Precuneus contributes to attentive control of finger movement[1]

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KEY WORDS functional magnetic resonance imaging; motor activity; parietal lobe

ABSTRACT

AIM: To examine whether precuneus subserves the attentive control of finger movement or whether it mediates the movement preparation and motor inhibition. **METHODS:** In the Preparation Stage, subjects were shown with a 5-number string in which each number stood for a key-pressing response, the number strings included a complex pattern (eg, 4-1-4-2-3), or a simple one (eg, 2-2-2-2-2), or a null one (ie, x-x-x-x-x). In the Execution Stage, five reaction signs were presented one by one and subjects were required to press the corresponding key to each sign sequentially (eg, in the 4-1-4-2-3 preparation example, subjects press key 4 to the first sign, press key 1 to the second sign, key 4 to the third sign and so on). For the null preparation pattern, five numbers, rather than the reaction signs, were shown at the same pace as in the other two conditions and subjects were to press the corresponding keys. **RESULTS:** Left medial frontal gyrus (BA 6) and precentral gyrus (BA 6) were involved in both of the Preparation Stage and the Execution Stage, whereas left precuneus (BA 7) was activated only in the Execution Stage. **CONCLUSION:** Precuneus mediates the attentive control of finger movement, but not the movement preparation or motor inhibition.

INTRODUCTION

The posterior part of the parietal cortex, including the precuneus, has been reported to be active during tasks involving motor imagery, implicitly[1-3] or explicitly[4]. In particular, the precuneus was observed to be more responsive during motor imagery of finger movement than during real execution of the movement [5,6]. For example, in their recent neuroimage study in which the imagery performance could be objectively assessed, Hanakawa *et al* observed stronger activation in precuneus during motor imagery of finger movement than during execution[6]. However, it is still unclear whether the precuneus subserved the attention to hand-centered space or the motor inhibition in motor imagery. On one hand, precuneus may subserve the attention to hand-centered space in motor imagery[6], given (a) the imagery of finger movement calls for more hand-centered spatial attention than the real execution of finger movement, and (b) precuneus may correspond to the parietal area V6a in nonhuman primates and this area is known to mediate the detection self-motion[7]. On the

[1] Project supported by the National Natural Science Foundation Of China (30270464, 30325026), Chinese Academy of Sciences (KSCX2-SW-221), and by the Ministry of Science and Technology of China (2002CCA01000).
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Received 2003-06-06 Accepted 2004-01-14

other hand, precuneus may subserve motor inhibition, given the imagery of finger movement involved more components of inhibition on explicit motor response than the real execution. Besides, other functions such as preparation for movement, passive observations of action, and mental operations of sensorimotor representations are also possible, because motor imagery is defined as the mental simulation of a motor act[8-10] and this definition can include those processes.

In this fMRI (functional magnetic resonance imaging) study, we examined the role of precuneus in finger movement by using a preparation-execution task. In the Preparation Stage, we showed subjects 5-number strings in which each number stood for a key-pressing response (number 1, 2, 3, 4 represented the first, second, third and fourth keys pressed by the index, middle, ring, and little fingers of the right hand respectively). Number strings could include a complex pattern (eg, 4-1-4-2-3) in the Complex Preparation Condition (CPC), or a simple one (eg, 2-2-2-2-2) in the Simple Preparation Condition (SPC), or a null one (x-x-x-x-x) in the Null Preparation Condition (NPC). In the Execution Stage, five reaction signs (the mark of "!") were presented one by one and subjects were required to press the corresponding key to each sign sequentially. For example, in the above-mentioned CPC example, 4-1-4-2-3, subjects pressed key 4 to the first sign, pressed key 1 to the second sign, key 4 to the third sign and so on. In the Execution Stage of NPC, five different numbers, instead of the reaction signs, were shown at the same pace and subject were asked to press the corresponding keys.

In the Preparation Stage, relative to NPC, CPC and SPC evoked the processes of number-string encoding and movement preparation. Because subjects were required not to response in this stage, CPC and SPC in the Preparation Stage also involve components of motor inhibition. The contrast of CPC with SPC in the Preparation Stage could highlight the areas involved in the processes of converting the number into corresponding key-pressing response and that of complex movement preparations. In the Execution Stage, subjects conducted the corresponding responses when they saw the reaction signs. CPC and NPC contained complex key-pressing patterns that included different numbers; whereas SPC contained simple ones-subjects who invariably pressed the same key when saw the reaction signs. Therefore, the Execution Stage of CPC and NPC called for more attentive control of finger movement relative the SPC.

We predicted that, if the precuneus functioned as attention to hand-centered space, then it would only be involved the Execution Stage when the CPC or NPC were contrasted with SPC. However, if the motor inhibition or movement preparation hypothesis of precuneus were correct, then the precuneus will be activated in both of the Execution Stage and of the Preparation Stage — when CPC and SPC were contrasted with NPC in their Preparation Stage.

MATERIALS AND METHODS

Subjects Seven healthy, right-handed volunteers (4 female and 3 male), aged from 21 to 23, participated in this experiment. Subjects were interviewed one or two days before they attended the fMRI experiment and given informed consent in accordance with the MRI ethics committee guidelines of the Electrotechnical Laboratory (now Neuroscience Research Institute), National Institute of Advanced Industrial Science and Technology.

Tasks There were three kinds of trials in the experiment, the Complex Preparation Condition (CPC), the Simple Preparation Condition (SPC), and the Null Preparation Condition (NPC) (Fig 1). There was a Preparation Stage and an Execution Stage on each trial. In the Preparation Stage of CPC, subjects encoded a complex number string like 2-4-3-2-1 for 2500 ms followed by a 1000-ms cross-viewing delay. Each number in the string stood for a key-pressing response, number 1, 2, 3, and 4 represented the first, second, third, and fourth keys on the response box pressed by the index, middle, ring, and little fingers of the right hand respectively. In the whole experimental session, subjects were required to slightly put their fingers on the corresponding response keys. The response recording system with optics fibers was adjusted to high sensitivity level that it could detect any slight finger movements. Through this way, we ensured that subjects did not move their fingers during the Preparation Stage. In the Execution Stage, subjects pressed the corresponding key when they saw the five reaction signs ("!" mark) sequentially presented at the pace of 1700 ms per sign (1000 ms sign presentation +700 ms cross-viewing delay), the final (the fifth) reaction sign was followed by 1500-ms unfilled delay. In the Preparation Stage of SPC, subjects viewed a simple number string like 2-2-2-2-2, and pressed the same key when they

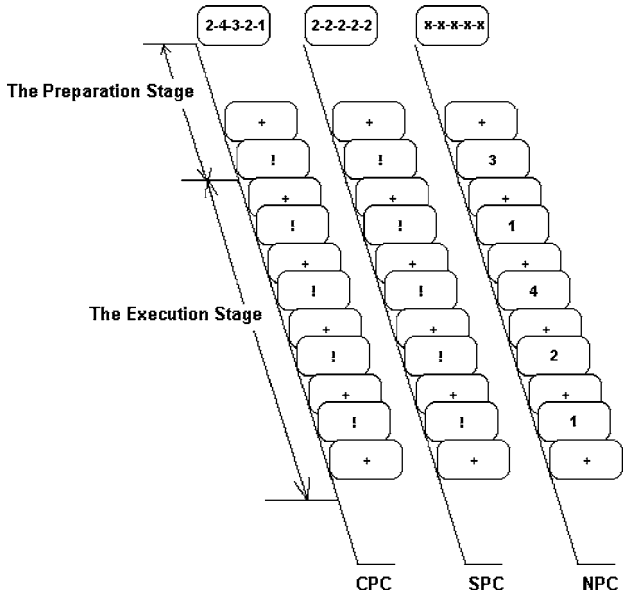

Fig 1. Examples of task. There were three kinds of trials, the Complex Preparation Condition (CPC), the Simple Preparation Condition (SPC), and the Null Preparation Condition (NPC). In each trial, there was a Preparation Stage in which subjects encoded a number string standing for a key-pressing response sequence, and an Execution Stage in which subjects pressed the corresponding keys once seeing the reaction signs ("!"). For CPC, subjects encoded a complex number string; for SPC subjects encoded a simple one; and for NPC, subjects encoded a null string x-x-x-x-x that did not have meaning; in the Execution Stage of NPC, five different numbers, instead of the reaction signs, were shown one by one and subjects pressed the corresponding keys.

saw the reaction signs in the Execution Stage. In the Preparation Stage of NPC, subjects encoded a null string x-x-x-x-x that did not have meaning. In the Execution Stage, five different numbers, rather than the reaction signs, were shown one by one and subjects were to press the corresponding keys. There were two blocks in each condition and each block contained 12 trials, so, there were 24 trials in each condition. The six blocks were presented in the sequence of CPC-SPC-NPC-SPC-NPC-CPC. To familiarize the subjects with the procedure and pace of the task, they were trained with another set of similar materials in the same procedure before the formal experiment.

fMRI scanning All scanning was performed on a 3.0-T MRI Scanner (GE 3T Sigma) equipped with echo planar imaging (EPI) capability. Eighteen axial slices (5.5-mm thick, interleaved) were prescribed to cover the whole brain. A T2* weighted gradient echo EPI was employed. The imaging parameters were TR=2500 ms, TE=35 ms, FA=80 degrees, FOV=20 cm×20 cm (64 mesh×64 mesh). To avoid head movement, subjects were asked not to talk during scanning, and to wear a neck brace.

fMRI data analysis The image data of the seven subjects were analyzed by SPM99. Images data of each subject were individually pre-processed (timeslice adjusted, realigned, normalized, and smoothed). The spatially pre-processed data of seven subjects were then estimated to establish a fixed-effects model. Conjunction analysis, which is used to make inferences about a population from a relative small number of subjects[11], was conducted to examine the differences between conditions. Given in both the Preparation Stage and the Execution Stage, the stimulus were presented in short duration and each stage contained complicated mental events, both stages were defined as small epochs/blocks modeled with boxcar. Length of the epoch for the Preparation Stage was 3500 ms and that for the Execution Stage was 8500 ms. There were six types of blocks in all (2 stages [the Preparation Stage, the Execution Stage]×3 conditions [CPC, SPC, and NPC]). The threshold was set at $P<0.001$ (uncorrected for multiple comparisons) and four or more contiguous voxels. Locations reported by SPM were converted into Talairach coordinates[12] by the transform specified in the mni2tal.m program[13]. These coordinates were used to determine the nearest gray matter (region and corresponding Brodmann area) using the Talairach Daemon program version 1.1 with the maximum range of 11 mm[14].

RESULTS

The Preparation Stage To define the neural network involved in movement preparation, we contrasted the Preparation Stage of CPC and SPC to that of NPC. Relative to NPC, the Preparation Stage of CPC and SPC were associated with activities in left medial frontal gyrus and precentral gyrus. The contrast of the CPC and SPC in the Preparation Stage revealed that the CPC was associated with more activities in left inferior frontal gyrus (BA 9) (Tab 1, Fig 2).

The Execution Stage In the Execution Stage, relative to SPC, both CPC and NPC showed extra activities in left medial frontal gyrus, precentral gyrus, and precuneus (Fig 3, Tab 2). The only detectable difference between CPC and NPC was that NPC was associated with left inferior frontal gyrus activity (Fig 4).

Tab 1. List of locations that showed significant difference in the Preparation Stage.

Number of voxels	Z	Talairach coordinates (x, y, z)			Area
Preparation Stage: (CPC+SPC)>NPC					
295	Inf	-2	-5	56	L Medial Frontal Gyrus, BA 6
35	6.34	-32	-14	60	L Precentral Gyrus, BA 6
4	5.41	-53	6	40	L Middle Frontal Gyrus, BA 6
Preparation Stage: CPC > SPC					
160	Inf	-48	7	31	L Inferior Frontal Gyrus, BA 9

L, left; R, right; BA, Brodmann area. Inf: Z value is infinite. Voxel size: 2.0 mm×2.0 mm×2.0 mm.

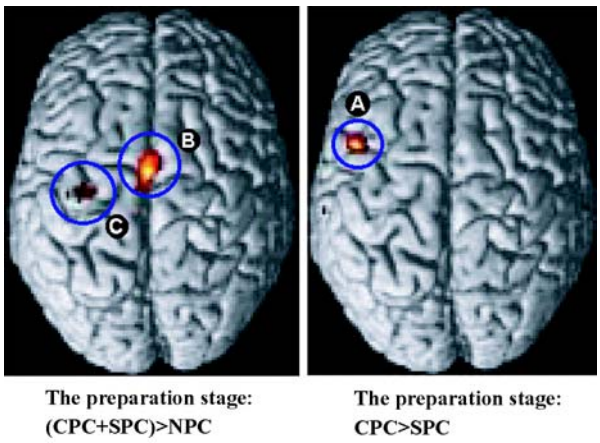

Fig 2. Areas showed significant difference in the Preparation Stage. Thresholded at *P*<0.001 (uncorrected). A: Left inferior frontal gyrus (BA 9); B: Left medial frontal gyrus (BA 6); C: Left precentral gyrus (BA 6).

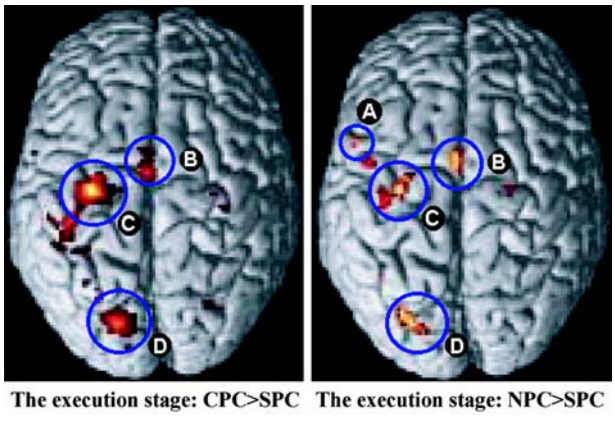

Fig 3. Areas showed significant difference in the Execution Stage. Thresholded at *P*<0.001 (uncorrected). A: Left inferior frontal gyrus (BA 9); B: Left medial frontal gyrus (BA 6); C: Left precentral gyrus (BA 6); D: Left precuneus (BA 7).

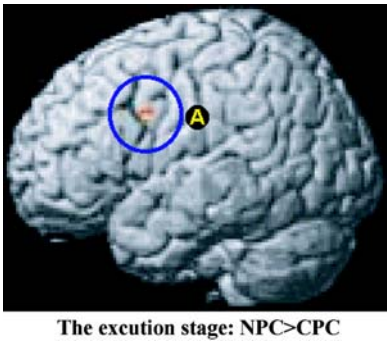

Fig 4. Area showed significant difference in the Execution Stage between NPC and CPC. Thresholded at *P*<0.001 (uncorrected). A: Left inferior frontal gyrus (BA 9).

DISCUSSION

In the present study, four critical areas were highlighted, they were: left inferior frontal gyrus (BA 9), left medial frontal gyrus (BA 6), left precentral gyrus (BA 6), and left precuneus (BA 7). These areas showed three different response patterns in our experimental situation.

Firstly, left medial frontal gyrus (BA 6) and left precentral gyrus (BA 6) was involved in both the Preparation Stage and the Execution Stage, they were activated when the motor preparation conditions (CPC and SPC) were contrasted with null preparation condition (NPC) and when complex response patterns (CPC and NPC) were contrasted with simple ones (SPC). This result was consistent with the observation that these areas participated in both motor movement and motor movement imagery[15].

Secondly, left inferior frontal gyrus (BA 9) was

Tab 2. List of locations that showed significant difference in the Execution Stage.

Number of voxels	Z	Talairach coordinates (x, y, z)			Area
Execution Stage: CPC > SPC					
622	Inf	-30	-12	61	L Precentral Gyrus, BA 6
	Inf	-32	-13	52	L Precentral Gyrus, BA 4
	Inf	-44	-29	36	L Postcentral Gyrus, BA 2
160	Inf	-18	-75	46	L Precuneus, BA 7
111	Inf	-4	-3	52	L Medial Frontal Gyrus, BA 6
45	6.91	-32	-43	37	L Inferior Parietal Lobule, BA 40
8	5.95	34	-20	62	R Precentral Gyrus, BA 4
12	5.66	30	-68	44	R Precuneus, BA 19
8	5.55	-48	-39	41	L Inferior Parietal Lobule, BA 40
4	5.53	28	-15	56	R Precentral Gyrus, BA 6
6	5.48	-28	-65	51	L Superior Parietal Lobule, BA 7
9	5.26	40	-43	37	R Supramarginal Gyrus, BA 40
Execution Stage: NPC > SPC					
60	Inf	-4	1	53	L Medial Frontal Gyrus, BA 6
67	7.5	-32	-11	59	L Precentral Gyrus, BA 6
	6.7	-32	-15	52	L Precentral Gyrus, BA 4
	6.16	-28	-5	50	L Middle Frontal Gyrus, BA 6
27	7.46	-38	-16	62	L Precentral Gyrus, BA 4
87	7.27	-22	-77	46	L Precuneus, BA 7
7	-30	-72	42		L Precuneus, BA 19
6	6.82	22	-11	59	R Middle Frontal Gyrus, BA 6
11	6.54	-53	9	31	L Inferior Frontal Gyrus, BA 9
8	6.2	-42	-29	35	L Postcentral Gyrus, BA 2
18	5.8	-46	0	42	L Precentral Gyrus, BA 6
4	5.55	-34	-41	37	L Sub-Gyral, BA 40
Execution Stage: NPC > CPC					
6	5.44	-46	7	27	L Inferior Frontal Gyrus, BA 9

L, left; R, right; BA, Brodmann area. Inf: Z value is infinite. Voxel size: 2.0 mm×2.0 mm×2.0 mm.

also involved in both the Preparation Stage and the Execution Stage. It was activated in the complex motor preparations (CPC) and in the Execution Stage of NPC in which the numbers, instead of reaction signs, were presented. Given it was well established that this area mediated various types of semantic processing[16-21], the function of left inferior frontal gyrus in the present study might be related to the number encoding process in which the numbers were verbally processed and interpretively converted into the representation of corresponding key-pressing pattern.

Finally, left precuneus was only involved in the Execution Stage of complex response patterns (CPC and NPC). Precuneus was known to participate in visuospatial tasks, including eye movement[22], displacement of visual attention[23,24], spatial working memory[25-27], mental imagery[28], mental rotation of three-dimensional objects or body parts[29-31], and mental navigation on an internal map[32]. Precuneus was also proposed to mediate the shifting of spatial attention between feature dimensions[33], locations[34], or multiple items that were maintained in working memory[35]. In the Execution Stage of the complex key-pressing response patterns (CPC and NPC), subjects continuously shifted their attention to the presented reaction signs and made the suitable finger movements; this response pattern challenged the precuneus.

Precuneus was observed to be more responsive during motor imagery of finger movement than during real execution of the movement[6]. But given motor

imagery could evoke both the process of attention to hand-centered space and the process of motor inhibition, the exact function of precuneus is still unclear. Our results that left precuneus was only activated in the Execution Stage when the execution of complex key-pressing sequence (CPC and NPC) was compared with that of the simple key-pressing sequence (SPC), proved that the function of precuneus in motor movement was the attentive control of finger movement, rather than the movement preparation or inhibition. However, one may argue that absence of precuneus activation in the Preparation Stage was attributed to the possibility that subjects might not do movement preparation in this stage. In other word, subjects might simply maintain the number string in their working memory in the Preparation Stage, and then, in the Execution Stage, they retrieved the corresponding number when they saw the reaction signs, converted the numbers into specific key-pressing responses, and performed these responses. But his hypothesis was inconsistent with several lines of evidences. Firstly, subjects reported that they always did movement preparation in the Preparation Stage and executed these preparations in the Execution Stage. Secondly, in the Preparation Stage, when compared with NPC, both CPC and SPC had significant activities in left medial frontal gyrus and precentral gyrus. These areas could be activated only when subjects did some movement-related preparations. If they simply remembered the number string, then a different neural network, ie, the areas involved in working memory encoding (eg, left ventral prefrontal cortex and medial prefrontal cortex) would be highlighted. Finally, if subjects simply memorized the number string in their mind during the Preparation Stage and retrieved the corresponding number in the Execution Stage, then, the Execution Stage of CPC, relative to that of NPC, should at least involve the areas subserved in working memory retrieval. However, the Execution Stage of CPC was not associated with any super-threshold activities relative to that of NPC. Based on these considerations, we thought the lack of difference in precuneus in the Preparation Stage could not be attributed to the possibility that there was no movement preparation in this stage.

Other possibilities, such as eye movements, which were known to evoke the activities in precuneus, were also implausible, because the three conditions contained the same visual stimulus pattern and our subjects were required to fix their eyes on the center of the screen.

However, there was not a motor imagery condition in the present study, we still could not directly contrast the complex motor movement with the motor imagery. Further studies are needed to compare the process of attention to hand-centered space and the involvements of precuneus in complex motor movement and in motor imagery.

REFERENCES

1 Bonda E, Petrides M, Frey S, Evans A. Neural correlates of mental transformations of the body-in-space. Proc Natl Acad Sci USA 1995; 92: 11180-4.

2 Hanakawa T, Honda M, Okada T, Sawamoto N, Fukuyama H, Konishi J, *et al*. Involvement of network for visuomotor control during mental calculation in Japanese abacus experts. Soc Neurosci Abstr 1999; 25: 1893.

3 Parsons LM, Fox PT, Downs JH, Glass T, Hirsch TB, Martin CC, *et al*. Use of implicit motor imagery for visual shape discrimination as revealed by PET. Nature 1995; 375: 54-8.

4 Ruby P, Decety J. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nat Neurosci 2001; 4: 546-50.

5 Gerardin E, Sirigu A, Lehericy S, Poline JB, Gaymard B, Marsault C, *et al*. Partially overlapping neural networks for real and imagined hand movements. Cereb Cortex 2000; 10: 1093-104.

6 Hanakawa T, Immisch I, Toma K, Dimyan MA, Van Gelderen P, Hallett M. Functional properties of brain areas associated with motor execution and imagery. J Neurophysiol 2003; 89: 989-1002.

7 Rosa MG, Tweedale R. The dorsomedial visual areas in New World and Old World monkeys: homology and function. Eur J Neurosci 2001; 13: 421-7.

8 Crammond DJ. Motor imagery: never in your wildest dream. Trends Neurosci 1997; 20: 54-5.

9 Decety J. The neurophysiological basis of motor imagery. Behav Brain Res 1996; 77: 45-52.

10 Jeannerod M. The representing brain. Neural correlates of motor intention and imagery. Behav Brain Sci 1994; 17: 187-245.

11 Friston KJ, Holmes AP, Worsley KJ. How many subjects constitute a study? Neuroimage 1999; 10: 1-5.

12 Talairach J, Tournoux P. Co-planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System: An Approach to Cerebral Imaging. New York: Thieme Medical Publishers; 1988.

13 Brett, M. The MNI Brain and the Talairach Atlas. 1999. (http:// www.mrc-cbu.cam.ac.uk/Imaging/common/mnispace.html. Retrieved 08/05/1999, updated 14/02/2002).

14 Lancaster JL, Woldorff MG, Parsons LM, Liotti M, Rainey CSFL, Kochunov PV, *et al*. Automated Talairach Atlas labels for functional brain mapping. Hum Brain Mapping 2000; 10: 120-31.

15 Porro CA, Cettolo V, Francescato MP, Baraldi P. Ipsilateral involvement of primary motor cortex during motor imagery. Eur J Neurosci 2000; 12: 3059-63.

16 Buckner RL, Petersen SE, Ojemann JG, Miezin FM, Squire LR, Raichle ME. Functional anatomical studies of explicit and implicit memory retrieval tasks. J Neurosci 1995; 15: 12-29.
17 Demb JB, Desmond JE, Wagner AD, Vaidya CJ, Glover GH, Gabrieli JD. Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. J Neurosci 1995; 15: 5870 - 8.
18 Demonet JF, Chollet F, Ramsay S, Cardebat D, Nespoulous JL, Wise R, *et al*. The anatomy of phonological and semantic processing in normal subjects. Brain 1992; 115: 1753-68.
19 Kapur S, Craik FI, Tulving E, Wilson AA, Houle S, Brown GM. Neuroanatomical correlates of encoding in episodic memory: levels of processing effect. Proc Natl Acad Sci USA 1994; 91: 2008 -11.
20 Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proc Natl Acad Sci USA 1997; 94: 14792-7.
21 Luo J, Niki K. Role of medial temporal lobe in extensive retrieval of task-related knowledge. Hippocampus 2002; 12: 487- 94.
22 Kawashima R, Naitoh E, Matsumura M, Itoh H, Ono S, Satoh K, *et al*. Topographic representation in human intraparietal sulcus of reaching and saccade. Neuroreport 1996; 7: 1253 - 56.
23 Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, *et al*. A common network of functional areas for attention and eye movements. Neuron 1998; 21: 761-73.
24 Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nat Neurosci 2000; 3: 292- 7.
25 Diwadkar VA, Carpenter PA, Just MA. Collaborative activity between parietal and dorso-lateral prefrontal cortex in dynamic spatial working memory revealed by fMRI. Neuroimage 2000; 12: 85-99.
26 Postle BR, Stern CE, Rosen BR, Corkin S. An fMRI investigation of cortical contributions to spatial and nonspatial visual working memory. Neuroimage 2000; 11: 409-23.
27 Thomas KM, King SW, Franzen PL, Welsh TF, Berkowitz AL, Noll DC, *et al*. A developmental functional MRI study of spatial working memory. Neuroimage 1999; 10: 327-38.
28 Mellet E, Tzourio N, Crivello F, Joliot M, Denis M, Mazoyer B. Functional anatomy of spatial mental imagery generated from verbal instructions. J Neurosci 1996; 16: 6504-12.
29 Carpenter PA, Just MA, Keller TA, Eddy W, Thulborn K. Graded functional activation in the visuospatial system with the amount of task demand. J Cogn Neurosci 1999; 11: 9-24.
30 Kosslyn SM, DiGirolamo GJ, Thompson WL, Alpert NM. Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. Psychophysiology 1998; 35: 151-61.
31 Richter W, Somorjai R, Summers R, Jarmasz M, Menon RS, Gati JS, *et al*. Motor area activity during mental rotation studied by time-resolved single-trial fMRI. J Cogn Neurosci 2000; 12: 310-20.
32 Ghaem O, Mellet E, Crivello F, Tzourio N, Mazoyer B, Berthoz A, *et al*. Mental navigation along memorized routes activates the hippocampus, precuneus, and insula. Neuroreport 1997; 8: 739-44.
33 Nagahama Y, Okada T, Katsumi Y, Hayashi T, Yamauchi H, Sawamoto N, *et al*. Transient neural activity in the medial superior frontal gyrus and precuneus time locked with attention shift between object features. Neuroimage 1999; 10: 193-9.
34 Culham JC, Brandt SA, Cavanagh P, Kanwisher NG, Dale AM, Tootell RB. Cortical fMRI activation produced by attentive tracking of moving targets. J Neurophysiol 1998; 80: 2657-70.
35 Phillips S, Niki K. Separating relational from item load effects in paired recognition: temporoparietal and middle frontal gyral activity with increased associates, but not items during encoding and retention. Neuroimage 2002; 17: 1031-55.