A Positron Emission Tomography Study of Visual and Mental Spatial Exploration

E. Mellet and N. Tzourio
CEA-DRM, Orsay, France

M. Denis
LIMSI-CNRS, Orsay, France

B. Mazoyer
CEA-DRM, Orsay and Université, Paris 7, France

Abstract

■ We measured normalized regional cerebral blood flow (NrCBF) using positron emission tomography (PET) and oxygen-15-labeled water in eight young right-handed healthy volunteers selected as high-imagers, during 2 runs of 3 different conditions: 1, rest in total darkness 2; visual exploration of a map 3; mental exploration of the same map in total darkness. NrCBF images were aligned with individual magnetic resonance images (MRI), and NrCBF variations between pairs of measurements ($N = 15$) were computed in regions of interest having anatomical boundaries that were defined using a three-dimensional (3-D) reconstruction of each subject MRI. During visual exploration, we found bilateral activations of primary visual areas, superior and inferior occipital gyri, fusiform and lingual gyri, cuneus and precuneus, bilateral superior parietal, and angular gyri. The right lateral premotor area was also activated during this task while superior temporal gyri and Broca's area were deactivated. By contrast, mental exploration activated the right superior occipital cortex, the supplementary motor area, and the cerebellar vermis. No activation was observed in the primary visual area. These results argue for a specific participation of the superior occipital cortex in the generation and maintenance of visual mental images. ■

INTRODUCTION

Despite Henri Bergson's famous statement in *Matière et Mémoire* (Bergson, 1896) that the nervous system is not a machine to create representations, cognitive psychology has found in people's abilities to generate and manipulate internal representations a wide field of investigations. The concept of mental representation has become increasingly important in theories advanced to account for mechanisms of brain activity (Rumelhart & Norman, 1988; Kosslyn & Koenig, 1992). Representations are now viewed as psychological entities resulting from subject's interactions with the external world, and standing for absent or distant objects. Some representations are highly symbolic by nature, as is the case for linguistic or conceptual representations, whereas others preserve features as well as the internal structure of perceptual events in an highly analog fashion.

This is typically the case for visual mental images for which recent theories assume the existence of stored representations common to visual perception, and a similarity of processes that access and manipulate these representations (Kosslyn, 1980, 1987). Indeed, most investigations about visual mental imagery postulate strong functional relationships between mechanisms serving imagery and those serving perception (Finke, 1989; Denis, 1991; Kosslyn & Koenig, 1992). Neuropsychological studies have shown that bilateral lesions in the occipital cortex give rise to similar impairments in visual perception and image generation (Farah, 1984). Strong arguments are also provided by studies showing similar deficits in perceptual and imaginal tasks in patients suffering from hemineglect (Basso, Bisiach, & Luzzati, 1980; Bisiach & Berti, 1988). Finally, the use of imaging techniques in healthy volunteers, such as measurements of regional cerebral blood flow (rCBF) variations by single photon emission tomography (SPECT), has provided data supporting the involvement of temporooccipital areas in mental imagery tasks (Goldenberg, Podreka, Steiner, & Willms, 1987; Charlot, Tzourio, Zilbovicius, Mazoyer, & Denis, 1992; Goldenberg, Steiner, Podreka, & Deecke, 1992). Moreover, using positron emission tomography (PET), the current most sensitive technique for investigating human functional neuroanatomy (Posner, 1993), Kosslyn recently reported that an area located near the primary visual area was more

Journal of Cognitive Neuroscience 7:4, pp. 433-445

activated when subjects projected a mental image of a letter on a perceived grid than when they actually perceived the letter on the grid (Kosslyn et al., 1993).

In the present experiment, we designed a PET activation protocol in which subjects were invited to perform a mental imagery task in such a way that the contribution of perception to possible activation of visual areas could be ruled out. The task consisted in the mental exploration of the visual image of a previously learned schematic geographic map containing six landmarks (Fig. 1). Subjects were asked to execute the task in total darkness without any time constraint, in contrast to the classic mental scanning paradigm, which also calls for mental exploration (Kosslyn, Ball, & Reiser, 1978; Denis & Cocude, 1992). Task execution was evaluated by asking subjects to pinpoint landmarks on a blank map within minutes following the NrCBF measurement. This imaginal task was contrasted with a perceptual condition in which subjects performed the same visual exploration on an actually perceived map. A common reference condition, resting silently in total darkness, was selected to serve as a basis for comparing the activation patterns observed during imaginal and perceptual conditions. Eye movements and heart rate were controlled in all conditions. The three tasks will be referred to as "Imagery," "Perception," and "Control".

The eight right-handed normal volunteers who participated in this study were selected from a larger population as exhibiting high mental imagery abilities. Indeed, in a previous SPECT study we showed that different individual abilities in visuospatial imagery result in distinct rCBF patterns, emphasizing the need for careful population selection (Charlot et al., 1992). Each subject was first given a magnetic resonance imaging (MRI) study of his brain anatomy and then received six injections of oxygen-15-labeled water, replicating the series of the three conditions described above in the following order: 1, Control 2; Perception 3; Imagery (Fig. 2). Data analysis consisted in detecting task-specific variations of NrCBF in regions of interest (ROIs) having anatomical boundaries defined with the help of each subject's MRI (Fig. 3).

RESULTS

Task Performance

The mean error in locating landmarks on blank maps during the postsession control was 4 ± 3 cm for the first map (mean ± SD, map perimeter = 173 cm) and 2 ± 2 cm for the second map (map perimeter = 206 cm).

Eye movements mean amplitude was found to be significantly larger in Imagery than in Perception (Imagery, 7 ± 2°, Perception, 4 ± 0.4°, $p < 0.01$, Student's t test), the perceptual support probably compelling eye movements in a tighter manner during the perceptual task. During Control, eye movements mean amplitude did not significantly differ from both Perception and Imagery conditions (Control: 6 ± 1°). In addition, we

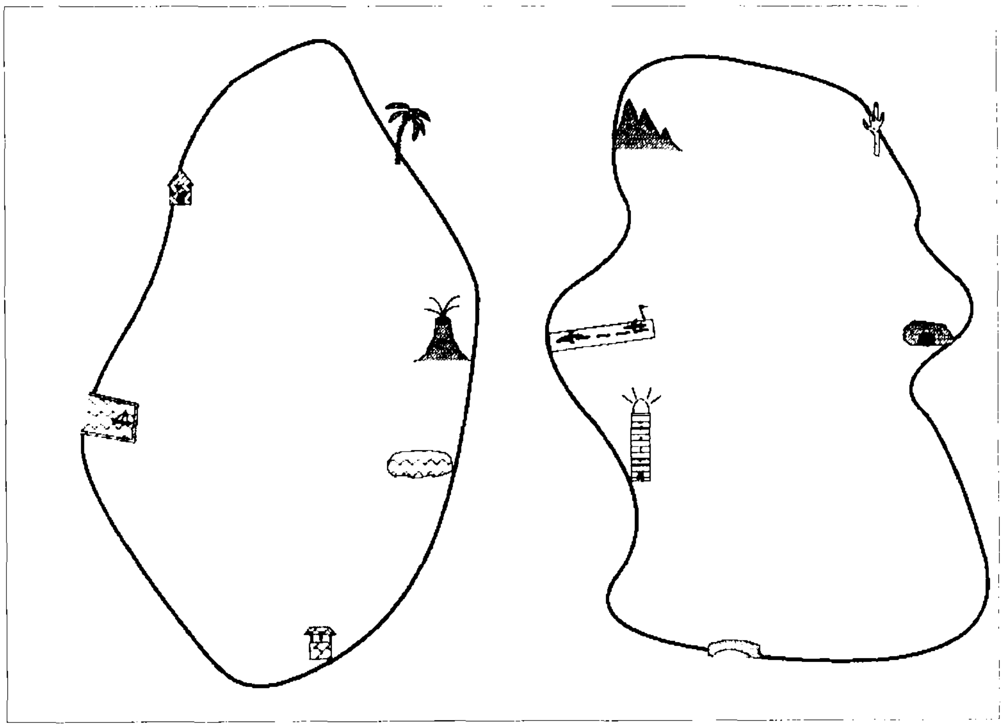

Figure 1. Maps used in Perception. Subjects had to move their gaze from landmark to landmark pausing a few seconds on each one. During Imagery, they had to generate a mental image of the recently perceived island and to mentally execute the same exploration task as in Perception.

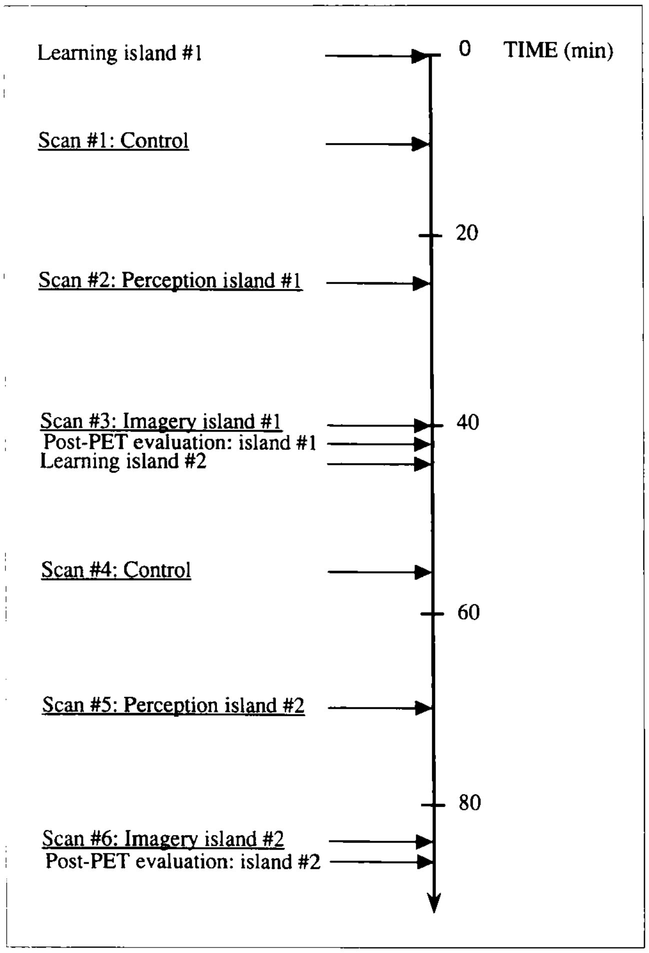

Figure 2. Experimental design. Three conditions (Control, Perception, and Imagery) were replicated twice in the same order. Cerebral blood flow measurements were preceded by a learning phase and followed by a post-PET task evaluation.

found a significant replication effect on heart rate ($p = 0.001$), heart rate during the second set of measurements being lower than during the first one.

Regional Cerebral Blood Flow Variations

Average NrCBF values during the three different conditions are reported in Table 1. Average NrCBF variations between pairs of tasks are shown in Table 2 (Perception versus Control), Table 3 (Imagery versus Control), and Table 4 (Imagery versus Perception) while individual regional variations of NrCBF values are depicted in Figure 4a and 4b for a selected set of ROIs.

Perception Versus Control

Occipital Lobe. All ROIs belonging to the occipital lobe showed very significant NrCBF increases during Perception. The primary visual area presented a bilateral activation in all subjects with values ranging from 2 to 10% in the left hemisphere (L: $p = 0.0001$), and from 2 to 6.5% in the right hemisphere (R: $p = 0.0001$). Bilateral NrCBF increases in the inferior (R: $p < 0.0001$, L: $p < 0.0001$) and superior (R: $p < 0.0001$, L: $p < 0.0001$) occipital regions were larger than 2% in all subjects. Figure 5 (bottom left) shows the location of the superior external occipital activation in subject 8. The cuneus (R: $p = 0.0001$, L: $p = 0.0001$) and the lingual and fusiform gyri (R: $p = 0.0001$, L: $p = 0.0001$) also showed bilateral significant NrCBF increases that were detected in all subjects.

Parietal Lobe. Three areas in the parietal lobe were found to be bilaterally activated, namely the superior parietal lobe (R: $p = 0.01$, range −3 to 9%; L: $p = 0.002$, range −3 to 15%), the angular gyrus (R: $p = 0.01$, range 0 to 6%; L: $p = 0.009$, range 0 to 7%), and the precuneus (R: $p = 0.001$, range −1 to 5%; L: $p = 0.03$, range −4 to 6%).

Temporal Lobe. No NrCBF increase was detected. Rather, a very significant and bilateral decrease in the superior temporal gyrus was observed (R: $p = 0.0003$, range −1 to −5%; L: $p < 0.0001$, range −2 to −5%).

Frontal Lobe. The right lateral premotor region, corresponding to Brodmann's area 6, showed a significant NrCBF increase ($p = 0.01$, range 0 to 3%). However, significant NrCBF decreases were observed in the left dorsolateral prefrontal area ($p = 0.02$, range 0 to −3%) and in the left inferior frontal gyrus ($p = 0.005$, range 1 to −7%). No significant activation of the supplementary motor area (SMA) was detected.

Cingulate Cortex. NrCBF was found significantly decreased in the anterior and median cingulate ($p = 0.002$ and $p = 0.01$, respectively).

Imagery Versus Control

As usually observed, NrCBF variations during Imagery were markedly lower than those observed during Perception.

Occipital Lobe. The mean NrCBF variation in the primary visual area during Imagery was slightly negative and not significantly different from 0 (R: $p = 0.32$, range −8 to 3%; L: $p = 0.25$, range −5 to 4%). On the other hand, a significant NrCBF increase was observed in the right superior occipital area ($p = 0.02$, range −1 to 3%) while the controlateral region failed to reach the 0.05 significance level ($p = 0.09$, range −2 to 4%). However, no significant difference was found between the right and left superior occipital area ($p = 0.3$). Figure 5 shows the

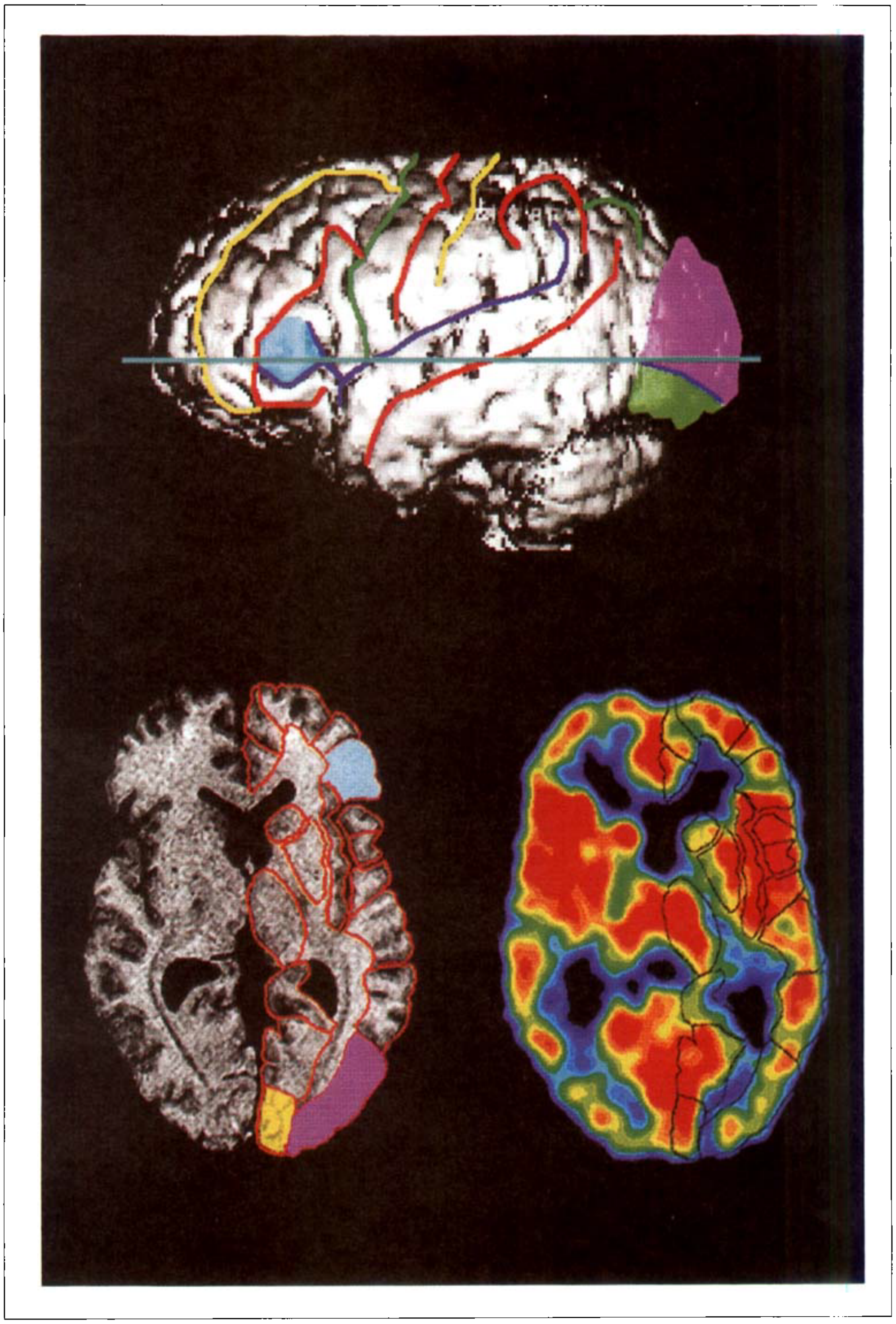

Figure 3. Illustration of the ROIs definition strategy. MRI axial slices are used to reconstruct a three-dimensional brain volume that is further segmented using a dedicated software. The external and internal surfaces of both hemispheres together with sections in three orthogonal directions allow the main gyri (top) to be identified; their limits are then automatically marked onto the MRI axial slices. Using these anatomical landmarks, cortical regions of interest with anatomical boundaries, corresponding to the intersection of the gyri with the MRI axial slices, are delineated on each subject's MRI images (bottom, left). Pars triangularis of inferior frontal gyrus (blue), superior and inferior occipital gyri (respectively, purple and green), and primary visual area (yellow) are displayed on a three-dimensional and axial view. Within each ROI, NrCBF is then estimated as the ratio (in percent) of the radioactivity concentration in the region to that of the whole brain as measured in the PET images and pieces of cortical ROIs belonging to the same brain structure are averaged (bottom, right).

location of the superior external occipital activation (bottom right) in subject 8.

Parietal Lobe. The left precuneus presented a moderate average NrCBF increase, which failed to reach significance ($p = 0.07$). Note that for subjects 6 and 7, there was no increase in left precuneus either during Perception or during Imagery (see Fig. 4a).

Frontal Lobe. The supplementary motor area was found to be significantly activated ($p = 0.01$, range −1 to 9%). This region and the cerebellar vermis (see below) were the only areas found activated during Imagery solely.

Cerebellar Vermis. NrCBF significantly increased in the cerebellar vermis during Imagery ($p = 0.05$, range −1 to 6%).

Table 1. Averaged Normalized Regional Cerebral Blood Flow in Each of the Three Conditions[a]

	Control		*Perception*		*Imagery*	
ROIs	*Mean*	*(SD)*	*Mean*	*(SD)*	*Mean*	*(SD)*
Primary visual area						
Left	102.9	(4.4)	108.9	(4.3)	101.6	(4.1)
Right	105.2	(4.1)	109.9	(5.6)	104.2	(4.2)
Superior occipital gyrus						
Left	89.4	(3.2)	96.0	(3.7)	90.2	(3.4)
Right	86.7	(3.8)	93.5	(4.5)	88.1	(4.2)
Inferior occipital gyrus						
Left	92.6	(3.6)	100.9	(5.4)	93.3	(4.3)
Right	88.1	(4.3)	95.3	(4.6)	87.2	(3.2)
Cuneus						
Left	104.8	(6.5)	109.7	(5.1)	105.0	(5.5)
Right	107.0	(7.7)	111.1	(7.7)	107.5	(6.9)
Fusiform and lingual gyri						
Left	107.1	(5.7)	110.9	(7.0)	105.8	(6.3)
Right	105.3	(5.2)	108.8	(6.0)	104.6	(4.9)
Superior parietal lobule						
Left	94.9	(7.0)	100.4	(8.7)	95.7	(9.8)
Right	90.7	(5.1)	94.6	(6.6)	91.2	(8.3)
Precuneus						
Left	111.6	(3.8)	114.0	(6.1)	113.5	(5.3)
Right	112.9	(4.7)	115.3	(5.0)	113.9	(6.2)
Angularis gyrus						
Left	103.0	(5.5)	105.4	(4.8)	104.8	(6.1)
Right	100.6	(4.9)	103.4	(4.5)	102.3	(5.4)
Superior temporal gyrus						
Left	104.8	(5.8)	102.0	(6.1)	103.9	(6.5)
Right	103.0	(3.2)	99.5	(3.5)	101.6	(4.0)
Middle temporal gyrus						
Left	94.7	(4.5)	93.8	(3.4)	94.9	(4.5)
Right	94.5	(2.9)	93.7	(2.7)	94.0	(3.1)
Inferior temporal gyrus						
Left	98.3	(6.7)	96.8	(7.7)	97.7	(7.2)
Right	97.6	(6.3)	98.8	(5.2)	98.4	(4.8)
Parahyppocampical gyrus						
Left	102.1	(4.6)	100.3	(4.2)	100.3	(3.4)
Right	100.5	(1.9)	100.0	(2.2)	100.1	(1.5)
Precentral gyrus						
Left	109.5	(4.9)	109.3	(6.0)	110.9	(6.8)
Right	108.3	(3.8)	107.9	(3.4)	109.5	(5.0)
Dorsolateral prefrontal area						
Left	104.2	(4.1)	102.7	(4.4)	104.4	(4.6)
Right	103.0	(4.2)	102.3	(5.1)	102.6	(4.5)
Inferior frontal gyrus						
Left	111.9	(5.7)	109.4	(5.5)	111.4	(6.6)
Right	109.5	(4.2)	108.0	(3.2)	109.0	(4.8)
Lateral premotor area						
Left	114.1	(4.2)	115.4	(4.7)	115.8	(6.5)
Right	112.4	(4.8)	114.3	(5.2)	112.8	(6.1)
Supplementary motor area	122.3	(4.3)	123.1	(5.0)	125.3	(5.9)
Anterior cingulate	124.2	(5.1)	120.8	(4.5)	123.9	(4.5)
Median cingulate	124.3	(3.9)	122.7	(3.7)	125.1	(3.4)
Cerebellar vermis	112.0	(5.7)	111.2	(3.4)	113.6	(5.1)

[a] NrCBF is the regional radioactive concentration expressed as a percentage of the whole brain radioactive concentration.

Table 2. Perception Minus Control[a]

ROIs	*Mean*	*(SD)*
Primary visual area		
Left	6.0‡	(4.0)
Right	4.6‡	(3.3)
Superior occipital gyrus		
Left	6.6‡	(2.7)
Right	6.8‡	(2.2)
Inferior occipital gyrus		
Left	8.3‡	(3.3)
Right	7.2‡	(2.7)
Cuneus		
Left	4.9‡	(3.4)
Right	4.1‡	(3.1)
Fusiform and lingual gyri		
Left	3.8‡	(2.6)
Right	3.6‡	(2.5)
Superior parietal lobule		
Left	5.5‡	(5.7)
Right	4.0*	(5.3)
Precuneus		
Left	2.3*	(3.9)
Right	2.4†	(2.3)
Angularis gyrus		
Left	2.3*	(3.0)
Right	2.8*	(3.8)
Superior temporal gyrus		
Left	−2.8‡	(1.8)
Right	−3.5‡	(2.8)
Middle temporal gyrus		
Left	−0.9	(2.5)
Right	−0.8	(2.0)
Inferior temporal gyrus		
Left	−1.5	(6.5)
Right	1.2	(3.6)
Parahyppocampical gyrus		
Left	−1.7	(3.3)
Right	−0.5	(2.5)
Precentral gyrus		
Left	−0.2	(3.1)
Right	−0.4	(2.5)
Dorsolateral prefrontal area		
Left	−1.5*	(2.3)
Right	−0.6	(3.4)
Inferior frontal gyrus		
Left	−2.5*	(2.9)
Right	−1.5	(3.0)
Lateral premotor area		
Left	1.3	(3.4)
Right	1.9*	(2.6)
Supplementary motor area	0.8	(3.0)
Anterior cingulate	−3.4†	(3.4)
Median cingulate	−1.6*	(2.2)
Cerebellar vermis	−0.1	(3.5)

[a] Average percentage variations of NrCBF in selected regions of interest while subjects executed the perception task as compared to Control in total darkness. p values are for Student's paired t test with $N = 15$.

* $p < 0.05$.

† $p < 0.005$.

‡ $p < 0.0005$.

Table 3. Imagery Minus Control[a]

ROIs	*Mean*	*(SD)*
Primary visual area		
Left	−1.3	(4.0)
Right	−1.0	(3.8)
Superior occipital gyrus		
Left	0.8	(1.8)
Right	1.4*	(2.0)
Inferior occipital gyrus		
Left	0.6	(2.2)
Right	−0.9	(3.0)
Cuneus		
Left	0.1	(2.6)
Right	0.5	(3.7)
Fusiform and lingual gyri		
Left	−1.3	(2.0)
Right	−0.7	(2.8)
Superior parietal lobule		
Left	0.8	(7.3)
Right	−0.5	(7.3)
Precuneus		
Left	1.9	(3.7)
Right	0.9	(3.7)
Angularis gyrus		
Left	1.8	(4.5)
Right	1.7	(3.8)
Superior temporal gyrus		
Left	−0.9	(2.0)
Right	−1.4	(2.8)
Middle temporal gyrus		
Left	0.2	(2.1)
Right	−0.5	(2.3)
Inferior temporal gyrus		
Left	−0.5	(4.4)
Right	0.8	(4.3)
Parahyppocampical gyrus		
Left	−1.8*	(2.3)
Right	−0.4	(1.6)
Precentral gyrus		
Left	1.4	(3.8)
Right	1.2	(3.8)
Dorsolateral prefrontal area		
Left	0.2	(2.5)
Right	−0.4	(2.2)
Inferior frontal gyrus		
Left	−0.5	(2.8)
Right	−0.5	(2.0)
Lateral premotor area		
Left	1.7	(0.4)
Right	0.4	(3.9)
Supplementary motor area	3.0*	(4.2)
Anterior cingulate	−0.3	(4.6)
Median cingulate	0.8	(3.4)
Cerebellar vermis	1.54*	(2.8)

[a] Average percentage variations of NrCBF in selected regions of interest while subjects executed the imagery task as compared to Control in total darkness. p values are for Student's paired t test with $N = 15$.

* $p < 0.05$.

Table 4. Imagery Minus Perception[a]

ROIs	*Mean*	*(SD)*
Primary visual area		
Left	−7.3‡	(4.7)
Right	−5.6‡	(5.8)
Superior occipital gyrus		
Left	−5.6‡	(3.2)
Right	−5.4‡	(2.7)
Inferior occipital gyrus		
Left	−7.6‡	(3.1)
Right	−8.2‡	(3.9)
Cuneus		
Left	−4.7‡	(2.6)
Right	−3.6†	(3.0)
Fusiform and lingual gyri		
Left	−5.1‡	(2.2)
Right	−4.2‡	(2.5)
Superior parietal lobule		
Left	−4.7‡	(3.6)
Right	−3.4†	(3.8)
Precuneus		
Left	−0.5	(3.1)
Right	−1.4	(2.3)
Angularis gyrus		
Left	−0.6	(3.4)
Right	−1.1	(3.6)
Superior temporal gyrus		
Left	1.9†	(2.1)
Right	2.1†	(2.2)
Middle temporal gyrus		
Left	1.1	(2.6)
Right	0.3	(1.7)
Inferior temporal gyrus		
Left	1.0	(3.7)
Right	−0.4	(3.5)
Parahyppocampical gyrus		
Left	−0.1	(3.0)
Right	0.1	(2.6)
Precentral gyrus		
Left	1.6*	(2.7)
Right	1.6*	(2.6)
Dorsolateral prefrontal area		
Left	1.7*	(2.0)
Right	0.2	(2.7)
Inferior frontal gyrus		
Left	2.0*	(3.4)
Right	1.0	(3.0)
Lateral premotor area		
Left	0.4	(3.7)
Right	1.6	(5.0)
Supplementary motor area	2.2†	(2.9)
Anterior cingulate	3.1†	(3.0)
Median cingulate	1.8†	(1.8)
Cerebellar vermis	2.3‡	(3.7)

[a] Average percentage variations of NrCBF in selected regions of interest while subjects executed the imagery task as compared to the perception condition. p values are for Student's paired t test with $N = 15$.

*$p < 0.05$.

†$p < 0.005$.

‡$p < 0.0005$.

Imagery Versus Perception

For the sake of comparison, we thought it would also be interesting to search for NrCBF activations during Imagery taking Perception as a control.

Frontal Lobe. NrCBF was found significantly increased in the supplementary motor area, the left dorsolateral prefrontal region, and the left inferior frontal gyrus. For these last two areas, these relative activations during Imagery reflect in fact deactivations during Perception (see Tables 1 and 2 and Fig. 4b), whereas the result observed in SMA corresponds to a significantly larger activation of this area during Imagery. In addition, a bilateral activation of the precentral gyrus was observed (R: $p = 0.03$, L: $p = 0.04$).

Temporal Lobe. NrCBF was found significantly bilaterally increased in the superior temporal gyrus, this relative activation again reflecting the deactivation of this area during Perception (see Tables 1 and 2).

Cingulate Cortex. Similarly, NrCBF was found significantly increased in the anterior and median cingulate ($p = 0.001$ and $p = 0.004$, respectively).

DISCUSSION

In the present study, visual exploration of a map activated a wide network of occipital, parietal, and frontal areas. Occipital activations occurred in the whole occipital lobe including its internal part. Primary visual area activations have already been described in a PET study contrasting a visual task to a condition where subjects had to keep their eyes closed (Lueck et al., 1989). External occipital cortex activations were also expected, these two areas being known to be engaged whenever a complex visual stimulus is processed (Petersen, Fox, Posner, Mintun, & Raichle, 1988; Haxby et al., 1991; Sergent, Ohta, & MacDonald, 1992). The cuneus activation could be related to visual scanning that was explicitly required from the subjects: cuneus has been shown to be involved in the spatial processing of visual information and, more particularly, in the coding of the relative positions of several objects in space (Damasio & Damasio, 1989). Fusiform and lingual gyri activations are probably related to the shape recognition process that was engaged during visual exploration of the map and its landmarks. Indeed, these regions have been reported to be responsive to changes in geometric shapes (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991), and to the shape of words independently of their meaning (Petersen, Fox, Snyder, & Raichle, 1990). Moreover their lesion causes object agnosia (Damasio & Damasio, 1989).

The superior parietal gyrus, the precuneus, and the angular gyrus belong to the dorsal pathway first described in the monkey (Mishkin, Ungerleider, & Macko,

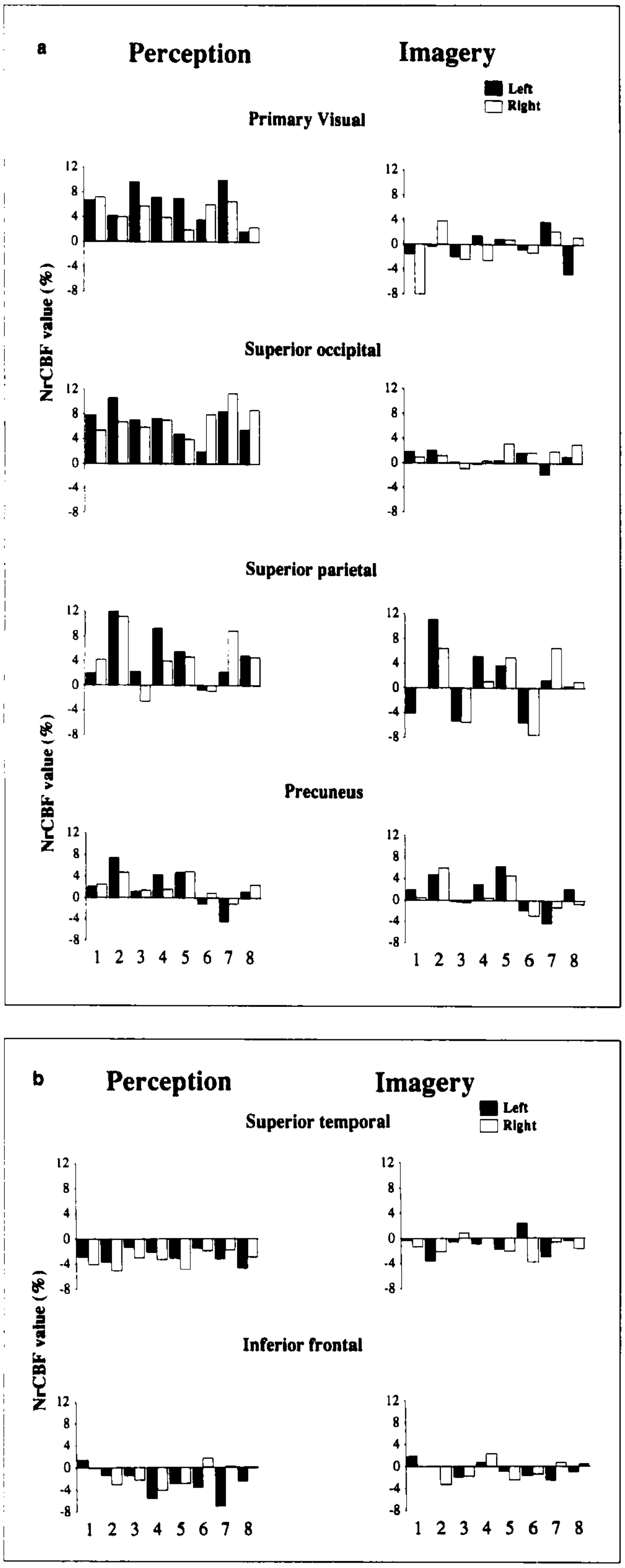

Figure 4. (a) Individual percent normalized regional cerebral blood flow variations in the different anatomical regions active during the Perception and/or Imagery as compared with Control (subject 1 to 8). Closed bar: left hemisphere. Open bar: right hemisphere. (b) Individual percent normalized regional cerebral blood flow variations in inferior frontal and superior temporal regions during the Perception and/or Imagery as compared with Control (subject 1 to 8). Closed bar: left hemisphere. Open bar: right hemisphere.

1983) then in man with PET (Haxby et al., 1991), which is assumed to be involved in the processing of the spatial component of visual stimuli. We think activations detected in the parietal lobe are related to the visuospatial nature of the perceptual task we designed.

In addition, the parietal lobe is part of the visual attention system (Posner & Dehaene, 1994) and the parietal activations could express the involvement of this system. Posner has described the difficulty evidenced by patients suffering from a posterior parietal trouble, in turning their attention from one visual stimulus to another (Posner, Walker, Friedrich, & Rafal, 1984). Furthermore, in a recent PET study, an activation in the superior parietal cortex and the precuneus was described while subjects had to shift their attention from one spot to another (Corbetta, Miezin, Shulman, & Petersen, 1993). Such an attentional movement is normally required in the present study during Perception and could be responsible in part for parietal activations.

Apart from these occipital and parietal activations, we observed a right lateral premotor area NrCBF increase during visual exploration. Eye movements, although not significantly different in amplitude when compared to Control, were qualitatively distinct because they were compelled by the scanning of the external stimulus. Activation in this region could then be related to the visuomotor activity consisting in moving the gaze along the limits of the island, the lateral premotor cortex having been previously reported to be involved in externally cued movements (Deiber et al., 1991; Grafton, Woods, Mazziotta, & Phelps, 1991).

Contrasting with the large network activated during visual exploration, mental exploration of a map resulted in activations of small amplitude in a reduced set of regions including the right superior occipital gyrus, the supplementary motor area, and the cerebellar vermis. A possible explanation for the paucity of activated areas during the mental Imagery task of the present study could be that this task would be too easy for subjects having high mental imagery capacities. Although one cannot totally rule out this hypothesis, we previously reported that high imagers do modify their rCBF during island map exploration (Charlot et al., 1992).

In particular, no activation was observed either in the primary visual area or in nearby regions. The fact that, in our data analysis strategy, primary visual area has been defined using MRI in each individual (see Methods) makes mispositioning an unlikely explanation for this absence of activation. In addition, the small and slightly negative average NrCBF variation in primary visual area during Imagery in our protocol argues against a possible statistical power limitation of our experimental design. In this respect, note that Perception gave rise to large and highly significant NrCBF increases in primary visual area, consistent with previous PET protocols on visual perception (Fox & Raichle, 1984; Lueck et al., 1989). In addition, although it is difficult to be entirely sure that

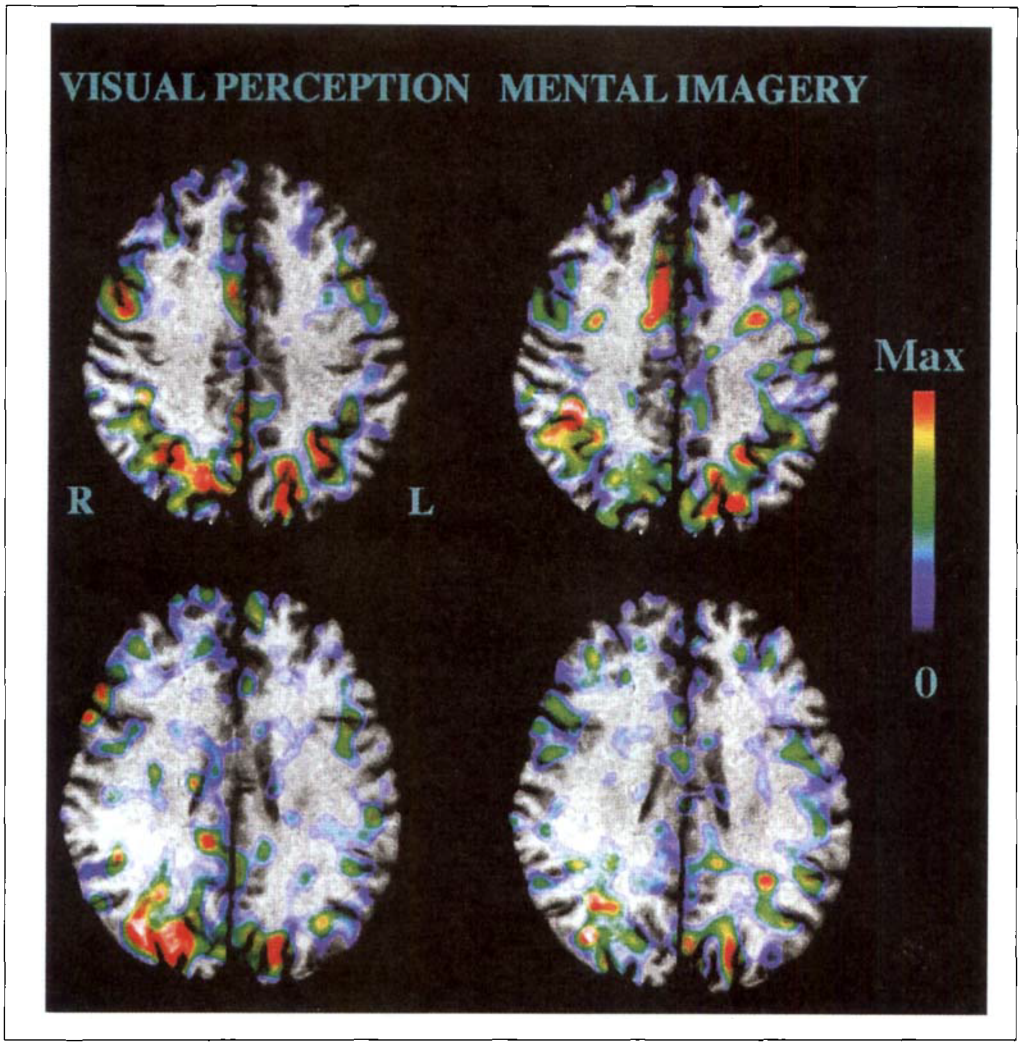

Figure 5. Single subject blood flow activation images superimposed on the corresponding axial MRI slice. The axial slice passes through the parietal (top) and superior occipital areas (bottom) of subject 8. Activation maps were obtained by subtracting averaged NrCBF images during Control from the average NrCBF images during Perception (left) and Imagery (right). Color scale represents NrCBF increase in pixel counts normalized by whole brain counts. R: Right, L: Left. Note that in this subject, the occipital activation in both Perception and Imagery tasks is accompanied by a parietal (intraparietal sulcus and precuneus) activation.

subjects did perform the mental imagery task, there are indirect elements such as the post-PET control sessions indicating that it was indeed the case. Finally, one could raise the hypothesis that mental imagery was already present during the control condition because our subjects were good imagers, thereby masking a primary visual area activation during the mental imagery condition. However, we have used this rest control condition in more than 100 PET experiments and found no difference in the occipital cortex CBF at rest in high imagers as opposed to standard normal volunteers.

We think thus that the apparent discrepancy between this result and a previous report of primary visual area activation during mental imagery (Kosslyn et al., 1993) may be found in differences between the designs of the two studies. In Kosslyn's study, the first imagery task required the mental projection of an image on an actually perceived support. Such a task closely entangles perception and imagery, and may require activation of the primary visual area to combine and adjust image and percept. Alternately, attentional effects could explain the NrCBF increase in primary visual area: several reports have indeed shown that flow increases in primary visual area were larger when attention to external stimuli was sustained as compared to passive viewing (Corbetta et al., 1991; Sergent et al., 1992; Dupont et al., 1993). In a second experiment, Kosslyn did describe an activation of the primary visual region while subjects built a mental image with eyes closed (Kosslyn et al., 1993), but this activation was observed when two mental imagery conditions were subtracted from one another and thus remains difficult to interpret. On the contrary, our result suggests that no top-down activation is needed in the absence of external stimulus.

The superior occipital lobe involvement in mental Imagery observed in the present study, although obtained on a small set of subjects, is fully compatible with neuropsychological studies that reported imagery deficits in patients with occipital lesions (Farah, 1984; Farah, Levine, & Calvanio, 1988; Goldenberg, 1992). It also goes together with evoked potential (Farah & Péronnet, 1989; Farah, Weisberg, Monheit, & Péronnet, 1990) and SPECT studies (Goldenberg et al., 1987; Charlot et al., 1992; Goldenberg et al., 1992) in healthy subjects showing that imagery activity develops in the posterior parts of the brain. Similarly in PET studies, activations of the right external side of the occipital lobe were observed when subjects created a mental image (Kosslyn et al., 1993) or when they implicitly used mental imagery to perform a spatial memory task (Jonides et al., 1993).

It is noteworthy that it is the upper part of the right lateral occipital cortex that was found activated in the mental Imagery task of our protocol: the upper external occipital is a subset of the dorsal pathway described above, engaged in visuospatial activities. With this respect, neuropsychological data have shown that occipitoparietal lesions cause disorders in mental imagery of the spatial type (Levine, Warach, & Farah, 1985).

Moreover, although not significantly activated at the 0.05 confidence level, the precuneus showed an NrCBF increase in 5 over the 8 subjects and PET protocols reported activations in the precuneus associated with the spatial (Haxby et al., 1991) or attentional (Corbetta et al., 1993) aspects of visual perception. We propose that the role of external occipital in mental imagery would be the generation and maintaining of the mental image, while the precuneus would be involved in the exploration of the image and the attention required by this task.

Despite the fact that eye movement amplitude did not differ significantly between the rest control and the imagery conditions, the activation of SMA during mental exploration may be attributed to the saccadic eye movements that were performed by the subjects. Although SMA has been found to play a role in motor imagery (Decety & Ingvar, 1990; Lang et al., 1994), mental exploration in the present study did not include motor imagery but explicitly required ocular exploration of visual mental images, resulting in internally cued movements in which SMA has been shown to play a major role (Goldberg, 1985; Deiber et al., 1991). Consistent with this interpretation, a recent neuropsychological study reported a selective impairment in the exploration of visual mental images, in the absence of any perceptual deficit, in a patient suffering from a frontal lesion encompassing SMA (Guariglia, Padovani, Pantano, & Pizzamiglio, 1993).

In this context, the cerebellar vermis activation added to the bilateral precentral gyri and the median cingulate gyrus activations that were observed when comparing mental and visual exploration probably reflect the involvement of the saccadic eye movement network (Petit et al., 1993; Lang et al., 1994).

Finally, when subtracting visual from mental exploration conditions, we found a significant activation of Broca's area similar to that previously described by Kosslyn in an imagery task when compared to a perceptual task (Kosslyn et al., 1993). However, NrCBF values (Table 1) and comparison with Control (Table 2) demonstrate that this finding is in fact due to a very significant deactivation of Broca's area in Perception. It is noticeable that this Broca's area deactivation during Perception is associated with bilateral superior temporal gyri deactivations similar to those previously described in a PET protocol studying visual perception (Dupont et al., 1993). This deactivation of a network of regions known to be involved in language processing (Mazoyer et al., 1993) during visual processing may reflect the dichotomy between verbal and visual representations as theorized by Paivio (1986).

METHODS

Subject Selection

Eight right-handed young male volunteers (age: 24 ± 5.6 years) participated in the study. They were selected among a population of 93 subjects on the basis of their high scores on the Minnesota Paper Form Board (MPFB, Likert & Quasha, 1941) and the Mental Rotations Test (MRT, Vandenberg & Kuse, 1978). These are objective tests of visuospatial mental abilities. The MPFB requires mental reconstruction of figures while MRT essentially deals with mental rotation. The eight selected subjects were high visuospatial imagers since they belonged to the superior quartile of the whole population distribution for both tests. Their MPFB mean score was 23.6 ± 2.8 (mean ± SD, whole population 19.2 ± 4.2), and the MRT mean score was 16.3 ± 2.2 (whole population 9.6 ± 4.3).

Tasks Design

NrCBF was measured six times for each subject replicating a series of three conditions: control in total darkness, visual perceptual exploration of a map, and mental exploration of the same map (Figs. 1 and 2).

Control

Subjects were lying in the camera, eyes closed, in total darkness, a black and opaque cloth covered the whole camera to turn it into a black chamber. No particular instruction was given to them, except not to move. After the PET session, subjects were debriefed to make sure they did not have systematic cognitive activity during this control condition, in particular that they were not engaged in visual mental imagery .

Perception

A black and white map of an imaginary island (71 × 42 cm) was placed in a black chamber attached to the back of the PET camera. Six landmarks were located on the periphery of the island (Fig. 1). A mirror placed in front of the subject allowed him to see the map, which covered his whole visual field. The subjects received the following instruction: starting from the northern extremity of the island and following its periphery, they had to move their gaze clockwise from landmark to landmark, pausing a few seconds on each one; after completing clockwise exploration in about 40 sec, subjects were to explore it again in counterclockwise direction at the same speed. Such alternate exploration began 45 sec prior to the rCBF measurements and was pursued during the scan acquisition.

Imagery

Subjects in total darkness with their eyes closed were first instructed to generate a mental image of the previously explored map, as accurate and vivid as possible, including each landmark. They then had to explore the image of the map in the same way and at the same speed as during Perception.

In this experiment, free continuous mental exploration was thought to be more appropriate than other tasks, in particular more constrained mental scanning tasks that typically consist for subjects in listening repeatedly to names of pairs of landmarks and indicating by pressing a button that they have scanned the interval separating these landmarks (Kosslyn et al., 1978; Denis & Cocude, 1992). Obviously, the intrinsic value of these tasks is that they provide experimenters with scanning times whose correlation with lengths of intervals may reflect the structural properties of subjects' visual images. However, we thought it preferable to leave subjects free of exploring their images for two reasons: (1) this procedure was exactly like the procedure used in the perceptual condition, which should be expected to increase the comparability of the two conditions; (2) it avoids any sensory inputs (name of landmarks) and motor outputs (motor responses) that might result in more complex brain activation patterns. In addition, previous experiments have shown that when subjects have listened to verbal descriptions of visual patterns, accuracy of graphic reproduction reflects prior active mental exploration of these patterns (Denis & Cocude, 1992).

Replicates of the Perception and Imagery tasks were performed with two maps to avoid overlearning effects with a single map (Fig. 1).

Training Session. During the few minutes preceding CBF measurements, each subject went through the perception and the imagery tasks twice.

Tasks Control. During each condition, eye movements and heart rate were recorded using, respectively, electrooculogram and electrocardiogram. Following each Imagery task, subjects were presented with a blank map of the corresponding island, and were requested to pinpoint the location of each landmark as accurately as possible. This was used as a check that subjects really paid attention to the tasks they executed and that they memorized the map. The accuracy of mental images was evaluated by calculating an error measure, i.e., the distance between the position of the landmarks indicated by the subjects and their actual location.

Scanning Procedure

For each condition, 31 contiguous brain slices were acquired simultaneously on an ECAT 953B/31 PET camera (Mazoyer, Trebossen, Deutch, & Blohm, 1991). Following intravenous bolus injection of oxygen-15-labeled water (Herscovitch, Markham, & Raichle, 1983), a single 80-sec scan was reconstructed (including correction for head attenuation) starting at the arrival of the radioactivity in the brain, the scan duration being chosen to improve the signal-to-noise ratio in the difference images (Kanno, Iida, Miura, & Murakami, 1991). Interscan interval was 15 min. A set of 3-mm-thick T1-weighted magnetic resonance axial slices covering the whole brain was acquired for each subject, using a 0.5 T MRMAX imager (General Electric). This protocol was approved by the Atomic Energy Commission Ethic Committee and all subjects gave a written informed consent.

Image Analysis

Our data analysis method has been described in detail elsewhere (Mazoyer et al., 1993). It is aimed at detecting task-specific increases of cerebral blood flow in cerebral structures having anatomical boundaries, based on a parcellation of the brain similar to that recently proposed by others (Rademacher, Galaburda, Kennedy, Filipek, & Caviness, 1992). In a first step, a detailed analysis of each subject's brain anatomy was performed. Using a dedicated software (Voxtool, General Electric, Buc, France), MRI axial slices were used to reconstruct a three-dimensional brain volume that was further segmented and allowed the display of both hemispheres' surfaces rendering and sections in three orthogonal directions. The major gyri could then be identified and their limits automatically marked onto the MRI axial slices. Using these anatomical landmarks, cortical ROIs with anatomical boundaries, corresponding to the intersection of the gyri with the MRI axial slices, were delineated on each subject's MRI images (Fig. 3).

The way some of the occipital and frontal regions were drawn needs further details. The location and the run of calcarine sulcus is known to show a great interindividual variability (Steinmetz, Furst, & Freund, 1990). The primary visual area was delineated around the banks of the calcarine sulcus, identified on axial, sagittal, and coronal views, including its side branches. The calcarine plane divides the mesial occipital lobe in a superior part: cuneus, and in an inferior part the fusiform and lingual gyri. The lateral part of the occipital lobe was separated in superior and inferior regions using the external occipital sulcus as a limit (Ono, Kubik, & Abernathey, 1990). In the frontal lobe, a region called lateral premotor was defined, corresponding to the lateral part of Brodmann's area 6 as defined in Talairach's atlas (Talairach & Tournoux, 1988).

This method does not require complex operations of normalization to a fixed brain atlas, and takes into account interindividual anatomical differences (Steinmetz & Seitz, 1991) as well as hemispheric anatomical asymmetries (Steinmetz, Volkmann, Jänke, & Freund, 1991). It also makes the ROI boundaries independent of the CBF PET images and provides regional activation values for each individual (Fig. 4a and b).

Statistical Analysis

To compute regional normalized regional cerebral blood flow values, the PET slices acquired on each trial were then aligned with the subject high resolution magnetic resonance images using the software developed by Pietrzyk, Herholz, and Wolf-Dieter (1990). Within each anatomical ROI, NrCBF was estimated as the ratio (in percent) of the radioactivity concentration in the region to that of the whole brain as measured in the PET images.

In each region, an analysis of variance with repeated measures was conducted with a three-level task factor and a two-level replication factor. Whenever task main effect was found significant at the 0.05 level, a post hoc paired *t* test was used to compare each visual task to Control. Due to technical reasons, the second Control of subject 7 was not suitable for analysis.

Acknowledgments

We thank Laurent Petit, Laurence Raynaud, Monique Crouzel, and the Orsay radiochemistry staff for technical assistance. This work has been supported by the Réseau Régional Paris-Sud (CNRS, Programme Cognisciences).

Reprint request should be sent to Pr. Bernard Mazoyer, Service Hospitalier Frédéric Joliot, CEA-DRIPP, 4, place du Général Leclerc 91406, Orsay Cedex, France.

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