

Learning through Hand- or Typewriting Influences Visual Recognition of New Graphic Shapes: Behavioral and Functional Imaging Evidence

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Abstract

■ Fast and accurate visual recognition of single characters is crucial for efficient reading. We explored the possible contribution of writing memory to character recognition processes. We evaluated the ability of adults to discriminate new characters from their mirror images after being taught how to produce the characters either by traditional pen-and-paper writing or with a computer keyboard. After training, we found stronger and longer lasting (several weeks) facilitation in recognizing the orientation of characters that had been written by hand compared to those typed. Functional magnetic resonance im-

aging recordings indicated that the response mode during learning is associated with distinct pathways during recognition of graphic shapes. Greater activity related to handwriting learning and normal letter identification was observed in several brain regions known to be involved in the execution, imagery, and observation of actions, in particular, the left Broca's area and bilateral inferior parietal lobules. Taken together, these results provide strong arguments in favor of the view that the specific movements memorized when learning how to write participate in the visual recognition of graphic shapes and letters. ■

INTRODUCTION

Several decades ago, the seminal work of Held and Hein (1963) with “motorically” deprived kittens experimentally proved that motor knowledge acquired through active exploration is important in processing spatial information from vision (see also Paillard, 1991). This view is now widely accepted as can be seen from more recent reports of activations in different parts of the cortical motor system during perception (Mecklinger, Gruenewald, Besson, Magnié, & von Cramon, 2002; Chao & Martin, 2000), mental rotation (Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Richter et al., 2000), and judgment of spatio-temporal features of objects (Schubotz & von Cramon, 2002). In addition, some studies have directly assessed the role of motor learning in the reorganization of the neural networks involved in object processing (Weisberg, van Turenout, & Martin, 2007; Pollmann & Maertens, 2005; Wolfensteller, Schubotz, & von Cramon, 2004) with results showing that after learning, visual presentation of the stimuli elicits activations in brain regions involved in the programming of the response specifically associated to the stimuli during learning.

Visual processing of graphic shapes is a very fine spatial skill because graphic shapes have precisely defined configurations and orientations that are crucial features for quick recognition, hence, for efficient reading (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). Results of several studies strongly suggest that motor knowledge acquired through learning how to write contributes to the visual recognition of letters. Firstly, neuroimaging and brain-damaged patient studies showed that regions of the cortical motor system participate in recognition (Longcamp, Anton, Roth, & Velay, 2003, 2005; Kato et al., 1999; Anderson, Damasio, & Damasio, 1990) and visual imagery of characters (Raij, 1999; Kosslyn, Thompson, & Alpert, 1997). Secondly behavioral studies have indicated that handwriting memory facilitates recognition (Longcamp, Boucard, Gilhodes, & Velay, 2006; Longcamp, Zerbato-Poudou, & Velay, 2005; Flores d'Arcais, 1994; Hulme, 1979) and mental imagery of characters (Kosslyn, Cave, Provost, & Von Gierke, 1988).

The issue of the contribution of handwriting movements to visual perception of characters is of primary importance when one considers the striking change arising in our writing habits with the extended use of computer keyboards, and the progressive disappearance of traditional handwriting from our everyday lives. Computers are now being increasingly used at school, even by very young children in kindergarten. If children happen to learn how to write with a keyboard before they

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master handwriting, this may affect the way they perceive written language. Longcamp et al. previously investigated this handwriting/typing distinction in two behavioral studies, one in prereaders (Longcamp et al., 2005) and one in adults (Longcamp et al., 2006). Both studies confirmed that letters or characters learned through typing were subsequently recognized less accurately than letters or characters written by hand. In addition, the writing knowledge associated with a character influenced the recognition of its orientation. Orientation is a critical parameter when readers have to discriminate between mirror letters (“d” and “b” for instance). Interestingly, confusions between letters and their mirror images are errors most frequently made by young children and “poor readers” (Terepocki, Kruk, & Willows, 2002; Adams, 1990). The difference between a letter and its mirror image is not immediately obvious visually, whereas writing a letter and its mirror image requires two very different movements. The motor program drawn up while learning a letter does not match that associated with its mirror image. For that reason, handwriting memory may help to prevent confusion between a letter and its mirror image, which is important for reading accuracy.

Typing is a complex form of spatial learning in which the beginner has to build a “keypress schema” transforming the visual form of each character into the position of a given key in keyboard centered coordinates, and specify the movement required to reach this location (Logan, 1999; Gentner, 1983). Therefore, learning how to type also creates an association between a character and a pointing movement. However, because the trajectory of the finger to a given key largely depends on its position before movement, the relationship cannot be very specific. Moreover, there is nothing in this pointing movement that informs about the orientation of the characters. The visuomotor association involved in typewriting should therefore have little contribution to its visual recognition.

Hence, arguments in favor of a motor contribution in visual recognition of alphabetic characters, although sparse, are convincing. However, to date, the neural basis of this motor contribution has never been investigated. It was the aim of the present study to further explore the contribution of acquired writing knowledge to visual recognition of characters by linking behavior with brain function and (re)organization. For that purpose, we taught adult subjects how to produce sets of unknown characters either by traditional pen-and-paper writing or with a computer keyboard. Following learning, we tested their ability to explicitly recognize the orientation of the newly learned characters and measured their brain activity using functional magnetic resonance imaging (fMRI). We also used normal overtrained letters as a third category of stimuli in the recognition tests. By identifying the activations common to handwritten and typewritten new characters with respect to overtrained letters, we were able to determine

which brain areas were involved in processing newly learned characters. In addition, differences in recognition performance between shapes acquired by handwriting and shapes acquired by typewriting should be associated with different patterns of brain activity. This was tested by analyzing the activations specific to each learning modality relative to the other two conditions. Finally, we predicted that the specific sensorimotor coding acquired through handwriting would be reactivated during visual recognition. Handwritten characters and letters had in common the associated handwriting knowledge despite otherwise very different properties (phonological or linguistic valence with more or less complex configuration). By identifying the activations common to handwritten characters and letters relative to typewritten characters, we were able to determine which brain areas sustain the possible reactivation of handwriting memory during letter recognition.

METHODS

Participants

Twelve subjects (6 men, 6 women, mean age \pm SD, 26 \pm 3) took part in the experiment. All subjects were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), and consistently used their right hand to write. Participants were free from neurological disease with no history of dyslexia or other language disability. They all gave their informed consent and the study was approved by the local ethics committee.

Procedure

The subjects underwent three training sessions (one per week) where they learned how to write new characters either by handwriting or by typewriting. These training sessions were followed by four behavioral recognition tests for new characters and normal letters: that were run immediately, 1, 3, and 5 weeks following training. An additional recognition test was conducted while fMRI was recorded 1 week following training. Finally, a sensorimotor test for writing knowledge was conducted 6 weeks after training.

Training

Two distinct sets of 10 unknown characters modified from the Bengali and Gujarati alphabets were learned (Figure 1). Subjects were isolated in a quiet room for one 1-hr session per week for 3 weeks. Sequential training of both writing modalities occurred in the same session in an order counterbalanced between subjects and between sessions. The association between a set of characters and a learning modality was counterbalanced between subjects. The visual presentation of the characters was rigorously identical in both learning modalities. In

Set 1:	ल	ळ	ज़	च	छ	ह	ड	ढ	ट	ड
Set 2:	झ	ण	ड	त	र	क	ख	ग	ज	झ
Letters:	a	e	f	g	h	k	r	s	z	y

Figure 1. The two sets of 10 characters used for learning and the 10 letters used as control. The same characters and letters were used in the recognition tests.

both cases, a series of 3-cm-high characters was displayed for 4 sec each on a computer monitor. Overall, each of the 10 characters was written (or typed) 20 times a session, and the characters were presented in random order. For each set, the 200 presentations were divided into four blocks of 50 with 5 min rest in-between. No constraints were imposed on the writing (or typing) speed. A sound signaled the beginning of the trials: If the character was not completed when the following one was displayed, subjects had to stop writing and look at the monitor for the following character.

In the typing modality, subjects were required to find the appropriate character on a predesigned keyboard where all the 10 new characters had been placed on the uppermost row, and to type it with their right hand. At each trial, the time between the onset of the visual display and the keypress was measured. No instruction was given relative to the finger to be used, and most subjects spontaneously used their index fingers to type the characters. In the handwriting modality, subjects were required to write the characters on a paper sheet, which was fixed on a digitizing tablet (Wacom, Intuos 2). The position of the pen tip in bidimensional space was recorded over the whole session with a sampling frequency of 100 Hz. Subjects were free to use the most comfortable stroke direction and order. Data from one of the subjects had to be discarded because of a measurement failure.

Sensorimotor Tests

We evaluated the long-term sensorimotor memory for both handwriting and typewriting 6 weeks after the last training session, when all the behavioral recognition tests had been completed. In the typing modality, subjects were given a keyboard from which the previous characters had been erased. They were then presented sequentially with the 10 characters in random order and had to hit a key according to the remembered location. The responses were scored according to the distance between the responded key and the correct key (0 if no error, 1 if distance of one key, etc.) and the sample obtained was compared to the theoretical score that would have been obtained for responses at chance. In the handwriting modality, subjects were presented briefly (100 msec) and sequentially with the 10 previously learned characters and had to write each of them at normal speed on the digitizing tablet. The writing speed

was measured and compared to the speeds produced during the last training session and at the beginning of learning.

Behavioral Recognition Tests

A first test was run immediately following the last learning session (W0) and repeated three times: 1 week (W1), 3 weeks (W3), and 5 weeks (W5) later. During the tests, subjects were seated at a distance of 57 cm from the computer monitor with their head in a chin and forehead restraint and their eyes fixed on the center of the screen. Stimuli were centrally displayed for 100 msec and subtended a vertical visual angle of 3°. Subjects held a cylinder in each hand on top of which a highly sensitive button could be pressed with either the left or the right thumb in order to give the response. In both learning modalities, the response mode used in the recognition test was therefore different from the movements performed during training or the sensorimotor test.

The test consisted of a mirror-normal judgment task. First, as a control condition, we carried out the task with familiar Latin letters as stimuli. The letters were presented either in normal or in mirror-reversed form and the subjects were instructed to respond as quickly and precisely as possible whether the letter was normally oriented or mirror-reversed. We then ran the same mirror-normal judgment task with the previously learned characters. Handwritten and typed characters were mixed in the same block and the correspondence between the responding hand and the response (normal vs. mirror) was counterbalanced between subjects.

Responses were recorded on a stimulus-control computer. If no response was made within 2 sec, the trial was coded as an error. Overall, 40 characters (20 normal and 20 mirrored) were presented three times each in random order for a total of 120 trials (60 in each modality). We first measured and then subsequently analyzed reaction times (RT) and correct response rates using a two-way within-subject analysis of variance (ANOVA), with the factors “learning modality” (handwritten and typed) and “time of testing” (W0, W1, W3, and W5). RTs with values exceeding mean \pm 2 standard deviation of a given condition were discarded from the analysis and considered as errors. In addition, arcsine transformation of the correct response rates was performed in order to take into account the fact that the rates were close to ceiling, and thus, not normally distributed. In both ANOVAs, the effects were adjusted for nonsphericity using the Greenhouse–Geisser (1959) adjustment factor. Only effects with $p \leq .05$ are reported.

fMRI Recognition Test

fMRI measurements were carried out one week following the end of training. We used a block design with

alternated blocks of handwritten characters, printed characters and letters, with rest periods of variable duration (12, 13.5 or 15 sec, to allow distributed sampling of the hemodynamic response; Veltman, Mechelli, Friston, & Price, 2002).

In each task block, characters or letters were sequentially presented for 1 sec and separated by a 0.5-sec fixation. Zero, one, or two of the presented stimuli were correctly oriented and the rest were mirror-oriented. Subjects were required to mentally note the number of correctly oriented stimuli and give their response with the left hand (thumb for 0, index finger for 1, and middle finger for 2) at the end of the block following a go signal. The response was recorded. The delay between the end of the block and the go signal, and the delay between the go signal and the following block were varied randomly from 3 to 6 sec. This procedure introduced time-incertitude for preparation of the response, and allowed to separate the activations related to the processing of the characters or letters from the activations related to the manual response preparation and execution.

fMRI Acquisition and Analysis

Brain activity was measured on a 3-T MEDSPEC 30/80 AVANCE whole-body imager (Bruker, Ettlingen, Germany), equipped with a circular polarized head coil. For each participant, we acquired a high-resolution structural T1-weighted image (inversion-recovery sequence, $1 \times 0.75 \times 1.22$ mm) parallel to the AC-PC plane, covering the whole brain. For functional imaging, we used a T2*-weighted echo-planar sequence, covering the whole brain with 36 interleaved 3-mm-thick/0.5 mm-gap axial slices (repetition time = 3000 msec, echo time = 35 msec, flip angle = 80° , field of view = 19.2×19.2 cm, 64×64 matrix of 3×3 mm voxels). We acquired 167 functional volumes per session during four sessions, leading to a total of 668 volumes per subject.

Data were processed using SPM2 software (www.fil.ion.ucl.ac.uk/spm/), according to the general linear model (Friston et al., 1995). The first four functional volumes of each session were removed to eliminate nonequilibrium effects of magnetization. The remaining 163 images were corrected for differences in slice acquisition time and the first and last two volumes were discarded to prevent invalid temporal interpolation. Images were then corrected for head movement by realignment with the first image using rigid body transformations, summarized into a mean functional image, normalized by matching to the standardized MNI EPI-template, then spatially smoothed with an isotropic Gaussian filter (9-mm full width at half maximum).

The experimental conditions were modeled as box-car functions convolved with the hemodynamic response function. The manual responses were modeled as separate events. At the first level, data were summarized

into three linear contrasts per subject, that is, contrasts between each of the three conditions and the resting baseline. Group analyses were performed with a random effects model (one-way within-subject ANOVA, with non-sphericity correction and adjustment for correlated repeated measures). The aim of the fMRI data analysis was to differentiate the characters according to the type of associated motor activity. We therefore used five conjunction analyses between *t*-contrasts: (1) “handwritten characters versus letters” and “typed characters versus letters” for new characters compared to overlearned letters; (2) “handwritten versus typed” and “handwritten versus letters” for previously written new characters compared to the other two conditions; (3) “typed versus handwritten” and “typed versus letters” for previously typed new characters compared to the other two conditions; (4) “handwritten versus typed characters” and “letters versus typed characters” for stimuli associated with handwriting movements in memory; (5) “typed versus handwritten characters” and “letters versus handwritten” for stimuli not associated in memory with handwriting but with typing movements. The effects reported have a height threshold of $p < .001$, uncorrected for multiple comparisons and an extent threshold of 10 voxels. It should be noted that the reported activations survive a threshold of $p < .05$, corrected for multiple comparisons (false discovery rate), when the original *t* contrasts are considered individually. In addition, the original *t* values were transformed into *Z* scores via the corresponding *p* values, in order to provide a statistical indicator independent of the degrees of freedom. Significant clusters were localized using a standard stereotaxic anatomical brain atlas (Talairach & Tournoux, 1988).

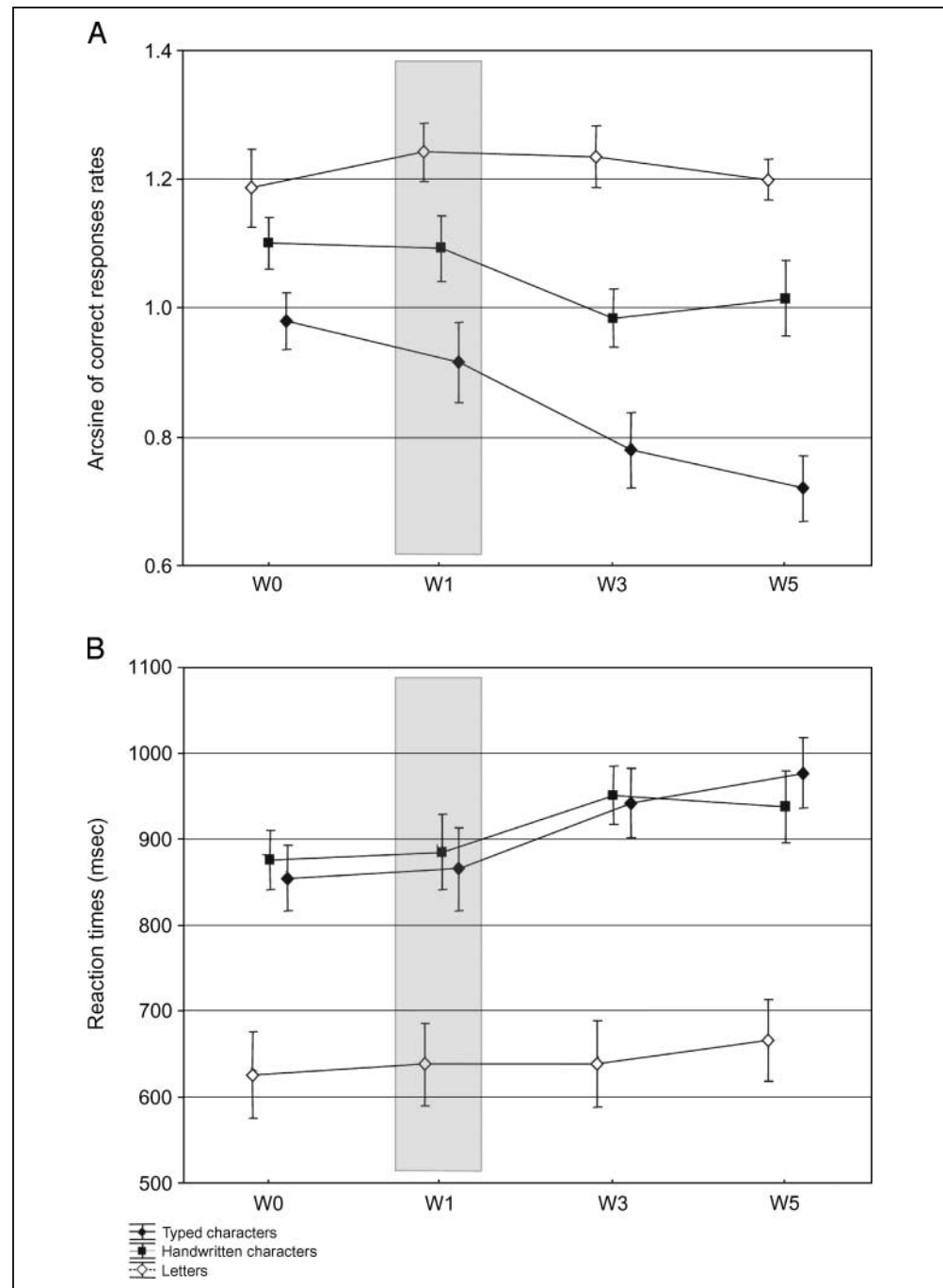
RESULTS

In the following sections, the characters learned through handwriting will be referred to as “handwritten characters” and the characters learned through typing as “typed characters.”

Behavioral Recognition Tests

Behavioral results are reported in Figure 2. Overall, correct response rates (Figure 2A) indicated a good level of performance at the end of training (around 85% correct for the new characters, and 90% correct for the letters). Note that a score below 38 correct responses out of 60 trials (i.e., 63.3%), corresponded to chance level (χ^2 test with $p \leq .05$). Results of the ANOVA on the arcsine transform of response accuracies showed that correct response rates were higher when the characters had been written by hand than typewritten [main effect of modality, $F(1, 11) = 25.6$, $p = .001$]. Moreover, response accuracy decreased with time [main effect of time of testing, $F(2.2, 24.4) = 13.9$, $p \leq .001$] with a

Figure 2. Behavioral results. (A) Arcsine transform of the correct response rates as a function of time of testing (for relationship with the correct response ratios: 100% correct responses corresponds to a value of 1.571, 80% correct to a value of 0.927, and 60% correct to a value of 0.644). (B) Reaction times as a function of time of testing. In both graphs the error bars represent the standard error of means. Abbreviations: W0 = test at Week 0 (immediately after the last training session); W1 = test at Week 1; W3 = test at Week 3; and W5 = test at Week 5, all relative to the last training session. The results for Letters are represented but were not included in the statistical analysis.



larger decrease for typed than handwritten characters, as shown in Figure 2A [Modality \times Time of testing interaction, $F(2.8, 30.8) = 4.1, p = .02$]. Post hoc comparisons between the two modalities at each time level using Scheffé's test revealed no significant difference at W0 ($p = .18$) and significant differences with subsequent tests ($p = .008$ at W1; $p \leq .001$ at W3 and W5). In order to check whether the response accuracies decreased similarly with time, we used Scheffé's test to compare the recognition performance between each possible pair of time levels for each modality. For the handwritten characters, the performance was stable over

the 5 weeks with no significant differences for any of the comparisons, whereas the performance decreased with time for the typed characters (significant difference between W0 and W3, $p = .002$; W0 and W5, $p \leq .001$; W1 and W5, $p = .003$). Five weeks following the end of training, response accuracy for typed characters approached chance level (6 subjects out of 12 responded below chance level for typed characters, whereas only one subject responded below chance level for handwritten characters). To summarize, analysis of the correct response rates indicated that handwritten characters were overall better discriminated from their mirror images

than typed characters, and were better remembered over the course of time.

RTs (Figure 2B) increased with time [main effect of time of testing, $F(2.6, 28.2) = 6.9, p = .001$]. Moreover, a significant interaction between time of testing and learning modality [$F(1, 11) = 8.4, p = .01$] indicates that the effect of learning modality was not the same across the four tests. Figure 2B shows that at W5, RT increased more for handwritten than for printed characters. However, post hoc comparisons failed to reveal a significant difference between the two modalities in any of the tests. Finally, the task was performed faster for letters (RTs around 650 msec) than for new characters with a stable performance across the four tests.

It should be noted that at W1, the time where the fMRI measurement was conducted, the response accuracies for handwritten and typed characters were significantly different whereas the response times were not.

Writing Performance (Training and Sensorimotor Tests)

Typed Characters

The typing speed increased significantly between the first and the last training sessions [average response time was 1622 msec at Session 1 and 1400 msec at Session 3; $t(11) = 4.65, p = .001$].

It was not possible to directly compare the typing responses obtained during the sensorimotor test (6 weeks after the last training session) with the typing responses in the course of training given the discrepancy between the tasks. Subjects were scored according to the distance between the responded key and the correct key (0 if no error, 1 if distance of one key, etc.). The sample obtained (mean = 1.57) was compared to the theoretical score for responses at chance (3.30). This analysis showed that the subjects could remember the position of the characters on the keyboard significantly better than chance [comparison between a single sample and a norm; $t(11) = -2.63, p = .03$].

Handwritten Characters

The handwriting speeds at the beginning and the end of training and then 6 weeks following the last training session were subjected to a repeated measures ANOVA.

This analysis yielded a significant main effect of time [average speed was 2.95 cm/sec at Session 1, 3.60 cm/sec at Session 3, and 3.33 cm/sec 6 weeks following the end of training; $F(2, 20) = 4.83, p = .02$]. Post hoc comparisons showed that the speed at the end of training differed significantly from that at the beginning ($p = .02$, Scheffé's test), but did not differ significantly from the speed measured 6 weeks following the end of training. In addition, visual inspection of the character shapes produced showed an improvement in spatial accuracy over time (see Figure 3).

Relationship between Writing Performance during Training and Behavioral Recognition Tests

In order to determine whether the orientation judgment for characters was related to writing speed reached at the end of learning, we averaged the writing speed for the last 10 repetitions of each character in the last training session of both training modalities and correlated these measures with the recognition performances at the four time levels (Table 1). The correlation coefficients were transformed to r' values according to Fisher's method, to compensate for violations of the normal distribution. No significant correlations were observed for typed characters. For handwritten characters, a significant correlation was evident 5 weeks following the end of training ($r' = .87; z = 2.46; p = .007$). Thus, the faster the subjects wrote at the end of learning, the better the handwritten characters were remembered at Week 5.

fMRI Results

Recognition performance recorded during the fMRI session was consistent with recognition performance observed outside the scanner. The level of performance (number of correctly responded blocks out of 20) was significantly higher for handwritten than for typed characters (Wilcoxon's rank-order test, $z = 2.45; p \leq .008$). Responses to blocks of letters approached the maximum accuracy for all subjects.

Figure 4A and Table 2 show the results of the conjunction between contrasts "handwritten versus letters" and "typed versus letters" aimed at investigating the areas with strongest involvement when subjects processed the orientation of new and more complex characters,

Figure 3. Evolution of the spatial accuracy for the handwritten characters over the course of learning for two characters written by two different subjects.

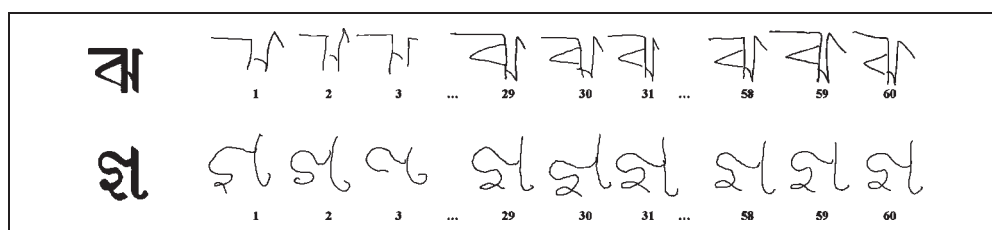


Table 1. Values of the Correlation Coefficients Calculated between the Correct Response Rates at the Different Time Delays and the Writing Speed Achieved at the End of Training for Both Learning Modalities

	<i>Time of Testing</i>			
	<i>Week 0</i>	<i>Week 1</i>	<i>Week 3</i>	<i>Week 5</i>
Handwritten	-.12	.24	.38	.87*
Typed	-.40	-.26	.09	-.17

* $p < .01$.

irrespective of the learning modality. This analysis revealed a bilateral, right-dominant parietofrontal network, composed of a number of regions. Activations included bilateral dorsolateral and rostral prefrontal cortices (BA 9 and 10), bilateral ventrolateral prefrontal cortices (BA 45/47), bilateral superior parietal lobules (BA 7), left cerebellum, presupplementary motor area (medial BA 6), as well as several occipital and temporal areas.

In a second step, we checked whether certain activations were specific to each learning modality. We found several clusters of activation when handwritten characters were compared to letters and typed characters (conjunction between contrasts “handwritten vs. typed” and “handwritten vs. letters”; Figure 4B), bilaterally in the precuneus (BA 19), the superior parietal lobule (BA 7), and the postcentral gyrus (BA 3), as well as in the middle temporal gyrus (BA 37) with left side predominance, and in the cerebellum. When the opposite comparison was performed (i.e., areas more activated by typed characters, conjunction between “typed vs. handwritten” and “typed vs. letters”; Figure 4C and Table 2), a single activation was evident in the right supramarginal gyrus (BA 40).

Activations commonly associated with handwriting knowledge and letter recognition were assessed with the conjunction between contrasts “handwritten versus typed” and “letters versus typed” (Figure 4D and Table 2), assuming that both letters and handwritten characters were associated with handwriting movements in memory. This analysis revealed a restricted set of regions, mostly left-lateralized, including bilateral inferior parietal lobules (BA 40), the left Broca’s area (BA 44), the left dorsal premotor cortex (BA 6), the left postcentral gyrus (BA 7), the medial posterior regions of both hemispheres (BA 5 and 31), and the pons.

Assuming that the subjects had experience with typing on normal keyboards in their everyday life, we used the conjunction between contrasts “typed versus handwritten” and “letters versus handwritten” to check whether letters and typed characters processing had some neural substrates in common. This conjunction revealed no significant activation.

Finally, the relationship between fMRI results and behavior was explored through correlation analyses. Differ-

ences in blood oxygenation level dependent activity were correlated with differences in the recognition performance (number of correct blocks) in the fMRI test. Only brain regions that were activated for the conjunction analysis of “handwritten versus typed” and “letters versus typed”—areas that show common activity for handwriting knowledge and letter recognition—were included (Figure 4D). A significant positive correlation between activity in Broca’s area (BA 44) and the recognition performance was observed for the difference of characters learned by handwriting versus letters (Figure 5; $r = .86$; $p \leq .03$, corrected for multiple comparisons). No significant correlation was observed in any other area or for any other difference (handwritten characters vs. typed characters or letters vs. typed characters).

DISCUSSION

Behavioral Findings

We found a more accurate recognition of new characters that had been written by hand than those that had been typed. Because the characters were seen for exactly the same duration in both learning methods, it was not the familiarity with the character that determined the recognition performance, but the type of motor activity associated during training. This result is in agreement with previous behavioral investigations showing the greater efficiency of handwriting learning, both in children (Longcamp et al., 2005; Naka, 1998; Hulme, 1979) and in adults (Longcamp et al., 2006; Naka & Naoi, 1995).

When learning how to write, some features of the movement such as the number and direction of strokes are determined for a given character according to individual preferences (Meulenbroek & Thomassen, 1991; Goodnow & Levine, 1973), and are subsequently memorized into a motor program (allograph; van Galen, 1991). Assuming that this motor program is reactivated when the character is perceived (Longcamp et al., 2003, 2005; Kato et al., 1999; Flores d’Arcais, 1994) or visually imagined (Kosslyn et al., 1988, 1997), it can be stated that more efficient mirror-normal discrimination of the characters learned by handwriting is mediated by the detection of a match or a mismatch between the perceived shape and the memorized motor program. This interpretation fits well with reports of reading improvements in alexic patients who simultaneously trace the outline of the letters with their fingers (Bartolomeo, Bachoud-Lévi, Chokron, & Degos, 2002; Seki, Yajima, & Sugishita, 1995).

Although the benefit of handwriting learning was general, the differential evolution of the characters in memory over time depending on the learning modality further indicates a greater effect of the learning modality with increasing delay between training and test. The specific correlation between the recognition performance for handwritten characters and the writing speed

Figure 4. fMRI results for four conjunction analyses. Left: Glass brains (the statistical parametric maps are displayed on the normalized space as maximum intensity projections, viewed in transparency through the brain viewed from the side and the top). Right: Brain activations overlaid on slices of the MNI brain. Left side of the image is the left side of the brain. The main activation clusters are labeled and the error bars represent the Z-scores. (A) Conjunction between contrasts “handwritten characters versus letters” and “typed characters versus letters” shows the regions more strongly activated when the subjects were processing the new characters compared to overlearned letters. (B) Conjunction between contrasts “handwritten versus typed” and “handwritten versus letters” shows the regions more strongly activated for new characters that subjects had previously written compared to the other two conditions. (C) Conjunction between contrasts “typed versus handwritten characters” and “typed versus letters” shows the regions more strongly activated by the task when the stimuli were associated with typing movements in memory. The contrast estimates are the average of the weighted sum of parameter estimates of the statistical model, with reference to the whole brain mean signal for each experimental condition relative to rest at the local maximum of the cluster. The error bars are the standard error of the contrast estimates. (D) A conjunction between *t*-contrasts “handwritten versus typed characters” and “letters versus typed characters” shows the regions more strongly activated with stimuli associated with handwriting movements in memory. SPL = superior parietal lobule; SFG = superior frontal gyrus; IFG = inferior frontal gyrus; MedFG = medial frontal gyrus; MidFG = middle frontal gyrus; Cb = cerebellum; MTG = middle temporal gyrus; PoCG = postcentral gyrus; IPL = inferior parietal lobule; PCL = paracentral lobule.

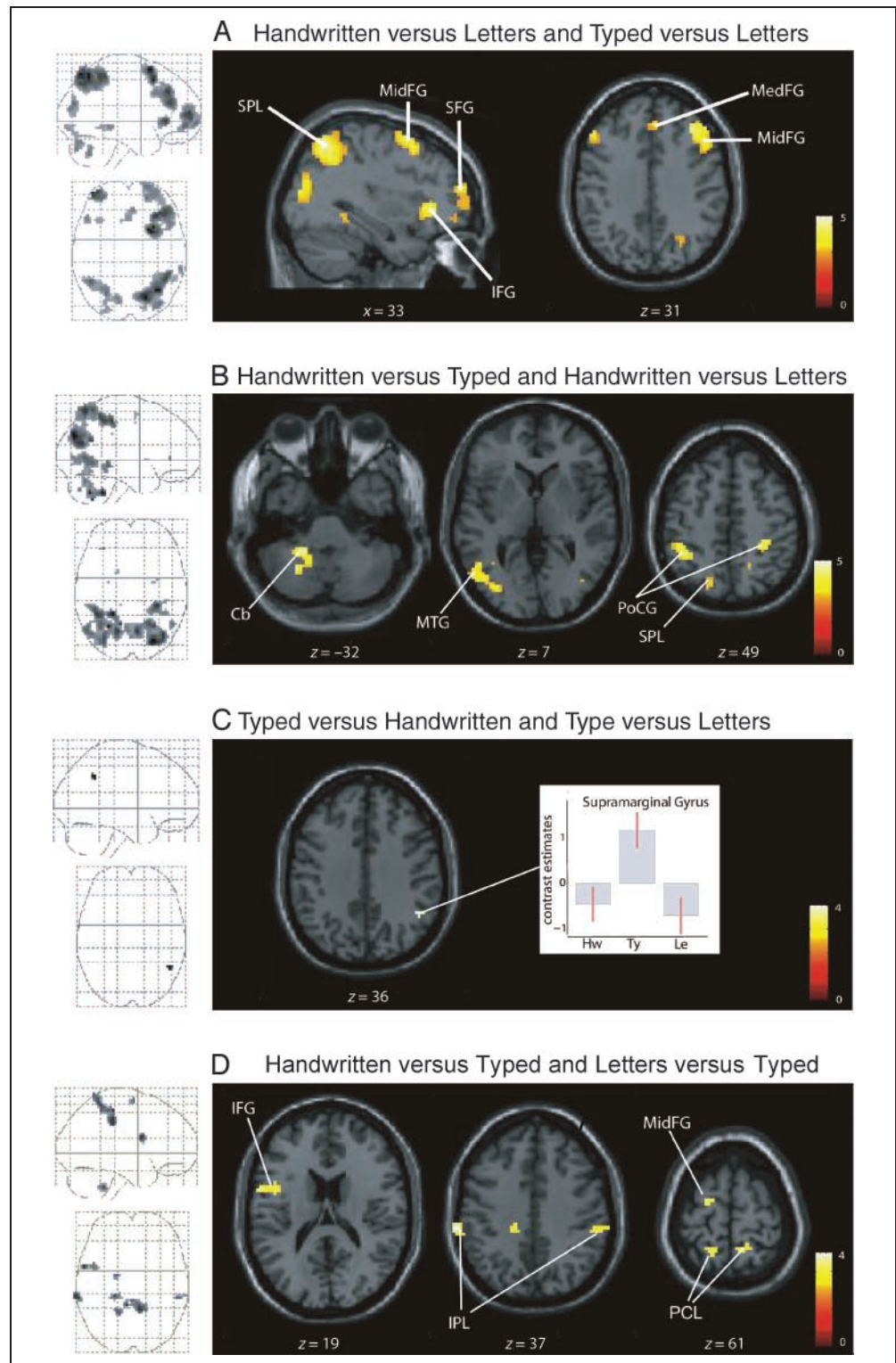


Table 2. Anatomical Location, Corresponding Brodmann's Area, Lateralization, Talairach Coordinates, and Z-score for the Activations Observed in the Five Conjunction Analyses Performed

Z	Talairach Coordinates			Brain Region	Brodmann's Area (BA)	Hemisphere
	x	y	z			
<i>Handwritten and Typed Characters Compared to Letters</i>						
4.86	24	15	57	Middle Frontal Gyrus	BA 6	Right
4.71	36	-59	53	Superior Parietal Lobule	BA 7	Right
4.61	36	34	31	Middle Frontal Gyrus	BA 9	Right
4.53	-42	56	6	Middle Frontal Gyrus	BA 10	Left
4.52	33	29	-1	Inferior Frontal Gyrus	BA 45/47	Right
4.18	-45	-50	47	Superior Parietal Lobule	BA 7	Left
3.96	24	64	-6	Superior Frontal Gyrus	BA 10	Right
3.92	36	-78	23	Middle Temporal Gyrus	BA 19	Right
3.88	6	37	31	Medial Frontal Gyrus	BA 6	Right
3.88	-30	-60	-30	Cerebellum		Left
3.88	-12	-77	-26	Cerebellum		Left
3.88	62	-35	-6	Middle Temporal Gyrus	BA 21	Right
3.85	-48	28	35	Middle Frontal Gyrus	BA 9	Left
3.51	-36	23	-1	Inferior Frontal Gyrus	BA 45/47	Left
3.43	18	-82	-6	Lingual Gyrus	BA 18	Right
3.38	30	-44	-5	Parahippocampal Gyrus	BA 37	Right
<i>Handwritten Compared to Typed and Letters</i>						
4.55	27	-74	34	Precuneus	BA 19	Right
4.48	-27	-60	-32	Cerebellum		Left
3.65	-3	-65	-19	Cerebellum		Middle
3.35	27	-59	-10	Cerebellum		Right
4.17	-15	-61	61	Superior Parietal Lobule	BA 7	Left
4.12	33	-30	48	Postcentral Gyrus	BA 3	Right
4.1	9	-61	58	Precuneus	BA 7	Right
3.82	-53	-61	3	Middle Temporal Gyrus	BA 37	Left
3.75	30	-38	-3	Parahippocampal Gyrus	BA 19	Right
3.61	50	-55	-2	Middle Temporal Gyrus	BA 37	Right
<i>Typed Compared to Handwritten and Letters</i>						
3.43	48	-48	36	Supramarginal Gyrus	BA 40	Right
<i>Handwritten and Letters Compared to Typed</i>						
4.05	-65	-27	37	Inferior Parietal Lobule	BA 40	Left
3.84	-56	4	19	Inferior Frontal Gyrus	BA 44	Left
3.76	12	-44	60	Paracentral Lobule	BA 5	Right
3.76	-21	-27	51	Paracentral Lobule/Cingulate Gyrus	BA 5/31	Left

Table 2. (continued)

Z	Talairach Coordinates			Brain Region	Brodmann's Area (BA)	Hemisphere
	x	y	z			
3.72	-6	-42	-33	Pons		
3.58	53	-30	37	Inferior Parietal Lobule	BA 40	Right
3.57	-18	-3	61	Middle Frontal Gyrus	BA 6	Left
3.57	-18	-46	63	Postcentral Gyrus	BA 7	Left

Typed and Letters Compared to Handwritten

No activation

The Talairach atlas was used to localize the significant clusters.

measured at the end of training, significant only 5 weeks following the end of the training, also supports this finding. These results can be explained by differential forgetting or consolidation processes dependent on the motor modality used for training. The motor memory specific to handwriting could be involved in this difference. Indeed, with sufficient practice, the internal model of a new motor skill gradually (within a few hours) becomes less fragile and this consolidation is accompanied by changes in its neural representation (Doyon & Benali, 2005; Shadmehr & Holcomb, 1997). Once it has been thoroughly learned and stabilized, motor memory can last for very long periods of time and even improve without any further practice (Shadmehr & Brashers-Krug, 1997; Brashers-Krug, Shadmehr, & Bizzi, 1996). The observed stability of the writing performance, measured 6 weeks following the end of training (sensorimotor test), argues for this interpretation.

Finally, behavioral recognition tests showed no significant difference in RTs between the two modalities. This indicates that despite differences in visual processing of the characters according to the learning modality, the response preparation was similar in both cases. The differences in response accuracy cannot therefore be explained by opposite differences in RTs.

fMRI Findings

Activations Related to Character Novelty

On comparing handwritten and typed characters to letters, greater activations were mostly evident in a parieto-prefrontal network, including the intraparietal sulcus and several prefrontal regions with right predominance, as well as some other occipital, temporal, and subcortical regions. Thus, this network seems to participate in the judgment of the orientation of newly learned characters. Activity in the right intraparietal sulcus has been linked to demands in attentional spatial processing (Pollmann & Maertens, 2005; Corbetta et al., 1998; Nobre et al., 1997) with increased strength likely for less familiar symbols such as new characters. This region is strongly activated when subjects are performing mirror-reading tasks (Dong et al., 2000). The role of prefrontal regions in memory procedures has been largely documented (for a review, see Shimamura, 1995). On the one hand, activation of the dorsolateral and ventrolateral prefrontal cortices has been linked to the formation of long-term episodic memories (Ranganath, Johnson, & D'Esposito, 2003) and, on the other hand, prefrontal, pre-SMA, and middle frontal activations have been evident during visual working memory tasks (Ranganath et al., 2003; Haxby, Petit, Ungerleider, & Courtney, 2000; Smith & Jonides, 1999). Both types of memories were likely involved in the present task for two reasons. Firstly, the number of correctly oriented stimuli within the sequence had to be held in working memory until the go signal was presented. Secondly, because the characters were newly learned, their

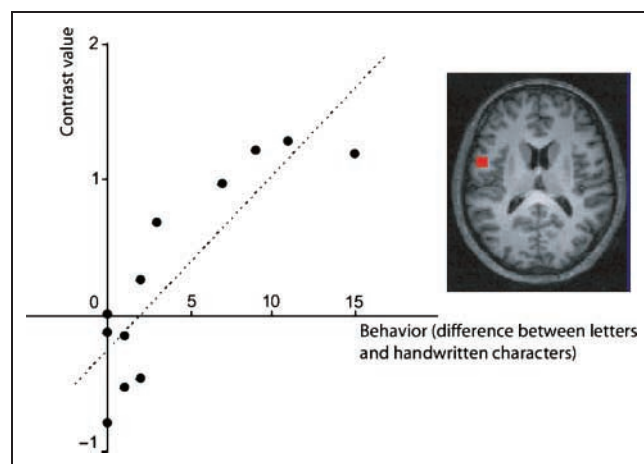


Figure 5. Correlation between behavioral performances (difference between the correct responses to letters and handwritten characters) and the level of activation in left Broca's area in the contrast letters versus handwritten characters.

processing could be facilitated by the reactivation of more “episodic” memories related to their context of acquisition. Altogether, these results indicate that the task was performed differently in terms of both memory and attentional processes on characters recently acquired compared to those items overlearned such as letters. In addition, activation within these parietal and prefrontal areas for typed characters indicates that despite poor recognition performance, typed characters were processed according to the task demands.

Activations Specific to Each Learning Modality

Several clusters of activation were specific to handwritten characters relative to letters and typed characters. Because the fMRI data were acquired 1 week following the end of training, we can assume that these activations were related to ongoing memory consolidation processes specific to the association between the visual shape of the characters and the movements performed during training. The cerebellum, where three distinct clusters of activation were found, is a critical structure for motor memory consolidation (Doyon & Benali, 2005; Shadmehr & Holcomb, 1997). In addition, several of the activations we report for handwritten characters have been described in studies where subjects learned an association between a visual stimulus and a motor response (Weisberg et al., 2007; Pollmann & Maertens, 2005). The activation of the posterior part of the middle temporal gyrus predominantly on the left hemisphere was equally observed by Weisberg et al. (2007) while subjects observed pictures of novel objects they had previously learned extensively how to use with their right hand. This region, more anterior and dorsal than the lateral occipital complex that processes all categories of visual objects (Malach et al., 1995), is thought to be involved in recognition and naming of manipulable objects such as tools relative to nonmanipulable objects such as animals or faces (Martin, Wiggs, Ungerleider, & Haxby, 1996), but also in action knowledge (Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). This could explain why the middle temporal gyrus is more activated for handwritten characters, to which specific and distinctive actions are associated. The postcentral gyrus (somatosensory cortex), activated in motor execution and imagery (Porro et al., 1996), also shows increased focal activation after subjects learn new object–response associations (Pollmann & Maertens, 2005). In addition, activation of the superior parietal lobule extending to the postcentral gyrus was also described by Weisberg et al.

The presentation of typed characters selectively activated one single area, the right supramarginal gyrus. This could simply reflect the greater difficulty in processing those characters, as attested by a decrease in behavioral performance in this study and previous evidence of involvement in generating saccades and attention shifts (Perry & Zeki, 2000). A more interesting alternative hypothesis could be an association with the

consolidation of typing movements in memory. Few data exist in the literature concerning the brain areas involved in typewriting. However, an interesting case of a professional typist, who was very disturbed in her typewriting production and much less in her handwriting production, has been described (Boyle & Canter, 1987). Such dissociation suggests that the two skills rely on distinct brain processes and structures. In addition, a recent study with highly skilled typists showed an increase in gray matter concentration following long-term typewriting practice in a region of the right hemisphere close to the area described in the present study (Cannonieri, Bonilha, Fernandes, Cendes, & Li, 2007).

Activations Related to Writing Knowledge and Letter Recognition

The most important finding in the fMRI study was the existence of activations common to the visual processing of handwritten characters and letters, and therefore, dependent on the writing knowledge associated with the stimulus. A striking finding in that context was the stronger activation of the left Broca’s area for letters and handwritten characters with respect to the characters learned on the keyboard. The only feature common to letters and handwritten characters, which was not shared by typewritten characters, was that subjects knew how to write them. Thus, left Broca’s area activation seems to depend on the motor knowledge associated with the characters. In addition, individual levels of activation in the left Broca’s area strongly correlated to individual behavioral differences between handwritten characters and letters, thereby underlining the sensitivity of this region to the similarity in processing letters and handwritten characters.

In contrast to the early concept of Broca’s region as an exclusive speech production area, today’s views suggest a role in much wider language- and motor-related functions (Nishitani, Schürmann, Hari, & Amunts, 2005). In a large number of studies, Broca’s area has been shown to be involved in various linguistic functions (for a review, see Nishitani et al., 2005). A possible explanation could be that through handwriting learning, the characters are categorized similarly as letters and acquire a “linguistic” status. However, such an interpretation remains very speculative. Broca’s area has also been recently implicated in perceptual and motor sequencing (Schubotz & von Cramon, 2004). According to these authors, tasks that rely on processing sequentially structured information may always converge on Broca’s area, be it in the context of planned, imagined, executed, or observed actions. It is therefore possible that the facilitation for recognizing the orientation of handwritten characters is based on implicit sequencing of the stimuli following the sequence used when they were written. This interpretation would be supported by results of behavioral studies indicating that the activation of the characters in memory is gradual and follows the order of strokes

in writing (Flores d'Arcais, 1994; Courrieu & De Falco, 1989; Kosslyn et al., 1988). A slightly different view is that the activation of Broca's area more generally reflects the reactivation of the unified motor representations of the different characters. According to Rizzolatti and Craighero (2004) and Rizzolatti, Fogassi, and Gallese (2002), Broca's area could be homologous to area F5 of the monkey, an area containing neurons coding for action "prototypes" and mirror neurons reacting to action observation. The role of Broca's region as an interface for action and perception generalized to non-verbal functions is now widely accepted. Broca's area is activated when actions are simulated, observed, or executed (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2002; Grèzes & Decety, 2001; Gerardin et al., 2000; Grafton, Arbib, Fadiga, & Rizzolatti, 1996).

The coordinates observed for the clusters in the inferior parietal lobule (BA 40) correspond well with the presumed location of the anterior intraparietal area (AIP), as defined by Simon, Mangin, Cohen, Le Bihan, and Dehaene (2002) in a series of tasks involving the parietal cortex ($\pm 60 -30 40$ vs. $-65 -27 37$ and $53 -30 37$ in the present study). In the monkey brain, together with area F5, area AIP is the core of the hand-objects interaction system (Gardner et al., 2007). The AIP neurons are involved in constructing an action-relevant representation that translates visual information into a form usable to specify motor actions (Colby & Goldberg, 1999). In humans, the equivalent of area AIP is very reliably activated in tasks requiring execution, imagery, and observation of hand actions (Rizzolatti & Craighero, 2004; Grèzes & Decety, 2001; Gerardin et al., 2000; Grafton et al., 1996). Also concordant with this view is the activation of both the left dorsal premotor and the left postcentral gyrus in the same action-related contexts (Grèzes & Decety, 2001). In addition, the activity observed in the dorsal premotor cortex was close to those previously reported in various fMRI studies involving writing movements (James & Gauthier, 2006; Sugihara, Kaminaga, & Sugishita, 2006; Longcamp et al., 2003; Katanoda, Yoshikawa, & Sugishita, 2001). Despite methodological differences between these studies and variations of the precise position, these activations might correspond to the same writing center, the so-called Exner's area (Lubrano, Roux, & Démonet, 2004; Tohgi et al., 1995; Anderson et al., 1990; Exner, 1881). The activation of this area during an orientation judgment for the handwritten characters might reflect a covert contribution of handwriting movements for achieving this task.

Finally, it should be noted that, even when lowering the statistical threshold, we observed no distinct activation of the letter- or object-processing occipito-temporal brain regions in relation to handwriting knowledge.

The lack of activation common to letters and typed characters indicates that the visual perception of letters did not spontaneously occur together with reactivation of the associated typing knowledge in memory. This may

be because the link between handwriting memory and visual shape of letters is learned very early in development and is therefore stronger in adults.

Conclusion

The behavioral data confirmed that handwriting memory facilitates the discrimination between characters and their mirror images for longer periods than typewriting memory. The fMRI results showed that the difference in recognition performance between characters learned by handwriting and characters learned by typewriting is related to different neural pathways. Part of the pathway activated during recognition of handwritten characters is also active during normal letter recognition. In particular, activity in the left Broca's area, together with activation of the bilateral AIP, left dorsal premotor, and left postcentral regions argue in favor of reactivation of motor knowledge during visual processing of new handwritten characters and overlearned letters. The left-sided lateralization of the activations further strengthens this interpretation. The present results support the findings of previous studies that focused on object learning (Weisberg et al., 2007; Pollmann & Maertens, 2005; Wolfensteller et al., 2004). They may have implications for written language education and rehabilitation.

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