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Hemispheric asymmetry emerges at distinct parts of the occipitotemporal cortex for objects, logograms and phonograms: A functional MRI study

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Behavioral and neuropsychological studies have suggested that the right hemisphere has a special advantage in the visual recognition of logograms. While this long-standing 'right hemisphere hypothesis' has never been investigated systematically by previous neuroimaging studies, a candidate neural substrate of such asymmetry might be found within the occipitotemporal cortex that is known to exhibit lateralized response to a certain class of stimuli, such as letters and faces. The present study examined the hemispheric specialization of brain activation during naming of objects, logograms and phonograms using functional magnetic resonance imaging. The three types of stimuli overall produced left-predominant activation of the perisylvian and inferior parietal regions relative to the resting baseline. This inter-hemispheric difference was significant irrespective of the stimuli type. In the occipitotemporal cortex, six subregions showing lateralized response were identified. That is, the three stimuli commonly produced left-lateralized response in the posterior fusiform and superior temporal gyri and right-lateralized response in the extrastriate cortex. Only logograms and objects produced a distinct cluster showing right-lateralized activation in the medial anterior fusiform gyrus associated with semantic knowledge, whereas only phonograms produced a left-lateralized activation in the posterior middle temporal cortex close to the site associated with visual perception of alphabetical letters. These findings suggest that while these stimuli similarly recruit the left perisylvian language area as a common neural component for naming, processing of objects and logograms becomes left-lateralized only in the downstream of the occipitotemporal cortex. By contrast, visual processing of phonograms is specialized to the left hemisphere in earlier stages of the area. The present data provide further evidence suggesting that both the left–right and anterior–posterior axes of the occipitotemporal cortex are differentially tuned according to the specific features of visual stimuli.

Keywords: Kana and kanji; Logograms; Occipitotemporal cortex

Introduction

Printed words constitute a specialized class of visual objects that can be rapidly recognized by human observers. Several lines of evidence indicate that the occipitotemporal cortex is differentially sensitive to visual objects of various categories, including faces and letters (Allison et al., 1994; Gauthier, 2000), and that such perceptual categorization occurs approximately 150–200 ms after the onset of the stimuli (Tarkiainen et al., 1999; Gros et al., 2002). Notably, faces and letterstrings each have been consistently associated with the right and left side of the region, suggesting that the inter-hemispheric difference already emerges at this part of the ventral temporal region for visual object recognition.

It remains unknown, however, whether such hemispheric specialization of object categories occurs similarly in visual perception of logographic characters. For instance, it has been postulated that the right hemisphere plays a special role in the visual recognition of Japanese kanji (Hatta, 1977; Sasanuma et al., 1977; Sugishita et al., 1986; Nakagawa, 1994). In fact, it is possible that neural representation of logograms is formed more like that of objects, because (1) this script system has evolved from the ancient pictograms and (2) reading of logograms and naming of objects have been thought to involve similar cognitive processes in

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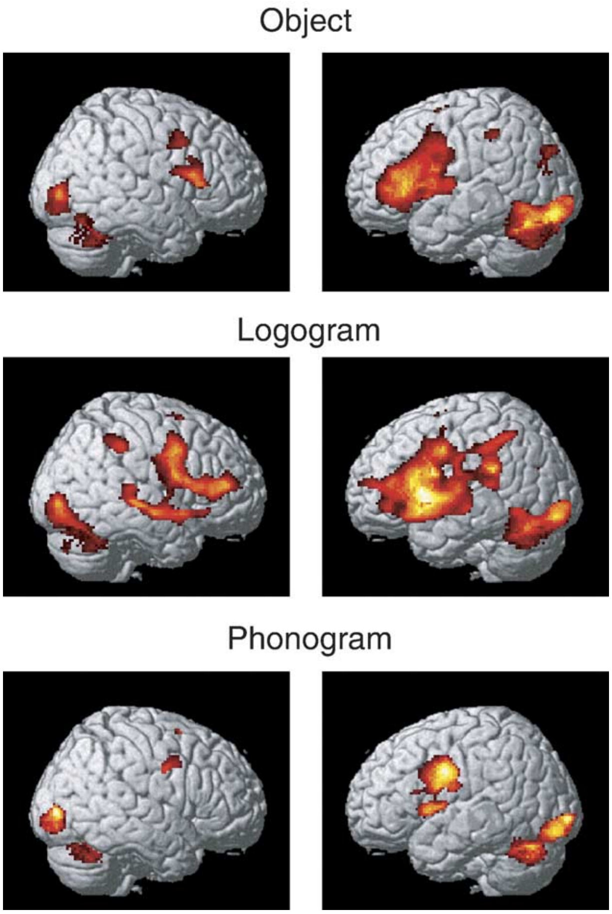

Fig. 1. Brain areas activated by the three naming tasks relative to their respective baseline (thresholded at voxel-level $P < 0.001$; spatial extent > 20 voxels). Irrespective of the stimulus type, activation of the fronto-parieto-temporal area spread more broadly in the left hemisphere.

the sense that both require the semantic access for phonological retrieval though some behavioral studies have shown that kanji phonology can be directly computed without recourse to semantics (Sasanuma et al., 1992; Wydell et al., 1993).

The main aim of the present study was to compare the pattern of hemispheric asymmetry in the occipitotemporal cortex among logograms, phonograms and objects. Although a few past studies have attempted to differentiate the brain activation during reading between logographic and phonographic writing systems (Chee et al., 2000; Sakurai et al., 2000; Fu et al., 2002), the possible inter-hemispheric difference of their respective neural representation has not been examined systematically using functional brain imaging. More importantly, several recent studies suggest that this region is composed of several subdivisions storing increasingly more abstract representations from posterior to anterior, not only for objects (Henson et al., 2000; Vuilleumier et al., 2002) but also for letterstrings (Dehaene et al., 2004). In this context, it will be expected that the lateralized neural response should appear at different stages of the ventral visual stream among the three types of stimuli, given the fact that they each should be associated with different kinds of representations (i.e., phonology for phonograms, phonology and semantics for logograms and visual semantics for objects).

Materials and methods

Participants

Eleven normal adults (age range 20–36 years) volunteered to participate in the present study. All of them were right handed, native Japanese speakers without history of neurological or psychiatric illness. Informed consent was obtained from each participant prior to the experiment. The protocol of this study was approved by the Committee of Medical Ethics, Fukui Medical University.

Behavioral tasks

Visual stimuli consisted of 30 line drawings of common objects, 30 kanji characters of high frequency and 30 kana characters. The objects were selected from the standardized set of Snodgrass and Vanderwart (1980). The kanji characters, each denoting a noun or morpheme of various categories, are pronounced most commonly in On-reading (a loaned pronunciation from Chinese), whereas the kana characters each represented a syllabic unit in Japanese. Participants named the objects or characters presented for 500 ms every 3 s in a pseudo-random

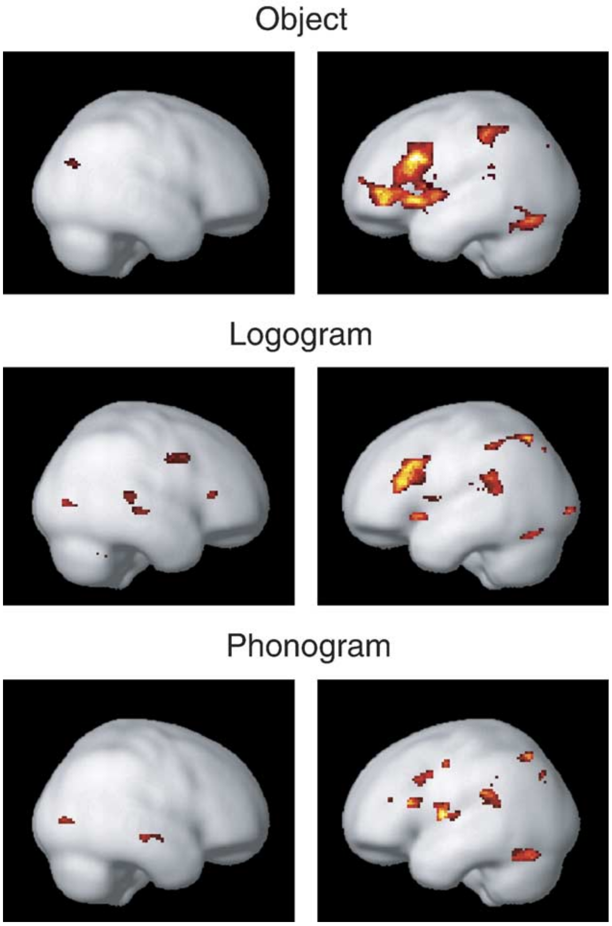

Fig. 2. Brain regions showing significant inter-hemispheric difference (thresholded at voxel-level $P < 0.001$; spatial extent > 20 voxels). Left and right panels each illustrate regions showing left- and right-predominant activations. The lateralized activations were overall distributed in the left fronto-temporo-parietal regions across the three tasks.

Table 1
Brain regions showing asymmetric activation for each type of the stimuli

Brain region	# voxels	*Z* score	Coordinates		
			x	*y*	*z*
Objects					
Left-predominant					
Insula	48	3.45	−40	4	9
Superior temporal gyrus	271	4.38	−46	−36	15
Supramarginal/angular gyri	385	4.38	−20	−62	36
Middle/inferior frontal gyri	1041	4.28	−44	28	13
	24	3.26	−32	6	49
	21	3.18	−30	4	40
Right-predominant					
Medial frontal gyrus	69	3.19	8	14	47
Middle temporal gyrus	24	3.34	36	−29	−7
Middle occipital gyrus	74	3.36	36	−76	28
	121	4.15	34	−81	6
Cerebellum	90	3.17	28	−58	−29
Logograms					
Left-predominant					
Superior temporal gyrus	232	4.03	−46	−36	15
Middle/inferior frontal gyri	1089	3.93	−44	21	27
Supramarginal/angular gyri	501	3.64	−20	−62	38
Right-predominant					
Medial frontal area	165	3.86	8	12	47
Mid occipital gyrus	26	3.78	34	−81	6
Phonograms					
Left-predominant					
Superior temporal gyrus	135	4.11	−46	−36	15
Supramarginal/angular gyri	59	3.29	−22	−64	35
	32	2.89	−50	18	16
	27	2.81	−55	−33	35
Right-predominant					
Medial frontal gyrus	77	3.52	10	12	47

order, and pressed an optical key with the right index finger immediately after the oral response (for kanji stimuli, participants were requested explicitly to pronounce them in On-reading). As a baseline condition, visual fixation of a central cross was used commonly for the three tasks.

fMRI procedure

Scanning was conducted with a 3 T whole-body MRI system (GE Signa, Horizon CX) using a standard head coil optimized for whole-brain echo-planar imaging (EPI). The blocked-design experiment for the naming tasks used a gradient echo EPI sequence with the following parameters: TR 3000 ms, TE 30 ms, flip angle 90°, field-of-view 22×22 cm^2 and pixel matrix 64×64. Thirty-six contiguous 3.5 mm thick slices with 0.5 mm gap were obtained in the axial plane for each participant. The three naming tasks each were performed in a separate scanning session. Each session included nine epochs alternating every ~30 s (four for task and five for baseline) and lasted 258 s, yielding 86 functional images per task per participant. Participants were reminded not to open the mouth wide to minimize the head motion during scanning. This same procedure has been employed in our previous studies (Nakamura et al., 2000, 2002). The visual stimuli for each task were presented in a pseudo-random order for each participant, while the task order was counterbalanced among participants.

Data analysis

After image reconstruction, the functional images were processed using the SPM99 software (Wellcome Department of Cognitive Neurology, London, UK). Three initial images were discarded to eliminate non-equilibrium effects of magnetization. Images were corrected for head motion, resampled every 2 mm using sinc interpolation, normalized to the standard brain space (Friston et al., 1995) and spatially smoothed with an isotropic Gaussian filter (7 mm full width at half maximum). The time-series for each voxel were high-pass filtered at 120 s and smoothed with a 4 s Gaussian kernel.

Random effect analysis (Friston et al., 1999) was used for the group-based statistical inference. For each participant, images of the weighted-sum of the parameter estimates were computed for each task relative to the baseline by fitting the fMRI time-series with a boxcar reference waveform convolved with a canonical hemodynamic response function. The contrast images per task per participant were subject to the second-level analysis using one-sample t test to examine overall brain regions activated by each task relative to the baseline (thresholded at voxel-level $P < 0.001$; spatial extent > 20 contiguous voxels). Also, the same contrast images were pooled across tasks and submitted to a one-sample t test to generate a masking image for subsequent analyses (voxelwise at $P = 0.05$).

For inter-hemispheric comparisons, the contrast images were flipped horizontally to create their respective left–right inverted images. A difference image for brain asymmetry was then computed per task per participant by subtracting these left–right inversions from the original contrast images. These difference images were submitted to one-sample t test to examine the overall pattern of hemispheric lateralization for each task (voxel-level $P = 0.001$; spatial extent > 20 voxels). For the specific purpose of the

Table 2
Regions showing asymmetric activation in the occipitotemporal cortex

Brain region	# voxels	*Z* score	Coordinates		
			x	*y*	*z*
Objects					
Left-predominant					
Superior temporal gyrus	170	3.47	−44	−34	15
Posterior fusiform gyrus	393	4.56	−42	−63	−14
Right-predominant					
Middle/inferior occipital gyri	206	3.51	40	−75	13
Anterior fusiform gyrus, medial	54	2.92	32	−35	−7
Middle temporal gyrus, lateral	26	2.86	59	−33	−3
Logograms					
Left-predominant					
Superior temporal gyrus	202	4.12	−42	−36	17
Posterior fusiform gyrus	182	3.58	−40	−69	−13
Right-predominant					
Anterior fusiform gyrus, medial	49	2.95	34	−35	−8
Middle occipital gyrus	126	3.60	32	−77	8
Phonograms					
Left-predominant					
Superior temporal gyrus	142	4.39	−42	−36	17
Posterior middle/inferior temporal gyri	56	3.43	−50	−68	0
Posterior fusiform gyrus	334	3.86	−42	−67	−17
Right-predominant					
Middle occipital gyrus	133	3.45	32	−75	7

study, clusters showing the hemispheric difference were searched in the occipitotemporal cortex using a volume of interest (VOI) covering most of the region (40 × 60 × 40 mm in dimension, centered at $x = \pm 40$ mm, $y = -60$ mm, $z = 0$ mm), for which a more lenient statistical cut-off was used to increase the sensitivity for detecting voxels showing the asymmetric response (voxelwise $P = 0.005$; spatial extent > 20 voxels). To protect against false positive errors, the inter-hemispheric difference at the locations identified in voxel-based analysis was further examined by comparing the percent signal change at the local maxima and 19 adjacent voxels (i.e., those located within 3 mm around the peak) obtained from the t statistics for each task. Only the regions surviving both voxelwise and VOI-based analyses were interpreted. Furthermore, for each of these regions, between-task difference in hemispheric asymmetry was confirmed voxelwise using one-way analysis of variance (ANOVA) in which the difference in brain asymmetry was measured as an interaction term between the three types of stimuli (i.e., object, logogram and phonogram). Brain regions were reported according to the stereotaxic atlas of Talairach and Tournoux (1988).

Results

Three naming tasks commonly activated the bilateral fronto-temporal and occipitotemporal areas, although these activation sites spread more broadly for logograms and objects than phonograms (Fig. 1). In the parietal regions, logograms and phonograms produced a larger activation site in the left supramarginal/angular gyrus than objects. Activation of the left inferior temporal/fusiform area was observed consistently across the three types of stimuli, while that of the right homologous area extended more anteriorly for objects and logograms than phonograms.

The inter-hemispheric comparison revealed that the brain activity during naming was overall lateralized to the left hemisphere regardless of the stimulus type (Fig. 2 and Table 1). This left-predominant response was distributed mainly in the perisylvian region and inferior parietal lobe, including the supramarginal gyrus. By contrast, right-predominant activation was found in the medial frontal area across the three types of stimuli. Additionally, objects and logograms showed right-lateralized response in the middle temporal and middle occipital gyri.

Asymmetric activations within the occipitotemporal areas are summarized in Table 2 and displayed in Figs. 3 and 4. Three types of stimuli commonly produced two distinct clusters showing left-lateralized activation in the middle portion of the superior temporal gyrus and the posterior fusiform gyrus. Right-predominant activation was observed in the lateral occipital area regardless of the stimulus type. In addition, objects produced two separate clusters showing right-predominant activation, one in a lateral part of the middle temporal gyrus and the other in a medial part of the anterior fusiform gyrus. The latter site exhibited a right-lateralized response similarly for logograms. These two stimuli produced no other cluster showing left-predominant activation. In contrast, phonograms produced a distinct cluster showing left-predominant activation in the posterior part of the middle/inferior temporal gyri,

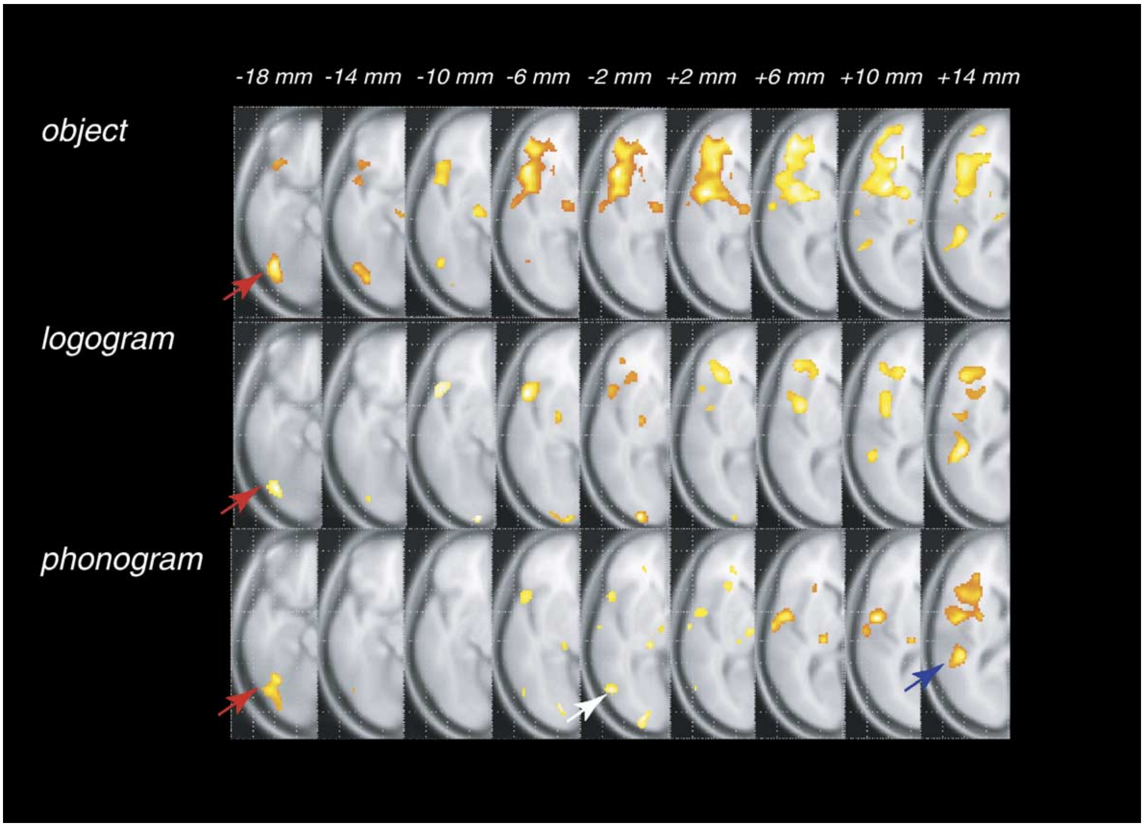

Fig. 3. Clusters showing left-predominant activation in the occipitotemporal cortex. The three types of stimuli commonly produced left-predominant activation in the superior temporal (blue) and posterior fusiform (red) gyri, while phonograms yielded an additional cluster in the posterior middle temporal region (white).

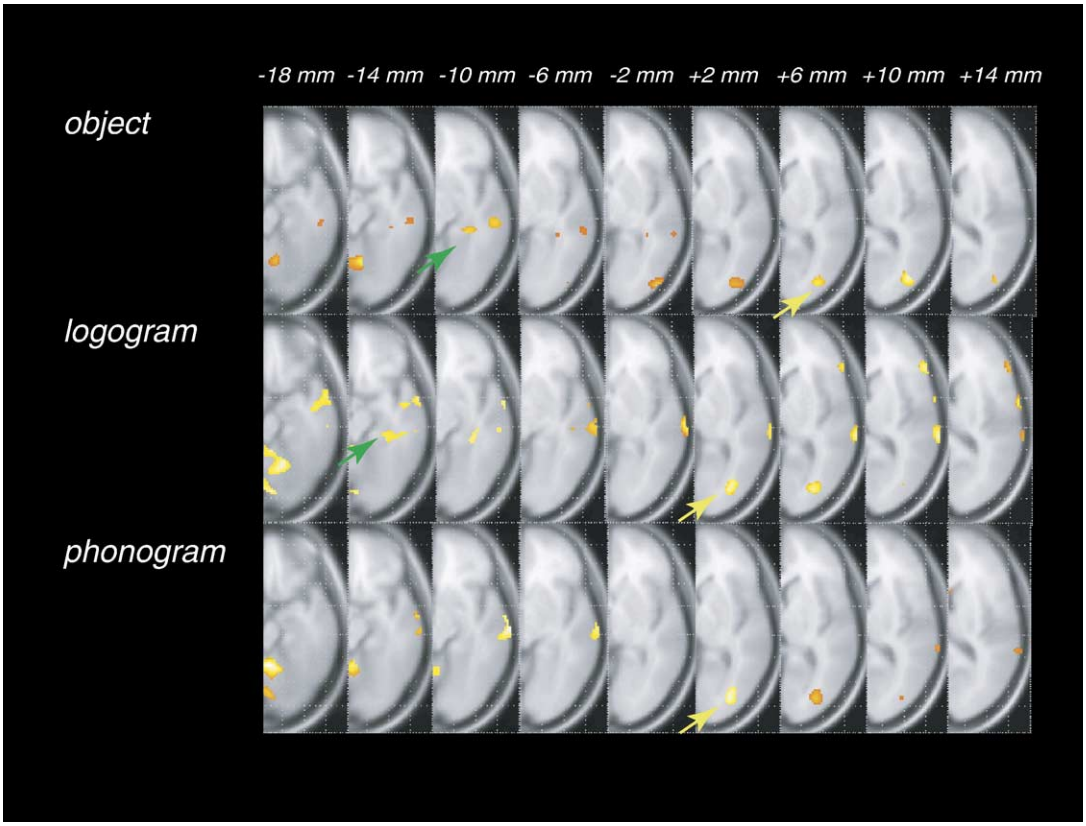

Fig. 4. Clusters showing right-predominant activation in the occipitotemporal cortex. The three stimuli produced right-lateralized response in the middle occipital gyrus (yellow). Only objects and logograms exhibited rightward lateralization in the anterior medial fusiform gyrus (green).

whereas they yielded no other cluster exhibiting right-predominant response.

As illustrated in Fig. 5, a paired *t* test for percent signal changes revealed a greater activation of the left hemisphere at the superior temporal gyrus and posterior fusiform area across the three types of stimuli ($P = 0.002$ for objects, $P < 0.001$ for logograms and $P < 0.001$ for phonograms; $P = 0.03$ for objects, $P = 0.006$ for logograms and $P < 0.001$ for phonograms, each respectively). The signal response from the lateral occipital area was significantly greater in the right hemisphere, irrespective of the stimulus type ($P = 0.005$ for objects, $P < 0.001$ for logograms and $P = 0.001$ for phonograms). The lateral middle temporal gyrus and medial anterior fusiform gyrus both exhibited greater response for objects and logograms ($P = 0007$ for objects $P = 0.006$ for logograms; $P = 0.02$ for objects and $P = 0.006$ for logograms, each respectively). The former area was inactive relative to the baseline during naming of phonograms, showing no inter-hemispheric difference ($P = 0.61$), while the latter area showed greater activation in the right side for phonograms ($P = 0.03$). By contrast, the posterior middle temporal gyrus responded more greatly in the left hemisphere only for phonograms ($P = 0.22$ for objects, $P = 0.75$ for logograms and $P = 0.001$ for phonograms). These results overall were in good accordance with those obtained from the voxel-based statistics.

Lastly, for the regions identified in the analyses above, the degree of hemispheric asymmetry was further compared among the three different stimuli. At the anterior part of the medial fusiform gyrus, objects and logograms showed greater trend of rightward lateralization than phonograms ($Z = 1.88$, $P = 0.03$ and $Z = 2.58$, $P = 0.005$, respectively), whereas the hemisphere lateralization did not differ between the former two stimuli ($Z = 0.93$, $P = 0.18$). The posterior middle temporal gyrus showed greater trend of leftward asymmetry for phonograms than the other two stimuli ($Z = 2.32$, $P = 0.010$ compared to objects and $Z = 2.11$, $P = 0.018$ compared to logograms, respectively). The inter-hemispheric asymmetry at this location did not differ between objects and logograms ($Z = 1.18$, $P = 0.12$). None of the other regions showed a significant hemispheric difference between the three types of stimuli ($P > 0.05$).

Discussion

Asymmetric activations common across the stimuli

The present data suggest that naming produces a similar, left-predominant activation of the fronto-parieto-temporal areas commonly across the three types of stimuli. This neural network comprises the inferior frontal gyrus, superior temporal gyrus and inferior parietal area in the left hemisphere that have been shown to be active during word production, including reading and naming (Price, 1998). In the occipitotemporal region, two different regions, one in the posterior end of the superior temporal cluster mentioned above and the other in the posterior fusiform

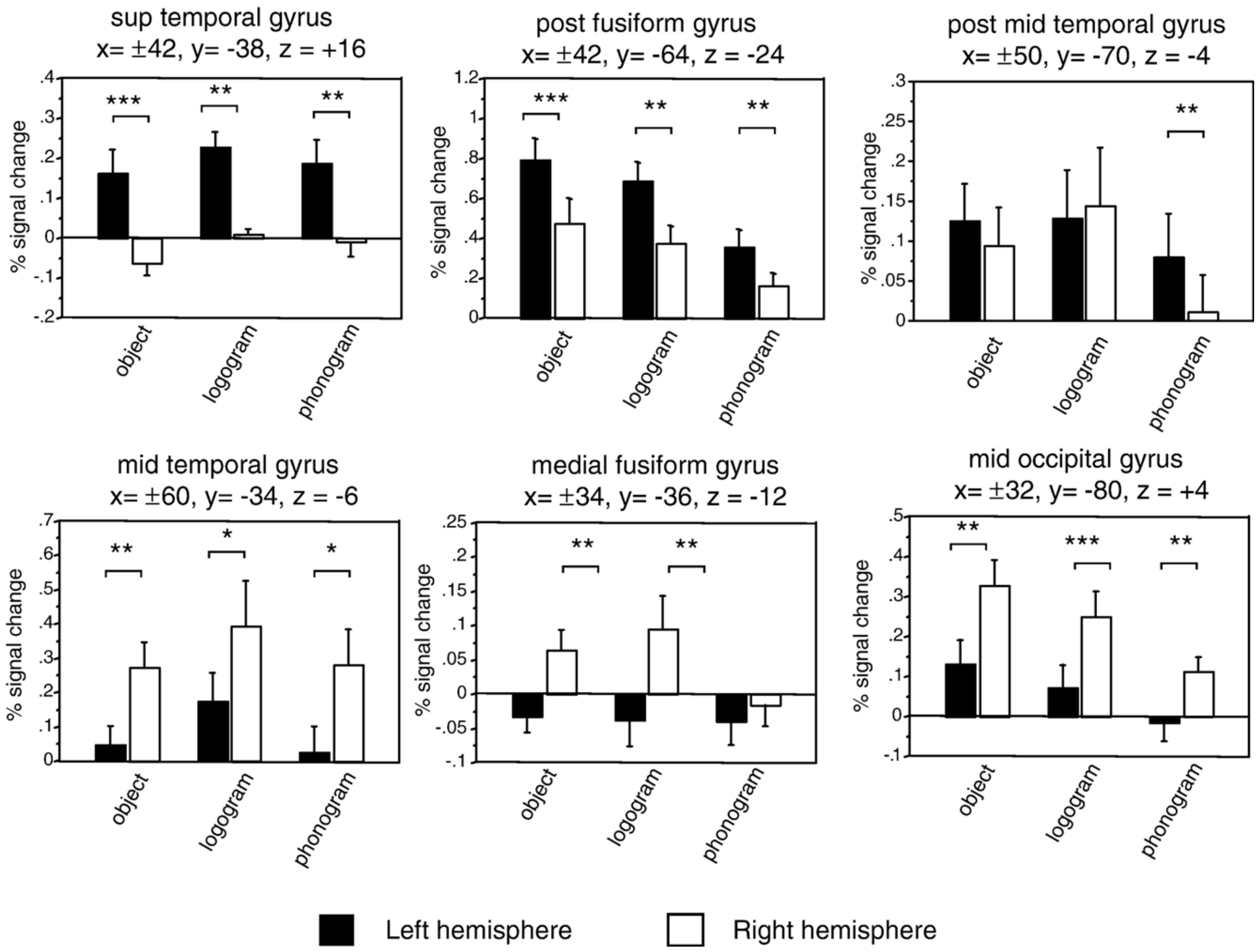

Fig. 5. Plots of percent signal change in the occipitotemporal cortex (inter-hemispheric difference significant at $P < 0.001$***, $P < 0.01$** and $P < 0.05$*). The superior temporal and posterior fusiform gyri showed left-predominant activation across the three types of stimuli, whereas the response of the middle occipital gyrus was greater in the right hemisphere irrespective of the stimulus type. Objects and logograms produced right-predominant response in the middle temporal and medial fusiform gyri, while phonograms left-predominant response in the posterior middle temporal gyrus.

gyrus, also exhibited left-lateralized response irrespective of the stimulus type.

Previous neuropsychological and brain imaging studies have consistently suggested that this left basal temporal area plays an important role in reading and naming (Fiez and Petersen, 1998; Foundas et al., 1998; Price, 1998). The present finding that the area showed a left-predominant response irrespective of the type of stimuli seems in accordance with the view that the area participates in word production by mediating the retrieval of phonology (Price, 1998). It is of note, however, that there is currently a controversy as to the precise nature of representation associated with this area (Cohen et al., 2000; Price and Devlin, 2003).

On the other hand, three types of stimuli commonly produced right-predominant activation in the medial frontal area and lateral occipital cortex. The former area is generally thought to be involved in motor aspect of speech production (Fiez and Petersen, 1998), of which it seems rather difficult at this point to give a physiological or psychological account for the observed right-dominance. In contrast, the rightward asymmetry of the latter area is consistent with a few neuroimaging studies suggesting that the lateral extrastriate cortex in the right hemisphere is sensitive to certain physical features of stimuli, such as changes of view-point for objects (Vuilleumier et al., 2002) and those of typographic case for letterstrings (Dehaene et al., 2001). Therefore, the observed asymmetry in this latter area is likely to reflect the process of computing the object shape that should work commonly across the three different stimuli.

Stimulus-specific asymmetries in the temporal cortex

We found that both objects and logograms produce right-predominant response in the medial anterior fusiform gyrus whereas phonograms did not exhibit this pattern of hemispheric asymmetry. Most neuroimaging studies to date have reported left-lateralized activation during reading of non-alphabetical orthographies such as Chinese (Tan et al., 2000; Kuo et al., 2001) and Japanese (Sakurai et al., 2000). However, the advantage of the right hemisphere in visual recognition of logograms has long been suggested by several lines of evidence, including behavioral (Hatta, 1977; Sasanuma et al., 1977; Nakagawa, 1994), neuropsychological (Sugishita and Yoshioka, 1987; Sugishita et al., 1986) and electrophysiological (Hatta et al., 1983; Hayashi et al., 1998; Yamaguchi et al., 2002) and magnetoencephalographic studies (Kamada et al., 1998), in which the right-predominant activity has been located in variously different brain regions, including fronto-central (Yamaguchi et al., 2002), parietal (Hayashi et al., 1998) and occipitotemporal cortices (Kamada et al., 1998). The present result therefore provides new evidence suggesting that logograms elicit a right-predominant activation at least in the medial part of the fusiform gyrus. It is interesting to note that this finding is comparable to a previous fMRI study suggesting the rightward asymmetry of this and adjacent area in the perception of logographic symbols such as '!' and '♂'(Henson et al., 2000).

Activation of the right medial fusiform gyrus has been reported by several neuroimaging studies using behavioral tasks requiring semantic processing of visual objects, including naming (Chao et al., 1999; Martin and Chao, 2001; Tyler et al., 2003). The notion that the anterior part of the ventral temporal cortex is associated with increasingly more abstract representations such as semantics has been suggested for different categories of visual stimuli, including faces (Henson et al., 2000; Vuilleumier et al., 2002) and words (Dehaene et al., 2004). In this context, the right-predominant activation of the anterior medial fusiform gyrus can be interpreted as reflecting the activation of semantic knowledge that both logograms and objects induce in the process of visual recognition, while the absence of such asymmetry for phonograms can be explained by the fact that this latter script is not directly associated with semantic properties. It is likely, however, that this right-predominant activation at this location represents a rather incidental phenomenon and not a mandatory process required for naming, since damage to this area usually causes no measurable impairment of this particular ability.

By contrast, phonograms produced a left-predominant response in the inferior occipitotemporal cortex. At this location, neither logograms nor objects exhibited the trend of lateralization. This finding suggests that the Japanese phonograms produce a similar pattern of hemispheric asymmetry as alphabetical letters, including single letters, non-word letterstrings and words (Dehaene et al., 2002; Gros et al., 2002; Tarkiainen et al., 2002). It is interesting to note that the observed focus showing the left-lateralized response is located in a part of the posterior temporal cortex approximately 15 mm superior to the region associated with the perception of alphabetical words (Cohen et al., 2000). This spatial discrepancy may relate to the fact that the phonographic characters of Japanese each represent a syllabic, that is, more coarse phonetic unit than phonemes, because it has been suggested that the left temporal cortex is differentially tuned according to the specific cognitive demand placed by the writing systems used (Paulesu et al., 2000; Cohen et al., 2002). In fact, neurolinguistic studies of Japanese have suggested that this dorsal lateral occipitotemporal area is important for reading of phonograms as a pathway linking the visual cortex and the inferior parietal area involved in orthography-to-phonology conversion (Iwata, 1986; Sakurai et al., 2001).

Conclusion

The present data suggest that naming of objects, logograms and phonograms activates the left perisylvian area quite similarly but recruits the bilateral occipitotemporal cortex to a different degree. In the latter region, logograms and objects showed a similar pattern of hemispheric asymmetry that is distinct from the one observed for phonograms. In this sense, it might be said that logograms act like objects or symbols within this region associated with more stimulus-specific cognitive processes whereas the leftward-lateralization common to the three types of stimuli appears only at more global or later processing stages associated with the perisylvian cortex.

Given the recent evidence that different neuronal clusters of the occipitotemporal area respond to various categories of visual objects, including faces, letters, animals, tools, houses and so on (Gauthier, 2000; Martin and Chao, 2001) and that the organization of brain systems for object naming changes as a function to perceptual experience (van Turennout et al., 2000), it is not very surprising that the processing stream of objects, logograms and phonograms is shaped differently in this region. For example, for normal readers, phonograms are acquired at an earlier stage of life, and used extremely frequently in everyday life than logograms. Such differences might eventually lead to the differential, script-specific organization of the occipitotemporal region.

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