

Essential role of the right superior parietal cortex in Japanese *kana* mirror reading

An fMRI study

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Summary

Functional magnetic resonance imaging (fMRI) was used to investigate the neural substrates responsible for Japanese *kana* mirror reading. Japanese *kana* words, arranged vertically from top to bottom, were used in the mirror reading task in 10 normal right-handed Japanese adults. Since both mirror-reversed and normally oriented *kana* items are read in the same (top to bottom) direction, it was possible to minimize the oculomotor effects which often occur in the process of mirror reading of alphabetical language. By using the SPM96 random effect analysis method, a significant increase in the blood oxygen level-dependent signal during mirror reading relative to normal reading was detected in multiple brain regions, including the bilateral superior occipital gyri, bilateral middle occipital gyri corresponding to Brodmann area (BA) 18/19, bilateral lingual gyri (BA 19), left inferior occipital gyrus (BA 18), left inferior temporal cortex

(BA 37), bilateral fusiform gyri (BA 19), right superior parietal cortex (SPC) (BA 7), left inferior frontal gyrus (BA 44/45) and an inferior part of the left BA 6. In addition to these cortical regions, the right caudate nucleus and right cerebellum were also activated. The activation found in the right SPC and the left inferior temporal region is consistent with the hypothesis that mirror reading involves both the dorsal visuospatial and ventral object recognition pathways. In particular, a significant correlation was found between the fMRI signal change in the right SPC and the behavioural performance (error index) in the task. This may reflect increased demand on the right SPC for the spatial transformation which is required for the accurate recognition of mirror-reversed *kana* items. This relationship between the haemodynamic response in a specific brain area and the behavioural data provides new evidence for the essential role of the right SPC in Japanese *kana* mirror reading.

Keywords: mirror reading; Japanese *kana* words; right superior parietal cortex; fMRI

Abbreviations: BA = Brodmann area; EI = error index; ERm = error ratio for mirror-reversed items; ERn = error ratio for normally oriented items; FG = fusiform gyrus; fMRI = functional MRI; RT = reaction time; SPC = superior parietal cortex

Introduction

Mirror phenomena in language, which include mirror writing and reading, are characterized by writing or reading which runs in the opposite direction to normal writing or reading, with reversals of words and letters. Normal subjects can produce mirror writing when they are asked to write on their forehead or on the underside of a table (Wade and Hart, 1991) and can acquire the mirror writing skill with great initial improvement and relative long-term retention (Marks, 1996). Investigation of perceptual motor skill learning using mirror drawing in patients with Alzheimer's disease and

amnesia revealed intact acquisition and long-term retention of the skill similar to those in normal controls (Gabrieli *et al.*, 1993). Compared with mirror writing, mirror reading has been employed and examined more in the investigation of perceptual visual skill learning.

Knowledge about the neural basis involved in acquisition of the mirror reading skill comes from neuropsychological studies of patients and, more recently, from functional imaging studies in normal humans. Neuropsychological studies revealed that amnesic patients showed normal learning of

the mirror reading skill, despite their inability to recognize the previously presented items (Cohen and Squire, 1980; Martone *et al.*, 1984), and that patients with Huntington disease showed some impairment in learning the mirror reading skill (Martone *et al.*, 1984). Thus, acquisition of the mirror reading skill may not involve the cortical regions including the medial temporal lobes which are damaged in amnesia, but may involve the striatum which is primarily affected in Huntington disease. Neuroimaging studies provided some evidence for the function of various parietal regions in the mental rotation of two- or three-dimensional objects (Cohen *et al.*, 1996; Alivisatos and Petrides, 1997), as well as in reading mirror-reversed letter strings (Goebel *et al.*, 1998; Poldrack *et al.*, 1998a). The study done by Poldrack and colleagues suggested that mental processing of mirror reading may require an interaction of visuospatial transformation and linguistic recognition (Poldrack *et al.*, 1998a). Therefore, it is postulated that both the regions in the dorsal visual pathway, such as the superior parietal cortex (SPC), and those related to object recognition mediated by the ventral visual pathway might be involved in mirror reading. However, which brain areas are essential for the processing of mirror reading is still unknown.

In the mirror reading task employed in the study of Poldrack and colleagues, English words were presented in a mirror-reversed manner for the subjects to read (Poldrack *et al.*, 1998a). Thus, they had to read the mirror-reversed words from right to left, whereas they read the normally oriented words from left to right. To overcome the inconsistency in the reading direction between normally oriented and mirror-reversed English words, we chose Japanese *kana* words which could be arranged vertically. In the mirror reading task employed in this study, therefore, mirror-reversed words can be presented vertically and read in the same top to bottom direction as normally oriented words. In this way, we could minimize the effects of eye movements that often occur in the traditional mirror reading task employing the alphabet.

The purpose of this study was to clarify the functional anatomy of Japanese *kana* mirror reading without oculomotor effects by using functional MRI (fMRI). In particular, by examining the relationship between behavioural performance in the mirror reading task and the functional activation of brain areas related to the task, we identified the brain areas that are crucial for mirror reading.

Subjects and methods

Subjects

Ten normal volunteers (mean age 26.4 ± 4.5 years; seven male and three female) participated in this study. Handedness of the subjects was tested by the Edinburgh handedness inventory (Oldfield, 1971), and all of them were judged to be right-handed (mean handedness score = 1.84 ± 0.83). All the subjects were native Japanese speakers. The protocol of this study was in accordance with the guidelines issued by the Committee of Medical Ethics, Graduate School of Medicine and Faculty of

	Condition	
	Mirror-reversed	Normally Oriented
Word	ひ ま わ り	ひ ま わ り (sunflower)
Non-word	ち く ら	ち く ら

Fig. 1 Examples of Japanese *kana* words and non-words used in the mirror reading task. Each word is composed of three or four Japanese *kana* phonograms, and presented in the top to bottom direction. The non-word in this case was created from a real word (meaning cherry blossom) by replacing the top phonogram.

Medicine, Kyoto University. Informed consent was obtained from each subject after the details of the protocol had been explained to them.

Word stimuli

Japanese words written in *kana* were chosen from the vocabulary of a Japanese high school textbook. Each word used here was composed of three or four Japanese *kana* phonograms that were arranged vertically from top to bottom (Fig. 1). For each word, a pronounceable non-word was created by replacing just one or two *kana* phonogram(s) by other(s).

Experimental design

Each subject underwent two consecutive fMRI scanning sessions on the same day, and the time interval between the two sessions was 2 min. Each session consisted of six blocks, each block lasting 30 s. Within each session, three blocks each for the mirror-reversed and normally oriented conditions were given in alternating sequence (Fig. 2). Each subject underwent the same sequence for the two sessions, and the type of condition for the initial block was counterbalanced across the subjects. For both conditions, the subjects performed a lexical decision task (word/non-word judgement) on the visually presented items. Within each block, 12 items (six each for words and non-words) were presented in random order, each item for 2000 ms, with a 500 ms interstimulus interval. For each subject, all items presented within the two scanning sessions were novel, and none of them appeared in the training sessions. In order to monitor the subject's response, two keys were placed under the index and middle fingers of the right

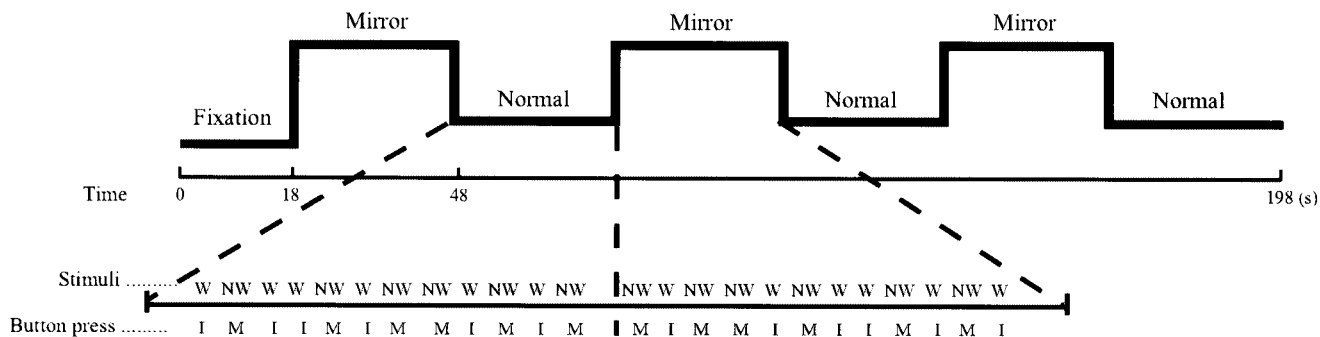


Fig. 2 Experimental block design used in the present fMRI study. Numbers indicate the time in seconds after the beginning of the session. After an 18 s fixation period, subjects performed a lexical decision task (word/non-word judgement) on the items presented in either the mirror-reversed or normally oriented condition, which alternated. In each block lasting 30 s, 12 items were presented, six each for words and non-words in random order. Each item was shown for 2000 ms with a 500 ms interstimulus interval. W, word; NW, non-word; I, index finger; M, middle finger.

hand. The subjects were told to press the key under the index finger if the item appearing on the screen was a word, and to press the key under the middle finger if it was a non-word. Before scanning, three training sessions similar to the scanning session were given to each subject.

The word stimuli were generated by using SuperLab software (Cedrus, Phoenix, Ariz., USA) on a Macintosh computer (Apple Computer Inc., Cupertino, Calif., USA), and back projected onto a screen located 40 cm in front of the subject's eyes by a video projector. During scanning sessions, the visual angle subtended by *kana* stimuli was 4° horizontally, and ranged between 17° (for three *kana* strings) and 24° (for four *kana* strings) vertically. An open circle presented in the centre of the screen served as the target for fixation. The response parameters consisting of reaction times (RTs) and accuracy of the lexical decision task were collected on a Macintosh computer interfaced with the above-described two keys through optical fibres.

fMRI procedure

After the three training sessions, the subjects lay supine on the MRI scanner. Head motion was minimized by applying foam padding. The fMRI scanning was performed with a 1.5 T whole-body scanner (Horizon, GE Medical, Milwaukee, Wis., USA) using a single shot EPI (echo planar imaging) sequence with parameters of TR = 6000 ms, TE = 43 ms, flip angle = 90° , field of view (FOV) = 220×220 mm, 64×64 matrix, 3.5 mm thickness without a gap, and 38 axial slices covering the whole brain. In each session lasting 198 s, 33 functional images were acquired. The first three images corresponding to the rest condition (fixation at a visual target) were excluded from the analysis because of the instability of the MRI signal. Thus, the remaining 30 images included three blocks of mirror reading alternated by three blocks of normal reading. A T_1 -weighted 3D anatomical image of each subject was obtained after the functional measurements.

Data analysis

Functional image processing was performed on an ULTRA-2 workstation (Sun Microsystems, Mountain View, Calif., USA). After image reconstruction, data were analysed with SPM96 (Wellcome Department of Cognitive Neurology, London, UK; Friston *et al.*, 1995). Images were realigned to correct for intrascan and interscan movements, co-registered with each subject's structural MRI and spatially normalized to allow group analysis. Afterwards, data were smoothed spatially in three dimensions with an isotropic 7.5 mm Gaussian filter in order to account for residual intersubject difference.

To detect the brain areas commonly activated among 10 subjects during mirror reading compared with normal reading, we used the random effect model kit of SPM96, which was designed for multi-subject statistical analysis (Holmes and Friston, 1998). In the random effect model, the fMRI series of each subject was correlated initially with a box-car reference function to compute individual level activation parameter α , where a high pass filter (0.5 cycles/min) and temporal smoothing were applied to remove low frequency noise or drift of MRI signals and to enhance the signal-to-noise ratio, respectively. As a result, images of the estimated activation α were computed as an adjusted mean image per condition for each subject. For the inter-subject analysis, a paired *t*-test was applied to the adjusted mean images by using the PET routine of SPM96. The threshold for statistics was set at $Z > 3.09$, i.e. $P < 0.05$ corrected for multiple comparisons following the theory of Gaussian fields. A statistical parametric map across subjects was created. Activated brain structures were identified by transforming the MNI (Montreal Neurological Institute) coordinate system of SPM96 into the standard brain atlas of Talairach and Tournoux (Talairach and Tournoux, 1988; Evans *et al.*, 1994).

RTs and accuracy in the lexical decision task were analysed by repeated measures ANOVA (analysis of variance). The accepted statistical significance level was $P < 0.05$. All *P*-values for repeated measures ANOVA reflect the Huynh-Feldt correction for non-sphericity. To determine the relation-

Table 1 Behavioural data of Japanese kana mirror and normal reading tasks for each of the two scanning sessions (mean \pm standard deviation)

Conditions	Session	Accuracy		RT (ms)
Mirror-reversed	1	0.88 \pm 0.02	Word	1296 \pm 171
			Non-word	1683 \pm 355
	2	0.88 \pm 0.03	Word	1294 \pm 205
			Non-word	1629 \pm 340
Normally orientated	1	0.94 \pm 0.01	Word	839 \pm 77
			Non-word	989 \pm 82
	2	0.95 \pm 0.02	Word	862 \pm 126
			Non-word	948 \pm 74

RT = reaction time.

ship between fMRI signal changes (signal intensities during the mirror-reversed condition minus those during the normally oriented condition) and behavioural performance in the mirror reading task, the error index (EI) was adopted as the representation of the behavioural parameters. Using the error ratio for mirror-reversed items (ER_m) and that for normally oriented items (ER_n), EI was calculated according to the formula; $EI = (ER_m - ER_n) / (ER_m + ER_n)$. ER_m was the number of errors divided by the total number of stimuli in the mirror-reversed condition, while ER_n was the number of errors divided by the total stimulus number in the normally oriented condition. In the calculation of fMRI signal change, we chose the local maxima (the voxel with peak *Z* value) in the activated regions and assigned each voxel to a region of interest based on its Talairach coordinate. The fMRI signal change as well as the EI across the two scan sessions was averaged for each subject. Pearson's correlation coefficient was calculated to examine the correlation between the EI and fMRI signal change at each assigned activated region. Furthermore, in terms of all the voxels showing significant activation during mirror reading relative to normal reading, the correlation between the EI and fMRI signal change was calculated on a voxel-by-voxel basis using the general linear model, in which the fMRI signal change at each voxel was explained by the EI as a covariate of interest. The threshold for the correlation map was set at $Z = 2.33$ without correction for multiple comparisons.

Results

Behavioural data

RTs and accuracy data for the two scanning sessions under each condition are presented in Table 1. There was no significant difference in RTs between the two successive sessions in either the mirror-reversed or normally oriented condition [$F(1,9) = 3.35, P > 0.05$]. Thus, no learning effect was found from the first to the second session in either condition. The mirror-reversed non-word decision required the longest RTs for correct responses (mean of the two sessions; 1656 ms), followed by the mirror-reversed word (1295 ms), the normally oriented non-word (969 ms) and the normally oriented word (851 ms)

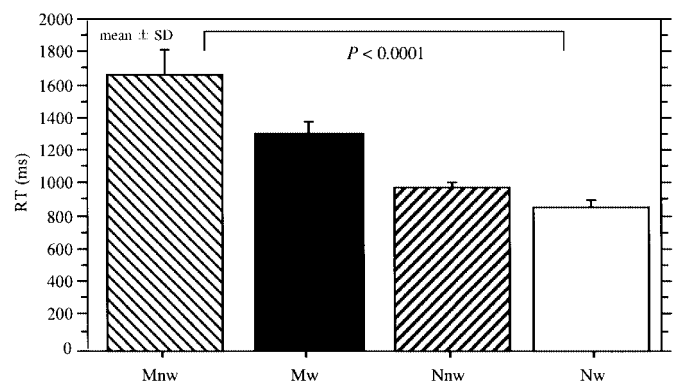


Fig. 3 Reaction times (RTs) in milliseconds (mean \pm standard deviation) for correct responses in the lexical decision task in Japanese *kana* mirror and normal reading in 10 subjects. Stimulus conditions are as follows: Mw, mirror-reversed words; Mnw, mirror-reversed non-words; Nw, normally oriented words; and Nnw, normally oriented non-words. A significant difference was found among conditions [$F(3,9) = 55.32, P < 0.0001$, repeated measures ANOVA].

[$F(3,9) = 55.32, P < 0.0001$] (Fig. 3). The stimulus condition \times session interaction for RTs was close to statistical significance [$F(3,27) = 2.33, P = 0.097$], which reflected the tendency that RTs for non-words decreased from session 1 to session 2, whereas RTs for words remained constant.

The accuracy for the normally oriented items was higher than that for the mirror-reversed items including both words and non-words [$F(1,9) = 96.20, P < 0.0001$], and there was no significant increase in accuracy from the first to the second session [$F(1,9) = 0.10, P > 0.05$] (Fig. 4). No significant stimulus condition \times session interaction was found for accuracy [$F(1,9) = 1.90, P > 0.05$].

fMRI findings

Enhanced activation during mirror reading relative to normal reading was found in the bilateral occipital regions, bilateral temporal regions, left frontal region, right superior parietal region, right caudate nucleus and right cerebellum (Fig. 5). The location of the activation on the Talairach and Tournoux coordinates is shown in Table 2. In the occipital lobe, activation

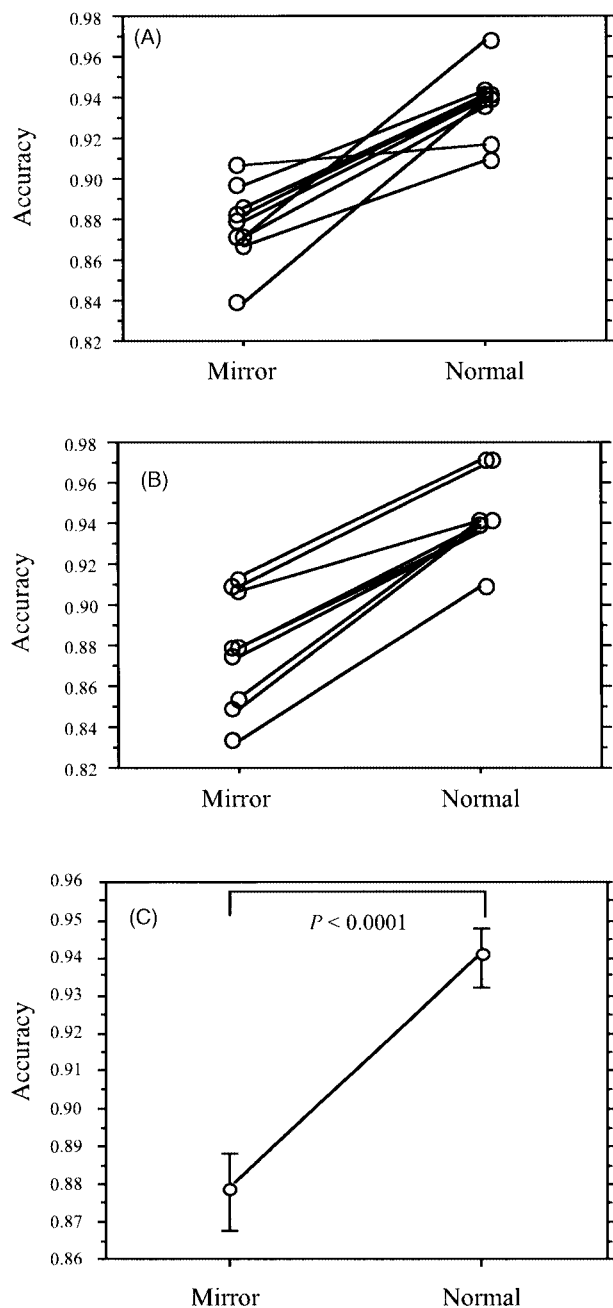


Fig. 4 Accuracy of the responses for mirror-reversed and normally oriented items in the first (A) and the second (B) scan session for each subject and the mean data across 10 subjects (C). (A and B) Accuracy for normally oriented items was higher than that for mirror-reversed items equally in the two sessions. (C) A significant difference in accuracy was found between mirror-reversed and normally oriented items [$F(1,9) = 96.20$, $P < 0.0001$, repeated measures ANOVA]. Accuracy = the number of correct responses including both words and non-words divided by the total number of stimuli.

was identified bilaterally in the superior and middle occipital gyri, which correspond to Brodmann area (BA) 18 or 19, partially extending to the parieto-occipital sulci. Additionally, activation in the left inferior occipital gyrus (BA 18) was observed, which extended laterally to the occipitotemporal

sulcus and ventrally from the lingual gyrus to the posterior part of the fusiform gyrus (FG). Temporal lobe activation was detected in a part of the left inferior temporal gyrus (BA 37) and bilateral FG (BA 19). In the parietal lobe, a consistent activation was found in the right SPC (BA 7), including a part of the intraparietal sulcus. Frontal lobe activation was observed in the inferior part of the left BA 6 and the left inferior frontal gyrus (Broca's area, BA 44/45). In addition to the cortical areas, activation was seen in the right cerebellum and the right caudate nucleus.

Among the activated brain regions, including the bilateral superior occipital gyri, bilateral middle occipital gyri, bilateral lingual gyri, left inferior occipital gyrus, bilateral FG, right SPC, left inferior temporal region, Broca's area, left inferior BA 6, right cerebellum and the right caudate nucleus, a statistically significant correlation between the EI in the mirror reading task and the fMRI signal change was found only in the right SPC by Pearson's correlation coefficient ($n = 10$, $r = 0.79$, $P < 0.005$) (Fig. 6A). Additionally, Broca's area showed a marginally significant correlation between fMRI signal change and the EI ($n = 10$, $r = 0.59$, $P = 0.075$). The r and P scores of Pearson's correlation coefficient for each activated region are listed in Table 2. Furthermore, significant correlation between fMRI signal change and the EI was evident in 73 contiguous voxels in the right SPC (Fig. 6B).

Discussion

In the present study, we employed the Japanese *kana* mirror reading task to demonstrate the functional anatomy involved in this special kind of reading skill. First of all, we emphasized the advantage of using Japanese *kana* words instead of English words in the mirror reading task. Japanese *kana* words can be arranged vertically from top to bottom, so that both normally oriented and mirror-reversed *kana* words can be read in the same top to bottom direction. This can help to minimize eye movements that are most probably related to the direction of the alphabetical mirror reading that is opposite to that of normal reading. In conventional English mirror reading, therefore, the oculomotion-related brain areas such as the frontal eye fields, intraparietal sulcus and posterior parietal regions might be activated.

Since visual transformation tasks often involve eye movements, the localization of the spatial process or spatial transformation requires the distinction between networks involved in each of the two processes (Milner and Goodale, 1995). Goebel and colleagues tried to separate the respective contributions of oculomotion and spatial transformation to mirror reading by means of a control condition involving the execution and suppression of eye movements (Goebel *et al.*, 1998). In their study, both the oculomotor control and the inverted reading tasks activated the frontal eye fields and superior parietal lobules bilaterally. Finally, the posterior part of the intraparietal sulcus, an area that showed high activation associated with inverted reading but not with the task involving eye movements, was specified to respond in the spatial

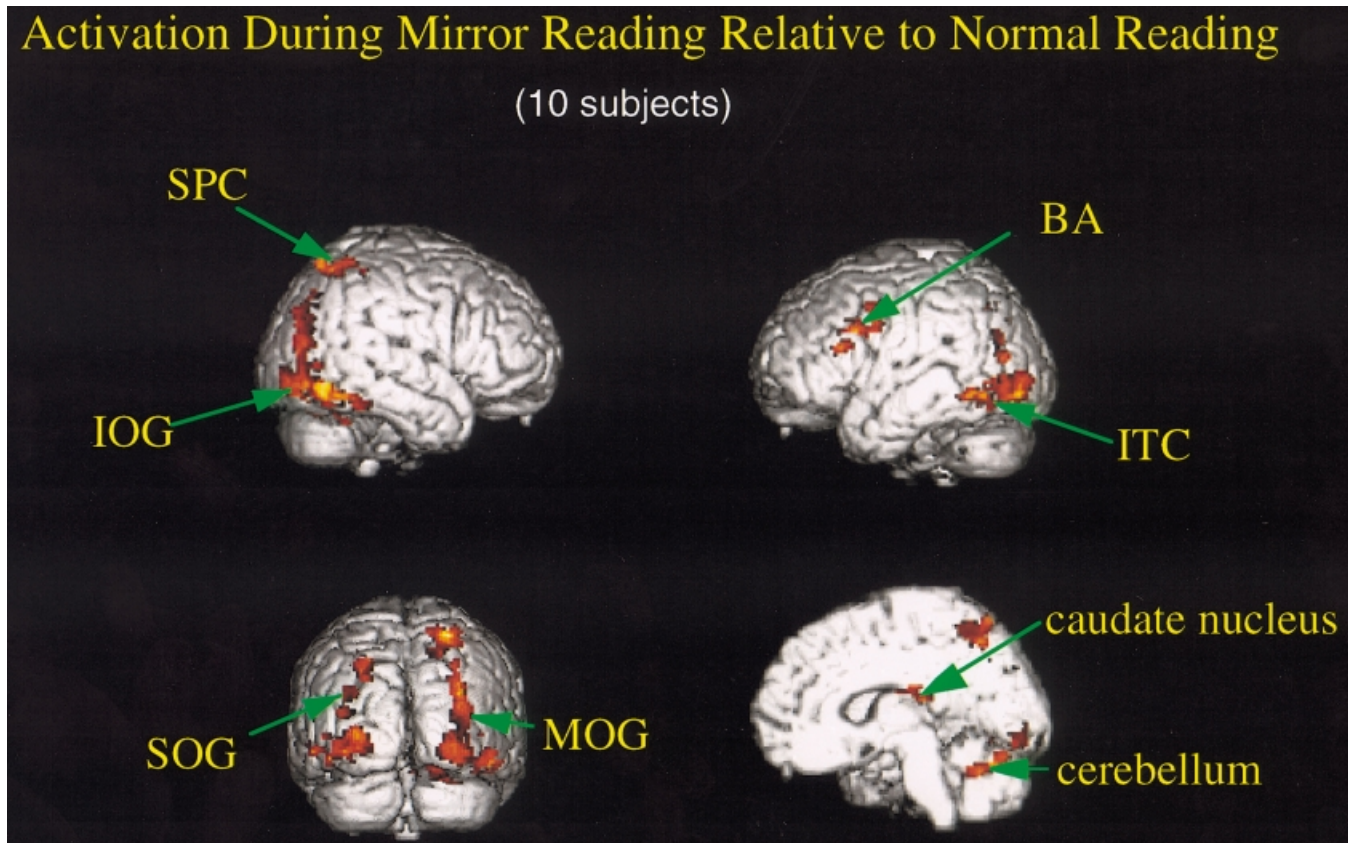


Fig. 5 Enhanced activation during mirror reading relative to normal reading, rendered onto a standard 3D anatomical template. The random effect model kit of SPM96 for multi-subject statistical analysis was used to detect the common activation among 10 subjects during mirror reading relative to normal reading, with the threshold of Z score > 3.09 . The activated cortical regions including the right superior parietal cortex (SPC), the right inferior occipital gyrus (IOG), the right middle occipital gyrus (MOG), the left superior occipital gyrus (SOG), the left inferior temporal cortex (ITC) and Broca's area (BA), and subcortical activation including the right cerebellum and the right caudate nucleus are shown.

Table 2 Significantly activated brain regions during Japanese kana mirror reading relative to normal reading and their correlation coefficient with EI

Location	BA	Talairach coordinates			Z score	Correlation coefficient ($n = 10$)	
		x	y	z		r-value	P-value
R inferior occipital/lingual gyrus	18, 19	34	-76	-4	6.67	0.353	0.329
R middle occipital gyrus	18	34	-78	18	4.70	0.239	0.519
R fusiform gyrus	19	30	-82	-10	5.23	-0.346	0.340
R superior occipital gyrus	19	28	-80	34	4.12	-0.016	0.967
R superior parietal cortex	7	26	-54	56	5.33	0.793	0.004
L superior occipital gyrus	19	-22	-66	42	6.00	0.261	0.481
L middle occipital gyrus	19	-44	-64	0	4.39	0.401	0.261
L inferior occipital gyrus	18	-28	-82	4	5.76	0.392	0.274
L lingual gyrus	19	-32	-74	0	4.61	0.217	0.561
L fusiform gyrus	19	-32	-78	-8	5.51	0.289	0.432
L inferior temporal gyrus	37	-46	-54	-6	4.79	-0.258	0.485
L inferior frontal gyrus	44, 45	-40	18	22	4.43	0.587	0.075
L precentral gyrus	6	-52	0	34	4.80	0.175	0.641
R cerebellum		22	-58	-24	4.50	0.076	0.841
R caudate nucleus		22	-20	22	4.62	0.239	0.519

BA = Brodmann area; EI = error index; r and P values calculated by Pearson's correlation coefficient.

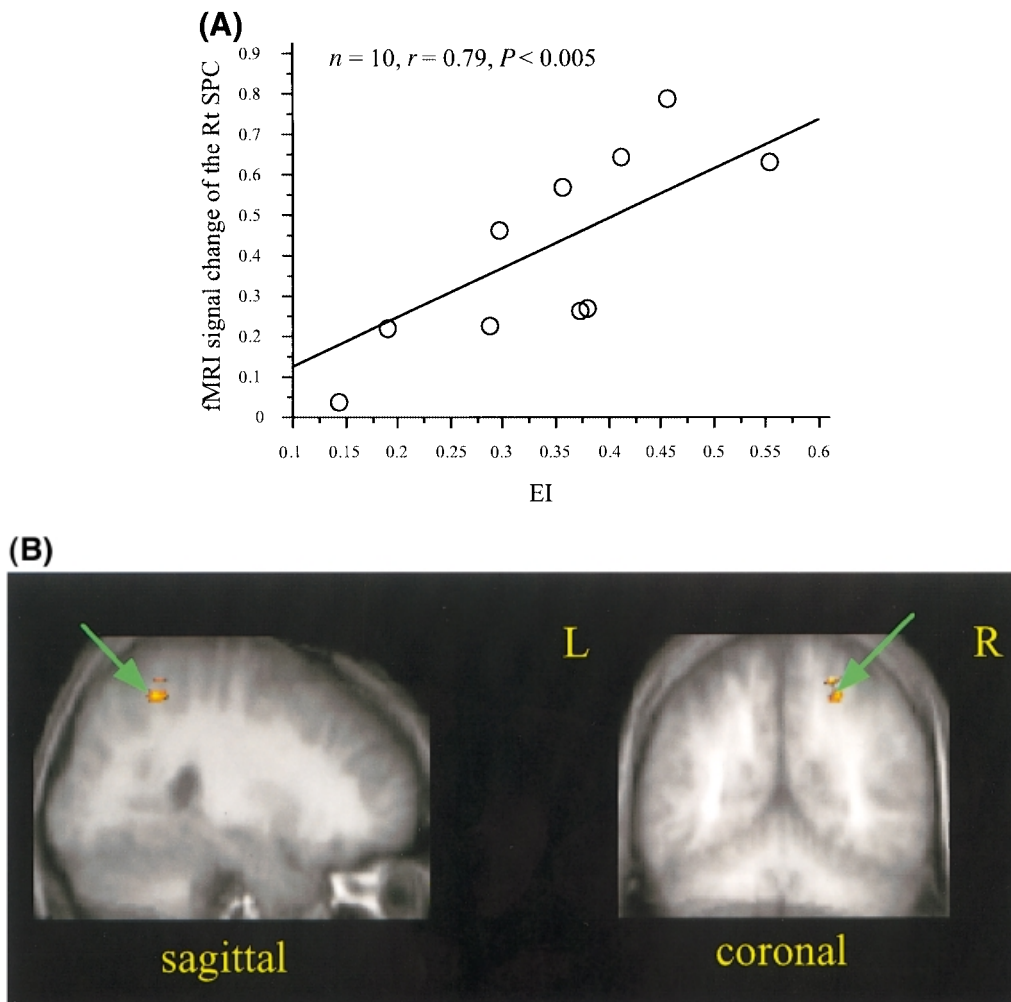


Fig. 6 Correlation between fMRI signal change in the right SPC ($x = 26, y = -54, z = 56$), corresponding to the local maxima in the right superior parietal region and the behavioural data (EI) in 10 subjects (A), and the right SPC activation which significantly correlated with EI (B). (A) There is a significant positive correlation between fMRI signal change in the right SPC and the EI (Pearson's correlation coefficient, $n = 10, r = 0.79, P < 0.005$). $EI = (ER_m - ER_n)/(ER_m + ER_n)$, where ER_m and ER_n are the error ratios for mirror-reversed and normally oriented items, respectively, including both words and non-words. (B) The right SPC activation showing significant correlation with EI includes 73 voxels in size. The activation is overlaid on the mean MRI of the subjects. The threshold for display was set to $P < 0.01$.

transformation of inverted letter strings. However, since the intraparietal sulcus was shown to be related to the direction of eye movements (Petit *et al.*, 1996), it seems that the postero-superior parietal region is a special area which is involved in co-activated networks of visuospatial transformation and oculomotion during mirror reading. Therefore, it is necessary to differentiate the two activation resources when investigating the neural basis of mirror reading. Thus, the Japanese *kana* mirror reading task, by minimizing the effect of 'contamination' due to eye movements, is useful for solving this problem. As we expected, there was no activation detected in the frontal and parietal eye fields in the present mirror reading task.

We focused on the activation in the right SPC, and investigated whether or not this area is responsible for successful mirror reading. When performing Japanese mirror reading, one needs to transform the individual mirror-reversed

kana spatially in order to match its normal representation, which seems to require substantial visuospatial transformation. Therefore, it is expected that the dorsal visuospatial stream, which is thought to project from the occipital cortex to the parietal region and to participate in the computation of extrapersonal and personal spatial localization (Mishkin *et al.*, 1983; Ungerleider and Haxby, 1994), is involved in the processing of mirror reading. We proposed that the activation detected in the right SPC is associated with spatial transformation of mirror-reversed *kana* items. This hypothesis is supported by recent neuroimaging studies. In a PET study carried out by Alivisatos and Petrides, activation in the right postero-SPC was observed in the discrimination task of the mirror image which required spatial transformation of reversed letters (Alivisatos and Petrides, 1997). More recently, Poldrack and colleagues reported bilateral parietal activation during mirror reading of letter strings, with the right superior parietal region showing a

learning-related decrease in activation (Poldrack *et al.*, 1998a). Our result suggests that the visuospatial transformation of Japanese *kana* might be implemented primarily in the right hemisphere.

In order to determine the brain areas essential for successful mirror reading, we evaluated the relationship between the behavioural performance represented by EI and the fMRI haemodynamic response in the activated brain regions. As a result, the right SPC was the only area where a statistically significant correlation between these two indices was found. In a PET study (Sadato *et al.*, 1996), the right dorsal premotor cortex and the right precuneus showed a linear increase of rCBF (regional cerebral blood flow) as the sequence complexity increased during complex finger movement. Their finding indicated that increased demands on brain activities due to performance of a difficult task result in the increase of haemodynamic response in the related brain areas. Recently, by adopting the mental rotation task of Shepard and Metzler (Shepard and Metzler, 1971), Carpenter and colleagues quantitatively investigated the relationship between the graded amount of rotation demand, as expressed in increasing angular disparity, and the amount of fMRI-measured cortical activation (Carpenter *et al.*, 1999). They found that activation in the bilateral parietal regions increased linearly with the increase of angular disparity. The results indicate that the amount of computational demands on visuospatial processes is related to fMRI-measured brain activation. In our study, since the EI was calculated from the difference between the error ratio for mirror reading and that for normal reading, this behavioural index could be considered to represent the degree of failure in spatial transformation of mirror-reversed items. It is reasonable to suppose that the more difficult stimuli would impose the higher demands on their spatial transformation, which could cause increased demands on processing by the SPC, resulting in its increased activation and, at the same time, would also increase the probability of errors. Thus, the correlation between fMRI signal change in the right SPC and the EI may reflect excessive demands on that area for the spatial transformation which is required for accurate recognition of mirror-reversed *kana*. Therefore, by determining the correlation between functional brain activity and behavioural performance, our study provided new evidence on the crucial role of the right SPC in Japanese *kana* mirror reading.

With regard to the activation of the frontal lobe in the Japanese *kana* mirror reading task, a part of the inferior frontal gyrus corresponding to Broca's area (BA 44/45) was activated during mirror reading relative to normal reading. Since none of the subjects spoke during the scan, it is unlikely that the activation is related to speech itself. However, one possibility is that this activation might reflect some internal speech (Hinze *et al.*, 1993). Recent neuroimaging studies provided some evidence that Broca's area mediates storage of verbal information (Fiez *et al.*, 1998; Smith and Jonides, 1998). Verbal storage can be decomposed further into a phonological buffer for short-term maintenance of phonological information and a subvocal rehearsal process that refreshes the contents of the

buffer (Smith and Jonides, 1999). We postulate that the activation of the inferior frontal gyrus might have resulted from phonological maintenance during performance of the lexical decision on mirror-reversed items compared with normally oriented items. As discussed above, it is especially noteworthy that normally oriented words can be recognized as a whole, while the mirror-reversed words have to be read at the phonogram-to-phonogram level, which obviously requires a temporary storage of the previously decoded *kana* phonograms in the short-term phonological working memory. Therefore, the activation in Broca's area may reflect extra demands on phonological working memory during mirror reading relative to normal reading. Additionally, the correlation between the activation in Broca's area and the EI deserves to be mentioned, although it is only marginally significant. This positive correlation indicates that successful preservation of individual decoded *kana* phonogram in short-term working memory may also play a role in the accurate recognition of mirror-reversed *kana* words.

Besides the Broca's area, activation was detected in the left inferior BA 6. As similar planning as well as execution of the motor response was required for both the control and mirror reading conditions, this result is unlikely to be related to motor planning for the behavioural response during the task performance. A similar area was reported to be activated in a visual attention paradigm (Buchel *et al.*, 1998). Taken together, this activation seems to be due to the substantial attention that is required for mirror reading relative to normal reading.

With regard to the activation observed in the occipital and temporal regions during mirror reading, it was especially prominent in the left inferior occipital gyrus, left postero-lateral FG and left inferior temporal region, which are implicated in visual object recognition. PET studies of reading revealed that the left FG and extrastriate cortex were involved in the processing of letter strings (Price *et al.*, 1996; Puce *et al.*, 1996). The activation of the FG and inferior temporal gyrus was greater on the left than the right hemisphere for Japanese *kana* reading (Sakurai *et al.*, 1993). During mirror reading, the subjects spatially transform the individual *kana*, and then match those *kana* to the existing *kana* representations. Thus, they may adopt a *kana*-to-*kana* level identification strategy for mirror-reversed items. However, a normally oriented *kana* word can be recognized as a whole. Therefore, compared with normal reading, mirror reading may require an additional process for *kana* recognition, leading to the greater activation of the left occipitotemporal *kana* recognition area. Alternatively, together with acquisition of the skill, new representations of individual mirror-reversed *kana* might be formed, which might also result in the increased involvement of *kana* recognition processing, and subsequently activate the occipitotemporal *kana* recognition area. The latter explanation is consistent with the finding that activation in the left FG increased with training in the mirror reading task (Poldrack *et al.*, 1998a).

Regarding the activation of the visual cortex, we did find activation in the so-called 'higher order' visual areas either in the dorsal pathway of visual information toward the parietal

cortex or in the ventral pathway leading to the temporal object recognition region (Baizer *et al.*, 1991). For example, the activation identified in the bilateral middle occipital gyri is close to V3a which was demonstrated in the fMRI studies of retinotopical stimuli (DeYoe *et al.*, 1996; Tootell *et al.*, 1997), and the area corresponding to the motion-sensitive area V5 (Watson *et al.*, 1993; Tootell *et al.*, 1995) was also activated in the present mirror-reversed condition. Neuroanatomical and behavioural studies suggest that parietal areas receive information from the orientation-sensitive cells in V2, V3 complex, V4 and the motion-selective cells in V5 (Morel and Bullier, 1990; Felleman and Van-Essen, 1991). Previous behavioural findings indicated that processes of mirror reading might not be the same as those involved in mental rotation (Koriat and Norman, 1985). However, there are brain areas related to visuospatial processes commonly involved in both mirror reading and mental rotation. For example, the cortical area V5 was also activated during mental rotation of three-dimensional figures (Cohen *et al.*, 1996). This is noteworthy because no actual motion was present either in the present mirror reading or previous mental rotation tasks. We postulate that the activation in V5 found in the present study might be associated with the orientation discrimination of mirror-reversed items.

Finally, activation of the right caudate nucleus found in the present task is of some interest. The caudate nucleus receives input from frontal and temporoparietal cortical areas (Kemp and Powell, 1970; Ragsdale and Graybiel, 1990) and sends the output fibres to the globus pallidus and other regions of the basal ganglia, forming anatomical loops with these structures (Alexander *et al.*, 1986). The head of the caudate nucleus seems to function similarly to the prefrontal cortex and even to share certain cognitive functions with it (Abdullaev *et al.*, 1998), whereas the tail of the caudate nucleus plays an important role in non-declarative learning (Brown *et al.*, 1995). Recently, by using an fMRI method, Poldrack *et al.* found increased activation in the right caudate nucleus from the pre-training to post-training session during English mirror reading, providing evidence for its function in visuoperceptual skill learning (Poldrack *et al.*, 1998b). In their experimental design, no training was given to the unskilled participants prior to the initial session, whereas a long training was given between the initial unskilled and the second skilled sessions. In our study, by contrast, three training sessions were given to each subject before the initial scanning session. Judging from the behavioural data which showed no learning effect between the two scanning sessions, we could assume that our mirror reading already belongs to an acquired or at least partially acquired skill compared with the unskilled mirror reading in the study of Poldrack and colleagues, although it might not have reached the level of skill comparable with theirs. Therefore, it is likely that the right caudate nucleus activation observed in our study might be associated with the visual skill learning resulting from the pre-scan training sessions. However, to clarify the function of the caudate nucleus in the acquisition of Japanese *kana* mirror reading, a new experimental design comparable with that in English mirror

reading by Poldrack and colleagues (Poldrack *et al.*, 1998b) would be necessary in any future study.

Conclusion

The present study used fMRI to demonstrate the functional anatomy that was responsible for Japanese *kana* mirror reading. Mirror reading was associated with activation in multiple cortical regions that included the bilateral occipital, bilateral temporal, right superior parietal and left inferior frontal cortices. The right cerebellum and the right caudate nucleus were also activated in the task. Activation found in the right SPC and left inferior temporal region is consistent with the hypothesis that mirror reading involves both the dorsal stream visuospatial and the ventral stream object recognition processes. By minimizing the effect of eye movements, our study clarified the function of the right SPC in the spatial transformation of mirror-reversed *kana*. Furthermore, a significant correlation was found between the fMRI signal change in the right SPC and behavioural performance in the mirror reading task. This may indicate that, among the brain regions that were activated during the task, the right SPC is of particular importance for the successful reading of mirror-reversed Japanese *kana* words. It is concluded that the right SPC plays an essential role in the spatial transformation required for Japanese *kana* mirror reading.

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