

DIFFERENT MENTAL IMAGERY ABILITIES RESULT IN DIFFERENT REGIONAL CEREBRAL BLOOD FLOW ACTIVATION PATTERNS DURING COGNITIVE TASKS

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(Received 13 June 1991; accepted 8 January 1992)

Abstract--Using regional cerebral blood flow (rCBF) imaging, two populations having high and low imagery abilities were compared at rest and while performing two cognitive tasks: silent verb conjugation and mental imagery. The imagery task produced an rCBF increase in the left visual association and left frontal cortices in both groups. Differences between high and low imagers were observed on global and regional flow responses to cognitive tasks: low imagers showed a whole cortex CBF increase during both tasks; high imagers showed a right dominance in the visual association cortex in all conditions, and in the parietal association cortex at rest.

INTRODUCTION

MENTAL IMAGES are psychological events whose specific capacity is to reconstruct the figural appearance of objects when these objects are outside subject's perceptual field. There is a variety of cognitive approaches to mental imagery [6, 9, 18, 28, 37, 47], most of them converging on the postulate of the existence of cognitive entities which represent in memory the visual information attached to objects. These representations can be transferred and transiently maintained in a "visual buffer" [28, 29] by specialized activating processes.

Cognitive research on imagery has so far devoted most of its efforts to evidence the similarity between mental activities involved in perception and imagery [8, 12, 19, 38, 39]. Experiments suggest that mental images do possess a structure which reflects the structure of represented objects. Furthermore, the existence of intimate functional interactions between images and percepts supports the idea that mental images result from the activation of structures and implementation of mechanisms which are similar to those involved in perception [7, 11, 12, 18, 29, 30].

Neuropsychological investigations of "imagery loss" have provided support to the assumption that deficits in image generation are associated with cortical lesions in the occipital region, mainly in the left hemisphere [1, 10, 14, 22]. The hypothesis of selective involvement of occipital regions in the generation of visual images is also supported by EEG studies [4] and by studies based on event-related potentials (ERP) [16, 17]. Obviously, techniques based on the assessment of variations of cerebral blood flow are suitable

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candidates for extending these investigations since they essentially aim at establishing whether the metabolism of specific populations of neurons can be modified by cognitive activity [33, 41].

Using single photon emission computerized tomography (SPECT), ROLAND and FRIBERG [45] reported the first attempt to measure variations of regional cerebral blood flow (rCBF) in connection with mental imagery. Besides an overall increase of cerebral blood flow, the visualization task produced blood flow increases in three regions, namely, the left inferior occipital cortex, the posterior inferior temporal cortex, and the posterior superior parietal cortex. These results were confirmed in a subsequent study with positron emission tomography (PET) [44].

Further indications regarding rCBF variations during cognitive tasks involving visual imagery were provided by GOLDENBERG *et al.* [24]. Their main finding was an increase of left to right hemisphere blood flow ratio during memorization of concrete nouns with imagery instructions. Furthermore, analysis of the pattern of covariations between regions revealed the existence of a correlation between occipital and inferior temporal regions. In a second study, GOLDENBERG *et al.* [23] showed that verification of high visual imagery sentences produced greater activity in the left inferior occipital cortex than verification of any other kinds of sentences.

The overall impression from the literature is that there may exist cortical structures more specifically concerned than others by mental imagery. However, while the results reported above have high internal consistency, they remain discrepant to each other to a large extent. In particular, the role of the parietal cortex in visual imagery, which was repeatedly documented by ROLAND *et al.* [44, 45], was not supported by the GOLDENBERG studies [23, 24]. The variety of the techniques and experimental paradigms used up till now may partly account for such discrepancies, but it could also be that variability in individual imaging capacities prevents clear-cut findings.

Actually, another approach has provided light on the processes under study in current imagery research. It consists of using natural variations among subject with respect to their imagery capacities. A large body of psychometric evidence is available regarding the measurement of individual imagery differences and their effects on cognitive performance [5, 32, 37]. For this reason, it seemed relevant to extend rCBF approach to the cortical structures involved in visual imagery by looking at differences between subjects characterized as "high" and "low imagers".

So far, all rCBF studies on cerebral regional involvement during mental activity have been performed on groups of normal volunteers without paying any particular attention to subject selection, except for left-right brain asymmetry, with the implicit assumption of the existence of a standard normal functioning as opposed to pathology. In fact, as emphasized by GALABURDA [20], variations among normal individuals regarding their cortical organization for specific cognitive tasks are very likely but difficult to investigate *in vivo*. Mental imagery appears then to be a prime model for such studies, since natural variations of imagery capacities exist and can be evaluated.

There is today little information available on this topic. One relevant study was reported by GOLDENBERG *et al.* [25], who found a positive correlation between the amount of rCBF in the inferior occipital cortex and the subjective vividness of mental images. This result is in line with the fact that more occipital ERP activity is found in subjects who report high vividness of visual imagery, as observed by FARAH and PÉRONNET [15].

It should, however, be underlined that in both Goldenberg's and Farah's studies, the

classification of subjects as high or low imagers was essentially based on subjects self-reports of vividness of their visual imagery. Although subjective reports of mental imagery have sometimes been shown to provide quite valid information, there is a growing need in the community of imagery researchers for more objective methodologies in the evaluation of subjects' imagery capacities. A number of objective tests, mainly spatial tests, are available and have been shown to be good predictors of the use people make of their visual imagery in tasks expected to require the generation and inspection of visual images. Furthermore it has been shown that performance on spatial tests is poorly correlated, if any, with scores on self-report imagery questionnaires [32, 40]. In this context, we decided to extend the approach involving subjective reports to a more objective methodology, and to classify subjects in our study on the basis of their scores on well-designed psychometric instruments.

A further decision was made with the expectation of reaching a satisfying level of contrast between subjects qualified as low and high imagers. In most of previous studies, subjects are classified as low and high imagers depending on their position either above or below the median of the criterion measure. This method, in particular, has the inconvenience of allocating to distinct groups subjects whose scores are just around the median of the criterion measure and by this very fact should be considered as quite close to each other. It seemed preferable to use a procedure which consisted in starting from a large population of subjects and selecting the two samples of subjects as contrasted as possible on relevant psychometric measures. A further justification of this procedure is that it is more manageable in terms of experimental costs, while still providing quite valid information.

METHOD

Subject selection

Two populations of subjects were selected from a larger population of healthy undergraduate volunteers from the Orsay campus ($n=69$). Subjects completed the Minnesota Paper Form Board (MPFB) [34] and the Mental Rotations Test (MRT) [50]. Distribution of scores on each of these tests were computed. Subjects from the lower third on both the MPFB and the MRT were considered to be "low imagers". Those who were among the upper third of scores on both tests were considered to be "high imagers". From each of these two subsets of subjects, an equal number of 11 subjects were selected. The mean scores of the low imagers were 12.5 on MPFB and 5.8 on MRT. The mean scores of the high imagers were 22.8 on MPFB and 12.2 on MRT. The two groups were of similar ages (high imagers: 20.6 ± 1.3 years; low imagers 21.2 ± 1.2 years), sex ratios (5 girls), cultural and social levels.

All subjects who participated in the experiment were right-handed as assessed by the Raczkowski questionnaire. Subjects completed the Spielberger Anxiety State Questionnaire concerning the first blood flow measurement and the Spielberger Anxiety Trait Questionnaire. No difference was found between the two groups on anxiety measures. Lastly, the absence of personality abnormality was checked by the Minnesota Multiphasic Personality Inventory.

Experimental protocol

For each subject the experimental protocol included three rCBF measurements, in the following order: at rest with eyes closed (R), 20 min later during the abstract verbal task (V), and 3 hr later during the imagery task (I). Subjects were taken out of the tomograph between rCBF studies and repositioned by aligning a reference line drawn on the subjects' skin and the tomograph laser beam.

The resting condition consisted in lying quietly with eyes closed in the dimmed light of the examination room and without any precise instruction except to relax. The ambient noise was coming from the cooling fans and could be considered as blank noise.

The two cognitive tasks were designed to contrast visual and verbal components of cognitive activity. The imagery task required a substantial amount of visual imagery with minimal implicit verbal activity, whereas the verbal task mainly involved implicit verbalization without visualization. The two tasks were assumed to involve comparable mental loads, and special attention was paid to design the two tasks according to exactly the same temporal pattern.

The verbal task consisted in performing covert conjugation of abstract verbs. Six verbs were chosen for their low imagery values: to presuppose, to deny, to know, to invert, to individualize, to conclude. Subjects were to mentally conjugate each verb at five tenses of the French indicative. Conjugation was started 30 sec before beginning

¹³³Xenon inhalation and pursued during acquisition. A new verb was given orally every 45 sec, which represented a conjugation of six verbs in a session. Before the session, subjects were reminded of the typical conjugation routines for French verbs and were informed that the same task would be executed during and after the rCBF measurement. After the session, subjects were asked to perform conjugation routines orally with a new verb, as a final control of their proficiency at conjugating.

The imagery task consisted in mentally exploring the visual image of a spatial configuration. One hour prior to the rCBF measurement, subjects were involved in a learning phase. They were orally presented with the description of the map of an imaginary island and were told they would have to create as vivid and accurate a visual image of the map as possible. The description told about an island circular in shape with six landmarks located at the periphery, at places which were specified in the conventional hour-dial terms of flight navigation (for instance, "At four o'clock, there is a lighthouse"). The description was presented four times. Subjects were informed that they would have to perform some (unspecified) tasks about this island during and after the rCBF measurement. During the rCBF task the subjects were required to form a vivid visual image of the island and to perform mental exploration over the distances separating the six landmarks (a lighthouse, a beach, a plantation, a village, a harbour, a farm). Upon hearing the name of one landmark, they were asked to mentally overflight from this landmark to each of the five others and return, while maintaining as vivid a visual image as possible. A new landmark was mentioned as a starting point every 45 sec. Thus, during the 5 min of examination, island exploration started from the six different landmarks successively.

After the whole session was terminated, subjects were involved in a task designed to check the accuracy of their mental image of the island that consisted in comparing the distances between the different landmarks of the island. This test showed that high imagers were more accurate and responded faster than low imagers, which confirmed that their mental image of the island was more precise and more vivid than that of low imagers.

Imaging protocol

Anatomical (X-ray CT) and functional SPECT rCBF images were acquired on the same day at the same brain levels. The orbito-meatal line (OM line) served as the reference line for subject positioning and for ensuring absence of motion during and right after image acquisition in both modalities. It was externally marked from the outer canthus of the eye to the midpoint of the projected outer external auditory meatus and aligned with the laser beam of each imaging system. In each modality, the lower slice was centered 20 mm above the OM line.

SPECT studies were performed with a brain-dedicated SPECT system (Tomomatic S64, Medimatic) that provides five 20 mm thick contiguous axial slices with an in-plane resolution of approx. 14 mm. rCBF measurements were obtained using ¹³³Xenon inhalation and the computational method designed by CHLISES *et al.* [2]. Duration of the blood flow measurement using this method is 4 min 30 sec, with a 20 min minimum delay between two consecutive examinations.

Anatomical images were acquired on an X-ray CT imager (CGR 9000), and consisted of ten 9 mm thick slices acquired parallel to the OM line every 10 mm. Images were obtained on standard radiograph films and further digitized in 256 × 256 matrices using an Hamamatsu camera and converter. Prior to this acquisition, the head size was evaluated on a scout view as the length between the auditory canal and the top of the vertex on a line perpendicular to the OM line. Absence of any brain abnormality was checked on the CT scans.

Data analysis

The data analysis method [49] included three major steps: (1) formatting the anatomical images to the same characteristics as flow images; (2) definition of regions of interest (ROI) on the anatomical images and registration of the two sets of images; and (3) rCBF computation. Only three from the five rCBF slices were processed, due to the presence of nasal contamination on the lowest slice and of partial volume effect on the OM - 100 mm slice. In order to perform an accurate image registration, images from both modalities were converted in a common format, e.g. 256 × 256 with a 0.8125 mm square pixel size.

The procedure to define regions of interest included four major steps. First a single Matsui's atlas slice was selected from the two or three slices predicted by MATSUI's method [35] for each SPECT slice. This was done using individual anatomical landmarks (such as the ventricles, the corpus callosum and large sulci like the sylvian sulcus) on the CT slice centred at the same level as the SPECT slice. In a second step, a 20 mm cortical ribbon was delineated on each CT slice using the internal skull contour, automatically drawn as an isodensity contour, and an inner contour obtained by erosion of the outer contour. In a third step this ribbon was cut into pieces corresponding to the various ROIs. Based on the fact that cortical lobes and gyri limits are clearly individualized on Matsui's atlas, each ROI limits could be expressed as percentages of the total length measured on the antero-posterior axis of the atlas section. These percentages were then used to automatically position the ROI limits and cut the CT ribbon (see Fig. 1).

Eleven cortical ROIs were defined this way according to Mesulam's hierarchical modular organization of the cortex [36]: left and right frontal (F), left and right visual association unimodal (ASSU) containing Brodmann's areas 21, 37, 19, 18, left and right association plurimodal (ASSP) corresponding to 39 and 40 Brodmann's areas, central (C) containing the sensory-motor cortex and 44 and 45 Brodmann's areas which corresponds to Broca's area

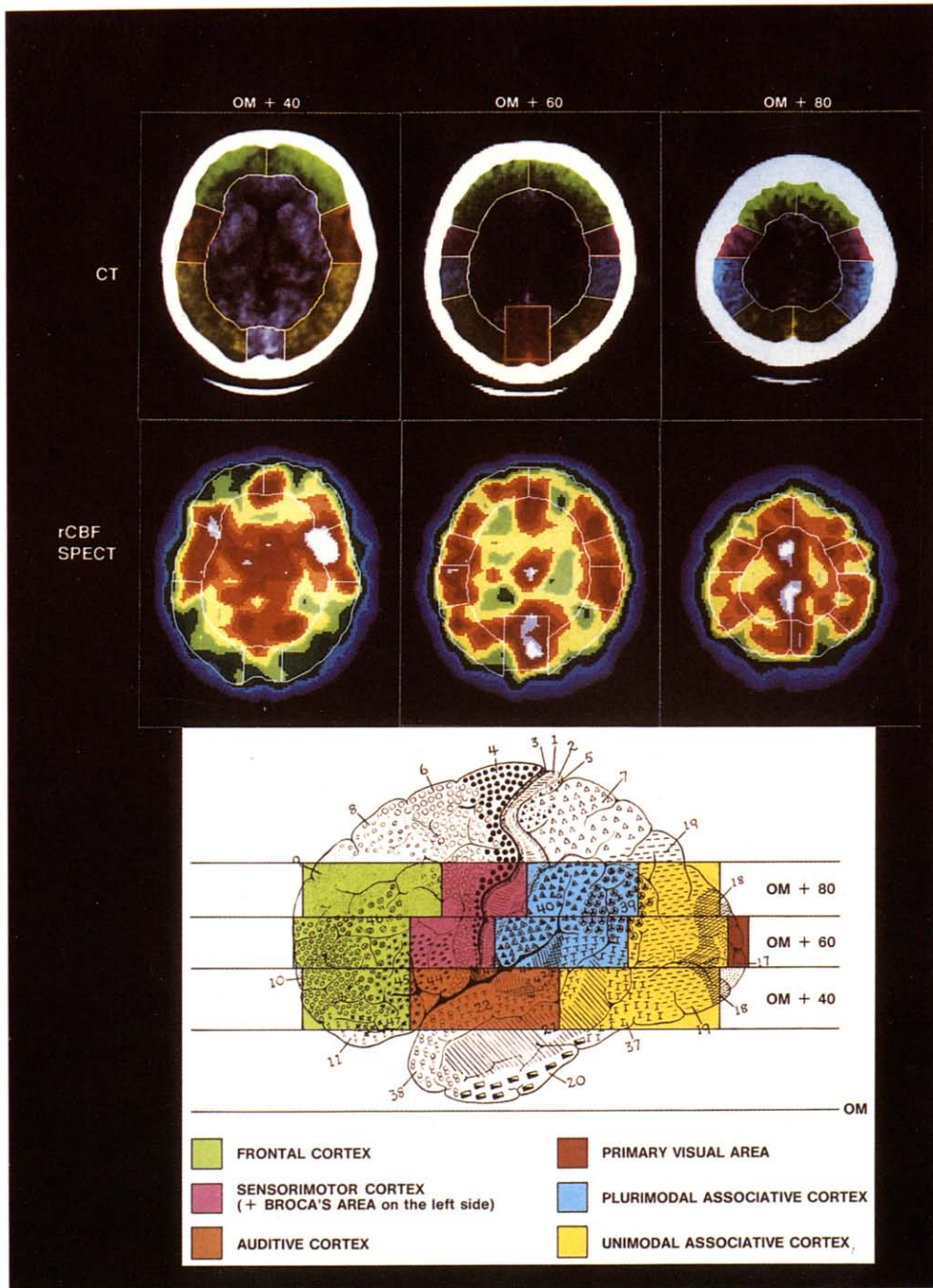


Fig. 1. Typical example of individual definition of functional regions of interest. Top: regions are defined as pieces of a cortical ribbon on CT images at three different brain levels. Colours correspond to the various regions. Middle: same regions copied onto SPECT images at the same brain levels. Bottom: brain lateral view illustrating the pooling of regions over the various levels and region relationships with Brodmann's areas.

on the left hemisphere, auditory area (AUD) containing 22, 41, 42 Brodmann's areas that corresponds to Wernicke's region (WER) on the left side, and a median occipital region corresponding to the primary visual area (PV).

Depending on the region and on subject's head size, a given region appeared on one or more slices, for example three for the frontal cortex and a single one for the primary visual area (see Fig. 1). The whole set of ROIs drawn on the CT slices was copied onto the corresponding flow image displayed on the Ramtek screen and manually repositioned by a physician. To register the two images, the physician manually displaced the CT elliptic ribbon over the SPECT rCBF image until it would fit "at best" the high rCBF cortical elliptical ring.

After rCBF computation in each ROI of each slice, values of CBF in the different pieces of the same ROI were averaged over slices (see Fig. 1).

No subcortical regions were included in the analysis, because, due to the inaccuracy of the attenuation correction algorithm of the Tomomatic system, CBF values are overestimated in these regions [42, 48].

Method reproducibility

Although use of anatomical images reduces investigator bias in ROI drawing that may exist when driven by the functional image only, operator intervention is still required at various steps of our image analysis protocol. For this reason, intra- and interobserver variabilities were both assessed by having two operators randomly process twice each a series of nine studies. Variance components were found to be overwhelmingly dominated by the between-subjects variance, the regional intraclass correlation coefficients ranging from 0.97 up to 0.99. The intraobserver reproducibility ranged from 0.986 up to 0.997 (0.963 in PV), and the interobserver reproducibility from 0.973 up to 0.995. These results demonstrate that the method is highly reproducible, this being due in part to the large size of the regions and in part to the use of individual anatomy for ROI definition and of a proportional system for ribbon-cutting.

Statistical analysis

Statistical analysis was conducted on different subsets of variables: (1) whole cortex cerebral blood flow (wCBF); (2) regional cerebral blood flow absolute values; (3) regional cerebral blood flow values relative to wCBF; and (4) rCBF right-to-left ratios. Subsets nos 3 and 4 were analysed in order to eliminate possible global blood flow effects.

For each subset of variables, a multivariate (regions) analysis of variance (MANOVA) with repeated measures was conducted with a 2-level Group factor (high and low imagers) and a 3-level within-group Task factor (rest, verbal, imagery). In each case, factor main effects and interactions were tested using a global multivariate *t*-test (WCP, within contrast pooled) and further analysed using *post-hoc t*-tests and profiles. In order to reduce type I error due to multiple testing, confidence levels were adjusted for each MANOVA by Bonferroni's method. All statistical procedures were conducted using the 4V program of the BMDP statistical package running on a Vax 8350.

RESULTS

Whole cortex cerebral blood flow

Significant Task effect ($P=0.0002$) and Task \times Group interaction ($P=0.03$) were found with no Group main effect ($P=0.83$). *Post-hoc* analysis showed that this interaction consisted in significant wCBF increases during both cognitive tasks in the low imagers group (Verbal vs Rest, $P=0.001$; Imagery vs Rest, $P=0.002$), while no significant variation was observed in the high imagers group (see Table 1). The absence of global Group effect was due to a somewhat lower wCBF value at rest in the low imagers group.

Table 1. Whole cortex blood flow values (ml/100 g/min) at rest (R) and their variations during the verbal (V) and imagery (I) tasks in the high and low imagers groups

	R		V		I	
	Mean	SD	Mean	SD	Mean	SD
High imagers	54.7	7.0	+1.5	4.5	+1.8	4.7
Low imagers	51.2	5.4	+6.6*	4.8	+5.6*	4.5

*Significantly different from 0, $P<0.002$.

Regional cerebral blood flow absolute values

Significant Task effects were found in all regions (P ranging from 0.03 to 0.0001), with Task \times Group interactions in the following regions: right association plurimodal ($P=0.004$), auditory ($P=0.01$), Wernicke ($P=0.02$), right central ($P=0.03$) and primary visual ($P=0.03$). No significant Group main effect and interactions consisted in variations similar to those observed on wCBF values, e.g. rCBF increases during both cognitive tasks in the low imagers group (see Tables 2(a) and 2(b)).

Table 2(a). Regional cerebral blood flow values (ml/100 g min) at rest (R) and their variations during the verbal (V) and imagery (I) tasks in the low imagers group ($n=11$)

Regions*	R		V R		I R	
	Mean	SD	Mean†	SD	Mean‡	SD
RASSP	51.8	5.9	-8.4	6.2	+6.0	5.7
LASSP	51.3	5.1	-7.0	5.5	+5.8	4.6
RASSU	45.7	5.1	-5.5	3.9	+5.2	3.8
LASSU	45.6	4.6	-5.9	3.4	+6.6	4.7
AUD	55.8	6.9	-8.8	7.0	+8.3	6.5
WER	56.9	5.7	-7.7	6.2	+7.5	5.3
RF	46.8	5.9	-5.9	4.1	+5.3	3.7
LF	46.6	5.5	-5.6	4.1	+6.2	3.1
RC	53.8	6.7	-8.1	5.8	+5.8	5.6
LC	54.2	5.0	-8.1	5.9	+6.1	4.9
PV	57.4	6.4	-6.2	5.4	+5.0	5.7

*ASSP: plurimodal association cortex; ASSU: unimodal association cortex; AUD: auditory cortex; WER: Wernicke's area; C: central cortex; PV: primary visual cortex; R: right; L: left.

†Significantly different from 0, $P < 0.006$ except PV $P < 0.02$.

Table 2(b). Regional cerebral blood flow values (ml/100 g min) at rest (R) and their variations during the verbal (V) and imagery (I) tasks in the low imagers group ($n=11$)

Regions*	R		V R		I R	
	Mean	SD	Mean	SD	Mean	SD
RASSP	56.9	9.6	+0.0	5.9	0.6	6.8
LASSP	53.9	9.4	-3.5	5.4	-3.5	7.1
RASSU	48.5	5.4	+1.9	4.5	-1.9	6.0
LASSU	47.8	5.7	-1.4	5.3	-2.3	5.7
AUD	62.1	6.3	-1.4	5.3	-0.7	7.6
WER	62.1	8.4	+0.7	6.1	-3.2	6.7
RF	49.4	6.9	+2.2	5.6	-1.2	6.5
LF	49.6	6.6	+2.5	4.6	-2.4	5.7
RC	58.5	9.6	+2.3	5.2	+3.1	5.3
LC	58.0	8.4	+4.2‡	5.0	+2.7	7.4
PV	59.5	7.7	0.4	5.2	+0.6	7.8

*ASSP: plurimodal association cortex; ASSU: unimodal association cortex; AUD: auditory cortex; WER: Wernicke's area; C: central cortex; PV: primary visual cortex; R: right; L: left.

‡Significantly different from 0, $P < 0.02$.

Regional cerebral blood flow values relative to wCBF

The MANOVA showed significant Task effects in two regions: left association unimodal ($P=0.016$) and left central ($P=0.005$), with no Group effects or interactions in any region. The Task effects consisted in significant increases in left central during the verbal task ($P=0.003$) and in left association unimodal ($P=0.004$) during the imagery task (see Table 3) in both groups.

Table 3. Regional cerebral blood flow values relative to whole cortex blood flow at rest (R) and their variations during the verbal (V) and imagery (I) tasks in the whole population ($n=22$)

Regions*	R		V R		I R	
	Mean	SD	Mean	SD	Mean	SD
RASSP	1.024	0.046	-0.000	0.047	-0.018	0.061
LASSP	0.992	0.054	-0.021	0.052	+0.017	0.043
RASSU	0.890	0.043	-0.002	0.045	+0.006	0.043
LASSU	0.884	0.033	+0.000	0.035	+0.020†	0.030
AUD	1.114	0.058	+0.009	0.052	+0.006	0.070
WER	1.160	0.113	-0.039	0.127	0.012	0.123
RF	0.908	0.034	+0.005	0.035	-0.001	0.040
LF	0.907	0.026	+0.006	0.041	+0.017	0.030
RC	1.057	0.057	+0.017	0.042	+0.013	0.049
LC	1.059	0.040	+0.031†	0.044	+0.008	0.046
PV	1.105	0.058	0.025	0.070	-0.024	0.063

*ASSP: plurimodal association cortex; ASSU: unimodal association cortex; AUD: auditory cortex; WER: Wernicke's area; C: central cortex; PV: primary visual cortex; R: right; L: left.

†Significantly different from 0, $P<0.003$.

Regional right-to-left rCBF ratios

A Group effect was found in the association unimodal region ($P=0.05$), a Task effect was found in the frontal ($P=0.03$) and association plurimodal ($P=0.05$) regions with a Task \times Group interaction in the latter region ($P=0.004$) (see Tables 4(a) and 4(b)). *Post-hoc* tests showed that the Group effect in the association unimodal region consisted of right-side dominance, independent of the task, in the high imagers group, while the right-left index was symmetrical in the low imagers group (see Fig. 2). The Task effect observed in the frontal

Table 4(a). Right to left ratios of regional cerebral blood flow values at rest (R) and their variations during the verbal (V) and imagery (I) tasks in the low imagers group ($n=11$)

Regions*	R		V R		I R	
	Mean	SD	Mean	SD	Mean	SD
ASSP	1.009	0.040	-0.022	0.060	+0.004	0.071
ASSU	1.000	0.033	-0.000	0.053	0.021	0.070
AUD	0.985	0.112	-0.017	0.105	+0.012	0.110
F	1.005	0.023	+0.004	0.033	-0.018	0.034
C	0.992	0.078	+0.002	0.081	-0.001	0.094

*ASSP: plurimodal association cortex; ASSU: unimodal association cortex; AUD: auditory cortex; C: central cortex; F: frontal cortex.

Table 4(b). Right to left ratios of regional cerebral blood flow values at rest (R) and their variations during the verbal (V) and imagery (I) tasks in the high imagers group ($n = 11$)

Regions*	R		V R		I R	
	Mean	SD	Mean	SD	Mean	SD
ASSP	1.050	0.041	- 0.068	0.057	- 0.075	0.071
ASSU	1.015	0.036	+ 0.011	0.050	- 0.009	0.032
AUD	1.005	0.070	+ 0.004	0.064	0.043	0.065
F	0.996	0.027	- 0.005	0.036	- 0.021	0.042
C	1.006	0.050	0.027	0.040	+ 0.011	0.052

*ASSP: plurimodal association cortex; ASSU: unimodal association cortex; AUD: auditory cortex; C: central cortex; F: frontal cortex.

region was characterized by a left dominance during the imagery task in both groups ($P=0.02$, see Fig. 3). Meanwhile, the Task effect and interaction observed on association plurimodal regions were due to very different behaviour of this variable in both groups (see profiles on Fig. 4): there was a significant right predominance in the high imagers group at rest ($P=0.001$) that disappeared under both cognitive tasks due to left association plurimodal increases. This means an implication of the left association plurimodal, that is the left inferior parietal including 39 and 40 areas of Brodmann, during both imagery and verbal tasks, in the high imagers group. On the opposite, the low imagers group demonstrated no asymmetry at rest nor in the imagery or verbal tasks.

DISCUSSION

The major point of interest of this study is the comparison of two groups of normal volunteers differing only in their imagery abilities. It is striking that the imagery ability tests succeeded so well in selecting two groups with such dramatic differences regarding their global rCBF responses. The two groups indeed show very different flow patterns during cognitive tasks: low imagers responded by global increase whereas high imagers responded by regional flow increases. Global flow increase has already been described during an imagery task by ROLAND [44, 45]. However, in the light of our results it is likely that this phenomenon is not specifically related to the imagery task but to the population under study. Anxiety is an unlikely explanation of this result, because first we did not observe any difference between the two groups concerning their anxiety scores and secondly because the relationship between global blood flow or metabolism and anxiety is very unclear: depending on authors, positive [26], negative [43] or absence of correlation was found [21]. What could be engaged in this blood flow response is a difference between the two groups regarding task difficulty, but previous rCBF study on this topic showed an absence of correlation between global blood flow and task difficulty [27].

A tentative interpretation can be advanced in light of the current componential approaches to mental imagery [10, 29, 30]. The hypothesis is that of low differentiation of cognitive functions in low imagers, whereas skilled visuo-spatial imagers would be characterized by more differentiated cognitive architecture. This feature would result in patterns of focalized cortical activation during high imagers' cognitive activity. Although this hypothesis is compatible with recent assumptions regarding the modular structure of

ASSOCIATIVE UNIMODAL REGION

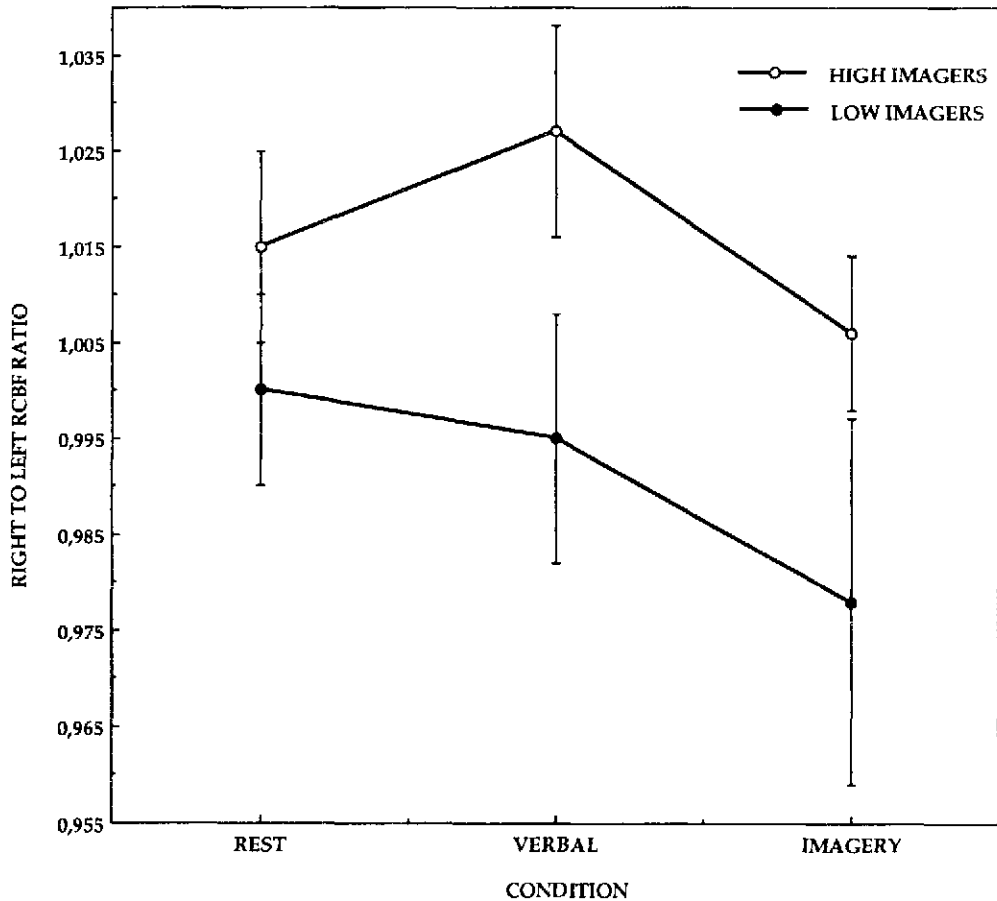


Fig. 2. Group effect in the association unimodal cortex. vertical bars indicate the standard error of the mean. There is a significant right dominance in the high imagers group (○) in all conditions when compared to low imagers (●). the increase of the left association unimodal region during the imagery task in both groups is clearly illustrated by the indices decrease.

imagery abilities, it obviously requires further empirical support. In any case, our findings underline the considerable heterogeneity of normal subjects' response patterns during cognitive processing.

Apart from this global blood flow response difference, high imagers and low imagers also showed different patterns of response in both posterior association plurimodal (39 and 40 Brodmann's areas) and visual unimodal regions. If we assume that blood flow dominance is a reflect of cortical functional dominance, the right association unimodal dominance in all conditions in high imagers could be a reflect of a preferential visuo-spatial strategy as opposed to strategies requiring verbalization. In addition, high imagers exhibit consistent dominance of right association plurimodal at rest, that shifts to left dominance when they are

ASSOCIATIVE PLURIMODAL REGION

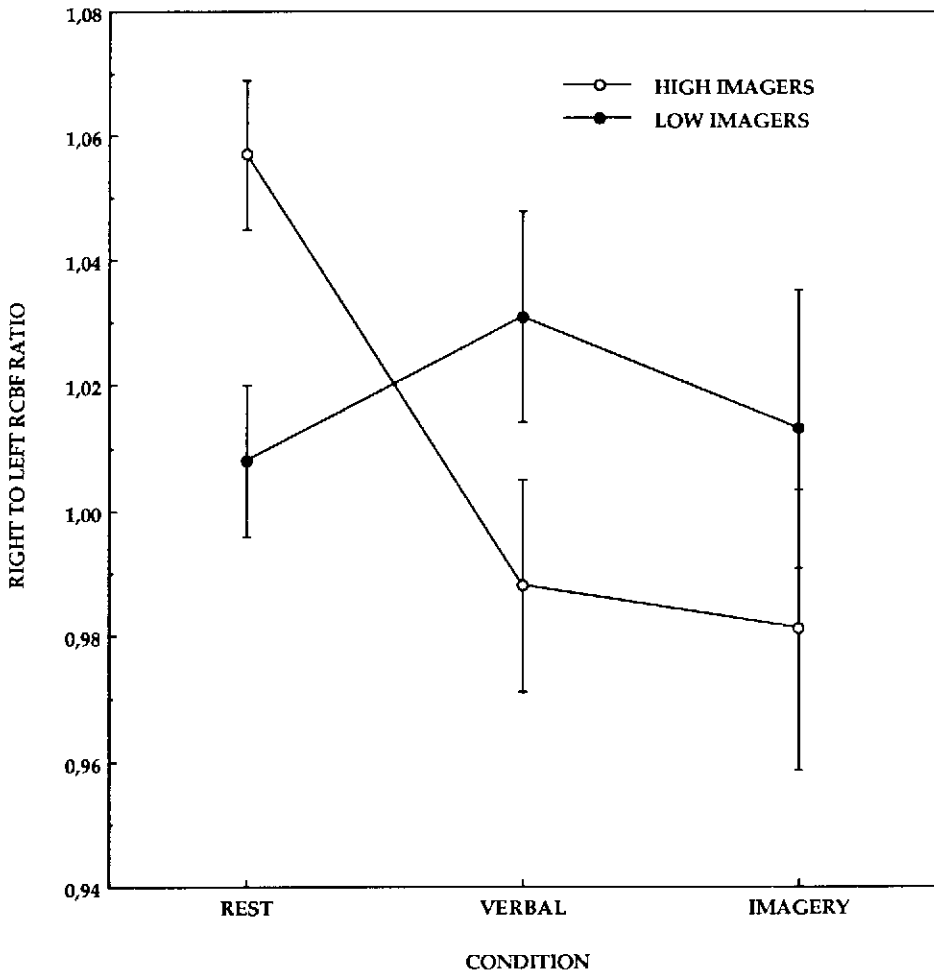


Fig. 3. Task effect in the frontal region. vertical bars indicate the standard error of the mean. There is a decrease in both high (○) and low (●) imagers groups during the imagery task.

engaged in either verbal or imagery activities. This is in line with the hypothesis advanced above, and should be paralleled with the notion that if the left hemisphere is engaged during verbal tasks, it has also been shown to be concerned by several image generation tasks (10).

A basic question raised by mental imagery activation studies is the specificity of the observed regional variations. In this work, when comparing verbal and imagery tasks in the entire population, regional modifications were definitely different in only two regions: left association unimodal and left central including Broca's area regions.

Activation of the left temporo-occipital region in an imagery task has already been described in previous SPFC rCBF studies of imagery tasks [23, 25, 44]. The constant

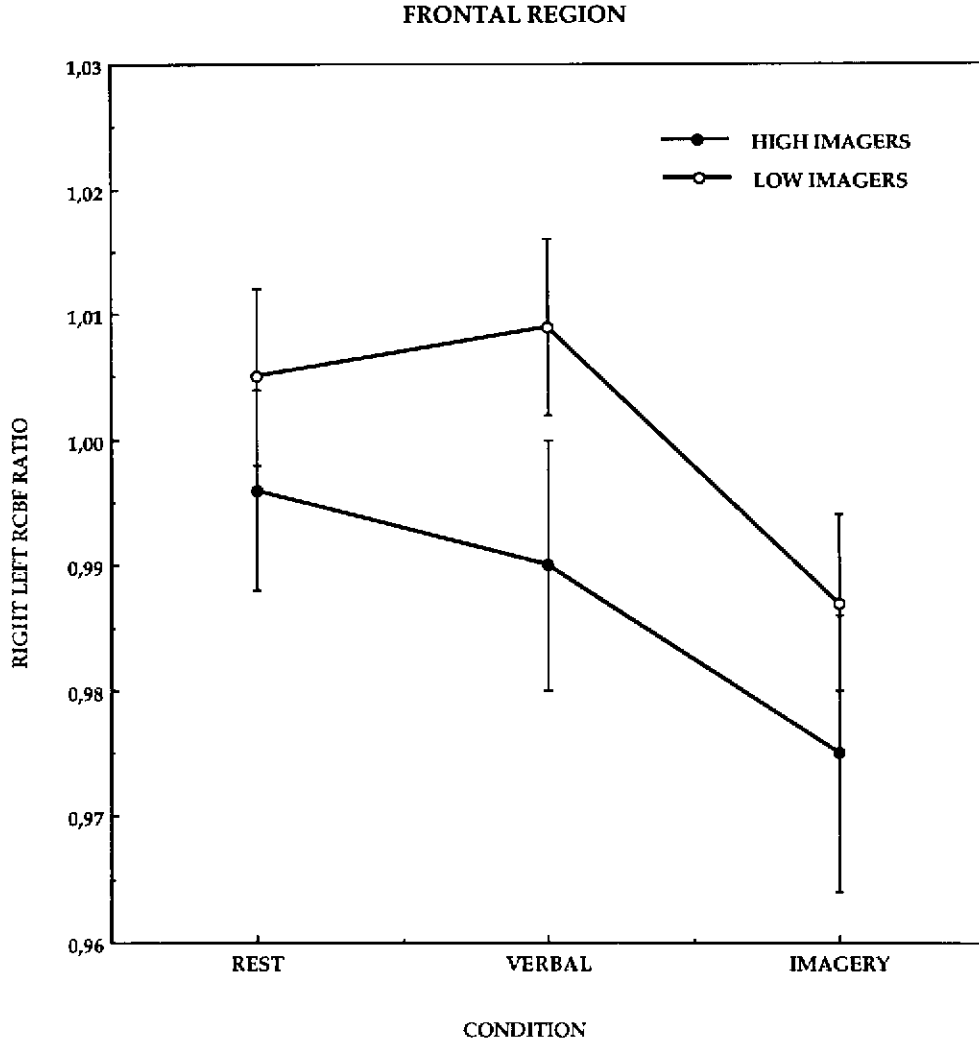


Fig. 4. Interaction between cognitive task and mental imagery ability in the association plurimodal cortex. vertical bars indicate the standard error of the mean. There is a significant right dominance in the high imagers group (○) at rest that disappears during both silent verb conjugation (verbal condition) and mental imagery. On the opposite, low imagers (●) demonstrate no significant asymmetry in either condition.

activation of the left inferior temporal and occipital lobe in these otherwise different experimental protocols reinforces the specific involvement of this region in mental imagery. These results also confirm the absence of involvement of the primary visual cortex during an imagery task, which underlines the difference between mental imagery and perception. Although the activation of parietal regions in the imagery task was not specific of the imagery task, it is in agreement with ROLAND's findings [44], who described the activation of the supra-marginalis gyrus (area 39) and of the upper part of the posterior parietal lobe, as compared with GOLDENBERG's results [23, 24] where no parietal involvement was evidenced.

Presence of a left frontal dominance during the imagery task only may reflect integrative processes which would not be required in the more automatized verbal task.

Finally, the activation in the left central region during the verbal task could be due to an increase of rCBF in Broca's area, because Broca's region constitutes a large component of our left central region (see Fig. 1). Another SPECT rCBF study concerning silent speech has shown an activation located in the middle of the left rolandic region during internal speech [46], which has been recently confirmed in a PET study during subvocalization [3]. However, the resolution of our SPECT machine does not allow to discriminate between motor, premotor or Broca's area increases.

There is a final point which requires further clarification, in relation with the distinction recently advocated by several researchers between the visual and spatial components of mental imagery. Neuropsychological arguments have been advanced in favour of distinct subsystems of imagery representation [13, 31]. One system, or "ventral system", is specialized on the processing of the visual appearance of mental images (mainly, shape and colour). This system runs from the occipital lobes down to the inferior temporal lobes. The other, or "dorsal system", is concerned with the spatial components of images (such as location, size and orientation). This system projects dorsally from the occipital lobes up to the parietal lobes. This distinction may explain some of the discrepancies between Goldenberg's and Roland's findings. In particular, it could reasonably be argued that the involvement of the parietal cortex in Roland's studies is due to the strong spatial component associated with the imagery task used in these studies.

The visual spatial distinction has other consequences if one considers the cognitive activities required by the imagery tests or questionnaires used for classifying subjects as high or low imagers. Typically, self-report questionnaires are based on the evocation and self-evaluation of visual experiences. On the other hand, spatial tests, which provide researchers with more objective measures, tend to place greater requirements on the spatial components of mental imagery. In the case of our study, spatial tests may have differentiated among subjects essentially in terms of their spatial capacities. Furthermore, the imagery task implied strong spatial components which could explain why parietal involvement was evident in the group of high imagers only, even if not specific to the imagery task. In any case, with the imaging instruments used both in our study and in Roland's studies it is impossible to precisely locate this parietal activation, a question that could be solved with more performant techniques such as positron emission tomography.

In conclusion, our results demonstrate the importance of the variability of flow response patterns during cognitive tasks within normals. They emphasize the need for a rigorous selection of population homogeneous with respect to the considered task, or for an individual analysis of flow activation studies.

Acknowledgements—The authors are deeply indebted to C. Raynaud, S. Ricard and B. Bruck for their help in data acquisition, to M. Joliot and M. C. Masure for their assistance during data analysis, and to J. D. Huret, J. L. Martinot, and two anonymous reviewers, for their thoughtful comments.

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