

A PET meta-analysis of object and spatial mental imagery

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Neuroimaging studies have described the functional neuroanatomy of mental imagery. Taken separately, specific studies vary in the nature of the task used and are limited by statistical power and sensitivity. We took advantage of a multistudy PET database of 54 subjects acquired in our laboratory to reveal the neural bases of spatial versus object mental imagery tasks. Our first goal was to evaluate to what extent the activated foci elicited by both object and spatial studies overlap. A second aim was to compare activations elicited by spatial imagery tasks to those elicited by object imagery tasks. We also explored applying regression analyses to the relationships between the scores on the Mental Rotations Test (MRT) and changes in regional cerebral blood flow (rCBF) during spatial and object imagery tasks. This meta-analysis yielded the following observations: (1) both spatial and object imagery tasks shared a common neural network composed of occipitotemporal (ventral pathway) and occipitoparietal (dorsal pathway) regions and also by a set of frontal regions (related to memory); (2) the superior parietal cortex was more strongly implicated during spatial imagery; (3) object imagery specifically engaged the anterior part of the ventral pathway, including the fusiform, parahippocampal, and hippocampal gyrus; (4) object imagery activated the early visual cortex, whereas spatial imagery induced a deactivation of the early visual cortex; (5) blood flow values in some of the regions noted above were positively correlated with scores on the MRT: the higher the subjects performed on the MRT, the more pronounced the rCBF was in these regions. These results may reconcile some of the apparent discrepancies among previous studies concerning the activation of early visual cortex in mental imagery. They also contribute to a better knowledge of the neural bases of object and spatial mental imagery.

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It is now well established that both visual mental imagery and visual perception rely on sets of distinct subsystems (Farah, 1984; Kosslyn, 1994). A major concern of neuroimaging studies that identified the cerebral bases of visual imagery has been to assess the extent to which visual imagery and visual perception share common cerebral structures (Kosslyn et al., 1993; Kosslyn, Thompson, & Alpert, 1997; Mellet, Tzourio, Denis, & Mazoyer, 1995). In agreement with the theoretical framework proposed by Kosslyn (1987, 1994), it has been established that both visual perception and visual imagery rely on a “what” and “where” functional dichotomy (see Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998, for a review). According to this dichotomy, figurative aspects of both mental images and visual percepts are processed along the ventral occipitotemporal route while the dorsal occipitoparietal route processes the spatial features. Note, however, that this distinction is not absolute since most of the neuroimaging studies that dealt with spatial imagery tasks not only reported dorsal activation but also activation along the ventral route. In the same vein, studies that focused on figurative imagery reported occipitoparietal activation together with the activation in the ventral pathway (Ishai, Ungerleider, & Haxby, 2000; Lambert, Sampaio, Scheiber, & Mauss, 2002).

In addition to these uncontroversial findings, divergent neuroimaging results were reported regarding the involvement of the early visual cortex (Brodmann Areas 17–18), within and around the calcarine fissure, during visual mental imagery. Some researchers have reported activation of the early visual cortex, whereas others have not (see Roland & Gulyas, 1994, for reviews; Kosslyn, Ganis, & Thompson, 2001; Kosslyn & Ochsner, 1994; Mellet et al., 1998; Sakai & Miyashita, 1994). These discrepancies have questioned some aspects of Kosslyn’s model since the early visual cortex had been proposed to be a key part of the neural substrate of the so-called visual buffer (Kosslyn, 1994). This buffer would be shared by both perception and imagery and is thought to implement a topographic representation of either a perceptual or a mental image. Various factors have been considered in the neuroimaging literature in order to explain these divergent reports: the nature of the baseline condition, the level of resolution of mental images and the type of neuroimaging techniques used (i.e., positron emission tomography, PET, or functional magnetic resonance imaging, fMRI), but no definite explanation has emerged. In the present paper we consider another alternative account, which is related to the spatial or object nature of the mental imagery task. Indeed, most studies dealing with spatial imagery have not reported early visual cortex activation whereas, in those studies in which an activation was noted, figurative imagery tasks were employed (Kosslyn et al., 2001; Thompson, Kosslyn, Sukel, & Alpert, 2001).

In the present paper, we report new analyses of PET data collected in our laboratory including nine mental imagery conditions, 54 subjects, and a total of 323 scans. The aim of this meta-analysis was two-fold. First, we wanted to discover which brain regions are activated during visual mental imagery in

general, whatever the nature of the imagery task. In the framework of the imagery debate, the large number of scans and subjects included in this analysis offers better sensitivity to small effects and allows one to detect even small activation of the early visual cortex. Our second goal was to compare two kinds of imagery tasks: tasks that mainly dealt with the spatial properties of the mental image, such as mental scanning or mental navigation, and those that required the subjects to imagine colour, shape, and texture of objects. This comparison will highlight the brain areas that are either specific to a given modality (i.e., spatial or figurative) or that are significantly more activated in one modality than in the other. Finally individual differences in imagery ability could also be partly responsible for the discrepancies in the literature. Adopting an exploratory approach, we investigated whether the individual ability for mental imagery, as assessed by the Mental Rotations Test (MRT; Vandenberg & Kuse, 1978), could explain the interindividual variability of regional blood flow increases during the mental imagery tasks.

MATERIALS AND METHODS

Experimental design

The data from nine mental imagery conditions were analysed with a multistudy statistical model. We distinguished two categories of mental imagery tasks in this analysis: the first included the tasks that relied on spatial properties of images, and the second comprised those that included a strong object component. More specifically, the spatial imagery tasks included mental scanning, mental navigation, or spatial construction. The object imagery tasks required the subjects to retrieve a representation of figurative attributes of the stimuli (e.g., shape, configuration). The nine imagery conditions are detailed below. Among the nine conditions, we have classified seven of them as spatial imagery conditions and two of them as object imagery conditions.

All conditions were conducted with eyes closed in total darkness; a black and opaque chamber covered the whole PET camera. All conditions except one (baseline condition of Study 6) were compared to a rest condition. During this rest condition, subjects were instructed to keep their eyes closed, to relax, to refrain from moving, and to avoid any structured mental activity such as counting or rehearsing. This condition has been widely used as a basic control condition in our laboratory (Mazoyer et al., 2001). It has recently been proposed as a good “baseline” physiological state (Gusnard & Raichle, 2001).

Spatial imagery conditions

Condition 1. Mental exploration (Mellet et al., 1995). Seven right-handed healthy male French students participated in this study. Normalised regional cerebral blood flow (NrCBF) was measured four times for each subject,

replicating a series of two conditions: mental exploration of an island map and rest in total darkness. For the mental exploration condition, the subjects were instructed to generate a mental image of a map of an island that they had previously visually explored; six landmarks were located on the periphery of the island. Then, they were asked to explore this mental map according to the following instructions: "Starting from the northern extremity of the island and following its periphery, you have to move mentally clockwise from landmark to landmark, pausing a few seconds on each one; after completing the clockwise exploration in about 40 s, you have to explore it again in a counterclockwise direction at the same speed."

Condition 2. Spatial mental construction (Mellet, Tzourio, Crivello, Joliot, Denis, & Mazoyer, 1996). Nine right-handed healthy male French students took part in this study. We obtained four sequential PET measurements of the NrCBF of each subject, replicating a series of two experimental conditions: a spatial mental construction task and a rest condition. During the mental construction task the subjects were requested to build four three-dimensional (3-D) mental objects made out of twelve cubes (Shepard & Metzler, 1971). The task itself consisted first in visualising one cube, which served as the starting point of the construction, and then adding eleven other cubes according to a list of directional words given verbally through earphones at 0.5 Hz. The lists were randomly generated using the six directional French words: "haut" ("up"), "bas" ("down"), "droite" ("right"), "gauche" ("left"), "avant" ("front"), "arrière" ("back"). At the end of the mental construction of the object, the subjects had to visualise the entire object during 5 s, and then delete it from their mind before visualising again the starting cube and building the next object from another list of directional words.

Condition 3. Mental navigation (Ghaëm et al., 1997). Five right-handed healthy male French students participated in this study. Four sequential measurements of the NrCBF were obtained from each subject, replicating a series of two experimental conditions: a rest condition and a mental navigation task. The day before the PET scanning, the subjects walked within an environment (a park) they had never seen before and were instructed to memorise key landmarks. The mental navigation task performed in the PET camera consisted of mentally recalling the visual and sensory-motor mental images of their walk from a route perspective, following the path between two named landmarks, and pressing a key when the second landmark was reached. Five different segments, randomly presented, were used during each replication of the mental navigation condition.

Condition 4. Mental scanning (Mellet et al., 2000a). Six right-handed healthy male French students took part in this study. Four to six sequential

measurements of NrCBF were obtained from each subject, replicating two or three times a series of two experimental conditions (because of technical problems, the PET camera did not start during part of the acquisition resulting in missing replications for some subjects). The two experimental conditions were rest and mental scanning of a map. During the mental map task, subjects were asked to keep eyes closed and to visualise a previously memorised map that included seven coloured dots. They were then given the name of two coloured dots (e.g., “red”, “blue”) through earphones and had to imagine a laser dot following the path segment drawn on the original map between the two dots. Once the second dot was reached, the subjects had to press a button with their right index finger—after they performed this action, the names of a second pair of dots were presented auditorily.

Condition 5. Mental scanning of verbally described environments (Mellet, Bricogne, Crivello, Mazoyer, Denis, & Tzourio-Mazoyer, 2002). This condition is similar to Condition 4 except that the mental map was mentally built after the subjects read a descriptive text. Six right-handed healthy male French students participated in this study. Eight measurements of NrCBF were obtained from each subject, replicating four times a series of two experimental conditions: a mental scanning task of verbally described environments and a rest condition. In this study, two different texts describing distinct environments (a leisure park and a town) were adapted from the study of Taylor and Tversky (1992). The texts described the environment from a survey perspective (i.e., using the canonical terms “north”, “south”, “east”, and “west”). During mental scanning, the subjects closed their eyes and were told to visualise the environment as accurately as possible. They were then given (through earphones) the names of two landmarks (e.g., “church”, “school”) and were to imagine a laser dot following the path segment between the two landmarks. Once the second landmark was reached, the subjects had to press a button with their right index finger—after they performed this action, the names of a second pair of landmarks were presented auditorily.

Condition 6. High-resolution mental imagery based on visual or verbal descriptions (Mellet, Tzourio-Mazoyer, Bricogne, Mazoyer, Kosslyn, & Denis, 2000b). Seven right-handed healthy male French students participated in this study. There were three PET conditions: imagery after visual learning (6a), imagery after verbal learning (6b), and a baseline condition. For the two mental imagery conditions, the subjects memorised two scenes during the 15 min prior to scanning. In the visual learning condition, the subjects were asked to study and memorise scenes. In the verbal learning condition, the subjects were instructed to listen to verbal descriptions of how shapes were to be arranged and to form and memorise a visual image for each of the described scenes. Each scene was composed of four simple geometric shapes, arranged on a base; the

scenes differed only in the ordering of the elements on the base. During the PET measurements, the subjects performed the imagery task, whatever the modality of learning, with the cues and comparison statements being delivered through earphones. Each condition consisted of nine comparison statements, alternating from one scene to the other. The comparison statements required the subjects to evaluate the relative height of the scene over two named points; the differences were subtle, and hence high resolution was required. The subjects had to respond by saying “right” or “wrong” into a microphone connected to a computer. After each response, the computer recorded the response time and then 750 ms later delivered the identification number of the next scene. Another 4 s later, a new comparison statement was delivered. Both imagery conditions (6a and 6b) were compared to a baseline task. During the baseline task, the subjects closed their eyes, listened to randomly chosen comparison statements delivered every 7 s, and alternatively said “right” and “wrong” after each term.

Condition 7. High-resolution mental imagery with different noise environments (Mazard, Mazoyer, Etard, Tzourio-Mazoyer, Kosslyn, & Mellet, 2002). Six right-handed healthy male French students took part in this study. This task was adapted from that used in the study just summarised (Mellet et al., 2000b). In the mental imagery task, subjects were asked to memorise 3-D sets of geometric forms on a base, which were presented visually, and then to judge subtle aspects of the scenes. In addition, we tested the effect of the “fMRI-like” noise environment on the mental imagery task. The sound produced by a clinical EPI-BOLD sequence was recorded using a nonmagnetic microphone near the radio frequency head coil (GE sigma 1.5T; TR = 6 s; TE = 60 ms; FA = 90°). We monitored rCBF in four different conditions. Two conditions were performed in a silent “PET-like” environment: a mental imagery task (7a) and a rest condition. During the other two conditions, the “fMRI-like” noise was played back from a digital audio tape and delivered through loudspeakers in the PET room. The remaining two conditions were a mental imagery task (7b) and a rest condition. All conditions were replicated twice in five subjects and once in one subject.

Object imagery conditions

Condition 8. Mental imagery of landmarks (Ghaëm et al., 1997). Five right-handed healthy male French students participated in this study. Four sequential measurements of rCBF were obtained from each subject, replicating a series of two experimental conditions: a rest condition and static visual imagery of landmarks. The day before PET scanning, subjects walked within an environment (a park) they had never seen before and had to memorise key landmarks. During the static visual imagery task, subjects were instructed to visualise a landmark upon hearing its name through earphones and to maintain its mental image until they heard another landmark name 10 s later.

Condition 9. Mental imagery from concrete word definitions versus rest (Mellet, Tzourio, Denis, & Mazoyer, 1998). Eight right-handed healthy male French students took part in this study. Six sequential measurements of NrCBF were obtained from each subject, replicating a series of two experimental conditions three times: listening to the definition of a concrete word and generating the corresponding mental image, and a rest condition. In the imagery task, the subjects were instructed to listen attentively to and understand 15 words and their definitions, taken from a French dictionary, verbally delivered through earphones. Each word and its accompanying definition were read in 6 s, followed by 2 s of silence before the next stimulus was delivered. The task duration was 120 s, starting 30 s before and maintained during the 90 s of the PET data acquisition. The words delivered during the imagery condition were of common use and easy to associate with an image, referring to objects or animals (such as ‘bottle’, ‘guitar’, ‘lion’). The definitions described figural, physical, or functional features of the objects or the animals. The definitions were thus very likely to result in spontaneous visual mental imagery activity. In addition, in order to induce sustained mental imagery, the subjects were explicitly encouraged to produce visual images evoked by words and to modify or refine each image as they listened to the definition following the word.

Subjects

A total of 54 right-handed male French students (age 18–35 years old) were included in this meta-analysis. Five of them performed both an object imagery task and a spatial imagery task (Conditions 3 and 5). More precisely, 13 subjects performed an object imagery condition and 46 performed a spatial imagery condition. Handedness was assessed with the Edinburgh Inventory (Oldfield, 1971). All subjects were free from neurological disease or injury and had no abnormalities in their T1-weighted magnetic resonance images (MRI). Written informed consent was obtained from each subject after the procedures had been fully explained. The local ethics committee approved all studies included in our meta-analysis.

In order to ensure optimal homogeneity of the sample of subjects with respect to their imagery abilities, subjects were selected as high visuospatial imagers on the basis of their scores on the MRT (Vandenberg & Kuse, 1978); all subjects scored beyond the 50th percentile of a population of 120 male subjects. The mean test score for all subjects was 16.46 ± 2.16 (mean \pm SD).

Imaging

Measurements of the normalised regional cerebral blood flow (NrCBF) were obtained from each subject on two different cameras: an ECAT 953B/31 PET camera for Conditions 1, 2, and 3 (time acquisition: 80 s); and an ECAT exact HR+ camera for the other six conditions (time acquisition: 90 s). A single scan

was acquired and reconstructed (including a correction for head attenuation using a measured transmission scan) with a Hanning filter of 0.5 mm^{-1} cut off frequency and a pixel size of $2 \times 2 \text{ mm}^2$. The time delay between scans was 8 min.

Data analysis

In order to be included in the analysis, all the 323 scans were processed using the same procedure. After automatic realignment (AIR; Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998), the original brain images were transformed into the MNI (Montreal National Institute) space (Friston, Holmes, Poline, Frith, & Frackowiak, 1995). The images were smoothed using a Gaussian filter of 12 mm FWHM leading to a final smoothness of 15 mm FWHM. The rCBF was normalised within and between subjects using a proportional model.

SPM-99 software was used to compute a multistudy analysis using the general linear model. Simple comparisons within each condition focused on the differences between a mental imagery task versus a baseline (rest in eight conditions, nonrest in one condition). All comparisons within each condition and within each study were computed and then combined in a conjunction analysis. Because activation and baseline conditions differed across studies, the conjunction analysis appears to be the most suitable approach to reveal effects common to the nine imagery conditions (Price & Friston, 1997). Conjunctions imply that activations must be present in all contrasts (mental imagery minus baseline) in order to be detected and it is thus a conservative approach, which avoids false-positive activations. In addition, outlying values did not influence the results (Friston, Holmes, Price, Büchel, & Worsley, 1999). The corresponding activation map was thresholded at $p < .001$ confidence level (uncorrected for multiple comparisons). The voxel amplitude t -map was transformed to a Z volume.

We also computed a comparison between the two types of tasks: (spatial tasks minus baselines) minus (object tasks minus baselines). In order to avoid any artifactual activation in the comparison caused by a deactivation during object imagery as compared to baseline, voxels that were not significant at $p = .05$ (uncorrected) in the spatial imagery versus baseline contrasts were excluded by masking. This activation map highlighted activations that were specific to the spatial imagery conditions, or more important in these conditions than in the object imagery conditions at $p < .001$ (uncorrected for multiple comparisons). The same procedure was used to reveal the specific activation map during object imagery conditions at $p < .001$ (uncorrected for multiple comparisons), using the comparison: (object tasks minus baselines) minus (spatial tasks minus baselines).

In addition, we performed two reverse comparisons, to discover the deactivations specific to spatial and to object imagery conditions, respectively at

$p < .001$ (uncorrected for multiple comparisons). These comparisons were thus: (baselines minus spatial tasks) minus (baselines minus object tasks) and (baselines minus object tasks) minus (baselines minus spatial tasks).

Linear regressions were computed between the difference noted in the scans of NrCBF during each imagery condition as compared to its baseline and the MRT scores recorded for each subject. Two regressions were performed separately for spatial imagery and object imagery conditions. Regression maps were thresholded at $p < .001$ (uncorrected for multiple comparisons).

Anatomical localisation of the maximum Z -score relied on the automated anatomical labelling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single subject brain (Tzourio-Mazoyer et al., 2002).

PET RESULTS

NrCBF increases: Conjunction of all the nine imagery conditions

(See Table 1 and Figure 1A.) This analysis revealed regions that were activated in all of the nine mental imagery conditions compared to their respective baseline conditions.

We found a widespread bilateral activation in the parietal lobe, including the intraparietal sulcus and the precuneus, extending to the right angular gyrus and to the left middle occipital gyrus. In addition, we detected several foci in the frontal lobe, including a bilateral activation in the depth of the superior frontal sulcus and an activation of the anterior part of the left superior frontal sulcus and of the right inferior frontal gyrus. Another focus of activation was detected in the right middle frontal gyrus. Activations were also evident in the left superior part of the temporal pole and bilaterally in the inferior temporal gyrus, belonging to the so-called ventral pathway. We also detected bilateral activation of the anterior insula and one focus of activation in the right anterior part of the anterior cingulate cortex. The cerebellar vermis was also activated. Note that this conjunction analysis did not reveal any activation of the early visual cortex.

Areas more activated in spatial imagery conditions than in object imagery conditions

(See Table 2 and Figure 1B.) These conditions elicited large bilateral activation of the entire superior part of the parietal lobe: the bilateral precuneus, extending to the bilateral superior parietal gyrus and the right superior occipital gyrus. The middle occipital gyrus was also activated. A focus of activation was observed in the right middle cingulate cortex. In the frontal lobe, blood flow increased in the left middle frontal gyrus and extended to the superior frontal gyrus.

TABLE 1
Conjunction analysis revealing foci of significant NrCBF increases common to all of the nine mental imagery conditions as compared to baseline ($p < .001$, uncorrected for multiple comparisons)

<i>Anatomical location of max. voxel activation</i>	<i>Coordinates</i>			<i>Z-score</i>
	<i>x</i>	<i>y</i>	<i>z</i>	
L. intraparietal sulcus	-22	-70	52	7.8
R. intraparietal sulcus/precuneus	32	-66	48	6.9
R. intraparietal sulcus/angular gyrus	42	-60	48	5.7
L. middle occipital gyrus/intraparietal sulcus	-32	-82	30	3.6
L. superior frontal sulcus	-28	0	56	6.8
L. middle cingulate cortex	-4	14	42	6.4
L. superior frontal gyrus	-16	8	48	5.7
R. superior frontal sulcus	36	-4	54	5.3
R. middle frontal gyrus	28	0	64	4.7
L. superior frontal sulcus—anterior part	-28	50	16	5.7
R. inferior frontal gyrus—orbital part	28	46	-18	5.3
R. middle frontal gyrus	44	38	22	4.7
R. middle frontal gyrus	42	44	16	4.4
L. superior temporal gyrus/temp. pole—sup. part	-62	4	-10	4.2
R. inferior temporal gyrus	72	-40	-16	4.9
L. inferior temporal gyrus	-60	-38	-16	3.9
L. anterior insula	-24	20	-4	6.2
R. anterior insula	30	16	-4	3.6
R. anterior cingulate cortex	10	36	12	3.5
Cerebellar vermis lobule IV–V	0	-58	-16	4.8
R. cerebellar vermis lobule IV–V	2	-50	-20	4.2
R. cerebellar vermis lobule I–II	6	-44	-24	4.1

The data are local maxima of activated region detected with SPM 99 software. The anatomical localisation of the maximum Z-scores of these regions is given on the basis of the MNI template, using their stereotactic coordinates in mm (R: right; L: left).

Figure 1 (opposite). (A) Left, right, and superior 3-D view rendering of the statistical map revealing the areas activated when subjects formed images compared to baseline conditions (conjunction analysis of spatial and object imagery, see Table 1). (B) Superior 3-D view rendering of the statistical map showing the areas activated when subjects formed spatial images compared to object conditions. Plots show the local maxima (Δ NrCBF as percentage of the baseline NrCBF value) during each imagery condition in the intraparietal sulcus (IPS, see Table 2). (C) Inferior 3-D view rendering of statistical map revealing the activation within the inferior temporal lobe when subjects formed object images compared to spatial conditions. Plots show the local maximum during each imagery condition in the inferior temporal lobe ($x = -44$, $y = -16$, $z = -26$; see Table 3). The Z-maps were thresholded at $Z = 3.09$ ($p < .001$; uncorrected for multiple comparison). Stereotactic coordinates of local maxima are given based on the MNI coordinates.

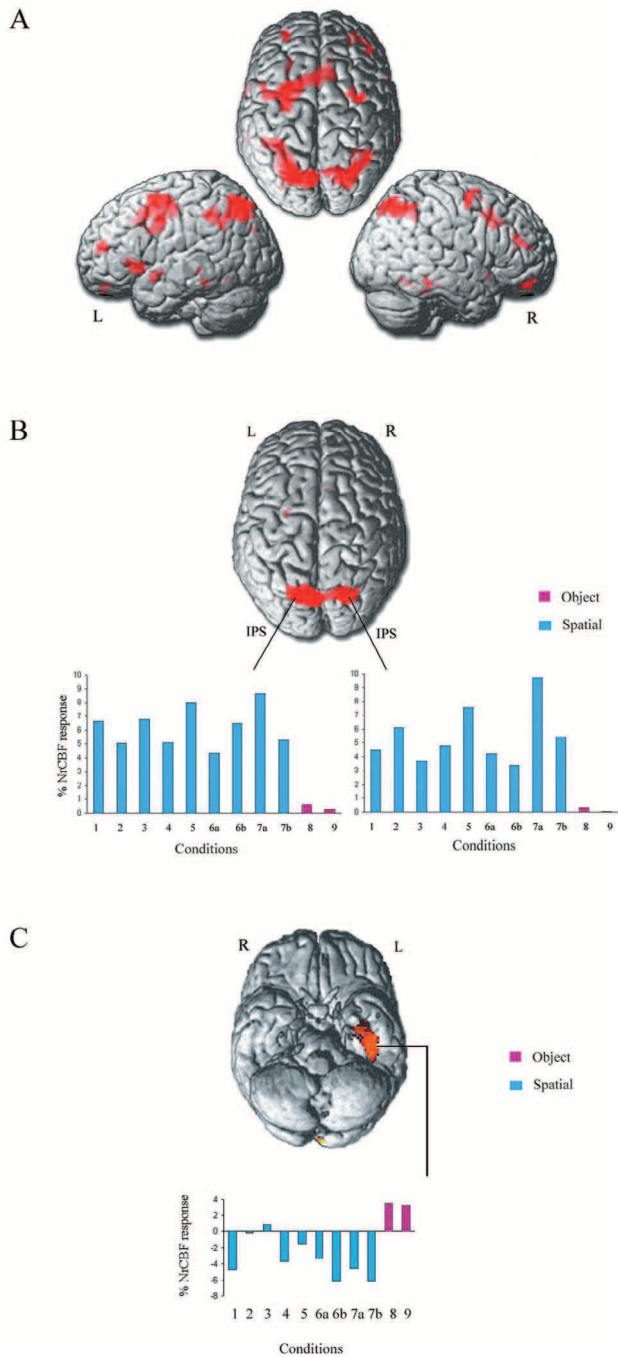


TABLE 2
Comparison analysis revealing foci of significant NrCBF increases between spatial imagery and object imagery ($p < .001$, uncorrected for multiple comparisons)

<i>Anatomical location of max. voxel activation</i>	<i>Coordinates</i>			<i>Z-score</i>
	<i>x</i>	<i>y</i>	<i>z</i>	
L. precuneus/superior parietal gyrus	-12	-70	46	>8.2
R. precuneus/superior parietal gyrus	18	-72	50	>8.2
R. superior occipital gyrus	32	-70	46	>8.2
R. middle occipital gyrus	40	-76	32	>8.2
R. middle cingulate cortex	8	18	38	7.6
L. middle/superior frontal gyrus	-28	-2	54	7.4

The data are local maxima of activated region detected with SPM 99 software. The anatomical localisation of the maximum Z -scores of these regions is given on the basis of the MNI template, using their stereotactic coordinates in mm (R: right; L: left).

TABLE 3
Comparison analysis revealing foci of significant NrCBF increases between object imagery and spatial imagery ($p < .001$, uncorrected for multiple comparisons)

<i>Anatomical location of max. voxel activation</i>	<i>Coordinates</i>			<i>Z-score</i>
	<i>x</i>	<i>y</i>	<i>z</i>	
L. Heschl's gyrus	-42	-20	8	5.6
L. superior temporal gyrus	-46	-24	14	5.3
R. Heschl's gyrus	40	-24	8	4.6
R. superior temporal gyrus	50	-24	10	4.3
L. inferior temporal gyrus/fusiform gyrus	-44	-16	-26	6.1
L. parahippocampal gyrus/hippocampus	-28	-10	-22	5.6
R. occipitotemporal junction	42	-50	-10	4.5
L. calcarine fissure	-2	-102	10	7.2
R. calcarine fissure	8	-88	12	4.7

The data are local maxima of activated region detected with SPM 99 software. The anatomical localisation of the maximum Z -scores of these regions is given on the basis of the MNI template, using their stereotactic coordinates in mm (R: right; L: left).

Areas more activated in object imagery conditions than in spatial imagery conditions

(See Table 3 and Figure 1C.) This comparison revealed that object imagery conditions induced a greater NrCBF increase in the temporal lobe, namely in the bilateral Heschl's gyrus extending to the superior temporal gyrus. Another focus

TABLE 4
Comparison analysis revealing foci of significant NrCBF decreases during spatial imagery ($p < .001$, uncorrected for multiple comparisons)

<i>Anatomical location of max. voxel activation</i>	<i>Coordinates</i>			<i>Z-score</i>
	<i>x</i>	<i>y</i>	<i>z</i>	
R. supramarginal gyrus/Rolandic operculum	58	-20	24	>8.2
L. calcarine fissure	-4	-100	10	7.2
L. cuneus/calcarine fissure	-2	-104	12	7.0
L. cuneus/superior occipital gyrus	-18	-100	12	6.0

The data are local maxima of deactivated region detected with SPM 99 software. The anatomical localisation of the maximum Z -scores of these regions is given on the basis of the MNI template, using their stereotactic coordinates in mm (R: right; L: left).

of activation was found in the posterior part of the right temporal lobe near its junction with the occipital lobe. In the left hemisphere, a cluster of activation spread to the inferior temporal gyrus, the parahippocampal gyrus and the hippocampus. This activation was specific to the object imagery conditions and this region was found to be deactivated in the spatial imagery conditions, as shown in Figure 1C. In the occipital lobe, two clusters of activated voxels were also detected within the calcarine fissure corresponding to primary visual area, as shown in Figure 2A.

Areas deactivated in spatial imagery conditions

(See Table 4 and Figure 2A.) A NrCBF decrease was observed in the right supramarginal gyrus near the right Rolandic operculum. In the occipital lobe, we found two foci of deactivation in the left cuneus near the superior occipital gyri. It is noteworthy that the calcarine fissure was found to be deactivated in these conditions. The calcarine cortex was thus deactivated in spatial imagery tasks whereas it was activated in object imagery tasks.

Areas deactivated in object imagery conditions

No cluster was identified in this analysis at $p < .001$ statistical threshold.

Regression analyses between MRT scores and CBF increases during the tasks

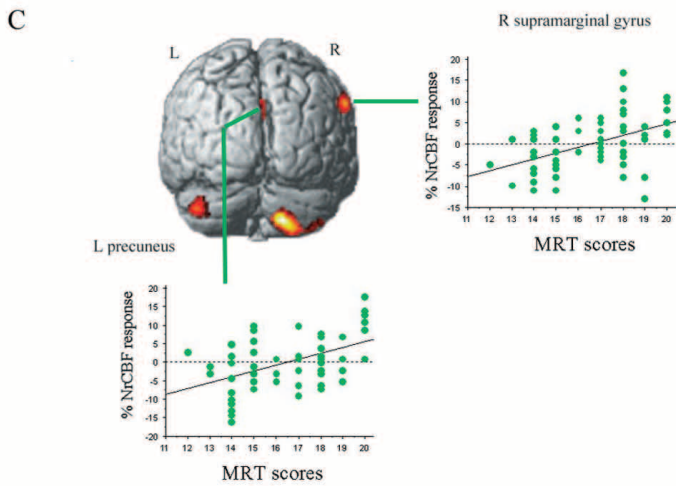
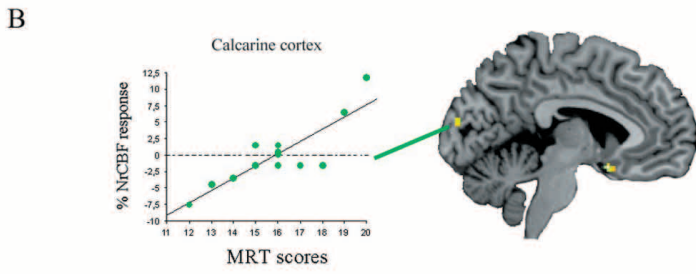
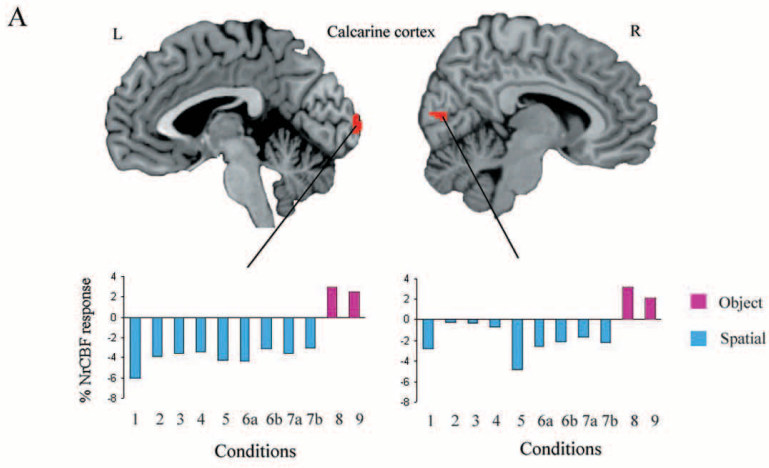
(See Table 5 and Figure 2B, C.) We computed two regression analyses between the scores obtained by subjects in the MRT and the degree of CBF increases. All results for the Z maps were thresholded at $p < .001$ (uncorrected for multiple comparisons) and are displayed in Table 5. Regarding the object imagery tasks,

TABLE 5
Peak coordinates of the significant positive regression between the MRT scores and blood flow values during object and spatial imagery tasks as compared to baseline conditions ($p < .001$, uncorrected for multiple comparisons)

<i>Anatomical location of max. voxel activation</i>	<i>Coordinates</i>			<i>Z-score</i>	<i>r₍₁₂₎</i>
	<i>x</i>	<i>y</i>	<i>z</i>		
Object MRT positive					
L. olfactory gyrus	-4	12	-16	4.5	0.923
L. putamen	-14	14	-10	3.5	0.825
R. thalamus	16	-18	14	3.9	0.875
L. inferior parietal gyrus/angular gyrus	-46	-58	42	4.3	0.906
L. cuneus/calcarine fissure	-4	-94	16	3.7	0.857
Spatial MRT positive					
R. cerebellum VIII	20	-72	-48	4.4	0.540
R. cerebellum VIII	34	-60	-54	3.3	0.419
R. cerebellum Crus II	42	-62	-48	3.3	0.417
L. cerebellum Crus I	-42	-64	-38	4.1	0.504
L. cerebellum Crus I	-28	-66	-32	3.2	0.410
R. cerebellum VIII	32	-36	-52	4.0	0.498
L. cerebellum VI	22	-66	-18	3.6	0.453
R. thalamus	12	-12	2	3.6	0.455
L. precuneus	2	-62	32	3.8	0.481
R. supramarginal gyrus	62	-46	34	3.8	0.470
R. angular gyrus	62	-56	36	3.3	0.419
R. anterior insula	46	18	-6	3.7	0.460
R. anterior insula	42	16	-14	3.5	0.445
R. inferior frontal sulcus	42	12	30	3.8	0.479
L. inferior frontal sulcus	-48	22	28	3.2	0.412
L. superior temporal gyrus	-58	-26	16	3.5	0.440
R. superior temporal gyrus	52	-30	18	3.2	0.409

The anatomical localisation of the maximum Z-scores of these regions is given on the basis of the MNI template, using their stereotactic coordinates in mm (R: right; L: left).

Figure 2 (opposite). (A) Plots show the activation of calcarine cortex during object imagery tasks (pink) and deactivation of calcarine cortex during spatial imagery tasks (blue) ($x = -2$, $y = -102$, $z = 10$ and $x = 8$, $y = -88$, $z = 12$). (B) Sagittal slice showing significant positive regression, in the calcarine cortex, between blood flow values during object imagery as compared to baseline and the MRT scores ($p < .001$). (C) 3-D rendering of the statistical map showing significant positive regressions between MRT scores and blood flow values in spatial imagery tasks as compared to baseline ($p < .001$). Plots show the positive regression between imagery conditions and MRT scores in areas indicated by arrows (see Table 5).



we found that CBF increases were positively correlated with the MRT scores in the left angular gyrus and in the dorsal bank of the left calcarine fissure.

Positive correlations in the spatial imagery tasks were found between MRT scores and activation in the cerebellar cortex bilaterally, the left inferior parietal lobe including the precuneus, the angular gyrus and the supramarginal gyrus, the right anterior insula, the bilateral inferior frontal sulcus and the left and right superior temporal gyrus.

DISCUSSION

The purpose of the present study was to assess the neural bases of two different types of mental imagery tasks as revealed by a multistudy of a large set of PET scans. We focused on three sets of results. The first set reflected the neural substrate common to both spatial and object imagery tasks, as revealed by a conjunction analysis. The second set of results compared each type of mental imagery (spatial and object), providing a direct measure of the effects of the tasks on brain areas involved in visual mental imagery. The third set of results explored the relationships between CBF increases and the individual ability of the subjects for mental imagery.

Common activations for object and spatial imagery conditions

Ventral and dorsal visual pathways. The first finding, in agreement with numerous previous reports, was that object and spatial imagery activated both ventral and dorsal visual pathways (Mellet et al., 1998). However, our results did not contradict the classical functional dichotomy between the “what” and “where” pathways putatively used in mental imagery. Rather, they indicated that even when the tasks are designed specifically to draw on spatial processing, they require some object processing and vice versa. The involvement of both dorsal and ventral pathways has been previously reported in spatial mental imagery (Larsen, Bundesen, Kyllingsbaek, Paulson, & Law, 2000; Roland & Gulyas, 1995) and also in object mental imagery tasks (Ishai et al., 2000; Kosslyn et al., 1997; Lambert et al., 2002). As emphasised by Kosslyn, this finding underlines that pure forms of imagery are rare (Kosslyn et al., 1997). For example, in the present analysis, the spatial imagery task of Condition 2 required the subjects to generate images of 3-D objects based on spatial instructions. Moreover, in the object imagery condition, 9, the subjects were to adjust and to add details to their mental image according to the verbal description they heard. These “online” modifications are likely to rely in part on spatial processing.

Frontal lobe. The activations detected in the frontal lobe overlapped clearly those observed in tasks that involve working memory (Haxby, Petit, Ungerleider, & Courtney, 2000; for a review, see Owen, 2000) and retrieval from episodic

memory (see Nyberg, 1998, for review; Buckner & Wheeler, 2001). These common activations reflect the fact that mental imagery, working memory and retrieval from episodic memory share common cognitive processes—and also underscore the fact that these three cognitive functions are difficult to disentangle. Baddeley has formalised the relationships between working and episodic memory in a revised version of his model, which now includes an episodic buffer (Baddeley, 2000). The generation of mental images commonly relies on the reactivation of representation stored in episodic memory, a process equivalent to retrieval (Buckner & Wheeler, 2001). Along the same lines, mental image maintenance appears very close, if not identical, to visuospatial working memory (Kosslyn, 1994). Indeed, the phenomenal experience of mental imagery could be seen as the result of an interaction between the retrieval of visual representations from episodic memory and the maintenance and transformation properties of working memory and may be revealed, in part, by the present frontal activation.

In addition to the frontal involvement, some other activations supported the participation of a memory network. These activations occurred in the anterior insular cortex, which has been shown to belong to an episodic memory network (Donaldson, Petersen, Ollinger, & Buckner, 2001). Moreover, reciprocal connections between the frontal lobe and the insular cortex have been well documented (Augustine, 1996). The anterior cingulate cortex also exhibited activation common to both spatial and object imagery tasks. This area has been reported as being activated in very different demanding cognitive tasks such as working memory and episodic retrieval (Cabeza & Nyberg, 2000; Duncan & Owen, 2000), and reflects a key role in evaluative processes (MacDonald, Cohen, Stenger, & Carter, 2000). It is likely that all the imagery tasks included in the present review required such processes. As a matter of fact, subjects performed the tasks in total darkness and were instructed to generate and maintain highly vivid and accurate mental images that rely on episodic and working memory.

The conscious experience of imagery probably does not arise from activation in frontal, insular, or cingulate cortex activity, but rather is likely to arise from the interaction of the frontal and anterior insular cortex (for the retrieval activity proper) with the associative visual areas belonging to the ventral pathway. This view is in agreement with Fuster's (1998) proposal that memory requires an interaction between the anterior cortex for executive memory and the posterior cortex for perceptual memory.

Differences between object and spatial imagery conditions

Early visual cortex. Our findings of an activation of the early visual cortex, which is specific to object imagery tasks, may be controversial. It has been shown, in the model originally proposed by Kosslyn, that the visual buffer is used to reconstruct the local geometry of the surface of visualised objects or

scenes (Kosslyn, 1994) and would thus be implemented within the early visual cortex. However, this activation together with the deactivation observed in spatial imagery tasks that we have already reported (Mazard et al., 2002; Mellet et al., 2000b), questions the exact role of the visual buffer. Kosslyn has recently suggested that mental images relying on spatial relations do not involve the visual buffer and that inspecting details of a mental image would be critical for the involvement of primary visual cortex (Kosslyn & Thompson, 2003). The present findings are thus compatible with this adaptation of the model. Note, however, that, as mentioned above, the mental images generated by the subjects during the spatial imagery tasks were not devoid of object features. Indeed the activation of the ventral pathway was observed in both types of imagery. Nevertheless, it is likely that successfully performing the tasks did not require an accurate evocation of shapes, colours, and textures incorporated in the mental image, a critical function of the visual buffer (Kosslyn et al., 2001; Thompson et al., 2001). Our results thus confirm that the type of imagery is a crucial feature for explaining the discrepancies among studies as well as the fact that most of the studies that reported activation in the early visual cortex dealt with object mental imagery (Bookheimer, Zeffiro, Blaxton, Gaillard, Malow, & Theodore, 1998; Klein, Paradis, Poline, Kosslyn, & Le Bihan, 2000; Kosslyn, Thompson, Kim, & Alpert, 1995; Kosslyn, Thompson, Kim, Rauch, & Alpert, 1996; Lambert et al., 2002).

Parietal cortex. Although present in both types of imagery tasks, the bilateral intraparietal sulcus was more activated in spatial imagery than in object imagery. The parietal activation reported here was located in the medial part of the intraparietal sulcus, including the precuneus. This localisation was in agreement with results recently reported that documented the fact that visuospatial tasks, such as attentional shifts and visually guided saccades, activated the medial part of the intraparietal sulcus (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). The present parietal activation thus suggests that spatial attention processes played a particularly important role in spatial imagery tasks.

Frontal cortex. Very few significant differences were detected in the frontal lobes in the comparison between the two types of tasks, suggesting that the type of images processed does not affect frontal activations. Frontal activation may mainly reflect processes common to both categories of tasks. Retrieval from episodic memory and maintenance in working memory are the most obvious such processes. The only major difference revealed that a region located at the intersection of the left precentral sulcus and the superior frontal sulcus was more activated in spatial imagery than in object imagery tasks. Activation of this region has been reported in various spatial working memory tasks (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Jonides, Smith, Koeppel, Awh,

Minoshima, & Mintun, 1993; Smith, Jonides, Koeppe, Awh, Schumacher, & Minoshima, 1995). Its activation during spatial imagery tasks is likely to reflect the large amount of spatial transformations required.

Left inferior temporal/fusiform cortex. We observed an activation of the left inferior temporal cortex specific to the object imagery tasks. This large activation spread from the left occipitotemporal sulcus to the left parahippocampal cortex and the left hippocampus. Using direct single neuron recordings in humans, a recent study has demonstrated that the hippocampus and the entorhinal cortex are involved in mental image generation of objects and faces (Kreiman, Koch, & Fried, 2000). Moreover, it has been suggested that this anterior part of the ventral visual pathway is engaged in multimodal integration, particularly between language and visual perception (Büchel, Price, & Friston, 1998; Papathanassiou, Etard, Mellet, Zago, Mazoyer, & Tzourio-Mazoyer, 2000; Price, 2000). It has been claimed that activations in this region raise “the intriguing possibility that semantic or conceptual representations of words may also be accessed directly within the ventral pathway” (Nobre, Allison, & McCarthy, 1994, p.262). Our findings are compatible with this suggestion. In fact, in the two studies dealing with object imagery included in the present analysis, the image generation process was driven by linguistic stimuli (as reflected by the primary and secondary auditory cortex activation): single words in Study 8 and descriptive sentences in Study 9.

In the present analysis, a leftward lateralisation was evident in the ventral pathway activation only when imagery of concrete items (object imagery) was compared to spatial imagery. This observation sheds light on the hemispheric lateralisation of mental imagery, an issue that remains unclear. It suggests that a strong component of object imagery is a prerequisite for a leftward lateralisation. Moreover, it supports a previous proposition that the left-lateralised ventral activation reflects the integration process between language and the retrieval processes required for imagery of concrete items (Mellet et al., 1998; Wise et al., 2000).

Individual variability

All subjects included in the present analysis were selected on the basis of their high scores obtained in the MRT. Although restricted to a sample of subjects who scored from 12 to 20 on the MRT (thus categorised as “high visuospatial imagers”), the correlations between the MRT scores and the amount of CBF increase during various imagery tasks begin to address the issue of the neural correlates of individual variability in visual imagery.

A first result showed that the better the subjects performed on the MRT, the higher their activation in the primary visual cortex during object imagery tasks. Negative correlations between reaction time and activation have been previously

reported (Klein et al., 2000; Kosslyn et al., 1996), which indicated that the fastest responses were associated with a more pronounced activation in the primary visual cortex. Taken together, these results emphasise that early visual cortex is affected by individual variability of imagery skills, a fact that should be considered when trying to explain discrepancies observed between studies.

Turning now to the spatial imagery tasks, significant positive correlations were evident in the inferior parietal cortex, anterior insular cortex, and precuneus. Activation in this set of cerebral regions was also evident in the conjunction analysis that included both the spatial and object imagery conditions. These areas were thought to be involved in the memory component of the imagery tasks. The present result suggests that this network is involved during both object and spatial imagery conditions and its activation varies according to one's individual imagery abilities.

Finally, CBF increases were positively correlated with imagery ability in the left parietal lobe in object imagery tasks whereas this correlation was with the right parietal lobe in the spatial imagery tasks. This observation may indicate that "high imagers" recruit substantially more effective brain regions than "lower performers" while performing imagery tasks. Consistent with this possibility, it has been suggested that the left parietal cortex is involved in image generation whereas the right parietal cortex is preferentially engaged in mental image manipulation that often characterises spatial imagery (Formisano et al., 2002).

CONCLUSIONS

We took advantage of a PET multistudy database of 54 subjects. The common pattern of activation of object and spatial imagery strongly implicates both the ventral and dorsal routes, regardless of the nature of the task. There is, however, variation in the level of activity in different tasks. Object imagery relied specifically on the anterior part of the ventral route, which may partly reflect the interaction between language and imagery. On the other hand, the dorsal route seemed to be more activated by the spatial than by the object imagery tasks, in agreement with its preferential role in the processing of spatial information. Finally, our study provides new insights regarding the debate about the involvement of the early visual cortex in mental imagery. First, it offers evidence that the early visual cortex (although not necessary for all types of imagery) may play a role in the imagery of figurative attributes. Secondly, the activity of the early visual cortex during the object imagery tasks varied among subjects. This finding provides evidence of the functional interindividual variability within the early visual cortex during object imagery. This functional variability should be taken into account in order to explain the divergent results found in previous studies.

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