The role of the vertical meridian in visual memory for objects

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Abstract

It is widely believed that, in human and nonhuman primates, visual memories of objects are stored in the temporal lobe. Electrophysiological results in monkeys, however, indicate that when a visual scene contains two or more objects, with at least one object in each visual hemifield, neurons in the temporal lobe of each hemisphere respond only to the objects that are in the contralateral visual hemifield, and their activity is unaffected by the objects in the ipsilateral hemifield. Putting these two premises together predicts that object memory should fail, or at least suffer a substantial decrement, when an object is presented for learning and retention as part of such a scene, but crosses the vertical meridian between the learning trial and the retention test. The effect of this change should be much greater than the effect of an equal retinal translation that crosses the horizontal rather than the vertical meridian. An experiment with normal human subjects verified this prediction under conventional conditions of tachistoscopic viewing, with a single constant fixation spot. A further condition in the same experiment, however, tested the same retinal translations in a more naturalistic condition, where the retinal changes were produced by varying the position on the display screen of the fixation spot rather than of the objects. Here, there was no significant special effect of crossing the vertical meridian. We conclude that visual memories are not stored exclusively in the temporal lobe.

1. Introduction

The medial and inferior temporal lobe, including the perirhinal and entorhinal cortex and the hippocampus as well as the white matter of the anterior temporal stem, is indispensable for normal memory processing in both human and nonhuman primates, as is shown by the severe memory impairments which follow lesions in these structures [5,13,18]. The inference that the temporal lobe contains a memory system [23], or multiple memory systems [8], in which memories are processed and stored, is widely accepted. The perirhinal cortex is the most important of these temporal-lobe structures in memory for visually presented objects, which is the most extensively studied kind of memory in nonhuman primates [16,18]; furthermore, the function of the perirhinal cortex has been doubly dissociated in the monkey from the function of adjacent structures in the temporal lobe [3,8]. On this basis it has been suggested [8] that the perirhinal cortex is a memory system, differentiated from other memory systems in the temporal lobe, and specialised

for the processing and storage of object memories. According to this view, memory for objects that are presented in complex visual scenes [9] is produced by the interaction within each temporal lobe between perirhinal cortex and the other memory systems of the temporal lobe, including the hippocampus [12]. Against the simplest version of this hypothesis of temporal-lobe memory systems for scene memory, however, is evidence that some of the effects of perirhinal cortex ablations in monkeys are perceptual deficits rather than memory deficits [2], and arguments that some or all of the memory deficits that are produced by perirhinal cortex ablations in monkeys can be seen as a secondary effect of the loss of high-level perceptual representations of objects, rather than as direct loss of memory storage [2,19]. The present experiment is concerned with one of the features of temporal-lobe function that seems most difficult to reconcile with the idea that memories of visual scenes are processed and stored exclusively or mainly within the temporal lobe, as the hypothesis of temporal-lobe memory systems suggests. This is the fact that the representation of complex visual scenes in the temporal lobes is divided at the vertical meridian of the visual field between the two hemispheres.

When a monkey sees a single object that is presented against a large blank background, neurons in the temporal

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lobe in both hemispheres respond to the object and signal its identity, even when the object is confined to one visual hemifield, and even though there are slight differences in strength of response favouring the neurons in the temporal lobe contralateral to the object [4]. However, a single object presented against a large blank background is not a natural condition of object vision and memory. In a more naturalistic scene-like condition, when two or more objects are presented, with at least one object in each visual hemifield, the difference between the two temporal lobes in the objects they respond to is stark. Neurons in the temporal lobe of each hemisphere now respond only to the objects that are in the contralateral visual hemifield, and their activity is unaffected by the objects in the ipsilateral hemifield [4]. This poses a problem for understanding the memory of objects that are presented in this fashion, that is, in scenes having at least one object in each visual hemifield. Consider the case where an object, a constituent of a visual scene that contains other objects, is presented for learning in one visual hemifield, but is subsequently presented for a recognition memory test in the opposite hemifield. In the learning trial, neurons in only one temporal lobe respond to the object, and in the retention test trial, neurons in only the other temporal lobe respond to the object. All proposals as to the neural basis of object memory assume that the memory of an object is stored as a modification in neurons that respond to the presentation of the object [1,17], and indeed it is difficult to see how neurons that do not respond to the presentation of an object could either lay down or retrieve a memory of it. It thus follows from the electrophysiological data, that neurons in neither of the two temporal lobes have both the opportunity to lay down and also the opportunity to retrieve a memory of the target object in the case we are considering, where the target object in a scene is presented in opposite hemifields at learning and at the retention test. Therefore, if object memories are stored either exclusively or mainly as modifications of neurons within the temporal lobe, memory for the object should either fail or suffer a substantial decrement in this case. The present experiment tested this counter-intuitive prediction in normal human subjects.

We administered two object recognition memory tasks. The trials were presented tachistoscopically, in order to control the retinal location of the presented objects. On every trial, both in learning and at the retention test, there were two different objects, one in each hemifield. Thus, each learning trial in these tasks presented two different objects, both to be remembered, and one in each visual hemifield. In each task a total of 128 objects were presented for learning in this fashion, and after all the objects had been presented for learning there was a retention test, at which the subjects had to recognise the objects they had seen in the learning trials by distinguishing them from novel foils. Each retention test trial presented one previously learned object together with one foil object that had not been seen before, one object in each hemifield. Some of the previously learned objects were presented at the retention test in the same location in

the visual field as they had occupied in the learning trials, in order to provide a baseline measure of object memory in these conditions. Other objects, however, were presented at the retention test in the hemifield opposite to that which they had occupied in the learning trials ("horizontal shift"). The prediction, derived above, is that memory for these objects should either fail or suffer a substantial decrement. To control for the possibility that a shift in an object's retinal location between learning and retention test is by itself sufficient to produce a memory decrement, even when it is not a shift across the vertical meridian, a third set of objects was presented at retention in the same hemifield as that which they had occupied in the learning trials, but shifted within that hemifield ("vertical shift"). In the monkey, temporal cortex neurons that fail to respond to objects in the ipsilateral hemifield, in the conditions we have discussed, respond in the same conditions to objects in the contralateral hemifield almost independently of their location within that hemifield [4]. Thus, the main question to be asked in each task is whether horizontal shifts produce worse memory performance than vertical shifts.

A further important aspect of the design of the two tasks was the means by which the shifts in the retinal location of objects were accomplished. To vary an object's retinal location, one can either change the position of the object while maintaining the position of the subject's eyes, or maintain the position of the object while changing the position of the subject's eyes; one cannot change only retinal position and nothing else. In tachistoscopic experiments, and in electrophysiological studies, there is usually a single constant fixation spot in the centre of the display screen, and objects are shifted from one retinal location to another by changing the object's position on the display screen. In the most usual natural condition, however, when stable complex scenes are viewed in free vision in one or more trials, changes in the retinal location of an object result from changes in the position of the subject's point of fixation, not from changes in the position of the object in the scene. Figs. 1 and 2 show how the two tasks instantiated these two different means by which an object can shift its retinal position. In tasks using the Square template there was a single central fixation point which was in the same position in all trials, and objects were shifted across the visual field, between learning and retention testing, by moving the objects on the display screen. But in tasks using the Lozenge template, exactly the same shifts of objects' positions in the visual field were accomplished by changing the position of the fixation spot, leaving the objects in an unchanged position on the display screen (the three pairs of learning and test trials using the Square template, that are illustrated in the leftmost two columns of Fig. 2, are identical, in terms of the retinal positions of the target and foil objects at learning and test, to the three pairs using the Lozenge template, that are illustrated in the rightmost two columns of Fig. 2).

Though identical in terms of the retinal positions of objects, these tasks are quite different from each other in the