

Memory and imagery in the temporal lobe

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Experimental and clinical studies in primates indicate that visual information is stored and retrieved by interactions between the temporal association area and the medial temporal lobe structures. Recent findings from single-neuron recordings have provided new evidence that perceptual aspects of the temporal neocortex are closely related to its memory function based on association. They further suggest that imagery is also implemented by the same neural mechanism that subserves memory retrieval.

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Introduction

The physical basis of memory and imagery is a fundamental and central issue in brain sciences. It is now widely known that there exist multiple memory systems, each of which is represented by distinct neural structures [1•,2,3]. In this review, we focus our attention on the visual declarative (explicit) memory in the primate temporal lobe. Recent studies on this topic extend from the molecular to the behavioural level. Single-neuron recordings provide one promising way to link these two extremes [4,5,6•]. We will summarize recent developments and propose a model based on the neural organization of perception, memory, and imagery.

Encoding, recoding, and decoding

Figure 1a shows a tripartite cognitive system that unifies memory and imagery. This scheme is based on structures and functions of the visual memory system for object recognition (Fig.1b). In the first place, the encoding process proceeds as information flows from a feature analyzer to a memory storehouse. The primary visual area and the prestriate area serve as the feature analyzer for visual perception (see a review by Van Essen *et al.* [7•]). A possible candidate for the memory storehouse is the temporal association area. To establish an enduring representation in the memory storehouse, a memory controller is responsible for consolidation. During this process, the memory code is dynamically reorganized (recoding) by the interaction between the memory storehouse and the memory controller. Medial temporal structures including the hippocampus are regarded as memory controllers, because of their plasticity (e.g. long-term potentiation), special neural networks (e.g. autoassociation), and clinical observations (e.g. amnesia after bilateral hippocampal lesions). A detailed discussion of these topics has been published elsewhere [4,5].

In the recall process, memory codes are decomposed into more elementary attributes (decoding) in the mem-

ory storehouse and feature analyzer. As Kosslyn [8] has pointed out, “imagery consists of brain states like those that arise during perception, but occurs in the absence of the appropriate immediate sensory input”. Moreover, neuropsychological evidence provides support for the top-down activation of perceptual representations by higher processing areas in the brain [9,10]. On the neurophysiological evidence described below, we hypothesize that imagery is implemented by the decoding mechanism, which enables retrieval of stored information. In summary, the cognitive memory process is divided into a feature analysis process and a memory control process; the former consists of encoding and decoding, the latter corresponds to recoding.

Memory storage in long-term memory (encoding)

Pair-coding neurons

To examine the possibility that the temporal association area is a memory storehouse, single-neuron responses have been recorded from the anterior temporal cortex of monkeys during memory tasks [11]. Recently, a pair-association task has been applied to the neurophysiological study [12••]. This task paradigm can directly assess long-term memory, because monkeys cannot select a paired associate correctly without memorizing and recalling pair combinations. One type of neuron (pair-coding neuron) manifests selective responses to both paired pictures. The properties of pair-coding neurons indicate that memory storage is organized such that single neurons can participate in the coding of both paired associates. The result provides new evidence that single neurons acquire selectivity for visual patterns in the long-term memory through associative learning. This type of coding is here termed associative coding, in which the involvement of associative learning is essential for memory storage.

Abbreviations

ERP—event-related potential; MRI—magnetic resonance imaging; PET—positron emission tomography.

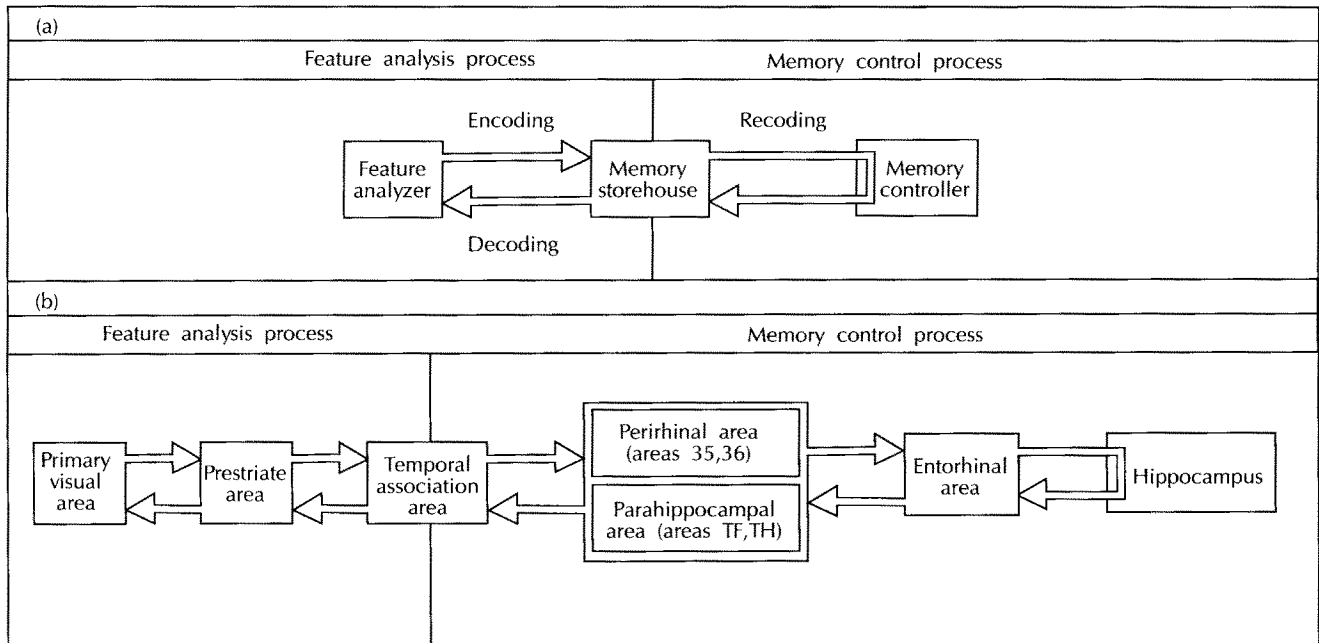


Fig. 1. (a) A model of the cognitive memory system that unifies memory and imagery. See text for an explanation. (b) The visual memory system for object recognition.

Face-responsive neurons

Neural responses to faces have been extensively studied in the monkey inferotemporal cortex and part of the superior temporal sulcus [13–17]. The relationships between face processing, face recognition impairments (prosopagnosia), and face-responsive neurons are still in dispute [18–22]. The associative coding described above could be applied as an organizing principle for these neurons. The response selectivity that neurons acquire through learning is a key feature in establishing association among different views of the same face or among different faces. The facial recognition properties of the temporal neocortex are thus likely to be a consequence of its essential memory-related capacity [23].

Non-sensory factors in encoding

Along with long-term memory, there is neurophysiological evidence for cortical representation of visual short-term memory in the temporal association area [24–26]. Some temporal neurons appear to function as adaptive mnemonic filters that preferentially pass information about new stimuli [27•]. This phenomenon could be closely coupled with priming, as suggested by a recent positron emission tomography (PET) study [28••]. The function of priming is to improve identification of perceptual objects [29]. It would be interesting to investigate whether encoding and priming share a common neural mechanism. The possibility that neurons are affected by non-sensory factors, such as attention to novel stimuli, should also be taken into account, because “working memory stands at the crossroads between memory, attention, and perception [30]”.

Retrograde amnesia

Lesion analysis of the temporal association area can test the possibility that this area is a memory storehouse.

If memories for past events are stored in the temporal neocortex, its disruption would result in significant retrograde memory impairment. Clear evidence for this impairment has been provided by Kapur *et al.* [31•]. They have reported that focal damage in the bilateral anterior temporal lobes (with an intact limbic-diencephalic system) causes marked loss of preoperative memory for information and events. As for autobiographical memory loss, there was no firm evidence of any temporal gradient. Moreover, McCarthy and Warrington [32•] have reported dissociation within retrograde amnesia, such that a patient has relatively good knowledge of people as individuals, but little knowledge of events or what people have done. Human long-term memory may also be organized in such distinct meaning systems, which are presumably modality-specific. Hart and Gordon [33•] have further confirmed that vision-based and language-based knowledge representations are segregated.

Memory retrieval and mental imagery (decoding)

Pair-recall neurons

In the anterior temporal cortex, another type of neuron (pair-recall neuron) is presumably involved in the process of memory retrieval [12••]. In each trial of the pair-association task, a cue picture is presented and the monkey is required to recognize the paired associate of that cue after a delay period. Pair-recall neurons exhibit picture-selective delay activity. This response is closely coupled with the paired associate that is not actually seen, but is retrieved by the cue stimulus. There are two possibilities for the critical process during the delay period. One is that a cue stimulus (retrospective code) is held in working memory. The other possibility is

that its paired associate (prospective code) is generated from stored memories. The increasing delay activity of the pair-recall neurons is consistent with the claim that subjects can employ a prospective code. On the ground that the anterior temporal cortex links the visual system and the medial temporal lobe memory system, these neurons could play an essential role in memory storage, and also be activated in memory retrieval.

Memory retrieval and the memory controller

The neuroimaging technique of PET has been successfully applied to the study of human memory. Squire and the group at Washington University Medical Center with Raichle [28••] have demonstrated activation of the right hippocampal region in normal subjects during a task of cued-recall (declarative memory). This result provides clear evidence for selective activation of the medial temporal lobe memory system in association with retrieval of explicit memory. The involvement of the memory controller in memory retrieval as well as memory storage is limited to the time span for memory consolidation. If a much longer interval between memorizing and retrieval is administered in the task, the loci of activation may differ.

Visual imagery and agnosia

Although the problem of mental imagery is still in dispute between pictorialism (a view that mental images are quasi-pictorial representations) and descriptionalism (a view that mental images are linguistic representations), plentiful evidence indicates that shared mechanisms exist in imagery and vision (see an excellent review by Tye [34]). For example, selective loss of imagery has been reported in associative visual agnosia, such that both visual recognition and mental imagery of living, in contrast with non-living items, are impaired [35•]. On the ground that pair-recall neurons can access to the prospective codes of visual imagery, we propose that imagery is implemented by the same neural mechanism that subserves memory retrieval in vision. Accordingly, there is a single set of visual representations for both object recognition and imagery. Within a single modality of vision, dissociation between recognition and imagery arises only from encoding and decoding processes. Neuropsychological studies have documented cases of impaired imagery in which visual recognition is intact. The other aspect of the double dissociation has been recently revealed by two studies [36•,37•]. These patients can draw objects well from memory but cannot identify visually presented material — even their own drawings. The deficit is probably of central origin at the intermediate level, because they show intact visual acuity and normal performances in various standard tests for mental imagery.

Parallel systems of imagery

In accord with multiple memory representations as discussed above, the cognitive memory system shown in Fig. 1a presumably functions in parallel for each modality-specific system. Therefore, imagery is likely to be segregated into vision-based and language-based channels. Furthermore, modality-specific cognitive memory systems

are not totally independent but interconnected with each other. There is psychological evidence that verbal encoding of visual stimuli affects subsequent visual image processing [38].

Memory consolidation and recognition (recoding)

Brain activity in recognition

In the human cortex, neuronal activity has been recorded extracellularly while a patient is performing several tasks. This opportunity is provided under local anaesthesia for the treatment of medically intractable epilepsy. One study has reported changes in neuronal activity related to object matching and/or face perception in the right anterior temporal cortex [39]. Recording of event-related potentials (ERPs) has proved that unilateral temporal lobectomy is associated with abnormally small ERP modulations in a recognition memory task with visually presented words [40]. In a face recognition task, active cortical sites were identified by a PET study in normal subjects: the fusiform gyrus and anterior temporal cortex along with the right parahippocampal gyrus and adjacent areas [41•]. These areas correspond to the site of radiologically identified lesions in prosopagnosia patients [42]. Recently, magnetic resonance imaging (MRI) of human brain activity, based on intrinsic sensitivity to cerebral blood flow and blood oxygenation, has been developed [43•]. With a precise three-dimensional imaging technique [44•], MRI will become a dynamic mapping tool for exploring memory and imagery in the near future.

Anterograde amnesia

There has been accumulating evidence that unilateral temporal lobectomy affects visual or verbal memory in epileptic patients [45–47]. These results have been further confirmed by case studies of object recognition impairment due to temporal lobe lesions or epilepsy [48–50]. It is well known that bilateral medial temporal lobe lesions cause marked anterograde amnesia that affects memory consolidation [51]. Further examination has indicated that forgetting of newly learned visual information within long-term memory (tested up to 30–32 h) occurs at a normal rate for amnesic patients [52]. This comparison was possible when much longer exposure to test stimuli was allowed to equate amnesic with normal subjects in the initial retention (10 min). Therefore, the forgetting rate within long-term memory is not the key parameter for anterograde amnesia.

Animal models of amnesia

Since the pioneering work by Mishkin [53], animal models of amnesia with specific brain lesions have provided substantial evidence for cortical localization of memory systems. Monkeys with rhinal cortex ablations (the hippocampus and amygdala were left intact) exhibit a severe impairment in visual short-term recognition memory [54]. Although these animals are impaired in remembering the preoperatively acquired set of object discrimina-

tions, they can normally learn a new set despite long-term (24 h) intertrial intervals. In a study of an animal model of cerebral ischemia, it has been shown that the hippocampus is a focal site of pathological change [55]. These ischemic monkeys exhibit memory impairment in the recognition memory task, although they show little impairment in the delayed (2 days) retention of object discrimination. Because monkeys with lesions of the hippocampus and adjacent parahippocampal cortices are also impaired in the latter object retention task, the perirhinal area and parahippocampal gyrus may play a pivotal role in the establishment of long-term memory needed for this task, as expected from the neural organization of the visual memory system (Fig. 1b).

Conclusions

Complementary and interdisciplinary approaches are crucial in studies of the neurobiology of memory and imagery because of the complexity of the problems to be studied. The data obtained from neuronal recording, neuroimaging, and lesion analysis are beginning to provide sufficient evidence to allow constructions of models that can be tested with further studies. The cognitive memory system proposed here emphasizes the shared neural mechanism of memory and imagery. The organizing principle of associative coding will be useful in constituting knowledge systems from vast numbers of long-term memories, which are linked to each other by chains of association.

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