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Functional Brain Imaging Studies of Cortical Mechanisms for Memory

Leslie G. Ungerleider

Recent functional brain imaging studies in humans indicate that learning and memory involve many of the same regions of the cortex that process sensory information and control motor output. The forms of perceptual and motor learning that can occur without conscious recollection are mediated in part by contractions and expansions of representations in the sensory and motor cortex. The same regions are also engaged during the conscious storage and retrieval of facts and events, but these types of memory also bring into play structures involved in the active maintenance of memories "on line" and in the establishment of associative links between the information stored in different sensory areas. Although the picture of memory that is emerging from functional imaging studies is consistent with current physiological accounts, there are puzzles and surprises that will be solved only through a combination of human and animal studies.

In the past few years, there has been an explosive growth in the field of human brain imaging (*1*). The goal of some of this work has been to "map" the brain, in the sense of assigning specific functions to structures by selectively activating (or "deactivating") them while people perform various tasks. However, from a neuroscientist's perspective, it is critical not only to ask where changes in activity occur but to understand the underlying mechanisms that produce the changes. To some extent, this question can be approached by new methods of analysis of brain imaging data, such as correlational, time-series, and path analyses (*2*). Probably the most powerful approach, however, is to use brain imaging data to test, where appropriate, specific hypotheses derived from physiological studies in animals, lesion studies in animals and humans, and cognitive theories.

It is important to acknowledge that what we measure in human brain imaging experiments is not neuronal activity but local hemodynamic changes: blood flow, in the case of positron emission tomography (PET) (*3*), and (typically) blood oxygenation, in the case of functional magnetic resonance imaging (fMRI) (*4*). The relation between these hemodynamic changes and the underlying physiology is still inadequately characterized. For simplicity, I will refer to hemodynamic changes as relative "activations" in this review. A further limitation of functional brain imaging is poor temporal and spatial resolution as compared with that obtained with physiological recordings of neuronal activity. Even with fMRI, which provides better resolution than PET, one is still dealing with signals that have latencies of 4 to 8 s and a spatial resolution of about 2 mm, which is a temporal and spatial scale at least one to two orders of magnitude coarser than that of the underlying physiological mechanisms. Nonetheless, functional brain imaging offers a way to study the human brain at work and, it is hoped, to bridge the gap between studies in animals and those in humans.

Because my primary focus will be on memory in the visual modality, I will first review the organization of the visual cortex in monkeys and humans and then examine how knowledge about objects may be stored in this cortex. I will then consider several mechanisms by which experience modifies the way the cortex processes information over both long and short time intervals.

Organization of the Monkey Visual Cortex

The monkey cortex contains at least 30 separate visual areas, occupying about one-half of the total cortex (*5*, *6*). These areas are organized into two functionally specialized processing pathways, each having the primary visual cortex (V1) as its source and each being composed of multiple areas beyond V1 (Fig. 1). The occipitotemporal pathway, or "ventral stream," is crucial for the identification of objects, whereas the occipitoparietal pathway, or "dorsal stream," is crucial for the appreciation of the spatial relations among objects (*7*) as well as the visual guidance of movements toward objects in space (*8*). A simple way to conceptualize the functions of the two streams is "what" versus "where." Both streams have reciprocal connections with systems beyond the modality-specific visual system, including prefrontal areas and the hippocampal region. I will consider the possible role of these connections in a later section.

Why are there so many visual areas, and what does each do? One view is that the pathways are organized hierarchically, in the sense that low-level inputs are transformed into progressively more useful representations through successive stages of processing. Within the ventral stream, for example, the processing of object features begins with simple spatial filtering by cells in V1, but by the time the inferior temporal cortex (area TE; see Fig. 1) is activated, the cells respond selectively to global or overall object features, such as shape, and some cells are even specialized for the analysis of faces (*5*). Likewise, within the dorsal stream, the processing of moving stimuli begins with simple direction-of-motion selectivity by V1 cells, but in the higher-order areas of the parietal cortex (such as LIP and MST; see Fig. 1) the cells respond selectively to complex patterns of motion, such as rotation, and to the optic flow patterns produced when one moves through an environment (*9*).

Organization of the Human Visual Cortex: Processing and Storage

To what extent is the human brain simply a bigger monkey brain, at least as far as the visual cortex is concerned? At the highest

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The author is with the Laboratory of Psychology and Psychopathology, National Institute of Mental Health, National Institutes of Health, Bethesda, MD 20892 USA. E-mail: lgu@ln.nimh.nih.gov

level of organization, functional imaging studies have tested for the existence of separate processing streams by having people perform object identity and spatial perceptual tasks analogous to the tasks that have been used in monkeys (*10–12*). Because both kinds of tasks involve a large number of extraneous operations, such as early visual processing of the sensory input, decision-making, and behavioral responses, one would expect both to cause activations in widespread areas of the cortex. Therefore, to isolate the activations that are unique to each task, these studies used the popular "subtraction" technique, in which the activations elicited in one task are subtracted from those elicited in the other. After such a subtraction, these studies revealed regions activated in the dorsal occipitoparietal cortex in the spatial perceptual tasks and regions activated in the ventral occipitotemporal cortex in the object identity tasks (Fig. 2), which is in agreement with the organization of the monkey cortex. As one would expect, damage to the dorsal and ventral streams by trauma or disease causes impairments in spatial vision and object recognition, respectively (*13*).

At a finer level of organization, functional imaging studies have begun to reveal the individual processing areas within the two streams, and many of these areas appear to be homologous to monkey visual areas, including V2, V3, V4, and the middle temporal area (MT) (*14*). Studies that measure activation in tasks requiring perception of, or attention to, color, shape, and faces tend to find foci in the vicinity of areas V2 and V4, as well as in more anterior ventral stream areas in the temporal lobe (*10*, *11*, *15–18*), all of which contain cells selective for these features in the monkey (*5*). Studies that measure activation during perception of, or attention to, motion often find foci in areas associated with the dorsal stream, particularly in a region that seems homologous to MT (*15*, *16*, *19*, *20*), an area in the monkey that contains a high proportion of cells selective for visual motion (*21*). Outside the visual cortex per se, functional imaging studies in humans, like physiological recording studies in monkeys (*22*), have also revealed additional zones in the prefrontal cortex that are activated during performance of object or spatial vision tasks (*23–26*). The possible roles of these regions in memory processes will be considered in a later section.

In further support of the hierarchical processing scheme derived from monkey research, functional imaging data argue for an increase in the complexity of processing as activity proceeds anteriorly through the ventral stream into the temporal lobe. Whereas posterior regions in the cortex are preferentially activated during the processing of object attributes, such as colors, shapes, and even scrambled faces (*15*, *16*, *27*, *28*), more anterior regions in the temporal lobe are activated during the processing of intact faces but not of scrambled ones (*27*, *29*). Further, the region activated during face processing shifts progressively more anteriorly within the temporal lobe as people classify faces on the basis of increasing specificity. Thus, identification based on facial features, as in gender discrimination, activates the ventral surface of the temporal cortex posteriorly; identification of a unique individual's face activates a more anterior ventral temporal region; and retrieving knowledge about an individual, as in naming the individual's profession, activates even more anterior regions in the parahippocampal gyrus and temporal pole (*10*, *18*), findings that are consistent with human lesion studies on the kinds of face recognition impairments produced by selective temporal lobe damage (*30*).

Thus, overall, the organization of the human and monkey visual cortex appears to be remarkably similar. The distinguishing feature between them may be the kinds of information processed and ultimately stored. One intriguing possibility, for example, is that the human visual cortex contains regions that are specialized for the processing of visual letters and word forms. Alexia, an inability to recognize words presented visually, is frequently associated with lesions affecting the left medial occipitotemporal cortex (*31*). Correspondingly, Petersen *et al.* (*32*) found a focus of activation within this same region of the cortex when people viewed written words but not other wordlike

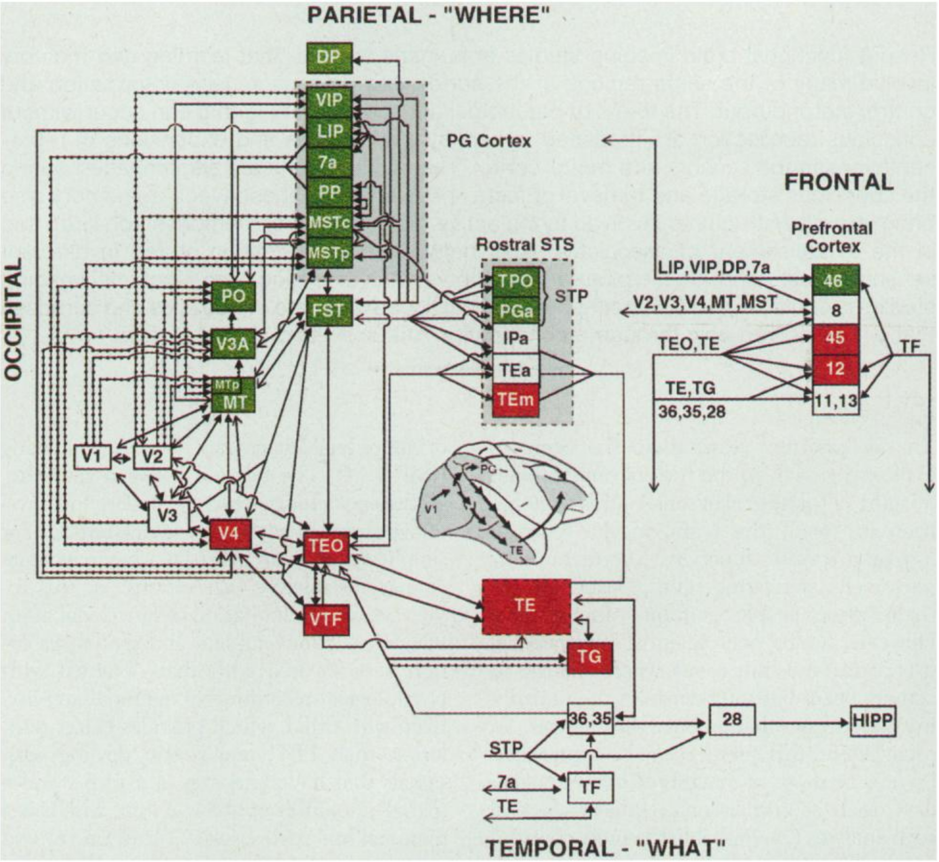

Fig. 1. Visual processing pathways in monkeys (*88*). Solid lines indicate connections arising from both central and peripheral visual field representations; dotted lines indicate connections restricted to peripheral field representations. Red boxes indicate ventral stream areas related primarily to object vision; green boxes indicate dorsal stream areas related primarily to spatial vision; and white boxes indicate areas not clearly allied with either stream. Shaded region on the lateral view of the brain represents the extent of the cortex included in the diagram. Abbreviations are as follows: DP, dorsal prelunate area; FST, fundus of superior temporal area; HIPP, hippocampus; LIP, lateral intraparietal area; MSTc, medial superior temporal area, central visual field representation; MSTp, medial superior temporal area, peripheral visual field representation; MT, middle temporal area; MTp, middle temporal area, peripheral visual field representation; PO, parieto-occipital area; PP, posterior parietal sulcal zone; STP, superior temporal polysensory area; V1, primary visual cortex; V2, visual area 2; V3, visual area 3; V3A, visual area 3, part A; V4, visual area 4; and VIP, ventral intraparietal area. Inferior parietal area 7a; prefrontal areas 8, 11 to 13, 45, and 46; perirhinal areas 35 and 36; and entorhinal area 28 are from Brodmann (*89*). Inferior temporal areas TEO and TE, parahippocampal area TF, temporal pole area TG, and inferior parietal area PG are from Bonin and Bailey (*90*). Rostral superior temporal sulcal (STS) areas are from Seltzer and Pandya (*91*) and VTF is the visually responsive portion of area TF (*92*).

stimuli, such as strings of random consonants or strings of letterlike forms (Fig. 2). Based on its location within the occipitotemporal cortex, this region would most likely subserve general-purpose visual pattern recognition functions in monkeys; however, in humans, it is distinct from regions activated during processing of other visual forms, such as faces and colored patterns (*33*). Because the region specialized for word forms clearly could not have evolved for the purpose of reading, it must develop in the course of learning to read.

The possibility that learning to read leads to specialization within visual processing areas brings us to the larger question of visual memory storage. For example, how and where is the information stored that a banana is yellow or that horses gallop? Recent functional imaging studies suggest that knowledge about the visual attributes of objects involves cortical areas closely associated with the processing areas in the ventral and dorsal streams (*34*). In one PET study, people were shown achromatic line drawings of objects and were asked to name either the color or the action typically associated with those objects. The generation of color names associated with objects selectively activated a region ventrally in the temporal cortex just in front of the area involved in the perception of color, whereas the generation of action names activated a region dorsally in the middle temporal gyrus just in front of the area involved in the perception of motion. These findings suggest that information about all the different visual attributes of an object is not stored in a unified fashion in any single area of the cortex. Rather, object knowledge seems to be stored in a distributed cortical system in which information about specific features is stored close to the regions of the cortex that mediate the perception of those features. How these stored features are linked to create complete object representations, such as the concept of "banana," will be considered in a later section.

In summary, the multiple visual areas within the dorsal and ventral streams of monkeys and humans provide a rich substrate not only for processing the visual features of objects but also for storing in memory the knowledge of object attributes, such as their color and action, which is accessed during identification, naming, and word generation. The extent to which the human visual cortex differs from that of the monkey presumably reflects the greater complexity and quantity of knowledge that humans are capable of acquiring through experience. The memory mechanisms that mediate this acquisition of knowledge will now be considered.

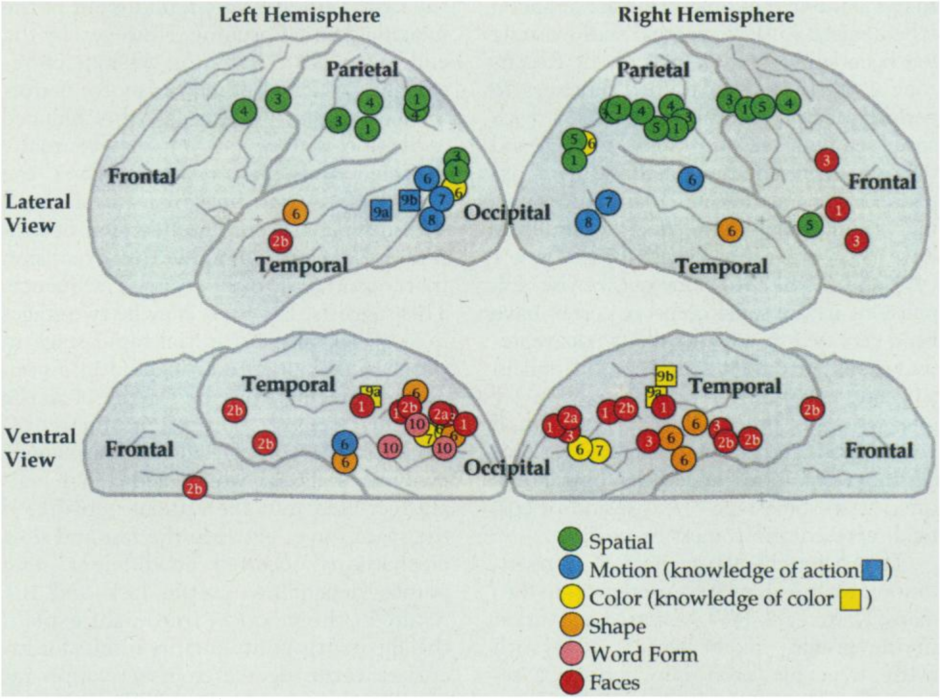

Fig. 2. Human visual processing streams identified in PET imaging studies (*93*). **(Top)** Lateral views of the left and right hemispheres. **(Bottom)** Ventral views of the hemispheres. Numbers in the symbols indicate the study reporting each activated focus of increased blood flow. Green and blue indicate foci activated in spatial vision tasks; yellow, orange, pink, and red indicate foci activated in object vision tasks. In some instances, multiple nearby foci of activation are shown as a single focus, representing their center of gravity. Study numbers are as follows: 1, face and location matching-to-sample (*10*); 2a, gender discrimination (*18*); 2b, face identity (*18*); 3, working memory for faces and locations (*24*); 4, shifting attention to spatial locations (*95*); 5, spatial working memory (*23*); 6, selective attention to color, shape, and velocity (*15*); 7, passive perception of color and motion (*16*); 8, passive perception of motion (*19*); 9a, word generation of object attributes from line drawings of objects (*34*); 9b, word generation of object attributes from object words (*34*); and 10, perception of word forms (*32*).

Priming

One type of memory thought to involve changes in sensory processing areas is termed perceptual fluency, or priming. Priming is often measured as an increase in the speed of naming or responding to stimuli that have been seen or heard on a previous occasion. This improvement occurs independently of whether people consciously recollect the stimuli or the original learning experience, a characteristic that distinguishes implicit memory mechanisms, such as priming, from explicit ones, such as episodic memory (*35*). The concept of priming derives from psychological studies in normal people (*36*), but its validity as a distinct memory mechanism is supported by the fact that it is preserved in patients suffering from amnesia after damage to the medial temporal lobe (*37*). Because the definition of priming depends in part on its independence from conscious recollection, which is difficult to assess in animals, animal models have been slow to develop. I will therefore review the imaging data first and then consider possible mechanisms in animals.

In one fMRI study of priming, people were shown line drawings of objects, which they silently named (*38*). Activation was measured in blocks of trials in which the line drawings were of the same objects, presented in randomly varying order, or in blocks of novel objects only. As expected, the time it took to name the objects (the reaction time) was faster for blocks of repeated objects, as compared with control blocks of novel objects. Surprisingly, as reaction time improved across blocks of repeated objects, the activation in the occipitotemporal cortex of the ventral stream actually declined. In contrast, the activation in this region remained constant when participants viewed only novel objects.

The same reduction in activation with stimulus repetition was found in PET studies using a word-stem completion priming paradigm (*39*, *40*). In one experiment, people studied a list of words before the scanning, and then in the priming condition were asked to complete a series of word stems (word beginnings). The control condition was a list of stems from words not previously studied. As in the experiment with line drawings of objects, reaction times to the primed stems were faster than those to the unprimed stems, and the cortical activation for the primed items was again reduced as compared with that for the control. The effects of priming on cortical activation by line drawings of objects and word stems appear to involve the same regions of the cortex in the ventral stream activated during perception of objects and visual word forms described in the previous section.

The fact that experience is associated with decreased cortical activation may at first seem paradoxical. It makes sense, however, if one considers the metabolically costly alternative, namely, that activation is maximal while an individual is living in an environment filled with familiar stimuli and activation shrinks when the individual enters a new environment filled with novel stimuli. Data from physiological studies in animals not only are consistent with the idea that less cortex is needed to process familiar stimuli than novel ones, but further suggest that the reason cortical activations shrink with familiarity is because the neural populations that represent the familiar stimuli have become more selective.

Studies of the inferior temporal cortex in monkeys have found that the responses of some cells steadily decline either as novel stimuli become familiar or as familiar stimuli are presented repeatedly over time (*41*, *42*). The cells are not novelty detectors in the sense that they respond to just any novel stimulus. Rather, the cells respond only to certain classes of stimuli but, within that class, their response to a given novel stimulus may drop out later as that stimulus becomes familiar. In contrast, the responses of many other cells in the same area do not change with familiarity. The overall reduction in the number of highly activated cells presumably explains the reduced activation found in imaging studies. As the critical features of a new object are learned through experience, cells coding noncritical features drop out of the pool of activated cells, making the remaining population smaller but more selective (*41*). The increased selectivity would then lead to better and faster behavioral performance. As is consistent with this idea, a recent study has found increased selectivity of inferior temporal neurons for highly familiar stimuli (*43*). Although this idea makes intuitive sense, it creates a problem with regard to another category of implicit memory, discussed in the next section.

Perceptual and Motor Skill Learning

In apparent contradiction to the priming and familiarity results showing reduced activation, another body of work has demonstrated that perceptual and motor skill learning, an apparently very similar type of implicit memory mechanism, leads to expansions of cortical representations. As in priming, skill learning is also independent of conscious recollection and is also spared in the amnesia that follows medial temporal lobe damage (*35*). Perceptual skill learning has been studied physiologically by Recanzone *et al.* (*44*), who trained monkeys to perform tactile discrimination tasks with specific digits on one hand. They found that the representation of those digits expanded over time in the somatosensory cortex. Similar long-term effects of training have been observed for cells in the motor (*45*) and visual (*46*) cortex. Likewise, expansions in the somatosensory cortex have been reported in adjacent body-part representations after digit removal (*47*) and in adjacent visual-field representations in V1 after lesions of the retina (*48*). Logically, if visual areas can become specialized for processing word forms and other object features, then some type of expansion of cortical representations must be possible.

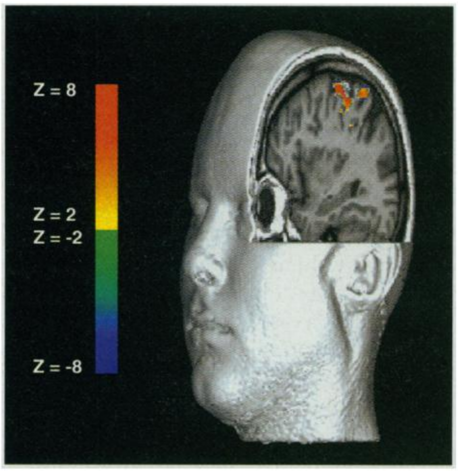

Fig. 3. Cortex activated during finger movement, identified with fMRI. The region activated in the motor cortex is shown in color [indicating relative (that is, standard deviations from the mean) values of Z scores], overlaid on a volume-rendered three-dimensional magnetic resonance data set from the same individual. The brain image shown is a parasaggital slice located 35 mm to the left of the midline. [Image courtesy of P. Jezzard, NIMH, NIH]

To test for changes in cortical representations after extensive experience in humans, Karni *et al.* (*49*) measured activation in the primary motor cortex (M1) with fMRI as people learned to perform a sequence of finger movements with one hand over the course of several weeks of training (Fig. 3). As participants practiced the movements outside the scanner, performance with the trained hand became faster and faster. At weekly intervals, the participants were scanned while performing the trained sequence and a control sequence, each at the same fixed slow rate. Before training, the experimental and control sequences each produced a patchy pattern of activation in the hand representation in the motor cortex, which is consistent with the results of both physiological mapping (*50*) and of other recent functional imaging studies (*51*). After training, the patches of activation expanded and tended to fill in the spaces between them. This expansion occurred only for the trained sequence and not the control sequence, which consisted of the same finger movements but in a different order. Thus, it was not the representation of the digits that expanded in the motor cortex but the representation of the specific motor sequence. The training apparently caused a recruitment of M1 neurons into the network that mediated performance of this sequence. Preliminary imaging data indicate a comparable expansion of a network mediating visual texture segmentation in V1 after long-term training (*52*).

How can we reconcile the apparently contradictory priming and skill learning results? One possibility is suggested by an observation in the motor learning study of Karni *et al.* (*49*). There it was found that, within the first scanning session (before training occurred), the size of the M1 activation was reduced the second time a sequence was performed as compared with the first, a finding very reminiscent of the imaging data on priming. However, by the end of the first scanning session, corresponding to about 30 min of motor performance within the scanner, this reduced activation with repetition was eventually canceled and even reversed. Over the course of several weeks of training, all within-session ordering effects on activation were overridden by the expansion that occurred for the trained sequence. This suggests that there may be two stages in skill learning: an initial rapid stage in which activity becomes focused in a population of cells that best represents the stimulus (sensory cortex) or the movement (motor cortex), and a later, slowly evolving stage in which additional cells are recruited into the critical network. If the switch-over between the fast and slow mechanisms occurred at different time points, depending on the task and the nature of the practice, this might explain the apparently contradictory results for increases versus decreases in activation reported in several earlier PET studies of short-term motor learning in M1 (*53*–*55*) and in the premotor and supplementary motor cortex (*54*–*56*).

In parallel with the changes occurring in M1, studies of two other structures thought to be important for learning, the cerebellum and prefrontal cortex, have consistently found that activation diminishes over the course of short-term learning of motor sequences (*54*, *57*). Because these changes occur in the same general time frame as the initial switch from reduced to enhanced activation with repetition that has been observed in M1, this raises the possibility that the relative roles of different structures shift during the different stages of learning. The cerebellum and prefrontal cortex may be preferentially engaged in tasks in which the initial learning is conscious and effortful, with the motor cortex gradually becoming predominant as the task becomes automatic. The final outcome is a more extensive representation of the skill in the motor cortex. The same principle might apply to many other procedural tasks that are not strictly motor. For example, Raichle *et al.* (*58*) have shown that generating verbs in response to nouns, which is initially conscious and effortful, is associated with activations in one set of structures (in the anterior cingulate cortex, in the left prefrontal and posterior temporal cortices, and in the right cerebellum). However, after practice, when the task has become automatic, activations in these structures fall in parallel with rising activations in a different set of structures (in the Sylvian insular cortex bilaterally and in the medial extrastriate cortex on the left) (*59*).

Declarative Memory

As indicated in previous sections, the mechanisms underlying priming and skill learning do not rely on the conscious recollection of the original experience and do not seem to involve medial temporal lobe structures. In contrast, declarative memory, which consists of the ability to store new memories of specific events (episodic memory) as well as new facts and knowledge (semantic memory) depends on medial temporal lobe structures in the hippocampal region (*60*). This region, including the hippocampus, parahippocampal cortex, perirhinal cortex, and entorhinal cortex, has reciprocal connections (directly or indirectly) with the dorsal and ventral stream visual areas as well as with equivalent areas in the other sensory systems (*61*). Because bilateral medial temporal lobe lesions in humans result in the loss of the ability to store new memories, but usually not in the ability to recall old ones, it is generally accepted that the hippocampal region plays a critical enabling role in the initial storage of information but is not critical for the retrieval of old memories and is not the ultimate storage site for this information (*35*). In contrast, damage to the higher-order sensory areas can result in a loss of recognition of previously known people and objects as well as in a loss of semantic knowledge about objects (*62*). Indeed, as described above, functional brain imaging studies indicate that knowledge of both object attributes and facial features is stored in regions of the cortex that are associated with the processing of those attributes and features. Within the hippocampal region itself, the role that different components of this system play in different forms of memory is an active area of research in animals and humans (*63*).

There is surprisingly little physiological evidence in animals concerning the role of the hippocampal region in declarative memory. The little information we have comes mainly from the "place fields" of cells recorded in the rat hippocampus (*64*). Different hippocampal cells fire when the rat enters different fields in its environment, and the cells develop new place fields over the course of several minutes when the rat enters a new environment (*65*). If the animal is removed from the environment and is later returned, the original place fields will be restored, indicating that the memory of the field has been retained, although not necessarily in the hippocampus (*66*).

Attempts to activate the hippocampal region while people perform tasks sensitive to medial temporal lobe damage have frequently been unsuccessful (*40, 67–69*). One possible explanation, suggested by others, is that the imaging subtraction technique is poorly suited for examination of the hippocampal region, because this structure may be just as active during baseline as during experimental conditions [see (*69*), for example]. If the hippocampal region is engaged in memory storage, for instance, it may not be possible to "turn off" memory storage during any condition. Two studies that did demonstrate activation of the hippocampal region used verbal tasks and found that the activation was related to the quantity of information held in long-term memory (*70*) and to the participants' performance on the long-term memory task (*71*).

Because neuropsychological studies indicate that the hippocampal region is more important for the initial storage, or encoding, of information than for its retrieval, one might expect to find this distinction reflected in the results of activation studies. In fact, there is some support for this idea from a recent study of face memory, which found right hippocampal activation during encoding but not during subsequent recognition of faces (*72*). It has been proposed that tasks that require people to process novel stimuli will also lead to hippocampal activation, because novel information is usually encoded for storage in memory (*73*). This might explain why memory tasks that have used unfamiliar faces or complex visual geometric patterns (*72, 74*) have found hippocampal activation, whereas most memory tasks involving verbal material, which is by definition familiar, typically have not (*40, 67–69*).

Alternatively, the fact that so many studies have failed to activate the hippocampal region with conventional memory tasks suggests that it may be only a part of the mechanism of declarative memory, at least in the normal brain. In particular, a large body of imaging work has demonstrated prefrontal participation in memory storage and retrieval, even though prefrontal lesions do not cause global amnesia (*35, 75*). The left prefrontal cortex is commonly activated during encoding of information, and the right prefrontal cortex is activated during retrieval, regardless of whether the material is verbal (*40, 67–69*) or visual (*72, 76*). It has been proposed that prefrontal activation during retrieval is correlated specifically with the effort of attempting to retrieve information from memory rather than the conscious recollection of the retrieved information (*77*).

In addition to prefrontal activation, several studies have noted activation of the medial aspect of the parietal lobe (the precuneus or retrosplenial cortex or both) during the retrieval of episodic (*67, 76, 78, 79*) but not of semantic memories (*67*). Fletcher *et al.* (*78*) have suggested that this medial parietal region is activated specifically in association with the visual imagery usually elicited with the retrieval of episodic memories.

Finally, as noted above, the ultimate storage sites for declarative memories must be cortical areas outside the hippocampal region. If these same cortical areas change with experience during priming and skill learning without any participation of the hippocampal region, why is this region needed for the initial storage of declarative memories? A possible answer is that priming and skill learning simply involve modifying a stimulus or motor representation within a single area, whereas declarative memory requires associative links between several types of information that are stored in different areas. For example, learning to distinguish among fine shades of yellow may lead to changes in the grain of color representation in a color area. However, learning that bananas are yellow requires linking the color yellow to other types of information, such as shape, food value, and so on, which are represented in many different areas. Because the hippocampal region is a convergence site for all types of information, it is in a unique position to help establish these links.

The Prefrontal Cortex and Working Memory

To this point, I have only considered the formation of long-term memories in the cortex. Often, however, we need to retain and use an item of information for only a short period before it is discarded. The active maintenance of short-term memories is commonly termed "working memory." In psychology, the concept of working memory embraces several interrelated ideas, including the covert rehearsal of verbal material, a visuospatial "sketch pad," and a "central executive" (*80*). Functional imaging studies have begun to identify the anatomical components of a verbal working memory system (*81*).

In monkeys, working memory has typically been studied in either delayed response or matching-to-sample tasks. In both types of tasks, the monkey is given a brief cue at the start of the trial, which it must maintain in memory during a delay of several seconds. At the end of the delay, the monkey is required to make a choice or differential response based on the previous cue. Many studies have found cells whose response to the initial cue is maintained at some level throughout the delay period (*22*). Thus, the memory of the cue appears to endure by maintaining the activity of cells that represent the cue. Depending on the type of cue, cells with such properties have been found in the inferior temporal cortex (visual patterns or color cues), the posterior parietal cortex (visuospatial cues), the premotor cortex (cues for particular responses), and the prefrontal cortex (all types of cues). The dorsal prefrontal regions that are reciprocally connected with dorsal stream visual areas exhibit maintained delay activity that is primarily related to spatial information, whereas the ventral prefrontal regions that are reciprocally connected with ventral stream visual areas exhibit maintained delay activity that is primarily related to color and object cues (*82*).

The degree of maintained activity in the prefrontal cortex during the delay is typically greater than that in the inferior temporal cortex (*83*), and, unlike activity in the temporal cortex, the prefrontal activity is not disrupted when the monkey processes other visual inputs during the delay period (*84*). These results suggest that prefrontal cells may be the major originators of the delay activity and may activate sensory representations in posterior processing areas during the delay via feedback projections to those areas. This idea has been tested explicitly by Goldman-Rakic and Chafee (*85*), who have found that delay activity for spatial information in the posterior parietal cortex is greatly diminished during reversible deactivation of the prefrontal cortex.

Several imaging studies have now found activation of the human frontal cortex during visual working memory tasks (*23–27*). As expected from monkey anatomy and physiology, when people are required to maintain spatial location information in memory during a delay, the results show that dorsal regions are activated, whereas when people are required to maintain information about faces, the regions activated are located more ventrally (*24*, *86*).

To explore the relative roles of prefrontal and visual cortical areas in working memory, Haxby *et al.* (*25*) parametrically varied the length of the delay interval between sample and choice faces. They found that the activation of occipitotemporal regions in the ventral stream declined systematically with increasing delay (presumably because there were fewer visual stimulus presentations during the longer delays), but activation of prefrontal areas did not, indicating that visual areas are involved mainly in the perceptual aspects of the task, and prefrontal areas are involved mainly in its mnemonic components. This idea is supported by a recent fMRI study of working memory, which found that signals evoked along the ventral surface of the occipitotemporal cortex were strongly coupled to the presentation of the visual stimuli, whereas the signals within the frontal lobe were sustained throughout the delay interval (*27*). Apparently, the imaging techniques were able to detect the strong activity of prefrontal neurons during the delay but were not sensitive enough to pick up the weaker maintained activity of ventral stream neurons in the same interval. It is possible that explicitly instructing participants to imagine a particular visual stimulus potentiates the maintenance of activity in the visual cortex. If so, it would account for PET data showing activation of the visual cortex during explicit imagery (*87*).

Concluding Remarks

The human data, like those from monkeys, suggest that when we see a visual stimulus, visual cortical areas become active; and then afterward, when we hold the memory of that stimulus "in mind," the prefrontal cortex becomes activated as well, presumably because its feedback projections are necessary for reactivating the representation of the stimulus in visual cortical areas. If prefrontal cells are involved in activating object representations in visual areas during working memory, they may have an analogous role during the retrieval of information from long-term memory. Such a role would explain the prefrontal activations that are commonly found in studies of long-term memory, as described earlier. The mystery is how prefrontal cells "know" which visual cells to activate, particularly because object representations in visual areas must be constantly changing as a result of the storage of new memories. Such questions only serve to emphasize how little we know about the coordination of activity across the multitude of interacting cortical areas. To address these issues, we will need the combined efforts of both human and animal studies.

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