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Cognitive Brain Research 24 (2005) 423-435

Research Report



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Neural impact of the semantic content of visual mental images and visual percepts

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Accepted 15 February 2005 Available online 8 April 2005

Abstract

The existence of hemispheric lateralization of visual mental imagery remains controversial. In light of the literature, we used fMRI to test whether processing of mental images of object drawings preferentially engages the left hemisphere to compared non-object drawings. An equivalent comparison was also made while participants actually perceived object and non-object drawings. Although these two conditions engaged both hemispheres, activation was significantly stronger in the left occipito-temporo-frontal network during mental inspection of object drawings. An interaction was nonetheless observed: this effect was stronger during imagery than during perception in the left inferior frontal and the left inferior temporal gyrus. Although the tasks subjects performed did not explicitly require semantic analysis, activation of this network probably reflected, at least in part, a semantic and possibly a verbal retrieval component when object drawings were processed. Mental imagery tasks elicited activation of early visual cortex at a lower level than perception tasks. In the context of the imagery debate, these findings indicate that, as previously suggested, figurative imagery could involve primary visual cortex and adjacent areas.

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Theme: Neural basis of behavior *Topic:* Cognition

Keywords: Visual mental imagery; Visual perception; Hemispheric lateralization; Semantic processing; fMRI; Ventral pathway; Early visual cortex

1. Introduction

During the last decade, the issue of how visual mental imagery is implemented in the brain has been widely studied [27,35]. There is now a consensus regarding the involvement of associative visual areas during various mental imagery tasks. While the hemispheric specialization of figurative (object) mental imagery has not yet been clearly established, advances have recently been made in the study of the spatial mental imagery domain (i.e., processing of spatial relations between objects or processing of part of

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objects such in mental navigation, mental rotation, etc.). It has been suggested that the right intraparietal sulcus is preferentially involved when spatial mental imagery tasks deal with metric spatial relations ("coordinates"), while the homologous region in the left hemisphere is preferentially involved in spatial tasks involving above/below or left/right ("categorical") judgments [46]. An alternative interpretation has recently been offered that the left posterior parietal cortex (PPC) is preferentially engaged in processes of mental image generation (i.e., visualization of previously memorized patterns), while the right PPC plays a role in mental image transformation (i.e., mental rotation of patterns) [14]. Altogether, these studies argue for bilateral involvement of the parietal cortex in spatial mental imagery, with a specific role for each hemisphere.

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Whether this type of organization exists in the ventral temporal cortex for figurative imagery has been a matter of intense debate [45]. It has been suggested that although both hemispheres might be involved in image generation, they act in different fashions. Early single case reports suggest the hypothesis that the left temporo-occipital cortex might be specialized for the generation of multipart mental images [13]. However, we have reported unilateral right activation of the occipito-temporal cortex in tasks that bear strongly on multipart image generation [34,37]. Interestingly, in one of these studies, the mental images involved represented three-dimensional shapes with no semantic attributes or lexical entries [34]. This suggests the hypothesis that the object and non-object types of mental imagery affect the lateralization of activation. Mental images that include semantic content or refer to a lexical entry might preferentially elicit left-sided activation. As a matter of fact, regarding the ventral pathway, most of the studies that have reported activation predominantly in the left hemisphere have used mental images that included some lexico-semantic information [3,9, 19,36]. Moreover, this effect might involve not only the ventral pathway but also the frontal region, in particular the left inferior frontal gyrus, which is known to play a key role in semantic processing of percepts. In the visual domain, it was found that this region was more activated by object than by non-object visual stimuli [29,51]. Accordingly, we postulated that figurative mental imagery with meaningful content (i.e., lexical and conceptual knowledge implicitly associated with the object drawn) would more strongly engage the left inferior frontal gyrus than meaningless images.

In summary, comparison of findings obtained with these two kinds of images suggests the existence of a left lateralized network including inferior temporal and fusiform gyrus belonging to the ventral pathway and the inferior frontal cortex, and indicates that processing of figurative mental imagery involves semantic processing networks. The purpose of the present study was to test this hypothesis using a mental imagery generation task involving drawings representing both usual objects and animals, and non-object drawings that do not represent an existing object or animal. It has been shown that visual perception and mental imagery share a common neural substrate ([26,35], for review). In order to compare the effect of type of drawing during imagery and actual perception, we also included a perceptive version of the task using the same object and non-object drawings. We paid particular attention to early visual cortex, considering the debate regarding its involvement in visual mental imagery. We have previously suggested that activation of early visual cortex could reflect the effort paid to maintain a clear and vivid mental image [30]. Assuming that this effort is more intense for imagery of non-object drawings than for that of object drawings, we expected that activation would be greater in the former than in the latter condition.

2. Materials and methods

2.1. Participants

Fifteen healthy volunteers (age: 18–27 years, 4 women) were included in this study. All were free of neurological disease and injury and had no abnormality on T1-weighted magnetic resonance imaging (MRI). The local Ethics Committee approved this study, and written informed consent was obtained from each subject after the procedures to be used in the study had been fully explained. All participants were right-handed as confirmed by the Edinburgh questionnaire (mean score: 77 ± 20). In order to ensure optimal homogeneity of subject sample with respect to imagery abilities, participants were selected as "high imagers" (having high spatial ability) on the basis of their scores on the Mental Rotations Test (mean MRT score: 17 ± 2.8) [49].

2.2. Materials

2.2.1. Stimuli

The first set of stimuli was composed of line drawings depicting objects belonging to various semantic categories (objects, tools, animals, etc.). These items were chosen from a French naming test [38]. The second set included nonobject drawings and was created by pseudo-random spatial shuffling of the object items. We attempted to match visually as closely as possible the complexity of the two sets of drawings (number of lines, etc.). Despite this effort, however, it is possible that some differences remain. For example, objects may have appeared more symmetric than non-objects. The difficulty here is that non-object drawings may be too suggestive of existing objects or symbols when symmetry is preserved (see below). Object and non-object drawings are presented in Fig. 1. We tested the non-object drawings in a pre-experimental study with 15 participants (differing from the participants included in the fMRI study) who were forced to name the non-object pictures. It was included in the set of non-object pictures only when the participants required more than 5 s to identify and name an existing object as present in a non-object drawing. In addition, we excluded non-object drawings that evoked the same objects for two participants (and were thus likely to actually evoke an existing object).

2.2.2. Learning and training phases out of the scanner

Prior to fMRI scanning, the participants memorized 12 object and 12 non-object drawings. They were informed that, during the fMRI experiment, they would have to create an accurate mental image of each drawing in order to evaluate some figurative properties. Each object drawing was associated with a letter (from A to L) and each non-object drawing with a number (from 1 to 12). The participants were requested to memorize a drawing and its paired symbol as accurately as possible and were then tested

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