

What Differs in Visual Recognition of Handwritten vs. Printed Letters? An fMRI Study

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Abstract: In models of letter recognition, handwritten letters are considered as a particular font exemplar, not qualitatively different in their processing from printed letters. Yet, some data suggest that recognizing handwritten letters might rely on distinct processes, possibly related to motor knowledge. We applied functional magnetic resonance imaging to compare the neural correlates of perceiving handwritten letters vs. standard printed letters. Statistical analysis circumscribed to frontal brain regions involved in hand-movement triggering and execution showed that processing of handwritten letters is supported by a stronger activation of the left primary motor cortex and the supplementary motor area. At the whole-brain level, additional differences between handwritten and printed letters were observed in the right superior frontal, middle occipital, and parahippocampal gyri, and in the left inferior precentral and the fusiform gyri. The results are suggested to indicate embodiment of the visual perception of handwritten letters. *Hum Brain Mapp* 32:1250–1259, 2011. © 2010 Wiley-Liss, Inc.

Key words: handwriting; letters recognition; embodied perception; fMRI

INTRODUCTION

The topic of visual letter recognition is currently gaining increased interest among specialists in object recognition [Grainger et al., 2008]. Accurate identification of a letter is indeed a fascinating skill given the multiplicity of forms a given letter can take. Among these forms, handwritten letters have received little attention, being considered as relying for their processing on the same cognitive architecture as machine-produced fonts [Grainger et al., 2008]. Yet, sparse data in the neuropsychological literature suggest that recognition of handwritten and printed characters can be distinctly disturbed following a brain lesion [van Atteveldt et al., 2002; Williams, 1984]. It is harder to recognize words when handwritten and printed exemplars are mixed in the same session, as if subjects had to apply different processes to recognize handwritten and printed words [Corcoran and Rouse, 1970]. A possible distinction

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between the two types of letters is that handwritten letters intrinsically carry production-related information that might be used by the visual system in the recognition processes. This hypothesis has already received empirical support in several psychophysical studies showing that the visual system reliably extracts production-related information from the dynamically displayed graphic trace [Knoblich et al., 2002; Li and Yeh, 2003; Orliaguët et al., 1997]. According to these studies, we spontaneously perceive dynamic configurations that are consistent with the rules we follow when we write [Li and Yeh, 2003], and we are able to use these configurations to predict forthcoming events [Knoblich et al., 2002; Orliaguët et al., 1997]. These effects are likely to rely on the more general sensitivity of the visual system to the laws driving movements that are strongly expressed in graphic movements [see for instance Kandel et al., 2000; Viviani and Stucchi, 1989 for the 2/3 power law relating the angular velocity and curvature of the movement, and Bidet-Ildei and Orliaguët, 2008; Meary et al., 2005 for the isochrony principle stating that the writing duration is independent of the trajectory length]. Noticeably, the same processes seem to be triggered by handwritten stimuli presented on a static form [Babcock and Freyd, 1988]: when subjects had to memorize handwritten pseudocharacters on a visual basis, they implicitly took into account the way the characters had been written (for instance with the last stroke upwards or downwards). According to Freyd [1987], such findings implicate that the underlying dynamic representations are formed during viewing of static handwritten traces.

Most of the studies dealing with letter perception have focused on the potential selectivity of the posterior cortical regions [the equivalent of the visual word form area for single letters: Flowers et al., 2004; Garrett et al., 2000; Gauthier et al., 2000; Gros et al., 2001; James et al., 2005; Pernet et al., 2005; Polk and Farah, 1998; Polk et al., 2002; Wong et al., 2009]. However, the investigation of whole-brain activations has established that visual perception of static single letters relies, not only on extrastriate brain areas, but also on cortical motor areas [James and Gauthier, 2006; Longcamp et al., 2003, 2006]. In functional magnetic resonance imaging (fMRI) studies, visually presented printed letters activated a part of the premotor cortex [James and Gauthier, 2006; Longcamp et al., 2003]. This activation pattern resembled activation associated with the actual writing movements and it thus appeared to reflect an implicit simulation of memory-stored motor programs needed to write each letter [Anderson et al., 1990; Longcamp et al., 2003]. As additional support for the psychophysical studies cited above, handwritten letters, compared with printed letters, have specific neural correlates. For example, magnetoencephalographic signals to handwritten letters imply involvement of the observer's own motor system in the visual perception: The reactivity of the ~ 20 -Hz oscillations, arising from the primary motor cortex, indicated a stronger excitation by handwritten than by printed letters [Longcamp et al., 2006]. Despite the cur-

rent lack of demonstration of single mirror neurons in the primary motor cortex [Kilner and Frith, 2007], such modulations of the ~ 20 -Hz oscillations have been associated with the mobilization of the mirror-neuron system [Caetano et al., 2007; Hari et al., 1998] because they occur both during observation and execution of an action, and even when only the sound of the action is presented [Caetano et al., 2007]. The results by Longcamp et al. [2006] indicate that a part of the system underlying action observation is also involved in the perception of static stimuli that only imply actions.

Here, we used fMRI in a similar experimental condition to identify in more detail the brain network that sustains the distinction between handwritten and printed letters. We expected that the motor and/or premotor cortices would display significantly different activations to the presentation of handwritten and printed letters. On the basis of recent studies on reading handwritten vs. printed words [Barton et al., 2010; Hellige and Adamson, 2007; Qiao et al., 2010], we also checked whether handwritten letters would be associated with more predominant right-hemispheric activations in the visual system, and especially in the fusiform gyrus.

METHODS

Participants

Eleven adults (mean age 27; age range 22–31; normal or corrected-to-normal visual acuity) participated in the experiment. One of the participants was removed from the final statistical analysis due to head motion artifacts. The remaining subjects were right-handed [handedness quotients 80–100%; mean 91%; Oldfield, 1971], and they consistently used their right hand to write. None of the participants reported history of neurological diseases. The study had a prior approval by the Ethics Committee of the Helsinki and Uusimaa Hospital District, and the subjects signed a written informed consent after the procedure was fully explained.

Stimuli and Experimental Design

The printed and handwritten letters used as stimuli were the same as in Longcamp et al. [2006]. The letters, matched in size and stroke thickness (Fig. 1a), were displayed as black symbols against white background. The presentation screen was grey, with the letters shown within a 5.5 cm \times 5.5 cm area in the middle of it. Stimulus presentation and its synchronization with the pulses of the fMRI scanner were controlled by Presentation[®] software version 0.81 (<http://www.neurobs.com>, Neurobehavioral Systems Inc., Albany, CA) run on a PC. The stimuli were displayed through a three-chip Digital Light Processing[™] (DLP) data projector VistaPro, Electrohome Ltd onto a rear projection screen attached to the head coil, and they were

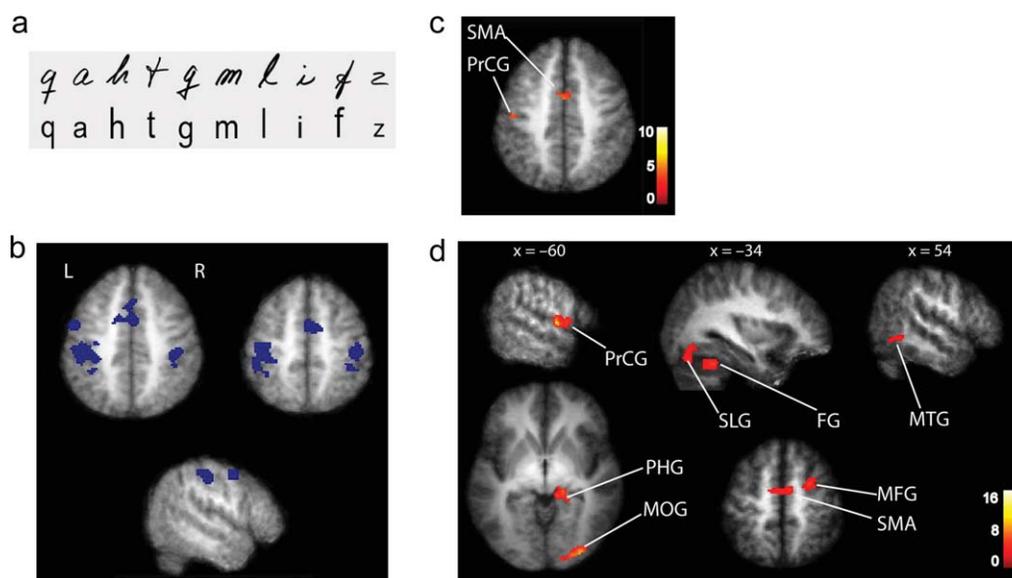


Figure 1.

a: Stimuli. **b:** Mask used for the analysis restricted to the frontal regions involved in hand movement triggering and execution, overlaid on the group average normalized anatomical image. **c:** Statistical map obtained in the masked analysis, for the contrast “Handwritten vs. Printed” overlaid on the group average normalized anatomical image. **d:** Statistical map obtained in the whole-brain analysis, for the contrast “Handwritten vs. Printed”,

overlaid on the group average normalized anatomical image. Abbreviations: SMA = supplementary motor area; PrCG = pre-central gyrus; FG = fusiform gyrus; SLG = superior lingual gyrus; PHG = parahippocampal gyrus; MOG = middle occipital gyrus; MFG = middle frontal gyrus; MTG = middle temporal gyrus. The color bars represent the t-values.

viewed through a mirror positioned in front of the participant’s eyes. The distance from the mirror to the screen was 35 cm.

In a block design, we alternated 21.6-s duration blocks of handwritten letters, printed letters, and rest (where only the white 5.5 cm × 5.5 cm background area was displayed). Each session included five blocks of each condition. Within a block, individual letters were presented for 0.4 s, separated by a 2-s fixation period. To ensure that the participants attended to the letters, we required them to detect the target letter “z” and to count the total number of its occurrences within a session. The participants were informed that the number of targets varied between 1, 2, and 3 (the last target was positioned close to the end of the session). They had to give their response after the scanning had stopped by pressing a response button either 1, or 2, or 3 times.

Immediately following the sessions of letter presentation, the participants performed a “motor localizer” task that aimed at identifying the frontal regions involved in the triggering and execution of self-initiated brisk finger movements, inspired from our previous MEG study [Longcamp et al., 2006]. Response buttons were placed under the participant’s left and right index fingers, and colored 5.5 cm² boxes on the screen signaled that the subject had to perform self-paced left (red box) or right (green box) index

finger presses once every 4 s, or to remain still (white box). Each task block (five blocks of three conditions) lasted for 21.6 s, and blocks were alternated randomly.

fMRI Acquisition and Analysis

Brain activity was measured with a Signa[®] EXCITE 3T MR-system (GE Medical systems, Milwaukee, WI) using a standard head coil. For each participant, a high-resolution structural T1-weighted image, covering the whole brain, was acquired with 3D fast spoiled gradient echo sequence (inversion-recovery prepared): repetition time (TR) = 9 ms, echo time (TE) = 1.9 ms, flip angle (FA) = 15°, 256 × 256 matrix, slice thickness 1.4 mm, in the sagittal plane. For functional imaging, we used a T2*-weighted gradient-echo echo-planar (EPI) sequence, covering the whole brain with 31 contiguous oblique axial slices (TR = 2,000 ms, TE = 32 ms, FA = 90, field of view = 200 × 200 mm², 64 × 64 matrix, slice thickness = 4 mm, no slice gap, interleaved acquisition, voxel size of 3.125 × 3.125 × 4 mm³). We acquired 168 functional volumes in each of the three sessions (two sessions of visual presentation of letters and one session of motor localizer), leading in a total of 504 volumes per subject.

The fMRI data were processed using SPM2 software (www.fil.ion.ucl.ac.uk/spm/) applying the general linear

model [Friston et al., 1995]. The first six functional volumes of each session were removed to eliminate nonequilibrium effects of magnetization. The remaining 162 images were corrected for differences in the slice acquisition time and for head movement by realignment with the first image using rigid body transformations. To improve the normalization hampered by intensity inhomogeneities of the signal in the occipital pole, the structural image was skull-stripped (Matthew Brett; <http://imaging.mrc-cbu.cam.ac.uk/imaging/NormalizeSkullStripped>), using the MRICro software (Chris Rorden; <http://www.sph.sc.edu/comd/rorden/mricro.html>), and only then normalized to a skull-stripped structural template. The normalization parameters were then applied to the functional images, and the normalized functional images were spatially smoothed with an isotropic Gaussian filter (8-mm full width at half maximum). A high-pass filter with a 128-s cut-off was finally applied to the functional series.

The experimental conditions were modeled as box-car functions convolved with the hemodynamic response function. For the sessions of letter presentation, four contrasts (“handwritten letters vs. rest”; “printed letters vs. rest”; “handwritten letters vs. printed letters”; “printed letters vs. handwritten letters”), and for the motor localizer, three contrasts (“left vs. right index finger lifts”; “right vs. left index finger lifts” and “left and right index finger lifts vs. rest”) were estimated for each subject and subsequently subjected to random-effects analyses.

The group analysis was carried out in two steps: first, in accordance with our *a priori* hypotheses, we restricted the calculation of one-sample *t*-tests to the central brain regions involved in finger movement triggering and execution. For that purpose, we used the MarsBar SPM Toolbox (<http://marsbar.sourceforge.net/>) to construct a binary image containing together the central activation clusters found in the above-mentioned “motor” contrasts: right–left finger movement (left primary sensorimotor cortex, 1,583 voxels); left–right finger movement (right primary sensorimotor cortex, 451 voxels), and left and right finger movements vs. rest (medial frontal cortex, containing the supplementary motor area (SMA), typically involved in such a self-triggered motor task [Roland et al., 1980] and part of the cingulate gyrus; 933 voxels). Because the pace of the finger movements was rather slow (about once every 4 s.), the statistical effects were not massive and the activation clusters were not corrected for multiple comparisons at the voxel level ($P < 0.001$). To investigate in parallel whether the blood-oxygenation-level-sensitive (BOLD) signals in the letter-sensitive left premotor cortex differed [Longcamp et al., 2003] to handwritten and printed letters, we also added to the binary image a sphere of 6-mm radius centered around Talairach coordinates ($[-54\ 2\ 44]$ /MNI $[-55\ 0\ 48]$) of the activation we previously found [Longcamp et al., 2003] to be common for perceiving letters and writing. We used the resulting binary image as an explicit mask during model estimation (Fig. 1b) and considered as activated areas brain regions with $P \leq 0.05$

(FWE corrected) at the cluster level (normalized voxel size $2 \times 2 \times 2\text{ mm}^3$).

Second, to evaluate the potential implications of other brain regions, we ran a whole-brain analysis in which we considered as activated all brain regions with $P \leq 0.05$ (FWE corrected) at the cluster level (normalized voxel size $2 \times 2 \times 2\text{ mm}^3$). Within a cluster, we report separately the local maxima if they occurred more than 10-mm apart in either the x , y , or z direction.

The coordinates of the statistically significant activations were expressed in the MNI space (according to recent recommendations [Devlin and Poldrack, 2007]). Significant activations were identified using a standard anatomical atlas [Duvernoy, 1991]. We indicate if the activations reached a voxel-level $P \leq 0.05$ (FWE corrected) or $P \leq 0.001$ (uncorrected). The results are displayed in neurological convention (left of the images is left of the brain).

RESULTS

All participants detected the target letters accurately in all task blocks, confirming that they sufficiently attended to the stimuli.

Masked Analysis: Letter Processing in the Hand-Related Central Regions

A conjunction between the contrasts “handwritten letters vs. rest” and “printed letters vs. rest” showed equal activations to the two types of stimuli in the left premotor cortex (peak coordinates: $[-54\ -4\ 44]$, $z = 2.98$, $P \leq 0.05$ FWE corrected at the voxel-level) and in a portion of the cingulate gyrus on the left hemisphere (peak coordinates: $[-8\ 4\ 46]$, $z = 2.95$, $P \leq 0.05$ FWE corrected at the voxel-level). In addition, handwritten letters triggered stronger activations in the medial frontal cortex, with y -coordinate posterior to the anterior commissure, corresponding to the supplementary motor area [SMA, Picard and Strick, 2001; Nachev et al., 2008] and in the precentral gyrus (PrCG) along the central sulcus (primary motor cortex, Fig. 1c and Table I).

No cluster survived the threshold in the reverse contrast (printed letters > handwritten letters).

Whole-Brain Analysis

A conjunction between the contrasts “handwritten letters vs. rest” and “printed letters vs. rest” showed a significant cluster in the left fusiform gyrus ($P \leq 0.001$, uncorrected at the voxel level and $P \leq 0.05$ FWE corrected at the cluster level, peak at $[-46\ -68\ -14]$, $z = 4.60$).

Whole-brain analysis (Fig. 1d and Table I) also revealed stronger activation of several posterior brain regions for handwritten than printed letters: the superior part of the middle occipital gyrus (MOG), the middle temporal gyrus (MTG), two sites of the parahippocampal gyrus (PHG) in

TABLE I. Cluster sizes (2-mm³ voxels), z-scores, MNI coordinates, hemispheric lateralization, anatomical locations for the activated regions in the “Handwritten vs. Printed” contrast

Cluster size (vx)	z-score	x	y	z	Hemisphere	Anatomical location
Masked analysis						
276	4.71**	8	-6	60	Medial	Medial frontal cortex
17	3.24**	-48	-16	46	Left	Precentral gyrus
Whole-brain analysis						
375	5.57**	34	-88	-4	Right	Middle occipital gyrus
	3.77*	48	-60	-10	Right	Middle temporal gyrus
170	4.91*	-60	-6	6	Left	Precentral gyrus
968	4.57*	-16	-82	-16	Left	Superior lingual gyrus
	4.25*	-42	-52	-26	Left	Fusiform gyrus
119	4.48*	26	0	60	Right	Middle frontal gyrus
189	4.21*	18	-34	2	Right	Parahippocampal gyrus
	3.55*	30	-34	6	Right	Parahippocampal gyrus

No cluster survived the threshold in the “Printed vs. Handwritten” contrast.

*corresponds to a voxel-level $P \leq 0.001$ (uncorrected);

**corresponds to a voxel-level $P \leq 0.05$ (FWE corrected).

the right hemisphere, and the fusiform gyrus (FG) and the superior lingual gyrus (SLG) in the left hemisphere. We also observed two frontal activation sites that were not included in the explicit mask analysis reported above: the right middle frontal gyrus (MFG) and the most inferior part of the left precentral gyrus (PrCG) extending to the subcentral gyrus and to the inferior frontal gyrus, pars opercularis.

In the reverse contrast (printed letters > handwritten letters), no cluster survived the threshold.

DISCUSSION

Hand-Related Frontal Regions and Letter Perception

Primary motor cortex

The present fMRI data strongly support our previous MEG study [Longcamp et al., 2006] by showing that the hand region of the left primary motor cortex is more strongly activated when the subject is viewing handwritten than printed letters. This result suggests that knowledge related to hand-movement execution is involved more in recognizing handwritten than printed letters presented on a static form, probably because the intrinsic traces of the writing actions are important cues for recognizing unfamiliar shapes, such as handwritten letters [Babcock and Freyd, 1988; Longcamp et al., 2006]. The participation of the primary motor cortex in action observation has been pointed out in several studies that used transcranial magnetic stimulation [Fadiga et al., 1995] monitored oscillatory cortical activity [Caetano et al. 2007; Hari et al., 1998; Kilner et al., 2009; Longcamp et al., 2006], or recorded single-unit activity in monkeys [Tkach et al., 2007]. Although the evidence of BOLD signal modulation in the primary motor cortex during action observation

remains scarce [Caspers et al., 2010; Grezes and Decety, 2001], our result is in line with previous findings of congruent modulations in the human visual and motor cortices for the BOLD signal and the MEG oscillations measured in similar experimental conditions [Singh et al., 2002; Winterer et al., 2007].

Premotor cortex and SMA

Two other findings might inform us on how motor information is used during perception of handwritten letters. First, both handwritten and printed letters activate the left premotor cortex to the same extent. The activation of the intermediate part of the left premotor cortex during the visual perception of letters is consistent with previous studies [James and Gauthier, 2006; Longcamp et al., 2003] that supposed this area to support the motor sequences necessary to write each letter and to be automatically recruited when the letters are visually perceived. Since this region is recruited by both printed and handwritten letters, reactivation of a given writing sequence could be automatically associated with the memory representations of letters. A second, and equally unexpected finding was that the SMA, an area known to be involved in the planning and control of voluntary actions [see Nachev et al., 2008, for a recent review], was more active to handwritten than printed letters. Although SMA activation has occasionally been reported during action observation [Gazzola and Keysers, 2009; Zentgraf et al., 2005], SMA does not belong to the core of the mirror-neuron system [Rizzolatti and Craighero, 2004]. The observed activation could nonetheless be related to the greater simulation of hand actions when handwritten shapes are viewed. The presumed functions of the SMA include planning of ordered sequential movements that require a high degree of coordination [Roland et al., 1980; Tanji and Shima, 1994], especially

when the sequence is performed from memory [Mushiaki et al., 1991]. Writing a letter is indeed a complex sequential action, which requires producing several strokes in different directions and in a specific order at high speed; in such a highly controlled gesture the SMA involvement is likely to be crucial [Menon and Desmond, 2001]. Moreover, the SMA directly targets the primary motor cortex [Luppino et al., 1993; Nachev et al., 2008], where both the oscillatory activity [Longcamp et al., 2006] and the BOLD signal (present study) are stronger for handwritten than printed letters. The SMA is assumed to play a key role in the automatic suppression of movements that are represented in the motor system but whose execution has to be prevented [such as during motor imagery, Kasess et al., 2008; Sumner et al., 2007]. It is thus plausible that the primary motor cortex needs to be controlled more by the SMA when handwritten than printed letters are perceived. In support of this hypothesis is the rare syndrome echographia [Berthier et al., 2006; Pick, 1924], characterized by automatic translation of visually (and more rarely, auditorily) perceived texts into writing, possibly caused by dysfunction of the medial frontal cortex that normally would inhibit the mirror-neuron system [see Berthier et al., 2006 for a review].

Other frontal regions

The activation site in the right middle frontal gyrus agrees with the position of the frontal eye field that is involved in programming eye movements [see Grosbras et al., 2005, for a review]. Although we tried to prevent eye movements by using small stimuli and by instructing the subjects to keep their eyes still, we cannot rule out the possibility that the level of visuospatial attention would have been different for handwritten and printed letters, especially because handwritten letters were much less familiar to the participants. In fact, strengthening of visuospatial attention can be associated with increased activation of the oculomotor cortical regions even if no overt eye movements are performed [Grosbras et al., 2005; Nobre et al., 1997]. Moreover, the frontal eye field is part of the dorsal attention network that supports top-down regulation of visual processing [Corbetta and Shulman, 2002]. Because tasks involving handwritten stimuli require enhanced processing effort [Corcoran and Rouse, 1970; Hellige and Adamson, 2007; Qiao et al., 2010; Wagner and Harris, 1994], frontal eye field could have become more activated in the present conditions. In addition, covert eye movements could have been associated with handwritten letters given their intrinsic dynamical character [Babcock and Freyd, 1988; Freyd, 1987]. In support of this interpretation, the right frontal cortex has recently been pointed as crucial for the ability to detect biological motion from point-light displays [Pavlova et al., 2009, see also Ptito et al., 2003]. However, without simultaneous eye-tracking data the present interpretations remain speculative.

The left ventral precentral activation is close to the motor representation of the articulators [either isolated tongue, lips or larynx movements, or speech-production movements; Brown et al., 2005, 2008, 2009], and could thus be related to subvocal articulation of the visually perceived letters. Although there is no a priori reason for a greater implication of phonological representations of letters when they are handwritten [Longcamp et al., 2006], a higher reliance on these articulatory motor representations might help to disambiguate the visual stimuli.

Altogether, our results suggest that the process of recognizing handwritten letters relies on the simulation of movements of several body parts (hands, eyes, and articulators), which implicates embodiment of the perception of handwritten letters: First, because handwritten letters contain traces of the writer's action, the observer's hand motor cortex gets more active. Second, the simulation of eye and articulatory movements may support the increased processing requirements for handwritten letters, although this hypothesis should be investigated in more detail.

Posterior Activations: Contribution of Left vs. Right Hemisphere

Several studies suggest that handwritten material may be identified through a greater contribution of the right than left hemisphere [Hellige and Adamson, 2007; Qiao et al., 2010]. In the present data, stronger right-hemispheric activations were found in the middle occipital and parahippocampal gyri. Both regions belong to the ventral visual pathway for processing objects [Joseph et al., 2006; Murray et al., 2000], and the parahippocampal region has also been associated to familiarity judgments and context [Diana et al., 2007; Epstein and Kanwisher, 1998], as well as processing of places [Epstein, 2008], but these regions have not previously been specifically pointed as crucial in letters processing. Conversely, the left fusiform gyrus, activated also in our study, has already been described as preferentially involved in processing of letters compared with other categories of objects [Flowers et al., 2004; James et al., 2005; Joseph et al., 2006; Pernet et al., 2005; Polk et al., 2002], at a location close but slightly anterior to that of the visual word form area [Cohen et al., 2000]. Here, we observed two activation foci in the left fusiform gyrus. The anterior one was more strongly activated by handwritten letters, while the posterior one was equally activated by handwritten and printed letters, in accordance with Barton et al. [2010] who used handwritten and printed words. Our results therefore tend to support the view that a part of the fusiform gyrus supports letter recognition, but given the lack of nonletter control stimuli, such as objects or faces, we cannot provide direct evidence that this region would be specifically sensitive to letters. The left fusiform activations further indicate that the right-hemispheric "superiority" observed by Hellige and Adamson [2007] in processing of handwritten material might not depend on

the right homologue of this “letter” fusiform area, but rather on the activity of other ventral visual areas (such as here the middle occipital and parahippocampal gyri). Such right occipital and parahippocampal activations have already been observed, although not extensively discussed, in studies that compared the perception of biological vs. non-biological motion [Dayan et al., 2007; Peelen et al., 2006, Ptito et al., 2003; Saygin et al., 2004] or investigated action observation [Calvo-Merino et al., 2005]. It is therefore possible that these right posterior activations constitute a gateway towards regions more directly involved in processing the “motor” status of handwritten letters. In addition, the Talairach coordinates (48 -59 -5, transformed from the MNI space using the `mni2tal.m` routine; <http://imaging.mrc-cbu.cam.ac.uk/downloads/MNI2tal/mni2tal.m>) of the right temporal activation for the group, as well as the macroanatomical landmarks checked for individual activations, are within 1 cm from the visual-motion sensitive area V5/MT in the vicinity of the ascending limb of the inferior temporal sulcus [coordinates 41 -67 2 in Watson et al., 1993 and 44 -67 0 in Dumoulin et al., 2000]. The stronger activation of the right V5/MT for handwritten than for printed letters would require further investigations using proper localizers, but it is nonetheless in line with V5/MT activations found for pictures that imply motion, such as snapshots of hand-objects interactions or photographs of athletes in motion [Kourtzi and Kanwisher, 2000; Senior et al., 2000].

What Differs Between Processing of Handwritten vs. Printed Letters? Possible Mechanisms

Several mechanisms could account for the present motor-related activations during the perception of handwritten letters. First, the activation of the primary motor cortex could be the consequence of associative Hebbian learning [Keysers and Perrett, 2004; Pulvermüller, 1999]. Clearly, the brain networks sustaining the perception and production of handwriting become coactivated very frequently during initial learning of handwriting, making it possible that later-on one entry (here the visually presented handwritten letter) would lead to automatic reactivation of the other (here the hand-movement representations in the primary motor cortex). This reactivation could well have no current functional impact, being just an epiphenomenon of the perceptual processes involved in analyzing the features of handwritten letters. However, a number of studies have demonstrated behavioral effects of handwriting knowledge on the recognition of handwritten traces [Babcock and Freyd, 1988; Bidet-Ildei and Orliaguet, 2008; Kandel et al., 2000; Knoblich et al., 2002; Li and Yeh, 2003; Meary et al., 2005; Orliaguet et al., 1997; Parkinson and Khurana, 2007; Viviani and Stucchi, 1989], although the direct relationship between these behavioral effects and the presently observed BOLD responses in motor brain regions remains to be demonstrated.

Alternatively, assuming that the motor activation is functionally relevant for processing handwritten letters, it is possible that the perceptual system would rely more on motor information to handle the lower familiarity of handwritten than printed letters, through covert simulation [Jeannerod, 2001] of handwriting movements. In that account, the processes involved for recognizing handwritten and printed letters would not be qualitatively different, but only accentuated for handwritten letters. This explanation would fit with the various data showing that motor knowledge does also play a role in processing printed letters [James and Gauthier, 2006; Longcamp et al., 2003; Parkinson and Khurana, 2007], simply because printed letters are potentially “writeable” objects (relative to unknown pseudoletters) and consequently afford writing. In that sense, handwritten letters would require a stronger internal motor simulation to be recognized, but this simulation would already be triggered, to a lesser extent, by printed letters.

In addition, it is also likely that qualitatively different processes subserve the recognition of handwritten and printed letters, because only handwritten letters contain traces of dynamic biological motion, and indirectly, of the laws of movement that are expressed very strongly in graphic movements and to which the visual system is sensitive [Bidet-Ildei and Orliaguet, 2008; Kandel et al., 2000; Meary et al., 2005; Viviani and Stucchi, 1989]. Both this mechanism and motor simulation might well support the recognition of handwritten letters, although we cannot disentangle the two due to the use of a subtractive design that aimed, as the first attempt, to demonstrate significantly stronger activity in regions related to hand movements during the perception of handwritten letters. In both cases, the reactivation of handwriting movements would demand stronger control in order to avoid overt movements, consistent with the presently observed activation of the SMA to handwritten letters [see Gazzola and Keysers, 2009]. Further work is required to uncover the fine interactions between the presently demonstrated cortical motor activations and visual processing of handwritten and printed letters of various familiarities.

CONCLUSIONS

First, we found fMRI support for our previous MEG study [Longcamp et al., 2006], demonstrating that the hand region of the primary motor cortex is more activated when the subject is viewing handwritten than printed letters. This finding suggests that action processing is automatically induced by visually presented handwritten letters, which themselves are static results of an action sequence. Second, as revealed by the stronger activation of the SMA for handwritten letters, action control mechanisms—likely needed to monitor the state of the primary motor cortex—are also triggered on a visual basis, when information about how the letter has been traced is

present. Third, the activations of two other action-related regions, the frontal eye field and the most inferior part of the left precentral gyrus, tend to indicate that the embodiment of visual perception of handwritten letters involves multiple effectors (the eyes and the articulators, in addition to the hand). Finally, the distinction between handwritten and printed letters was also evident in the activation of the left fusiform gyrus, but not in its right counterpart.

Overall, although the exact mechanisms underlying these observed patterns of difference between handwritten and printed letters remain to be determined, the results suggest that even if the action—here writing—is not directly accessible to the observer, it is likely reconstructed dynamically on the basis of a static input. Our results further support the view that visual perception is an embodied process, tightly linked to motor competencies.

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