



A functional MRI study of mental image generation

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Abstract—The neural substrates of mental image generation were investigated with functional MRI. Subjects listened to words under two different instructional conditions: to generate visual mental images of the words' referents, or to simply listen to each word and wait for the next word. Analyses were performed which directly compared the regional brain activity during each condition, with the goal of discovering whether mental image generation engages modality-specific visual areas, whether it engages primary visual cortex, and whether it recruits the left hemisphere to a greater extent than the right. Results revealed that visual association cortex, and not primary visual cortex, was engaged during the mental image generation condition. Left inferior temporal lobe (Brodmann's area 37) was the most reliably and robustly activated area across subjects, but some subjects had activity which extended superiorly into occipital association cortex (area 19). The results of this experiment support the hypothesis that visual mental imagery is a function of visual association cortex, and that image generation is asymmetrically localized to the left. © 1997 Elsevier Science Ltd.

Key Words: mental imagery; neuroimaging; hemispheric specialization; visual association cortex.

Introduction

Mental imagery, or 'seeing with the mind's eye,' has been the subject of intense study in cognitive psychology for decades (see, e.g. [21, 31]), and has more recently been investigated with the tools of cognitive neuroscience (see, e.g. [4, 11]). One issue of interest to both fields is the nature of imaginal representation: Is it a form of visual representation, or is it a more abstract, prepositional (i.e. language-like) form of representation? And, if imagery is visual, does it involve retinotopically-mapped visual representations of the kind found in occipital cortex, or only the more abstract representations of appearance found in temporal cortex? Are representations as peripheral as those of primary visual cortex involved in the centrally initiated process of mental imagery? In addition, cognitive neuroscientists have debated the hemispheric locus of mental imagery, with some studies suggesting a special role for the left hemisphere in the generation of images from memory, and others failing to support this hypothesis.

The goal of the present study is to address these issues of localization and laterality for mental imagery using fMRI in normal subjects who are engaged in a simple mental image generation task. Specifically, in the present study we test the hypothesis that generating an internal mental image activates modality-specific visual cortex. We also seek to determine whether imagery activation extends as far into the periphery of the visual system as primary visual cortex. Finally, we assess the laterality of mental image generation.

Our rationale for undertaking this project is that the existing neuroimaging literature on mental imagery yields conflicting results, and this may be due to particular aspects of the methods, experimental designs, and subjects used in each case. While many find evidence of occipital involvement in mental image generation [2, 5, 9, 14–18, 22, 24–36] not all do [13, 27, 29]. And among those that do find occipital activation, only a few find activation of primary visual cortex [22, 24] while most find evidence of no primary cortex activation (e.g. [25]). Furthermore, a number of studies find evidence of left temporo-occipital activation during image generation [2, 9, 10, 15, 16, 18, 22—Exp. 2, 36], but others show either no asymmetry or a right-sided focus [5, 13, 22—Exp. 1, 23–25].

It is likely that some of the discrepancies among these studies result from aspects of their experimental designs,

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methods or subjects that make them unsuitable for answering the questions of interest in the present article. First, not all studies are directly relevant to memory images, that is, to images of familiar objects called up from memory, but instead involved images generated from physically present models [2, 22—Exp. 1]. Second, studies in which maps were imaged may involve a more abstract spatial form of imagery than that of interest here [2, 17, 25, 36], and images of full-field color or pattern may also differ from images of objects [17, 29, 36]. Third, studies that require subjects to project or superimpose a mental image onto visual stimuli may engage forms of visual attention in addition to imagery that could lead to spurious visual area activation [5, 22]. Fourth, some studies lack the appropriate control conditions to make inferences about image generation *per se*, that is, conditions in which the subject carries out all of the mental operations of the imagery task except for generating an image [5, 17, 22—Exp. 3, 25, 29, 33]. Fifth, the neuro-imaging methods used in these previous studies vary in their localizing ability. Event related potentials offer only very crude localization [5, 36]. Single photon emission computed tomography (SPECT) offers better localization [2, 14–18], but is nevertheless inferior to positron emission tomography (PET) [13, 22, 25, 27, 29] and functional magnetic resonance imaging (fMRI) [24]. Sixth, subjects differ in the quality and nature of their mental imagery, and this can affect measures of regional brain activity [6, 23]. Subjects' handedness and the handedness of subjects' first-degree relatives will also affect the symmetry or asymmetry of regional brain activity. Many, but not all, studies select for subject handedness but none select for familial handedness, and few select for imagery ability [2, 8, 23, 25]. Finally, because neuro-imaging techniques other than fMRI usually require the averaging of multiple subjects to detect significant changes, previous studies (with the exception of [24]) could not draw conclusions from individual subject data.

The design, methods and subjects of the present study were chosen to minimize the problems just reviewed. First, subjects generated mental images from memory, cued by an aurally presented word. Second, the images were of common concrete objects, not maps or other forms of abstract spatial representation. Third, the images were not projected into the visual field (in fact, subjects' eyes were closed throughout the experiment) so that any visual area activation observed could be attributed to imagery. Fourth, the image generation condition was paired with a control condition that engaged the same mental processes as the imagery condition except for the imagery *per se*. Fifth, regional brain activity was measured using fMRI, to enable relatively precise localization of activity. Finally, ambiguity of results due to subject variability was minimized by testing only right-handed males with no left-handed first degree relatives, and by carrying out individual subject analyses as well as a group analysis.

Our task is one that has been used previously in an

ERP studies [8, 9]. In both conditions of the experiment, subjects listened to auditorially presented words. In the imagery condition, the words were concrete, in order to facilitate generation of an image, and subjects were told to listen to the words and generate mental images of the words' referents. For example, if the word were 'tree', subjects imagined a tree. In the baseline condition, the words were abstract, in order to discourage image generation, and subjects were told to listen to the words and wait passively between words.

Two aspects of this experimental design involved choices between nonideal alternatives, although the results of the previous ERP experiment vindicate the choices in both cases. First, we chose to use abstract words rather than concrete words for the baseline condition, even though concrete words would have made the baseline condition even more comparable to the imagery condition. This choice was made because subjects find it difficult to resist generating images of concrete words when told not to do so. The results of the earlier study support the use of abstract words for the baseline condition: when both types of baselines were used we found that they yielded similar results, although the image generation effects were more pronounced relative to the abstract words baseline. This is consistent with the idea that the two baseline conditions engaged similar processes but that there was some additional image generation in the concrete words baseline condition. The second tradeoff concerned the nature of the imagery task. We chose the very minimal task of listening to words and generating images of them, rather than a more complex task in which subjects would have to operate on their images and formulate a response. Although a more complex task could have given us a behavioral measure to verify imagery use, it would also increase the number of neural systems brought into play, thus complicating data interpretation. The risk of using this minimal task is that we could obtain null results because subjects did not comply with the instructions to generate images. However, the previous ERP experiments found positive results, and these results correlated with individual differences in vividness of imagery, suggesting that subjects did generate images.

Methods

Subjects

Seven male, right handed subjects (with right-handed parents), ages 18–37, were studied. Subjects were excluded if they had any medical, neurological or psychiatric illness or if they were taking any type of medication. All subjects gave their informed consent.

Functional MRI technique

Imaging was carried out on a 1.5T SIGNA scanner (G.E. Medical Systems) equipped with a prototype fast gradient sys-

tem for echo-planar imaging. A standard radiofrequency (RF) head coil was used with foam padding to comfortably restrict head motion. High resolution sagittal T1-weighted images and axial T1-weighted images were obtained in every subject. A total of 2880 gradient echo echoplanar images were then obtained per activation run using 16 contiguous 5 mm slices (TR = 2000 msec, TE = 50 msec) at a resolution of 64×64 pixels in a 24 cm field of view (3.75 mm resolution). Twenty seconds of 'dummy' gradient and RF pulses preceded the actual data acquisition. A motion correction method was utilized which removed spatially coherent signal changes (referenced to the first acquired image) in each slice which correlated with x and y shifts. In addition, spatially coherent signal changes in each slice that correlated with the difference between the first and last image were removed.

Experimental paradigm

Two sets of aurally presented nouns ('concrete' vs 'abstract') were used for this study. Words were selected from the dictionary with the constraint that they have between 1 and 3 syllables and assigned to the concrete or abstract condition on the basis of experimenters' intuitions. In the *concrete* condition subjects heard words that the experimenters judged easy to image (e.g. 'apple', 'house', 'horse'), while words presented during the *abstract* condition were judged difficult to image (e.g. 'treaty', 'guilt', 'tenure'). Each run consisted of alternations of 40-sec blocks of concrete words with 40-sec blocks of abstract words, repeated four times. A tone signaled the start of each new block. Subjects were instructed to imagine the appearance of the named object during the concrete condition and to listen passively to the words during the abstract condition. Stimuli were presented over a loud-speaker system at a rate of one word per second for both conditions. Scanning was performed in a darkened room and the subjects were instructed to keep their eyes closed during the experiment.

Individual subject data analysis

For each subject, an activation r map was calculated by assigning a correlation coefficient to each pixel versus a pre-defined task-related square reference function. The resulting correlation map was filtered to remove pixels not overlying brain parenchyma or with large intensity signal changes ($> 8\%$) which likely represent motion effects. A nearest-neighbor algorithm was then applied to remove any activations consisting of less than three contiguous pixels. The resulting functional maps were thresholded at $r = 0.2$ and overlaid upon axial T1-weighted anatomical images (TR = 600 msec, TE = 15 msec) which were acquired just prior to echo planar scanning. Our prior experience using identical filtering and thresholding on fMRI runs obtained without task activity has demonstrated infrequent false positive activation at this level. The anatomical coordinates for each activated region was determined by conversion through linear transformation into the proportional grid system of Talairach and Tournoux [33]. Note that no spatial smoothing was undertaken in the single subject analysis.

Group analysis

In addition to individual subject analyses, a group analysis was performed to identify anatomical areas of consistent activity across subjects. The raw data for all runs from each subject were transformed to standardized Talairach space [33] and spatially smoothed by convolution with a three-dimen-

sional, 18.75 mm FWHM gaussian kernel. A group statistical parametric map (SPM) was produced by concatenating data from all subjects. Voxel-wise analysis was performed using the general linear model for autocorrelated observations as described by Worsley and Friston [38]. Included within the model was an empirical estimate of intrinsic temporal autocorrelation and a global signal change covariate. Inclusion of both components has been demonstrated to result in false positive rates not greater than tabular values in human null-hypothesis data [1]. The t field result of Worsley [37] was utilized to derive a critical t -value for the entire map. Given values for effective degrees of freedom (505), smoothness (5 voxels FWHM), search volume (18000 voxels), and desired alpha value (0.01), we calculated a critical t -value of 4.5. The SPM map was thresholded at this t -level and the Talairach coordinates of local t maxima within the observed regions of activity were determined.

The axial T1 weighted localizer images from each subject were converted to Talairach space and averaged. The resulting anatomical map demonstrates the resolution of the spatial conversion routine and is used for display of the SPM results.

Results

Whereas subjects hear and understand words in both conditions, they generate mental images only in, or primarily in, the *concrete* condition. Individual subject analyses revealed several brain regions that were more active in the *concrete* condition as compared to the *abstract* condition, implicating these areas in the process of mental image generation (Fig. 1A). Left inferior temporal lobe (Brodmann's area 37) was the most reliably and robustly activated area across subjects. Five of seven subjects had supra-threshold activity in this region. In two subjects, the activated region in area 37 in the lateral temporal lobe extended superiorly into area 19 of the left lateral occipital lobe. As activity was confluent within areas 37 and 19, it was not possible to determine which area was the primary site of activation. No activity was observed for any subject within primary visual cortices (area 17).

The group SPM analysis confirmed the reliable presence of activity in left area 37. Positively correlated signal changes were also observed, on the left, in the precentral and anterior cingulate gyri. Figure 1B presents axial, sagittal and coronal slices through the left fusiform gyrus (area 37), while Fig. 1C shows axial slices through the centers of other areas of positively and negatively correlated activity. Table 1 provides the Talairach coordinates of the local maxima of these areas of activity. Significant signal changes in area 37 were present only on the left side; t -values within the homologous region on the right were well below significance.

Discussion

The results of this experiment support the hypothesis that mental imagery is a function of visual association cortex, and that image generation is asymmetrically local-

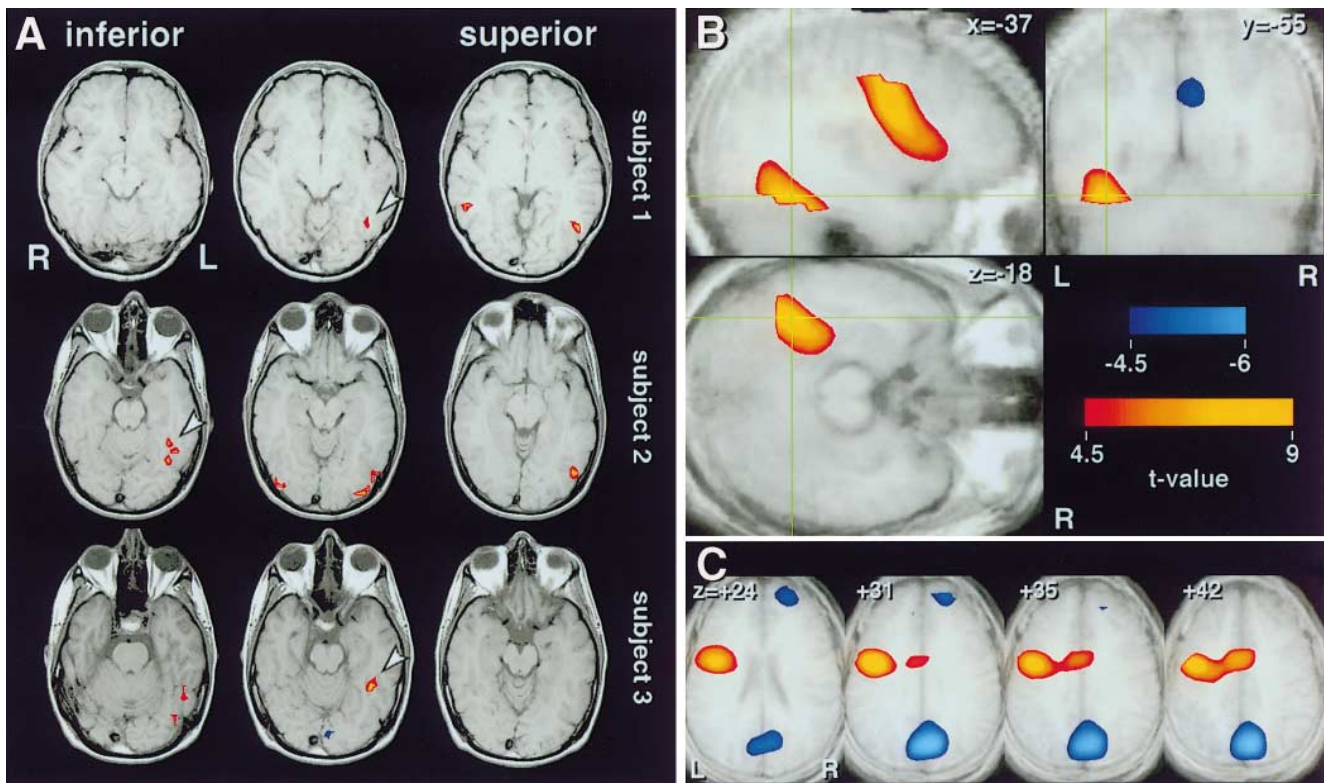


Fig. 1. (A) Axial slices from three of the five subjects demonstrating activity within the inferior occipital–temporal cortex. Three 5 mm slices, arranged inferior to superior from left to right, are shown for each subject. (B) Left area 37 locus of activity revealed by group SPM. Significant [$t > 4.5$, $\alpha < 0.01$ (corrected for multiple comparisons)] activity is shown in color superimposed upon averaged axial, sagittal and coronal slices converted to Talairach space. These slices pass through the local maxima of the activity present in the left fusiform gyrus. (C) Axial slices through the other five regions of activity.

Table 1. Local maxima for significant areas of activation

Region (Brodmann's area)		Talairach coordinates (x, y, z)			Cluster volume (cm^3)	t
Concrete > Abstract						
Fusiform gyrus (37)	L	-33	-48	-18	7.75	8.5
Premotor area (6)	L	-45	-3	31	23.9*	8.9
Anterior cingulate gyrus (24)	L	-7	-3	42		7.1
Abstract > concrete						
Superior frontal gyrus (10)	R	19	50	24	2.64	5.7
Precuneus (7)	R	4	-74	35	13.66	8.2

*A single cluster contained the local maxima for premotor area and anterior cingulate gyrus.

ized to the left. Five out of seven subjects showed activation at the temporal–occipital junction. The activation in these five subjects included the fusiform gyrus, area 37, a modality-specific visual area. The involvement of visual association cortex is consistent with the majority of neuroimaging studies reported earlier, as well as with a case study of the effects of occipital lobectomy on mental imagery [10]. In this study, a patient developed parallel perceptual and imaginal hemianopias after removal of her right occipital lobe.

The pronounced asymmetry found in this study addresses the controversial issue of laterality of image generation. In an early review of the literature, Farah noted a trend of left posterior damage when image gen-

eration was impaired [3], and a number of recent cases have had damage in the left temporo-occipital areas [7, 19, 20, 26]. Nevertheless, a range of opinion persists, with recent reviews concluding that both hemispheres contribute equally [30], that the left may have a slight advantage [34], and the left hemisphere is, in most people, specialized for image generation [12, 35]. Farah [12] reviews the case report and group study literature on the effects of focal brain damage on image generation. The present findings are in accord with a number of the neuroimaging findings cited earlier, as well as with the case and group studies just mentioned, in supporting left hemisphere specialization for image generation. The present asymmetry cannot be explained in any simple way by the

verbal nature of the stimulus materials, as the stimuli in both the imagery and baseline conditions were verbal. Furthermore, the use of verbal materials does not prevent right-sided asymmetries from being observed in functional neuroimaging [32].

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