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Premotor activations in response to visually presented single letters depend on the hand used to write: a study on left-handers

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Abstract

In a previous fMRI study on right-handers (Rhrs), we reported that part of the left ventral premotor cortex (BA6) was activated when alphabetical characters were passively observed and that the same region was also involved in handwriting [Longcamp, M., Anton, J. L., Roth, M., & Velay, J. L. (2003). Visual presentation of single letters activates a premotor area involved in writing. *NeuroImage*, 19, 1492–1500]. We therefore suggested that letter-viewing may induce automatic involvement of handwriting movements. In the present study, in order to confirm this hypothesis, we carried out a similar fMRI experiment on a group of left-handed subjects (Lhrs). We reasoned that if the above assumption was correct, visual perception of letters by Lhrs might automatically activate cortical motor areas coding for left-handed writing movements, i.e., areas located in the right hemisphere. The visual stimuli used here were either single letters, single pseudoletters, or a control stimulus. The subjects were asked to watch these stimuli attentively, and no response was required. The results showed that a ventral premotor cortical area (BA6) in the right hemisphere was specifically activated when Lhrs looked at letters and not at pseudoletters. This right area was symmetrically located with respect to the left one activated under the same circumstances in Rhrs. This finding supports the hypothesis that visual perception of written language evokes covert motor processes. In addition, a bilateral area, also located in the premotor cortex (BA6), but more ventrally and medially, was found to be activated in response to both letters and pseudoletters. This premotor region, which was not activated correspondingly in Rhrs, might be involved in the processing of graphic stimuli, whatever their degree of familiarity.

Keywords: Handedness; fMRI; Handwriting; Perceptual–motor interactions; Letter perception; Premotor cortex

1. Introduction

According to the motor theory of perception, perceptual processes are influenced and guided by the perceiver's own repertory of potential gestures (for a review, see Viviani & Stucchi, 1992). One of the assumptions made by motor theorists about the perception of space and objects is that motor–perceptual interactions are strongly determined by the way subjects interact within their environment (Paillard, 1991). One particular example of a strong association between a gesture and a category of objects is that between handwriting and graphic forms. Since we know how to write, each character we know is coded in memory under the form of a specific motor program (van Galen, 1991), and we might automatically refer to these writing programs even when we are simply looking at characters. If so, the nature of the motor–perceptual interactions involved in reading is likely to depend on the way we write: somebody who knows how to read but doesn't know how to write should not be able to associate the visual form of a character with any specific motor process. Someone who has learned how to write and usually writes with his/her right hand will probably associate a character with motor schemes specific to the right hand, whereas someone who has learned how to write and usually writes with his/her left hand will make use of motor schemes specific to the left hand. The present experiment was designed to test this idea.

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Several empirical findings support the hypothesis that motoric writing knowledge contributes automatically to the processing of visually perceived characters. From this viewpoint, Chinese and Japanese ideograms are striking examples. In these graphic systems, each character is composed of a number of strokes that must be written in a precise order when learning to read and write. The order of the strokes is subsequently used as a cue to retrieve the ideograms from memory (Flores d'Arcais, 1994), suggesting that the motor sequence of strokes specific to each ideogram may be an essential component of its central representation. Kanji ideogram retrieval has been found to activate several brain regions usually involved in handwriting (Kato et al., 1999). In alphabetical systems, a comparable example is provided by a case study by Anderson, Damasio, and Damasio (1990). The patient in question became agraphic as the result of a left premotor cortical lesion. The fact that her inability to write was associated with a specific visual letter identification deficit shows that the lack of the motor programs for writing can prevent subjects from being able to recognise letters and consequently, from reading.

In a previous neuroimaging study (Longcamp, Anton, Roth, & Velay, 2003), we directly assessed the possibility that motoric writing skills might be automatically involved in the visual perception of alphabetical letters. Using fMRI on a group of right-handed subjects (Rhrs), we checked whether passive letter-viewing induced any activation in the sensorimotor brain areas known to be involved in writing movements. We observed that part of the left ventral premotor cortex (Brodmann area 6) was activated when alphabetical characters were being passively observed and that the same region was also involved in handwriting. Interestingly, this area did not respond to the visual presentation of pseudoletters, to which no predetermined motor program could be associated. We therefore suggested that the premotor activation observed reflected the involvement of the motor programs for writing, corresponding to each letter, in agreement with the conclusions drawn by Anderson et al. (1990). Although our experimental results strongly support this conclusion, the premotor activation can also be explained in terms of linguistic processing. Subvocal articulatory processes are known to activate higher order motor areas, especially during silent or implicit reading (Price et al., 1994; Price, Wise, & Frackowiak, 1996) and working memory tasks (Chen, Cohen, & Hallet, 1997; Paulesu, Frith, & Frackowiak, 1993; Smith & Jonides, 1999).

In the present study, we were looking for stronger evidence in favor of our hypothesis. We therefore repeated the experiments previously carried out on Rhrs with a group of left-handers (Lhrs) who consistently used their left hand to write. One of the main characteristics of writing movements is their high degree of lateralization and dependence on handedness, whereas language and spatial abilities are thought to be more widely distributed over the whole brain in Lhrs. Although the cerebral organization of Lhrs is still a matter of discussion, it seems likely that, as in Rhrs, language is predominantly processed by the left hemisphere in a majority of Lhrs (Hécaen & Sauguet, 1971). For instance, in a recent study using functional transcranial Doppler ultrasonography, a perfusion-sensitive technique, Knecht et al. (2000) measured the incidence of right-hemispheric dominance for language in a phonological word generation task. These authors reported that in a sample of 326 individuals, the incidence of right-hemispheric language dominance increased with the degree of left-handedness from 4% in strong Rhrs (handedness = 100 in terms of the Edinburgh handedness inventory score (Oldfield, 1971)), to 15% in ambidextrous individuals and 27% in the strongest Lhrs (handedness = −100). The assumption about the localization of writing engrams in Lhrs requires some discussion, however although it is generally recognised that motor programs for writing are left-lateralized in most Rhrs (Katanoda, Yoshikawa, & Sugishita, 2001; Menon & Desmond, 2001; Rijntjes et al., 1999), since both their language and motor skills are controlled by the left hemisphere, the situation as far as Lhrs are concerned is less clear-cut and has been less well documented. Nonetheless, there exist several grounds for presuming that graphic motor representations are entirely right-lateralised in these subjects. First, according to Rijntjes et al. (1999), who examined the cerebral zones involved in signing, highly trained movements of this kind may be stored in the same brain areas as those controlling the movements of the limb ordinarily used for their execution (i.e., in the right hemisphere in Lhrs). Secondly, Herron, Galin, Johnstone, and Ornstein (1979) measured EEG asymmetry in handwriting as compared to other linguistic tasks such as listening to a story, relating it or reading it. The right central region was found to be consistently involved during handwriting in those subjects who usually wrote with their left hand, regardless of their pattern of lateralization for language and other motor abilities. Thirdly, studies on patients with apraxic agraphia, a disorder affecting motor aspects of writing but sparing other language functions (Roeltgen, 1985), have also provided some information about the lateralization of the neural basis of handwriting. For instance, Margolin (1980) described a fully left-handed patient who became apraxic and agraphic as the result of a right central lesion, but showed no associated language deficits. On similar lines, Margolin and Binder (1984) reported the case of a patient who wrote with his left hand and was mixed-handed when performing other activities. After having a right hemispheric stroke, he presented with apraxic agraphia without any limb–motor apraxia or aphasia. These cases point to the fact that motor programs for writing may be separate from other language and motor functions and suggest that they are probably set up in the hemisphere contralateral to the usual writing hand. Finally, a more direct piece of evidence comes from a study by Siebner et al. (2002) who found an exclusive activation of the right sensorimotor cortex when a group of Lhrs was performing a simple handwriting task.

On the basis of these data, we reasoned that if our previous interpretation was true, then there would be only one possible pattern of results for Lhrs: visual perception of sin-