The neural locus of mental image generation: Converging evidence from brain-damaged and normal subjects

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Abstract

Recent work with brain-damaged patients has provided evidence for a tentative neuroanatomical localization of mental image generation in the posterior left hemisphere. This evidence will be briefly summarized and critiqued, and a new test of the localization, using normal subjects, will be presented. When mental images of stimuli were used as templates to facilitate a visual discrimination, the effect of imagery was greater for stimuli presented in the right visual field (left hemisphere) than in the left visual field (right hemisphere). This result is discussed in relation to earlier claims about the hemisphericity of imagery.

Introduction

The ability to imagine the appearances of objects and scenes not currently in view requires more than simply having those appearances stored in long-term memory. It also requires the ability to generate, or reconstruct, from those long-term memory descriptions the short-term, array-format mental image (Kosslyn, 1980). Recent evidence from the study of two different neurological patient groups has suggested that these procedures may be critically dependent upon structures in the left hemisphere of the brain.

In this paper a third source of evidence is presented for the left-laterality of mental image generation, from a lateralized tachistoscopic stimulus presentation technique used with normal subjects. The objective of the experiment described here is to expand both quantitatively and qualitatively the evidence for the laterality of image generation; whereas each method of localization has its own weaknesses, one can decrease the liklihood of spurious or artifactual findings by using multiple different methods.

Previous findings

Evidence for a functional localization of imate generation in the left hemisphere came initially from Farah's (1984) review of published neurological case reports of imagery deficits. In this review, task analyses were constructed for the cognitive and perceptual tests that had been administered to the patients described in the case reports. By comparing the cognitive components that occurred in successfully and unsuccessfully performed tasks, it was possible to infer the particular component of mental imagery ability that was impaired. There were twelve patients who could recognize visually presented objects, yet could not imagine the appearances of the same or similar objects. To explain the imagery deficit in these patients we must postulate damage to some component of the imagery system that is not shared with visual recognition; that is, if visual recognition is intact then the long-term visual memories must be intact and so must the short-term visual memory medium in which both images and percepts occur (Farah, 1985; Finke, 1980). By a process of elimination, this leaves the image generation process, which converts the long-term memory information into a mental image in short-term visual memory, as the impaired component of imagery ability. In these twelve cases, the predominant site of brain damage was the posterior left hemisphere.

The laterality of image generation inferred from the effects of focal brain damage on imagery ability is supported by recent studies of two split-brain patients (Farah, Gazzaniga, Holtzman & Kosslyn, 1985; Kosslyn, Holtzman, Farah & Gazzaniga, in press). Whereas the disconnected left hemispheres of these patients were able to perform tasks requiring image generation, the right hemispheres were generally not, despite adequate performance on control tasks containing all of the processing steps of the imagery task except for image generation per se. For example, in each patient both hemispheres could classify a lower case letter as including or not including a long "stem" (e.g. "t" and "g" have long stems, "s" and "r" do not) and both hemispheres could use an upper case cue to select the associated lower case form from a set of lower case letters presented in free vision. However, the performances of the left and right hemispheres diverged sharply in the corresponding imagery task: only the left hemispheres of the split-brain patients could perform the lower case letter classification using the upper case form as a cue.

On the one hand, these preliminary results from patients with localized brain damage and with surgically separated but otherwise intact hemispheres represent a significant convergence of evidence for a left hemisphere locus for image generation. On the other hand, several facts warrant caution in our acceptance of this localization.

In the analysis of cases from the neurological literature, one might argue that the procedure of case selection by literature review has a systematic bias against right-hemisphere-damaged patients: such patients are initially less likely to come to the attention of neurologists and psychologists (because their language ability will not have been endangered) and this bias may be compounded by the tendency of right-hemisphere-damaged patients to deny the existence of neurological deficits, including those far more obvious than a loss of imagery, such as hemiplegia or cortical blindness (Hecaen & Albert, 1978).

In the case of the split-brain patients, interpretation of right-hemisphere failures on the imagery tasks is complicated by the lack of independent evidence that the right hemisphere, with its inferior logical and language comprehension abilities, understood the task. One of the "Catch 22's" of split-brain research is that there is in general no way to determine that the right hemisphere has understood a task that it has failed.

A new test: A cognitive paradigm with normal subjects

The purpose of the present experiment is to assess the laterality of image generation in a third way, with normal subjects in an imagery paradigm developed and validated within cognitive science. A finding of left-hemisphere superiority in this experiment cannot be attributed to any of the potential artifacts outlined above, and would therefore strengthen the hypothesis that image generation is lateralized to the left hemisphere.

The basic experimental paradigm is a lateralized visual discrimination task, in which the subject is to decide whether a stimulus, presented briefly and to one side of a fixation point, is or is not a pre-designated "target." Past studies have shown that a visual image of the target can be used as a template to facilitate discriminations between target and non-target stimuli (Cooper & Shepard, 1973, Posner, Boies, Eichelman & Taylor, 1969).

The two targets in this experiment are a plus sign and a rectangular-shaped capital "O" character. Non-targets are characters selected for being visually similar to either the plus or the "O": "*", "-", an oval-shaped "O" and "@". In this experiment, subjects perform two versions of the lateralized discrimination task. In the "Baseline" condition, they are pre-cued with the information about the side on which the stimulus will occur before the stimulus presentation. Their task is to respond "target" to either of the targets and "non-target" to nay of the non-targets. In the "Imagery" condition, they are pre-cued as before with the side on which the stimulus will occur, and they are also shown one of the two targets (in central vision), which they are instructed to image in the position of the up-coming stimulus. The task is the same as in the Baseline condition: Subjects respond "target" to either target, *whether or not it is the same as their image*, and "non-target" to all non-targets.

Subjects were given two blocks of 64 trials each of the Baseline condition, followed by two more blocks of the imagery condition. Subjects were right-handed males with no first-degree relatives known to be left-handed. As an objective criterion for determining whether or not subjects were o,agomg as omstricted. the mean latency of response to stimuli while holding similar and different images were compared for each subject. If a subject was successful at using an image as a template during the Imagery condition, then they should have responded more quickly to stimuli that were similar to the image than to stimuli that were different. Accordingly, any subject who showed an opposite trend would be eliminated from the analysis and replaced with a new subject. Data from twenty subjects is reported here. An additional six subjects were tested and replaced because they showed a negative effect of similarity (nonsignificant in all cases). Three of these subjects also estimated having imaged less than 75% of the time. All other subjects reported complying with the instructions at least 80% of the time.

The image should facilitate the visual discrimination between targets and non-targets, particularly when the image and stimulus are visually similar. Thus, there are two, independent measures of the effectiveness of imagery in the present experiment: the degree of facilitation with an image, relative to performance in the same visual discrimination task without an image, and the degree of facilitation with an image that is visually similar to the stimulus being presented, relative to performance in the same visual discrimination task with an image that is visually different from the stimulus being presented. If the left hemisphere is specialized for image generation, then these measures of image-mediated facilitation should be greatest when the image-stimulus overlap occurs in the right hemifield-left hemisphere, where the image was generated.

Results

Response latencies from incorrect responses were removed from the analysis, as were latencies that were more than 1.75 times the mean of the remaining response latencies from the same subject for comparable responses (i.e. responses from the same Order x Laterality x Response cell in the Baseline condition, and from the same Order x Similarity x Laterality x Response in the Imagery condition). Mean response latencies were then calculated for each subject in each subcondition of the experiment (i.e. each Imagery x Order x Similarity x Laterality x Response condition) and these means comprised the data upon which the statistical analyses reported below were performed.

The mean response times and error rates in the conditions of interest are shown in Table 1. The two predictions set out earlier for the differential effects of imagery on visual discrimination performance in the two hemifields were borne out by planned comparisons among the response latencies in this task. The first prediction concerned the overall effect of image generation on visual discrimination performance (i.e. the difference between performance in the Baseline and Imagery conditions). As predicted, there was a right visual field superiority only in the Imagery condition, $t=2.81$, $df=19$, $p<.01$. The mean response latencies to stimuli in the left and right hemifields in the Baseline condition were 818 msec and 815 msec respectively, and in the Imagery condition they were 776 msec and 754 msec respectively. Note that the small field difference in the Baseline response latencies was not by itself significant, $t<1$.

The second prediction concerned the effect of image-stimulus similarity in the Imagery condition (i.e. the difference between performance when the image and stimulus were visually similar and when they were visually different, in the Imagery condition). Also as predicted, there was a greater right visual field advantage when the image and the stimulus were visually similar than when they were visually different, $t=3.19$, $df=19$, $p<.005$. The response latencies to stimuli in the left and right hemifields after generating a different image were 797 msec and 790 msec respectively, and after generating a similar image they were 755 msec and 717 msec respectively.

The possibility that hemispheric differences in speed-accuracy trade-offs could account for the present findings was dispelled by an examination of each hemisphere's error rates in the experimental conditions of interest, shown in table 1. For the first of the contrasts above, the left hemisphere error rate was the same for the baseline and imagery conditions (20.5%), and the right hemisphere error rate was only 0.3 percentage points higher in the baseline condition than in the imagery condition (23.4% and 23.1% respectively). For the second of the contrasts above, the hemispheric error rates as well as response latencies reflected the predicted pattern of performance, with greater facilitation from similar than from different images in the left hemisphere (18.5% and 22.5%, respectively) than in the right hemisphere (24.4% and 21.8% respectively).

The response latencies were also submitted to a repeated measures analysis of variance, whose factors were presence or absence of imagery, laterality of stimulus presentation, response, similarity (of image to stimulus in the Imagery condition and the identical partitioning of trials in the Baseline condition) and order of occurence (i.e. first block or second block of the Baseline and Imagery conditions).

The overall interaction between laterality of stimulus presentation and presence or absence of imagery, a specific form of which was tested with the first planned comparison above, was of borderline significance, $F(1,19)=3.00$, $p= 1$. The overall three-way interaction between presence or absence of imagery, laterality, and similarity, a specific form of which was tested with the second planned comparison above, was significant, $F(1,19)=5.07$, $p<.05$.

Order of occurence had a significant effect, $F(1,19)=9.09$, $p<.01$, and an examination of the means shows this to be primarily a speeding-up between the first baseline block and the second: 850 msec mean latency for the first baseline block, 782 msec for the second baseline block, 780 msec for the first imagery block and 750 msec for the second imagery block. The disproportionate speeding-up between the first and second baseline blocks, compared with the first and second imagery blocks, is reflected in a significant interaction between order or occurence and presence or absence of imagery, $F(1,19)=4.88$, $p<.05$.

However, there was no interaction between order of occurence and laterality, $F(1,19)=0.08$, $p=.79$, and thus the laterality effect present in the imagery blocks and not in the baseline blocks cannot be accounted for as an artifact of order of occurence.

Similarity and its interactionm with presence or absence of imagery were highly significant, although this was at least partly artifactual, given the subject selection procedure described earlier of excluding subjects whose response times were slower when the image and stimulus were similar than when they were different. As expected, similarity had an effect only in the imagery condition, $F(1,19)=9.21$, $p<.01$ for the interaction of similarity and presence or absence of imagery: With a similar image, a stimulus could be classified as a target or nontarget in an average of 736 msec, whereas with a different image an average of 794 msec were required; when the same two groups of trials, administered in the same order, were performed without imagery, the comparable mean latencies were 818 msec and 814 msec respectively. The effect of similarity in the imagery condition led to a significant main effect of similarity in this experiment, $F(1,19)=20.06$, $p<.001$. Targets were responded to more quickly than nontargets, $F(1,19)=14.54$, $p<.005$, with an average of 750 msec required for targets and 831 msec required for nontargets. The three-way interaction between presence or absence of imagery, similarity, and response was significant, $F(1,19)=26.09$, $p<.001$, and an examination of the means in table 1 indicates that this results from the disproportionate facilitation with imagery for similar targets in the imagery condition, which, in contrast to both similar nontargets and different targets and nontargets, constitute a perfect, template-style match with the image. The two-way interaction between similarity and response is also significant, $F(1,19)=10.71$, $p<.01$, owing to the just-discussed effect of template-style matches in the trials of the imagery condition.

Finally, there were two four-way interactions of statistical significance: A presence or absence of imagery by similarity by order of occurence by response interaction, $F(1,19)=9.40$, $p<.01$, which the means of table 1 suggest reflects a progressive quickening in responding "no" to similar nontargets and "yes" to different targets in the imagery condition (i.e. with practice subjects became less inclined to false alarm to a nontarget that resembled their image and less inclined to miss a target that looked different from their image), and a presence or absence of imagery by order by laterality by response interaction, $F(1,19)=14.21$, $p<.01$, for which no simple interpretation suggests itself. No other effects were significant, $p>.1$.

Discussion

Visual discrimination performance was more strongly facilitated by the presence of an image in the right visual field (left hemisphere), and was more sensitive to the visual similarity between the image and the stimulus in the right visual field (left hemisphere). Both of these results were predicted by the hypothesis that the left hemisphere is required for image generation, because according to this hypothesis, image-stimulus interactions after a left visual field stimulus presentation require either the image or the percept to cross the corpus callosum, with attendent delay and degradation of information, whereas callosal transmission is not necessarily required after a right visual field stimulus presentation.

How do the present findings relate to other recent work on hemispheric differences in visual/spatial processing? Many authors have suggested that imagery is a right hemisphere function, although Ehrlichman and Barrett's (1983) survey of the neuropsychological literature found little empirical support for this hypothesis. As Ehrlichman and Barrett pointed out, most claims of right hemisphere specialization for imagery derive from a conflation of imagery with other forms of visual/spatial ability. When one considers the computational "problem" which must be solved in image generation, it is clearly of a different nature from the problems of maze learning, visual analogy solving, face recognition, and other typical examples of visual/spatial tasks for whicxh right hemisphere superiority has been found. In particular, the work of Kosslyn and his associates has shown that image generation involves the construction of the image from separately stored parts, even in the case of a seemingly unitary image, such as an image of a dog or the letter "a". (Farah & Kosslyn, 1981; Kosslyn, 1980; Kosslyn, Reiser, Farah & Fleigel, 1983; Kosslyn & Shwartz, 1978). Image generation therefore involves the integration of separate parts in functionally spatial array, an ability which has been identified with areas in the posterior left hemisphere (Kinsbourne & Warrington, 1962; Levine & Calvanio, 1978).

To summarize the outcome of the present experiment, the effect of image generation on visual discrimination performance was found to be asymmetrical in a direction consistent with a left hemisphere locus for image generation. Taken together with the results described earlier from neurological patients, the present result strengthens the hypothesis that image generation depends upon structures in the left hemisphere.

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Acknowledgements

The research reported here was supported by PHS fellowship F32 MH08876-01 and by the MIT Center for Cognitive Science under a grant from the Alfred P. Sloan Foundation. The author thanks Kaveri Suryanarayan and Ron Wilson for valuable technical assistance, and Howard Gardner for helpful comments on an earlier draft of this paper.

	BASELINE CONDITION		IMAGERY CONDITION			
			image & stimulus similar		image & stimulus different	
Response:	YES	NO	YES	NO	YES	NO
RVF (lh)	**777 ms** **20.6%** 821 ms 733 ms 20.6% 20.6%	**852 ms** **21.9%** 881 ms 824 ms 22.2% 21.6%	**646 ms** **13.8%** 651 ms 642 ms 16.9% 10.6%	**788 ms** **23.1%** 831 ms 746 ms 28.1% 18.1%	**802 ms** **24.7%** 809 ms 794 ms 24.4% 25.0%	**778 ms** **20.3%** 786 ms 770 ms 18.1% 22.5%
VISUAL FIELD (hemisphere)						
LVF (rh)	**775 ms** **20.8%** 797 ms 753 ms 23.4% 18.1%	**860 ms** **26.0%** 902 ms 818 ms 27.5% 24.4%	**683 ms** **18.2%** 704 ms 663 ms 16.9% 19.4%	**827 ms** **30.6%** 831 ms 823 ms 33.1% 28.1%	**763 ms** **21.6%** 798 ms 728 ms 23.8% 19.4%	**832 ms** **21.9%** 831 ms 833 ms 25.6% 18.1%