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Research Report

Distinct neural correlates underlying two- and three-dimensional mental rotations using three-dimensional objects

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ABSTRACT

Two strategies–motor and visual–are considered to be used for performing mental rotation. The former involves the functions of the motor-related areas of the brain, whereas the latter does not. It is known that subjects' experiences influence strategy selection during the mental rotation of three-dimensional (3D) shapes. However, it remains questionable as to whether the attributes of 3D objects enhance the motor-related activities. In this regard, using functional magnetic resonance imaging, we compared the brain activities during two types of mental rotations–two-dimensional (2D) and 3D rotations–using 3D objects. 2D rotation using 3D objects requires rotation in a screen plain, whereas 3D rotation requires in-depth rotation. Only 3D rotation implicitly requires subjects to construct and manipulate 3D images with visualizations of the hidden parts; this plays an important role in visuo-motor tasks such as preshaping. As a result, a wide area of the right superior parietal lobule (SPL) was activated in relation to a 2D rotation angle. Conversely, a wide area of the right dorsal premotor cortex (PMd) was activated in relation to a 3D rotation angle. The right PMd activity is related to visualization of the hidden parts of visual stimuli, which is required only for 3D rotation. This implies that task difficulty enhanced by rotation dimensionality is a major factor related to the selection of motor strategy. In addition, it implies that the right SPL and the right PMd play important roles in rotation imagery without visualization and in constructing and manipulating 3D images, respectively.

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Abbreviations: RT, response time; fMRI, functional magnetic resonance imaging; PET, positron emission tomography; MEG, magnetoencephalography; EEG, electroencephalography; 3D, three-dimensional; 2D, two-dimensional; SPL, superior parietal lobule; PMd, dorsal premotor cortex; SMA, supplementary motor area; IPL, inferior parietal lobule; ROI, region of interest; PO, parietooccipital; EPI, echo planar imaging; TE, echo time; TR, repetition time; FOV, field of view; Fast SPGR, fast spoiled gradient-recalled echo; SOA, stimulus onset asynchrony; MNI, Montreal Neurological Institute; PM, premotor; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; PMv, ventral premotor cortex; MOG, middle occipital gyrus; SFG, superior frontal gyrus; PreCG, precentral gyrus; STG, superior temporal gyrus

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1. Introduction

Psychological studies of mental rotation tasks have indicated the existence of mental analogue processes during these tasks. The mental rotation tasks required the subjects to decide whether the two shapes that were presented at various orientations were the same or mirror images. The results revealed that their RT increased with an increase in the angle of rotation between the shapes (Shepard and Metzler, 1971).

Various studies have aimed to reveal the neural mechanisms related to the mental analogue processes underlying the mental rotation task, by using noninvasive methods such as fMRI (Cohen et al., 1996; Gauthier et al., 2002; Jordan et al., 2001; Kosslyn et al., 2001a; Lamm et al., 2001; Podzebenko et al., 2002; Richter et al., 2000; Tagaris et al., 1996, 1997; Vingerhoets et al., 2002; Windischberger et al., 2003), PET (Alivisatos and Petrides, 1997; Bonda et al., 1995; Harris et al., 2000; Parsons et al., 1995), MEG (Iwaki et al., 1999; Kawamichi et al., 1998) and EEG (Inoue et al., 1998; Yoshino et al., 2000) to measure brain activity. The following two categories of visual stimuli were used in these studies: body parts (e.g., hands, feet) and inanimate objects (e.g., 3D shapes, characters). The mental rotation tasks that made use of body parts as visual stimuli were observed to activate the motor-related areas of the brain, in particular the left premotor area (Bonda et al., 1995; Kawamichi et al., 1998; Parsons et al., 1995) or both the premotor areas (Vingerhoets et al., 2002). The tasks that made use of inanimate objects as visual stimuli were observed to activate the visual information processing areas, particularly the right parietal association area (Harris et al., 2000; Inoue et al., 1998; Podzebenko et al., 2002; Tagaris et al., 1996; Yoshino et al., 2000), the left parietal association area (Alivisatos and Petrides, 1997; Iwaki et al., 1999) or both the parietal association areas (Cohen et al., 1996; Gauthier et al., 2002; Jordan et al., 2001; Tagaris et al., 1997). However, controversy has arisen as to whether motor-related areas are activated during the mental rotation tasks that make use of 3D shapes (inanimate objects) as visual stimuli. Some studies using fMRI (Lamm et al., 2001; Richter et al., 2000; Tagaris et al., 1997; Windischberger et al., 2003) reported the activities of the higher motor areas during the mental rotation of 3D shapes, while others (Cohen et al., 1996; Gauthier et al., 2002; Jordan et al., 2001) did not.

It is considered that two strategies are used to solve mental rotation tasks, namely, a motor strategy and a visual strategy (Kosslyn et al., 2001a,b; Tomasino and Rumiati, 2004), and that these two strategies can offer an explanation for the abovementioned disparity. Kosslyn et al. (2001a,b) demonstrated that motor-related areas were activated during the mental rotation of 3D shapes after the subjects had practiced the manual rotation of real objects that were similar in shape to those used as visual stimuli. On the other hand, they also demonstrated that motor-related areas were not activated during the mental rotation of 3D shapes after the subjects had viewed the rotation of the real objects. This implied that the implicit utilization of motor-related areas for visual information processing is influenced by the subject's experiences; i.e., subjects appear to select the motor strategy for the mental rotation of 3D shapes based on previous experience. This point of view suggests the possible activation of motor-related areas by the mental rotation of 3D shapes and that the activation of motor-related areas was enhanced by subjects' previous experience.

On the other hand, motor execution consists of two processes. The first process predetermines a course of actions aimed at achieving certain specific goals based on managerial knowledge. The second process involves the execution of the plan to a successful conclusion; this process includes environmental monitoring (Chevignard et al., 2000). A study conducted by Chevignard et al. (2000) demonstrated that an assessment using 'script execution' that is related to the latter process was effective for the assessment of dysexecutive syndrome. In contrast, experiences of manual movement before conducting mental rotation tasks, such as in the experiments of Kosslyn et al. (2001a,b), influenced the two processes of motor execution. Based on this viewpoint, it remains unclear as to whether the selection of the motor strategy is influenced by the attributes of 3D shapes related to the execution of a plan, particularly with respect to environmental monitoring.

The acquisition of environmental information from various viewpoints is important for environmental monitoring. In mental rotation task, subjects are implicitly required to monitor imagined rotation of visual stimuli. Accordingly, 3D mental transformation during the mental rotation of 3D objects would enhance motor-related activities. To investigate difference of brain activities based on mental transformation, Gauthier et al. (2002) investigated the brain activities during mental rotation task related to three rotation axes (*x*, *y* and *z*). In addition, Jordan et al. (2001) and Vingerhoets et al. (2002) investigated difference of brain activities during mental rotation of various visual stimuli. However, either 2D or 3D rotation was required during mental rotation of 3D shapes. In addition, the difference between brain activities during 2D and 3D rotation using 3D objects has not been investigated. Consequently, we aimed at the relation between motor-related activities and rotation methods in this study.

Therefore, in the present study, we focused on task difficulty based on rotation dimensionality. Specifically, we used fMRI to measure the subjects' brain activity during the 2D and 3D mental rotation of 3D objects [similar to those used by Shepard and Metzler (1971)] in order to estimate the effects of task difficulty based on rotation dimensionality on the activity of the motor-related areas. Of the two rotation types, only 3D rotation implicitly requires changing the viewpoint in order to visualize the hidden parts of the visual stimuli, using 3D information for constructing and manipulating the visual image.

2. Results

2.1. Exp. 1: performance results

As shown in Fig. 1, the RT of the subjects increased with an increase in the angle of rotation between the objects.

Regression analysis was performed for both 2D and 3D rotation tasks in order to evaluate the angular difference of the objects and the average RT of each subject. In both tasks, a correlation was observed between the angular differences and

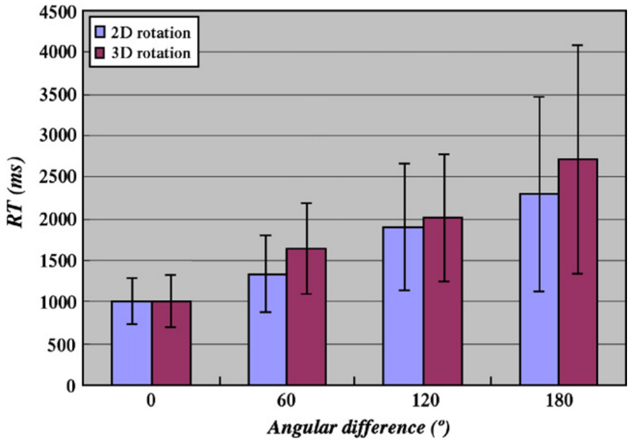

Fig. 1 – Average RTs of the subjects used to judge whether two objects presented at various orientations in 2D and 3D rotations were identical or mirror images. In both tasks, a correlation was observed between angular differences and RT [2D: $F(1,46)=23.759$, $r=0.584$, $P<0.05$; 3D: $F(1,46)=28.282$, $r=0.617$, $P<0.05$]. The RTs therefore increased with an increase in the angle of rotation between objects. The RTs of each subject were measured prior to the fMRI measurements.

RT (2D: $F(1,46)=23.759$, $r=0.584$, $P<0.05$; 3D: $F(1,46)=28.282$, $r=0.617$, $P<0.05$). For both tasks, more than 94% of the answers were correct.

2.2. *Exp. 2: fMRI results*

(1) Primary analysis of the four conditions
Fig. 2 and Table 1 display the results of the four conditions (3DL, 3DS, 2DL and 2DS) compared to the rest blocks.
Both the SPL (BA 7) and the cerebellum were activated under each condition. In addition, with the exception of 2DL, the right PMd (BA 6) was activated under each of the conditions. Activities in both the SPL and the right PMd during 3DL were the greatest among the four conditions.

(2) Comparative analysis of 2D and 3D rotations
Fig. 3 and Table 2 display the results of a comparison of brain activity between 2D (2DL+2DS) and 3D (3DL+3DS) rotations. 3D–2D demonstrated activity in the right insula (BA 13), the right SPL (BA 7) and the right cuneus (BA 19). However, 2D–3D resulted in no activity.

(3) Separate analysis of 2D and 3D rotations
Fig. 4 and Table 3 display the activities related to 2D (2DL–2DS) and 3D (3DL–3DS) rotations.
For a 3D rotation angle, the right PMd (BA 6) was observed to be broadly active, whereas the right SMA (BA 6), the right SPL (BA 7), the right cuneus (BA 19) and the left SPL (BA 7) were observed to be active. In contrast, for a 2D rotation angle, the right SPL (BA 7) was broadly active, whereas the right PMd (BA 6), the right IPL (BA 40), the left SPL (BA 7), the right precuneus (BA 7) and the left cerebellum were observed to be active.
On comparing 2D and 3D rotations, the right PMd activity increased and widened with an increase in 3D rotation angle, and the right SPL activity increased and widened with an increase in 2D rotation angle (Fig. 5).
In addition, we performed an ROI analysis to examine any possible differences between the two rotation methods in both the PMd and both the SPL. We traced a circle of 15.7 mm in radius around each of the two loci in both the PMd ((28, −12, 70), (−28, −12, 70)) and a circle of 17.7 mm in radius around each of the two loci in both the SPL ((24, −80, 52), (−24, −80, 52)). These centers and radii were determined based on the number of voxels of the right PMd activities in 3DL–3DS and that of the right SPL activities in 2DL–2DS. As a result, the right PMd ROI and left SPL ROI revealed significant activities in 3DL–3DS and the right SPL ROI revealed significant activities in 2DL–3DS ($P<0.05$, corrected). All of the findings from the whole brain analysis were confirmed.

3. Discussion

In the primary analysis of the four conditions, both the SPL were activated. This result is consistent with those of previous studies (Cohen et al., 1996; Gauthier et al., 2002; Jordan et al., 2001; Tagaris et al., 1997). Among the four conditions, the number of voxels in both the SPL during 3DL was the greatest. This result is related to the fact that 3D rotation is more difficult than 2D rotation for each angular difference and that mental rotation with a larger rotation angle is more difficult than that with a smaller rotation angle.

Additionally, in the comparative analysis, the right SPL was activated to a greater extent during the 3D rotation task as compared with that in the 2D rotation task. This result is consistent with a previous study that reported that the activities in the right SPL were influenced by the performance of mental rotation (Tagaris et al., 1996). This result is related to the fact that 3D rotation is more difficult than 2D rotation based on the difference of dimensionality. This result is also consistent with the result of a performance measurement demonstrating that the RT for 3D rotation with a 180° difference was longer than that for 2D rotation with a 180° difference.

In the separate analysis, the posterior parietal association area (BA 7, BA 40) was activated during the two rotation tasks. This result is consistent with those of previous studies (Cohen et al., 1996; Gauthier et al., 2002; Jordan et al., 2001; Tagaris et al., 1997) that reported activity in both the posterior parietal association areas during mental rotation tasks with 3D shapes related to task difficulty based on rotation angle. For a 2D rotation angle, a broad area of the right posterior parietal association region was activated. This result coincides with the result of the ROI analysis of separate analysis. On the other hand, this area was not broadly activated in response to a 3D rotation angle. However, the results of the comparative analysis demonstrated right SPL activity in 3D–2D. In addition, the number of voxels in both the SPL during 3D rotation was greater than those during 2D rotation in the primary analysis. Based on the results of these comparative and primary analyses, the right SPL was thought to be active even in the 3DS condition because of the difficulty of the 3D rotation task at small rotation angles.

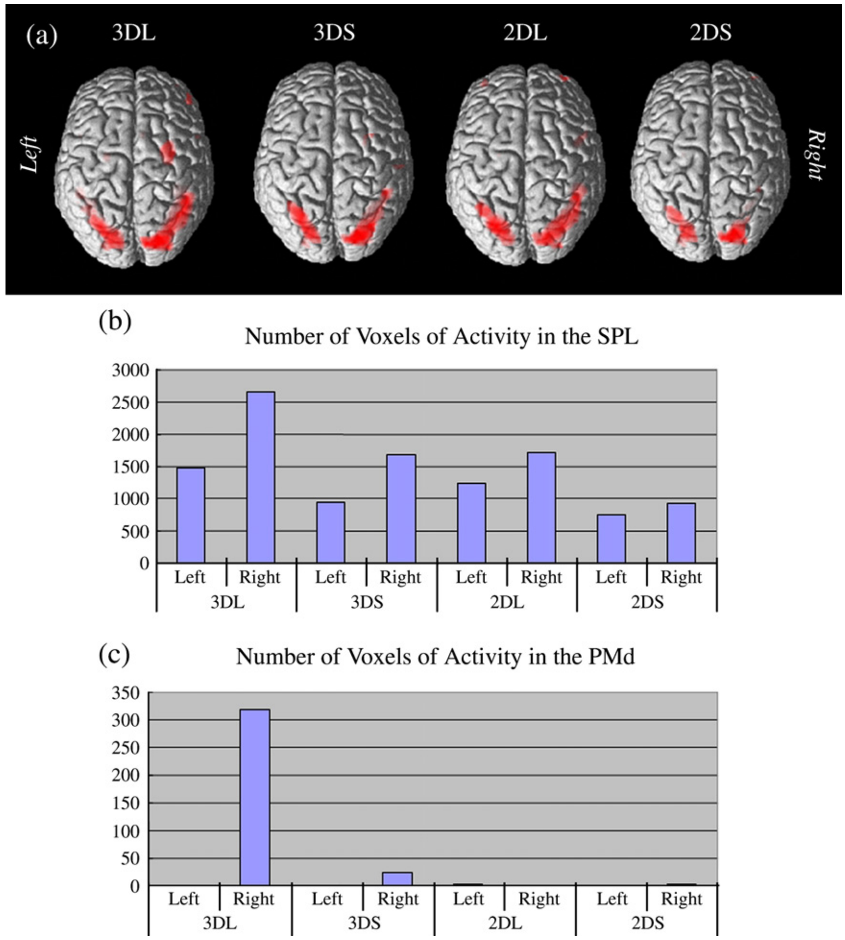

Fig. 2 – Results of group analysis of localized activation during the four conditions (3DL, 3DS, 2DL and 2DS) compared to those during rest blocks. (a) Shows the dorsal view of the activated areas. (b) Shows the number of voxels of activity in both the SPL (BA 7). (c) Shows the number of voxels of activity in both the PMd (BA 6). Both the SPL (BA 7) were activated in each condition. In addition, the right PMd (BA 6) was activated under all conditions, with the exception of 2DL. Activity in both the SPL and the right PMd was most prominent during 3DL.

In the separate analysis, the right PMd activity was broadly observed in relation to a 3D rotation angle. This result coincides with the result of the primary analysis; activities (number of voxels and *t* value) in the right PMd during 3DL were the greatest among the four conditions. In addition, this result coincides with the result of the ROI analysis of separate analysis. However, no PMd activity was observed in the 3D–2D of the comparative analysis. Further analysis with respect to PMd activity in 3DL–3DS, 2DL–2DS, 3DL–2DL and 3DS–2DS demonstrated a large activated area in 3DL–3DS (number of voxels = 127, *t* value = 5.72), a small activated area in 2DL–2DS (number of voxels = 1, *t* value = 4.09) and 3DL–2DL (number of voxels = 4, *t* value = 4.58) and no activity in 3DS–2DS (Fig. 6). In addition, in the primary analysis, small activities were demonstrated during 3DS and 2DS. From this point of view, during 2DL, there were potential broad activities in motor-related areas. These activities appear to be broad but weak. Calibration based on 3D information plays an important role (Clower et al., 1996) in visuo-motor tasks such as preshaping or visually guided reaching. In particular, preshaping requires a subject to construct 3D images of the objects by visualizing the hidden parts of the objects. Based on this result, the visualization of visual stimuli based on 3D information implicitly activates the motor-related area of the brain. In this study, four conditions (3DL, 3DS, 2DL and 2DS) required the construction of 3D images of visual stimuli and two conditions (3DL and 2DL) required a large angular rotation. However, only one condition (3DL) required large angular rotation in conjunction with the visualization of the hidden parts. Based on these results (Figs. 2 and 6), we considered that four conditions potentially activated the right PMd. Especially, during 2DL, there were potential broad activities in the right PMd. Furthermore, during 3DS and 2DS there were small activities in the right PMd. Based on this idea, 3DL–2DL revealed small PMd activities and 3DL–3DS revealed large PMd activities. Furthermore, the right PMd activity was potentially related to the rotation of 3D objects and enhanced by the task difficulty based on 3D rotation.

In contrast, a previous fMRI study (Gauthier et al., 2002) that revealed brain activity related to rotation axis failed to demonstrate constant activity of the right PMd in relation to mental rotation that required visualizations of the hidden parts of the visual stimuli. Furthermore, these authors demonstrated differences in brain activity by comparing the

Table 1 – Activated regions in the four conditions (3DL, 3DS, 2DL and 2DS) with comparing rest condition

	x-axis	y-axis	z-axis	Number of voxels	t value
3DL					
Right SPL (BA 7)	10	−86	46	2657	9.62
Left SPL (BA 7)	−14	−84	44	1468	7.22
Right PMd (BA 6)	28	−4	58	319	6.77
Left PM (BA 6)	−24	−8	50	35	6.25
Left cerebellum	−42	−74	−32	6	6.01
Right MFG (BA 46)	50	42	24	42	4.99
Right cerebellum	42	−62	−34	13	4.58
Left IFG (BA 44)	56	10	36	3	4.36
Left PMv (BA 6)	−48	10	24	3	4.33
Right SMA (BA 6)	8	12	48	7	4.22
Left IPL (BA 40)	−50	−48	42	1	4.05
3DS					
Right SPL (BA 7)	32	−58	34	1687	8.55
Left SPL (BA 7)	−30	−66	54	954	7.96
Right cerebellum	44	−62	−32	13	5.47
Right MOG (BA 17)	−24	−92	20	50	5.20
Right IPL (BA 2)	58	−22	36	19	5.04
Left cerebellum	−42	−74	−32	4	4.97
Right PMd (BA 6)	34	8	60	25	4.5
Right IPL (BA 7)	42	−38	30	4	4.18
Right SPL (BA 7)	44	−46	62	1	4.04
2DL					
Left SPL (BA 7)	−30	−70	56	1234	7.83
Right SPL (BA 7)	8	−80	52	1709	7.50
Right cerebellum	44	−62	−30	46	6.71
Left MFG (BA 10)	−38	56	22	22	5.78
Left cerebellum	−42	−74	−32	11	5.75
Right SFG (BA 10)	34	62	14	35	5.60
Right PreCG (BA 44)	54	10	34	69	4.92
Left IFG (BA 44)	−44	6	24	1	4.16
Right cerebellum	32	−68	−32	1	4.16
Left PMd (BA 6)	−24	−8	62	2	4.08
2DS					
Right SPL (BA 7)	10	−86	46	929	10.28
Right cerebellum	40	−62	−34	25	6.88
Left SPL (BA 7)	−32	−68	58	746	6.11
Left MOG (BA 18)	−28	−86	12	74	5.51
Right STG (BA 39)	34	−56	30	54	5.44
Right IPL (BA 7)	42	−42	36	28	5.21
Left cerebellum	−42	−74	−32	2	4.70
Right SPL (BA 7)	28	−64	36	6	4.25
Right MFG (BA 10)	38	58	10	8	4.19
Right PMd (BA 6)	−24	−10	54	2	4.06

activity observed with small (15° and 30°) and relatively large (75° and 90°) angular differences. Their experimental design failed to activate the right PMd constantly partly because the difference between the two conditions was smaller than that in our experiments.

There has been some controversy regarding the laterality of premotor activity in previous studies. Studies on the mental rotation of hands (Bonda et al., 1995; Kawamichi et al., 1998; Parsons et al., 1995; Vingerhoets et al., 2002) demonstrated activity in the left premotor area or both the premotor areas. Other studies on the mental rotation of 3D shapes (Lamm et al., 2001; Richter et al., 2000; Windischberger et al., 2003) demonstrated activity in both the premotor areas. However, an fMRI study (Tagaris et al., 1997) on the mental rotation of the shapes similar to the Shepard and Metzler experiment demonstrated a relationship between the activity in the right precentral gyrus and the speed of mental rotation. In addition, EEG studies of the mental rotation of 2D shapes (Inoue et al., 1998; Yoshino et al., 2000) revealed right frontocentral activities related to mental rotation. Another fMRI study (Ehrsson et al., 2000) measured human brain activity during power-grip and precision-grip tasks; this study reported activity in the left premotor area during the power-grip task and activity in the right premotor area during the precision-grip task. Furthermore, a PET study (Decety et al., 1997) revealed that the right premotor area was activated while the subjects memorized a meaningless series of actions; this task required the subjects to carefully and precisely memorize

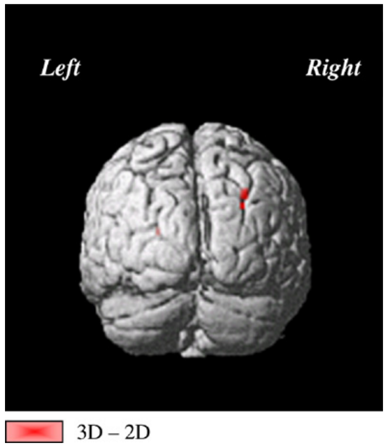

Fig. 3 – Results of group analysis of localized activation during the 3D rotation task as compared with that during the 2D rotation task. Activities in the right SPL (BA 7) and the right cuneus (BA 19) were exhibited in 3D–2D. On the other hand, there were no activities in 2D–3D.

the series of actions. In the 3D rotation tasks (3DL, 3DS), the subjects were thought to be unfamiliar with creating images of the manual rotation of the 3D objects; this was unlike other studies that used the mental rotation of hands. In addition, after the experiment, our subjects reported that they used trial and error to perform the mental rotation task. In this regard, the observed right PMd activity being related to 3D rotation implied that the subjects mentally rotated the 3D objects while considering the importance of precision.

In relation to 3D rotation, the right premotor activity was located on the dorsal side. The location of this activity coincides with the PMd activity during the mental rotation of hands (Bonda et al., 1995; Kawamichi et al., 1998; Parsons et al., 1995; Vingerhoets et al., 2002), tools (Vingerhoets et al., 2002) and 3D shapes (Kosslyn et al., 2001a,b; Lamm et al., 2001). A further study (Cisek and Kalaska, 2004) reported that the PMd was activated during the mental rehearsal of motor tasks. In addition, the right cuneus located near the PO area was activated in relation to 3D rotation. The neurons in the PO area project signals to the PMd (Nakamura et al., 2001). This area is thought to be related to a type of spatial processing that is required for mental rehearsal. Based on these results, it is suggested that the subjects in this study performed a mental simulation using visuo-motor networks related to 3D rotation.

Using fMRI, we measured brain activity during the mental rotation of 3D objects using two types of visual stimuli (2D rotation and 3D rotation). This was performed in order to investigate the effect of task difficulty based on rotation dimensionality. As a result, for a 3D rotation angle, a wide area of the right PMd was activated. On the other hand, for a 2D rotation angle, a wide area of the right SPL was activated. These results imply that visualization, which is implicitly required for 3D rotation, based on 3D information for conducting and manipulating visual images, is related to mental processing that enhances the right PMd activation for performing the mental rotation of 3D objects, such as the shapes used by Shepard and Metzler (1971), and is related to the selection of the motor strategy. Therefore, task difficulty based on rotation dimensionality enhanced motor-related activities. In addition, it is implied that the right SPL plays an important role in rotation imagery without visualization.

4. Experimental procedure

4.1. *Subjects*

Fourteen healthy male subjects (18–33 years old) participated in this study. All the subjects were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and had provided informed consent. Ethical approval for the present study was obtained from the Tokyo Metropolitan University Research Ethics Committee.

4.2. *Exp. 1: performance measurement*

Prior to fMRI, we measured the RT of the subjects.

(1) Visual stimuli
The visual stimuli in this experiment were generated by combining a basic image (0°)–3D objects comprising blocks, similar to those used by Shepard and Metzler (1971)–and a rotated image. There were three variations of the basic images. When generating the rotated images, two types of rotation methods were used—2D and 3D rotations. Only the 3D rotation method rotates the objects in a depth plane. Furthermore, six different rotation angles (0°, 60°, 120°, 180°, 240° and 300°) and two versions of the rotated image, namely, an identical version and its mirror image, were used. These visual stimuli were presented in a randomized order on a screen.

(2) Measurement of RT
In order to measure the RT, subjects were required to press a button based on their judgment. The interval between pressing the button and the presentation of the next visual stimuli was 500 ms. For each type of visual stimulus and rotation angle, a visual stimulus was presented at least 16 times.

4.3. *Exp. 2: fMRI experiments*

In the fMRI experiments, the subjects were only requested to make an implicit decision in order to exclude the brain motor-

Table 2 – Specific regions activated during the comparisons of 3D and 2D rotations

	x	y	z	Number of voxels	t value
3D–2D (red)					
Right insula (BA 13)	38	12	−4	7	4.76
Right SPL (BA 7)	30	−72	38	18	4.5
Right cuneus (BA 19)	30	−82	32	6	4.26
2D–3D					
–	–	–	–		–

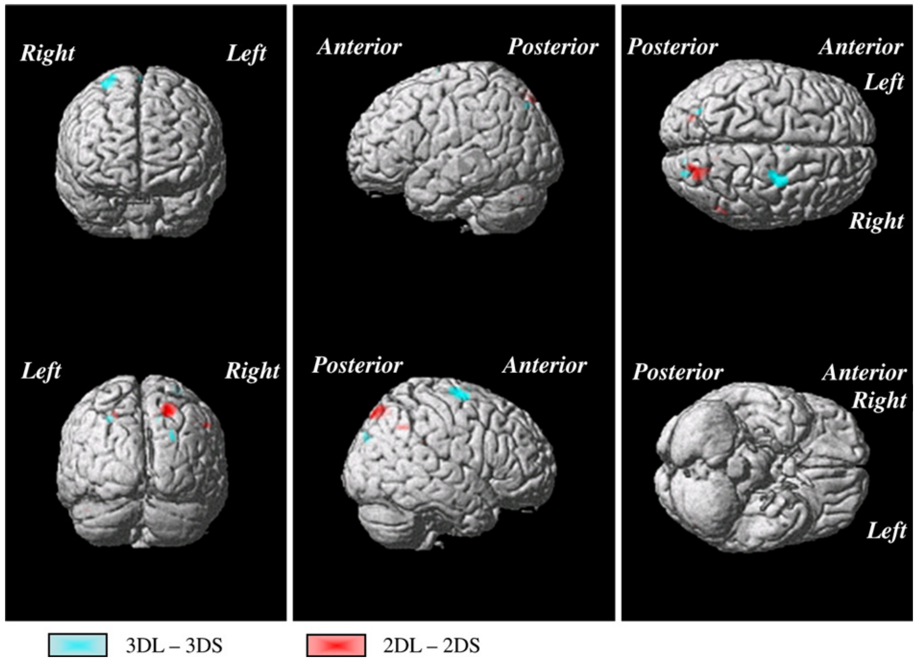

Fig. 4 – Results of group analysis of localized activation related to 3D and 2D rotation angles. For a 3D rotation angle, the right PMd (BA 6) was observed to be broadly active. In contrast, for a 2D rotation angle, the right SPL (BA 7) was broadly active.

related activity influenced by the pressing of the button. After the experiments, the subjects were interviewed in order to determine whether or not they actually performed mental rotation. Only the data of those subjects who indicated that they mentally rotated the 3D objects during the experiments were analyzed. In the present study, two subjects indicated that they did not conduct mental rotation. Consequently, the data from a total of 12 subjects were analyzed.

(1) Visual stimuli
The visual stimuli used in this experiment were generated by combining a basic image (0°)–3D objects comprising blocks, similar to those used by Shepard and Metzler (1971)–and a rotated image. There were six variations of the basic image. When generating the rotated images, two types of rotation methods were used—2D and 3D rotations. Furthermore, eight rotation angles (20°, 60°, 120°, 160°, 200°, 240°, 300° and 340°) and two versions of the rotated image, namely, an identical version and its mirror image, were used. In order to prevent familiarization of the subjects with the visual stimuli, the basic images used were different from those used in the performance measurement. These visual stimuli were presented in a randomized order on a screen. The horizontal length of the visual stimuli subtended the 2.8° visual angle and the 1.4° vertical visual angle.
The probabilities of presenting an identical pair or mirror images were equal. The probabilities of presenting the basic image on the right or left side were also equal. Examples of the visual stimuli are shown in Fig. 7.

(2) fMRI measurement
All the fMRI examinations were performed using a 1.5 T scanner (GE Signa Horizon LX). The subject's head was immobilized within a circularly polarized head coil. fMRI was performed using an EPI gradient-echo sequence (TE = 32.1 ms, TR = 4000 ms, FOV = 240 × 240 mm^2, flip angle = 80°, matrix size = 128 × 128 pixels and slice thickness = 7 mm) and oriented identically to the anatomical images. In addition, a whole brain high-resolution, T1-weighted anatomical MRI using a magnetization-prepared Fast SPGR 2D sequence was acquired for each subject (axial plane; TR = 26.0 ms, TE = 2.4 ms, flip angle = 30°, matrix size = 256 × 256 pixels, slice thickness = 2.3 mm and FOV = 240 × 240 mm^2).

Table 3 – Activated regions related to the 3D (3DL–3DS) and 2D (2DL–2DS) rotations

	x	y	z	Number of voxels	t value
3DL–3DS (light blue)					
Left SPL (BA 7)	−28	−74	44	10	6.25
Right PMd (BA 6)	28	−12	70	127	5.72
Right SMA (BA 6)	2	−7	72	6	4.75
Right cuneus (BA 19)	24	−86	32	24	4.64
Right SPL (BA 7)	14	−88	46	2	4.11
2DL–2DS (red)					
Right SPL (BA 7)	24	−80	52	182	8.32
Right precuneus (BA 7)	10	−60	48	6	5.18
Right IPL (BA 40)	56	−54	40	22	5.05
Left SPL (BA 7)	−22	−82	48	16	4.72
Right cerebellum	−46	−72	−30	2	4.41
Right PMd (BA 6)	22	−12	78	1	4.09
Right IPL (BA 40)	44	−52	42	2	4.07
Right IPL (BA 40)	58	−38	28	2	4.05
Right IPL (BA 40)	46	−50	44	1	4.04

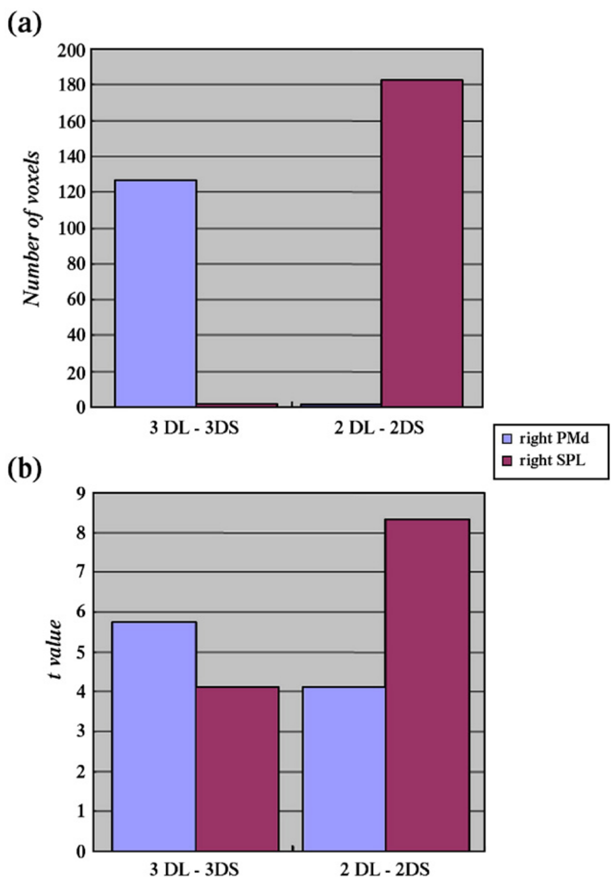

Fig. 5 – Results of a group analysis are shown. Comparison of the activities in the right PMd and right SPL related to 3D and 2D rotation angles ($P<0.001$, uncorrected). (a) Shows the number of voxels related to both the rotation angles in these two areas. (b) Shows the *t* value of the activity related to both the rotation angles in these two areas. The *t* value refers to the peak value of the activities. On comparing 2D and 3D rotations, the right PMd activity increased and widened with the increase of 3D rotation angle, and the right SPL activity increased and widened with the increase of 2D rotation angle.

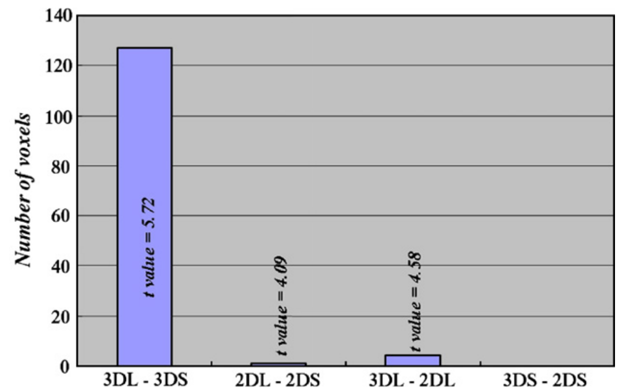

Fig. 6 – Results of a group analysis are shown. Right PMd activities in four comparison conditions (3DL–3DS, 2DL–2DS, 3DL–2DL, 3DS–2DS) ($P<0.001$, uncorrected). Only 3DL–3DS exhibited broad activities in the right PMd. 2DL–2DS and 3DL–2DL exhibited weak activities in the right PMd.

Each subject underwent fMRI under five different conditions: 2DL, 2D rotation with a large angular difference between the two objects; 2DS, 2D rotation with a small angular difference between the two objects; 3DL, 3D rotation with a large angular difference between the two objects; 3DS, 3D rotation with a small angular difference between the two objects; and rest, presenting a fixation cross, which allows the altered cerebral blood flow levels to return to a baseline between trials. The average rotation angle for the 2DL and 3DL conditions was 140° (utilizing four rotation angles: 120°, 160°, 200° and 240°) and was 40° for the 2DS and 3DS conditions (utilizing the other four rotation angles: 20°, 60°, 300° and 340°).

Each session consisted of one 2DL, one 2DS, one 3DL, one 3DS and four rest blocks (Fig. 8). The rest blocks comprised the second, fourth, sixth and eighth block in each session. The order of presentation of the other four blocks was randomized. Each subject underwent five sessions during the fMRI measurement. The duration of each block was 24 s and the total duration of the fMRI experiment was approximately 16 min. The visual stimuli were presented eight times in each block. Each visual stimulus was presented for 2.7 s. The SOA was 3 s. Therefore, from 2.7 s to 3 s after

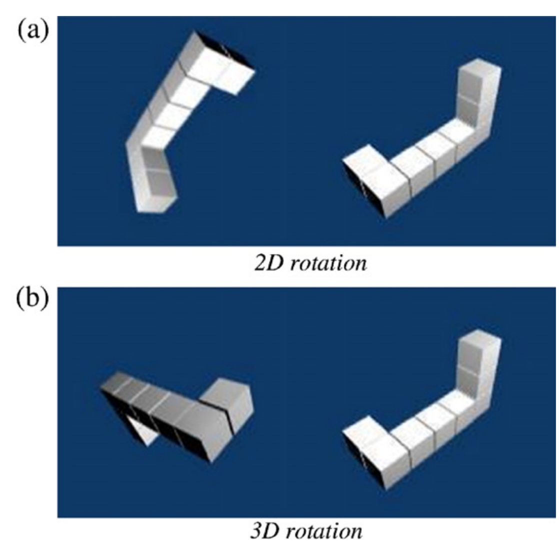

Fig. 7 – Examples of the visual stimuli. (a) An example of 2D rotation visual stimuli. (b) An example of the 3D rotation visual stimuli. These two types of visual stimuli were produced using the same 3D objects. However, different rotation methods were used for the two types of visual stimuli. Only the 3D rotation method rotates the objects in a depth plane. Therefore, only during the 3D rotation, subjects were implicitly required to change their viewpoint in order to visualize the hidden parts of the visual stimuli, using 3D information for conducting and manipulating the visual image.

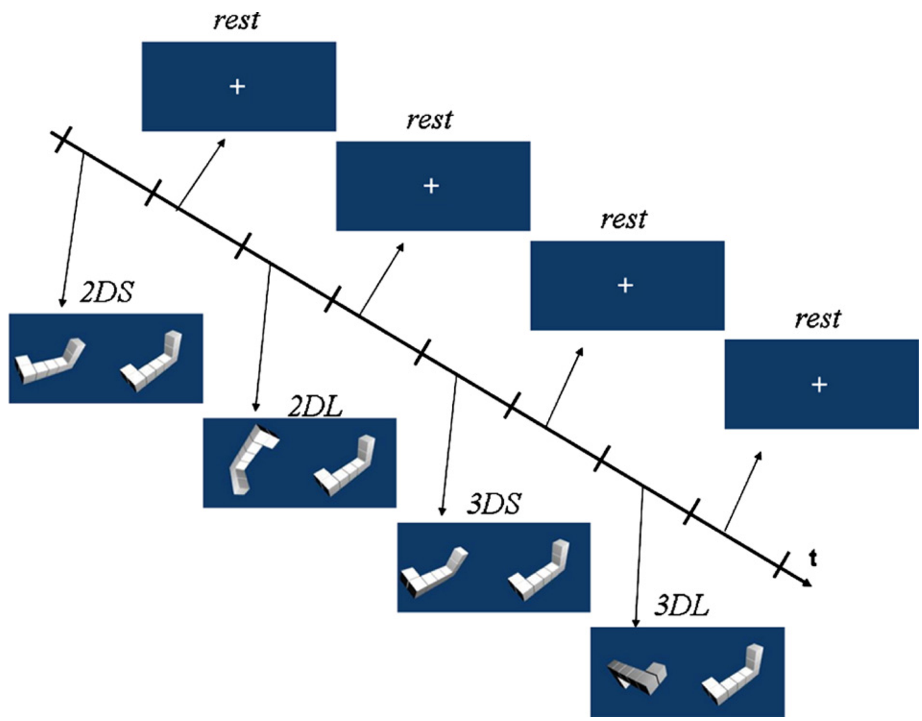

Fig. 8 – An example of the sequence of blocks in a session. This sequence shows that the second, fourth, sixth and eighth blocks are rest block and the first, third, fifth and seventh blocks are 2DS, 2DL, 3DS and 3DL blocks, respectively.

stimulus onset, only the fixation cross was presented. In each block, both an identical pair and a mirrored pair were presented four times.

(3) Statistical analyses

We used statistical parametric mapping (SPM99) software to analyze the functional images. The statistical significance of brain activation was evaluated based on voxel-wise signal changes by using random effects analysis based on a general linear model (Friston et al., 1995). Firstly, we performed motion correction, normalization to the MNI template and minimal spatial smoothing (10 mm). We then analyzed the brain activity of each subject during the five conditions.

Subsequently, we performed group analyses in which the brain activities related to the four conditions [3DL, 3DS, 2DL and 2DS; (1) primary analysis of the four conditions] were compared with those during the rest block. We then performed group analyses in which the brain activities related to the 2D and 3D rotation tasks were compared [3D–2D: (3DL+3DS)–(2DL+2DS), 2D–3D: (2DL+2DS)–(3DL+3DS); (2) comparative analysis of 2D and 3D rotations]. Thirdly, in order to investigate the detailed brain activity related to the two types of the visual stimuli, we separately analyzed the activity related to 2D and 3D rotations [2DL–2DS, 3DL–3DS; (3) separate analysis of 2D and 3D rotations].

The regions were reported to be significantly activated when all the voxels passed a threshold of $P<0.001$ (uncorrected), a state similar to that described in other fMRI studies investigating the mental rotation of 3D shapes (Gauthier et al., 2002; Jordan et al., 2001; Kosslyn et al., 2001a,b; Windischberger et al., 2003).

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