($p<0.001$) and as much as +28.3% for pseudo-fonts ($p<0.001$), which the participants found very difficult. Again, this effect did not vary with group.

In summary, those results confirm that, with respect to mirror-image invariance, participants behaved quite differently with written stimuli than with pictures of faces or objects. It is disproportionately difficult to decide whether two mirror-image samples of writing are or are not the same. The absence of any difference between the French and Japanese participants indicates that this lack of mirror invariance extends to unfamiliar scripts. To provide a more direct test of this hypothesis, we reanalyzed the critical interaction between group (French or Japanese) and stimulus category (alphabetic strings or Japanese characters), restricting the analysis only to the critical pairs where the same stimuli were presented in mirror image. There was no interaction on response times ($p=0.11$), but a marginally significant interaction on error rates ($p=0.051$). If anything, Japanese participants made more errors with alphabetic stimuli than with characters (24.8% versus 11.5%; $p=0.046$), while no such difference was found for French participants (7.5 versus 7.0%, n.s.). The overall result was that in expert readers, mirror generalization is difficult for all written scripts, familiar or unfamiliar.

Discussion

Taken together, the two behavioral tasks confirm that mirror-image invariance is present for pictures of faces, tools, or animals, but is absent for written stimuli in familiar or unfamiliar scripts. This difference between words and pictures is compatible with our hypothesis that symmetry generalization is partially inhibited or "unlearned" when learning to read. fMRI priming associated these effects with the left occipito-temporal VWFA: when pictures were presented, this region showed repetition priming for both identity and mirror primes, but when words were presented, only identity priming was found, not mirror priming.

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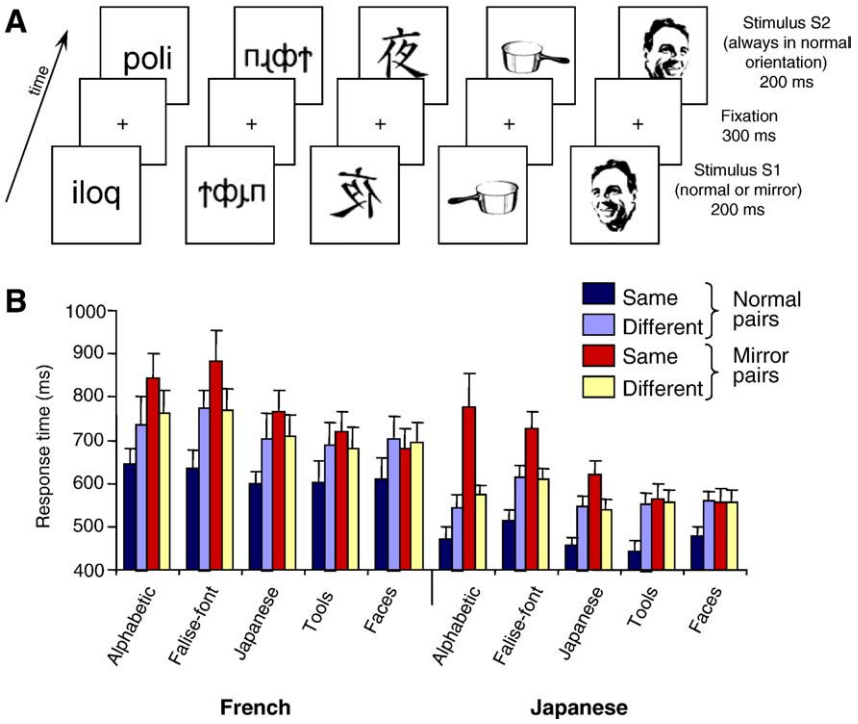

Fig. 7. Behavioral evidence that the unlearning of symmetry generalization extends to unfamiliar scripts. (A) participants decided whether two consecutive images belonging to 5 categories were "same" or "different." Crucially, they had to respond "same" to images that were identical up to a mirror-image transformation, as illustrated here. (B) responses times were fast (and accuracy high) for pictures of faces and tools, but worsened dramatically in the 'mirror-same' condition (red bar) when judging French words, Japanese characters, or strings in a pseudo-font. This effect did not differ across the two groups of participants, suggesting that even unfamiliar scripts cease to be invariantly recognized across a mirror transformation.

These findings were robust in two different cultural groups of Japanese and French readers. Cultural differences did exist—we observed a more similar response of the LOC to Kanji characters versus pictures in Japanese readers, than to alphabetic strings versus pictures in French readers, perhaps reflecting a remnant of pictographic or "holistic" processing in Kanji recognition. However, both groups exhibited the same profile of responses to words in the VWFA, including statistically indistinguishable contrasts for words versus pictures, left lateralization of the word responses, and priming patterns. These results are in keeping with a recent meta-analysis indicating a similar localization of the VWFA in readers of alphabetic and non-alphabetic scripts, to within a few millimetres (Bolger et al., 2005).

Past studies have shown extensive activations corresponding to mental rotation and effortful reading when expert readers attempt to read rotated or mirror-reversed words (Cohen et al., 2008; Goebel et al., 1998; Mochizuki-Kawai et al., 2006; Poldrack and Gabrieli, 2001). Such strategies, if present, would have confounded our goal of using priming to probe the spontaneous capacity of the visual system for invariant recognition of mirror images. We therefore attempted to minimize strategies by flashing the normal or reversed prime for 50 ms, only 100-ms prior to the target, thus making primes nearly invisible. Furthermore, participants were discouraged from actively processing them since their identity and orientation were task-irrelevant. Indeed, we found no significant activation difference between trials with normal primes and those with mirror-reversed primes, regardless of whether the stimulus was a picture or a word. It is thus unlikely that participants were engaged in detectable effortful strategies when the first stimulus was mirror reversed.

Under these conditions, our finding of mirror repetition suppression for pictures fits with previous fMRI studies which observed a high degree of generalization across mirror views of the same object in a long-term priming situation, particularly in the fusiform gyrus, at coordinates very close to the present ones (Eger et al., 2004; Vuilleumier et al., 2005). That this priming was due to an automatic encoding of object identity, invariant for object orientation, was supported by the finding that fusiform priming persisted even when the pictures were unattended (Vuilleumier et al., 2005).

To the best of our knowledge, mirror priming for words had not been studied under similar conditions probing invariant visual coding. We are only aware of two studies (Lin and Ryan, 2007; Ryan and Schnyer, 2007) of fMRI priming which, however, used an effortful task of mirror reading where the target word on trial *n* was presented previously in the list either in the same or in mirror orientation. These studies observed a reduced activation in various areas, including the fusiform gyrus at coordinates very close to the VWFA, even for mirror primes and especially in the mirror–mirror condition (when both prime and target words were in the unusual mirror format). These results suggest that, under effortful reading conditions, some of the perceptual resources provided by the VWFA can contribute to the reading of mirror words, perhaps through a slow serial identification of component letters (Cohen et al., 2008). However, they need not be seen as contradicting the present conclusion that, under fast and automatic priming conditions, the VWFA represents words only in their normal orientation and is unable to quickly generalize to the mirror image. The distinct status of words versus pictures with respect to mirror generalization has been also demonstrated by patients with orientation agnosia, often with parietal lobe lesions and intact occipito-temporal pathways (Davidoff and Warrington, 2001; Priftis et al., 2003; Turnbull and McCarthy, 1996; Vinckier et al., 2006). Such patients may fail to see any difference between mirrored pictures such as and . Remarkably, they are flawless in distinguishing mirrored letters or letter strings such as "quod" and "boup", thus offering a neuropsychological analogue of the present dissociation observed in normal subjects with fMRI.

Although we found the activation evoked by words and pictures to overlap in the left VWFA, the distinct patterns of mirror priming qualify the view that this region implements a domain-general function, for instance as a generic interface between visual form,

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sound and meaning (Devlin et al., 2006; Price and Devlin, 2003). As noted in our reply to Price and Devlin (Cohen and Dehaene, 2004), the issues of functional specialization and of regional selectivity must be carefully distinguished. Here, we observed functional specialization for words versus pictures within the same voxels, confirming that the visual computations needed for efficient word recognition differ markedly from those needed for efficient picture recognition (Cohen and Dehaene, 2004). Indeed, the capacity to distinguish otherwise identical mirror shapes such as p and q is just one of these specialized computations, which also include case-invariant letter recognition (knowing that A and a are the same letter), learning of specific letter shapes (e.g. Hebrew versus Roman script), and compiling statistics of letter co-occurrence (bigrams), all of which have now been related to the VWFA (Baker et al., 2007; Binder et al., 2006; Dehaene et al., 2001). These adaptations to reading observed in the adult VWFA fit with developmental studies indicating that VWFA is one of the main sites of enhanced activation during reading acquisition, and that its activation correlates with reading expertise (Shaywitz et al., 2007).

While functional specialization was obvious in our study, at the limited resolution afforded by a group analysis, we did not observe any visual response to words greater than to pictures (although our study did show that words activate a small left-lateralized subset of fusiform cortex compared to the broad bilateral activation evoked by pictures). Our findings are generally consistent with the hypothesis, derived from intracranial recordings, that the neural circuits for word and object recognition are not identical but are tightly intermingled in partially similar sectors of ventral occipito-temporal cortex (Allison et al., 1994). Indeed, scanning of individual subjects at a higher resolution has now revealed small patches of cortex with a specialization for visual word recognition (Baker et al., 2007), a finding that still needs to be confirmed by other groups.

The present study revealed an unexpected result in terms of cortical spatial organization. Although many occipito-temporal voxels show mirror priming for pictures, the effect peaks precisely at the same location as the VWFA. Thus, the cortical site essential for acquisition of expert visual word recognition in all cultures is precisely the site of greatest mirror-image invariance. This observation, together with the neuronal recycling view presented in the introduction, provides a speculative hypothesis for the high prevalence of mirror errors during reading acquisition. As children learn to read, visual word responses progressively focalize to the left occipito-temporal cortex (Maurer et al., 2006) The mirror-image generalization inherent in this region, if present early on in childhood or even infancy (Bornstein et al., 1978), would grant them an immediate ability to recognize letters regardless of their left–right orientation. This mirroring competence would have been useful in archaic scripts such hieroglyphs and ancient Greek, which could be written in both directions. However, it is now counterproductive given the presence of mirror or near-mirror graphemes in most present-day scripts (e.g. letters p and q; Kana characters さ [sa] and ち [ti]).

Behavioral and electrophysiological evidence concurs with the hypothesis that mirror generalization is a deeply entrenched evolutionary feature of the ventral visual system, rather than the result of a learned association of left and right views. Four-month-old babies already show behavioral evidence of recognizing the mirror image of a familiarized object (Bornstein et al., 1978). Adults also exhibit a poor memory for the orientation in which a picture was presented: even after training with only one orientation, they immediately generalize to the other (Fiser and Biederman, 2001; Tarr and Pinker, 1989). Mirror generalization is just as spontaneous in other animal species, suggesting an old evolutionary history, possibly with multiple convergent evolutions. After training with a single view of an object, pigeons and monkeys extend their responses to the mirror-image view (Beale et al., 1972; Mello, 1965, 1967; Noble, 1966). In macaque monkeys, inferotemporal neurons spontaneously exhibit highly correlated responses to novel mirror-image shapes (Baylis and Driver, 2001; Logothetis et al., 1995; Rollenhagen and Olson, 2000).

The monkey electrophysiological data help refute an alternative interpretation of the present data, which would attribute it to stimulus familiarity and learning. According to this view, inferotemporal cortex would progressively learn to associate the multiple views of objects, including their right and left profiles, which tend to be symmetrical views for many common objects (faces, cars, tools, etc.). However, words would never benefit from such mirror training, because they are almost always seen in one orientation. It thus seems possible that the VWFA site and neighboring cortex operate as an expertise site (Gauthier et al., 2000) capable of learning whichever features and invariance classes are useful for each category of object. Since we used only pictures of familiar objects and familiar scripts, we cannot directly refute this learning-based interpretation of the VWFA pattern in humans (although behaviorally, we did find that mirror generalization remained difficult for unfamiliar scripts; and, conversely, Tarr and Pinker (1989) found immediate mirror generalization for unfamiliar object shapes). Crucially, the familiarity interpretation was tested directly by Logothetis and Pauls (1995) in monkeys, in whom it is much easier to tightly control for past visual input. Logothetis and Pauls trained monkeys to recognize paperclip-like objects that were wholly unfamiliar and whose twisted 3-D shape made it difficult to anticipate how the object would look like from a different angle. During training, a given object was always presented at a fixed orientation, plus or minus a few degrees. Under these conditions, even after weeks of training, monkeys failed to recognize the same object when rotated by more than 40 degrees, thus demonstrating view-specific learning. However, the monkeys immediately generalized, both in their behavior and in their neural responses, when presented with the 180-degree view which they had never seen earlier, but which corresponded to the (near) mirror image of the learned wireframe object.

In summary, learning alone does not seem to explain mirror generalization. If anything, the monkey results would suggest that the acquisition of reading, if comparable to the recognition of random twisted shapes, should immediately generalize across a mirror transformation (as indeed seen in children's initial errors). That it no longer does in human adults, as observed here, suggests that, in the course of learning to read, a special interpretation must be given to letters as two-dimensional shapes, thus blocking mirror generalization (Dehaene, 2009; Lachmann and van Leeuwen, 2007).

Conclusion

Ever since Orton (1937), mirror errors have been erroneously associated with dyslexia. Our results, together with others (Baylis and Driver, 2001; Eger et al., 2004; Logothetis and Pauls, 1995; Rollenhagen and Olson, 2000; Vuilleumier et al., 2005), suggest that mirror generalization is a normal property of the primate ventral visual system. Only the excessive prolongation of letter mirroring, beyond the age of 8 or 10, may indicate a reading deficit (Lachmann and Geyer, 2003; Terepocki et al., 2002). The general consensus is that in most children, mirror confusions are not a cause of dyslexia, but a mere consequence of reduced expertise with reading. Indeed mirror errors have also been reported in illiterates (Kolinsky et al., 1987) and in readers of a curvilinear script such as Tamil that does not contain minimal mirror pairs (Danziger and Pederson, 1998). Excessive mirror generalization seems to be the primary cause of the reading deficit only in very rare dyslexia cases who exhibit severe visual inversions and spatial confusions extending to non-linguistic domains such as grasping and picture copying (McCloskey and Rapp, 2000). In the future, the present fMRI priming method, extended to simpler shapes such as individual letters, could provide a simple method to systematically investigate the neural mechanisms of mirror generalization in normal and dyslexic children.

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Method

Participants

We tested a total of 26 volunteers, 13 French (seven females; mean age = 23 years) and 13 Japanese (three females; mean age = 23 years). All were right-handed native speakers of their respective languages. All gave written informed consent, and the study was approved by the appropriate national and regional ethical committees.

Behavioral same-different task

The stimuli for the behavioral same-different task, performed after fMRI, were 14 French words, 14 Japanese characters, 14 pictures of tools, 14 pictures of faces, 14 unknown script stimuli, and their corresponding left–right reversed mirror images. On each trial, two stimuli from the same category were successively presented at the fixation (200 ms presentation of each image, 300 ms inter-stimulus interval with fixation cross). The participant's task was to decide whether the two stimuli depicted the same object, possibly in mirror-form. Thus, the participants had to respond "same" both to physically identical stimuli (1/4 of trials) and to mirror images (1/4 of trials). They had to respond "different" whenever the stimuli were unrelated, whether they were in the same orientation (e.g. two normally oriented words; two faces in the same orientation; 1/4 of trials), or whether they were in different orientations (e.g. one word followed by a mirror image of a word). The first stimulus, drawn from one of the five categories, was always in standard orientation, and the second stimulus was defined by a 2×2 factorial design with factors of identity (same or different object) and orientation (same or different left–right orientation). This design defined a list of $14\times5\times2\times2=280$ trials, which were run once in random order.

All stimuli were presented in black-and-white, and occupied similar locations on screen (approximate width and height : $2°\times2°$ for Japanese characters and faces; $1.5–4°\times1.5–4°$ for tools, depending on their compactness and vertical or horizontal main axis; $0.8°\times2.3°$ for French words). Several precautions were taken to ensure that the task required view-point invariant recognition and could not be performed using simple short-cuts. All stimuli were selected so that they were clearly asymmetrical and maximally distinct from their mirror images. In particular, the faces were not front views, but were viewed and lit from an angle intermediate between profile and front view. Likewise, the Japanese characters were presented in a curvy font ("HG Sei-Kaisho-Tai") so that they did not contain any vertical or horizontal bars that would be identical after left–right inversion. The French words had an even number of non-repeated letters, so that no letter was repeated at the same location in a word and its mirror-image. Finally, the French words were made of lower-case letters b, d, i, l, m, n, o, p, q, u, v, x, and were presented in an 20-point Arial font, slightly modified so that the above letters were exactly symmetrical on screen. As a result, even in mirror-image the words appeared as alphabetical strings made of essentially normal letters (non-French readers could not easily tell that they were not French words). A similar manipulation was not possible with Japanese characters, but we selected characters made of strokes that did not seem artificial once reversed (non-Japanese readers could not easily tell that these were not Japanese characters). French and Japanese words were matched on frequency (mean Log_{10} frequency = 1.14 versus 0.90, n.s.).

fMRI experiment: size judgment task

On different fMRI runs, the stimuli were either pictures or words written in the participant's language. The word stimuli were 116 common nouns, subdivided into 58 words referring to things larger than a computer screen (e.g. elephant, truck, goat), and 58 words referring to things smaller than a computer screen (e.g. mouse, pen, finger). French words were matched on frequency, letter and phonemic length, and number of orthographic neighbors. Japanese words were all written in a single Kanji (logographic) character and matched on frequency and syllabic length. The pictures were 116 line drawings of familiar objects, fruits, or animals, again subdivided into 56 small and 56 large things, all presented at the same screen size. All stimuli were presented in black-and-white, and occupied similar locations on screen (approximate width and height : $3.2°\times3.2°$ for Japanese characters; $2–4.5°\times2–4.5°$ for pictures, depending on their compactness and vertical or horizontal main axis; and $0.8°\times1.6–4°$ for French words, depending on character width and word length [4–7 letters]).

Each participant received three fMRI runs with pictures and three runs with words, in randomized order. On each trial, the participants saw a target word or drawing preceded by a brief presentation of the same or different image (50 ms prime presentation, 50 ms inter-stimulus interval with fixation cross, 500 ms target presentation, and 1400 ms post-trial fixation, for a total of 2 s per trials; see Fig. 2). The target was always in normal orientation (for pictures, one orientation was selected as the 'normal' target orientation, e.g. all target images of animals had their head pointing to the right). The prime, however, appeared in the normal or mirrored orientation on half the trials. The participants were told to neglect the first, barely visible stimulus and to judge the real-world size of the target. All words were presented in lower-case, in the same fonts as the above-described behavioral experiment (although for French stimuli all 26 letters of the alphabet could be included).

Stimuli were presented in six fMRI runs, each comprising a 2-s rest with fixation, 3 training trials, 200 experimental trials, and 7.8-s rest with fixation, for a total of 415.8 s or 297 TRs of 1.4 s each. Each run included 40 trials in each of the four trial types defined by the 2×2 combinations of prime orientation (normal or mirror) and stimulus repetition (same or different). On an additional 40 trials, the primes and targets were omitted, thus providing an event-related baseline condition relative to which we could compute activation in the other four trial types.

fMRI acquisition and analysis

The fMRI data was acquired on two 3 Tesla scanners in France (Bruker 3T, Service Hospitalier Frédéric Joliot, Orsay) and in Japan (Siemens Allegra 3T, Ogawa Laboratories for Brain Function Research, Tokyo). Identical sequences were used for fMRI: gradient echo-echo planar images with 25 contiguous axial slices, 4 mm thickness with 1 mm gap, TR = 1,400 ms, TE = 30 ms, flip angle = 80°, field-of-view = 256×256 mm2, 64×64 matrix.

A two-level analysis was implemented in SPM5. First, functional images were corrected for head motion, resampled every 3 mm using sinc interpolation, normalized to the standard MNI brain space, and spatially smoothed with an isotropic Gaussian filter (5 mm full width at half maximum). Each individual participant's data was then modelled, within each fMRI run, by eight regressors obtained by convolution of the four experimental conditions with the canonical SPM hemodynamic response function and its time derivative. The model included high-pass filtering (cutoff 128 s). Then a second-level group ANOVA was performed with factors of participants and group (French or Japanese), and within-subject factors of stimulus category (words or pictures), repetition (same or different prime) and orientation of the first stimulus (normal or mirror). Unless otherwise stated, we used a voxelwise threshold of $p<0.001$ uncorrected, and a cluster-level threshold of $p<0.05$ corrected for multiple comparisons across the brain volume.

For testing inter-hemispheric differences in neural activation, we further created a left–right flipped image for each contrast for each participant, by applying to each original contrast image a spatial

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transformation specific to each participant and appropriate to align his flipped anatomical image to the MNI template. For each contrast, we then computed a hemispheric difference image for each participant by subtracting the flipped contrast images from the original contrast images. These difference images were submitted to the same ANOVA model to estimate the hemispheric differences for each effect of interest. For interpretation, those images were systematically masked by the corresponding image of activation relative to rest (for instance, the word>picture hemispheric difference analysis was masked by words>rest).

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