

# Visual Perception and Memory: A New View of Medial Temporal Lobe Function in Primates and Rodents\*

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## Key Words

declarative memory, object perception, object recognition, spatial memory, feature conjunctions, configural learning

## Abstract

The prevailing view of medial temporal lobe (MTL) function has two principal elements: first, that the MTL subserves memory but not perception, and second, that the many anatomically distinctive parts of the MTL function together in the service of declarative memory. Recent neuropsychological studies have, however, challenged both opinions. First, studies in rodents, nonhuman primates, and humans suggest that the perirhinal cortex represents information about objects for both mnemonic and perceptual purposes. Second, the idea that MTL components contribute to declarative memory in similar ways has also been contradicted. Whereas the perirhinal cortex plays an essential role in familiarity-based object recognition, the hippocampus contributes little, if at all, to this function. In both primates and rodents, the hippocampus contributes to the memory and perception of places and paths, whereas the perirhinal cortex does so for objects and the contents of scenes.

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**MTL:** medial temporal lobe

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## INTRODUCTION

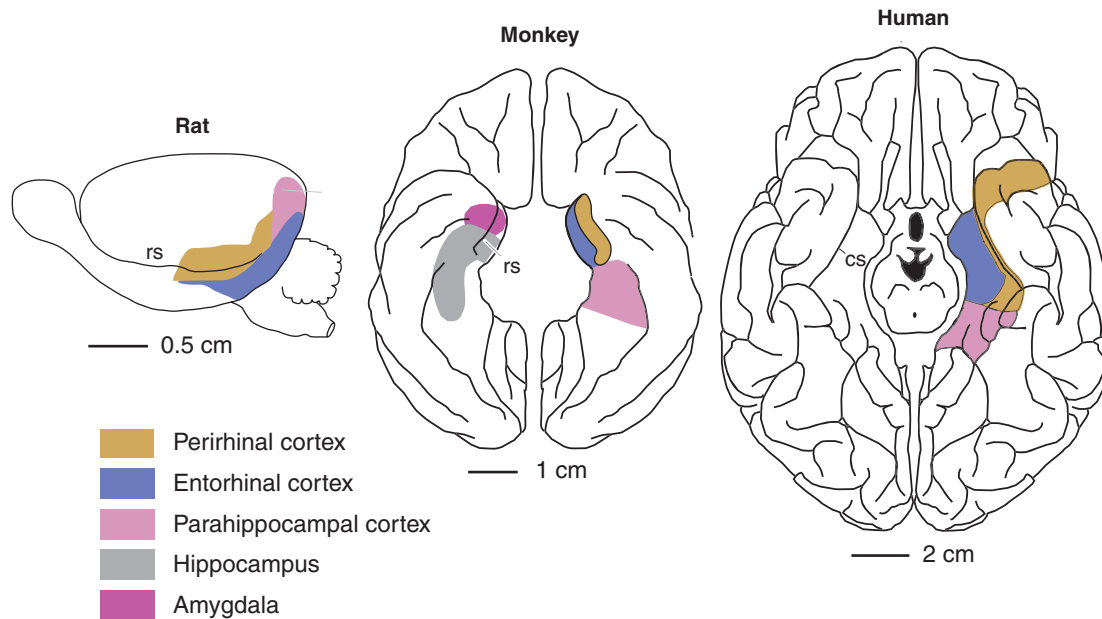
Vision dominates the sensory life of primates, as it has since early in our history (Radinsky 1979). We and our fellow primates have excellent visual acuity, color vision, and—thanks in large part to binocularity—distance perception. Vision so strongly governs our understanding of the world that to say “I see” suffices to express cognizance.

Visual information processing occurs in a group of anatomically linked cortical fields in primates. By one count, as many as 23 separate visual cortical fields have been identified in macaque monkeys by anatomical and physiological methods (Van Essen et al. 2001). The so-called object-analyzer system, often called the “ventral visual stream,” comprises several of these areas, including the primary visual (or striate) cortex, several prestriate areas, and the inferior temporal cortex. These areas play an essential role in visual perception.

All the same, there is much more to vision than visual perception. We not only de-

velop a sensory awareness that depends on colors, shapes, spatial relations, and other visually perceived qualities, but we remember these features in several ways: as elements, in various combinations, and as coherent wholes we call objects. Visual perception and visual memory, then, seem at first glance to be two sides of the same coin. Yet, the prevailing neuropsychological theory holds that perceptual and mnemonic functions are segregated in the brain, with inferior temporal cortex and certain other visual areas underlying the perception of objects and structures in the medial temporal lobe (MTL) underlying the memory of objects. One aspect of this second proposition is that the specific kind of memory supported by the MTL is declarative memory or explicit knowledge, a form of information storage available to conscious awareness. Although these are popular and deeply entrenched views of the organization of perception and memory, recent research has begun to yield a new idea, one that unites the mechanisms of perception and memory rather than relegating them to segregated brain structures.

The concept of the MTL as a system has many weaknesses from a neuroanatomical perspective (Murray & Wise 2004), and the idea that it houses one of the major memory systems—declarative memory—has been challenged effectively (Gaffan 2002). Nevertheless, MTL remains a term of convenience for referring collectively to the hippocampus proper; dentate gyrus; subicular complex; amygdala; and perirhinal, entorhinal, and parahippocampal cortical fields (**Figure 1**). Because this review focuses on regions in the MTL that are known to contribute to visual perception and memory, we exclude from consideration the amygdala and parahippocampal cortex. According to the current evidence, although the amygdala influences the processing of sensory information and its storage, and plays a role in assigning biological significance to objects and events, it is not essential for accurate perception or memory of the visual attributes of



**Figure 1**

View of the lateral surface of the brain of a rat (*left*) and the ventral surface of the brain of a rhesus monkey (*middle*) and a human (*right*) depicting the location and extent of selected structures in or homologous to those in the medial temporal lobe. The entorhinal cortex is shown in blue, the perirhinal cortex is shown in gold, and the parahippocampal cortex is shown in pink. (The region homologous with the parahippocampal cortex of monkeys is known as postrhinal cortex in rats.) In the brain of a macaque monkey (*middle*), the approximate locations of the amygdala and hippocampus, which lie deep in the temporal lobe, are shown in magenta and gray, respectively, on the left side of the drawing. The boundary between the entorhinal and the perirhinal cortex is located near the fundus of the rhinal sulcus (rs) in rats (Burwell 2001) and macaque monkeys. In human brains, much of the perirhinal cortex lies within the collateral sulcus (cs).

objects. As for the parahippocampal cortex, there is little information about its role in the visual life of nonhuman primates, although in the human it is thought by some to house representations of places (parahippocampal place area, e.g., Epstein et al. 1999).

By exploring a new view of visual processing, one that eliminates the stark anatomical separation of perceptual and mnemonic functions, we aim to move beyond the established views to achieve a deeper understanding of the way the cerebral cortex enables monkeys, humans, and rats to interpret the world and behave adaptively. Accordingly, this review considers two ideas:

- First, the MTL is not just for memory. Recent evidence suggests, to the con-

trary, that the perirhinal cortex, which lies at the interface of the putative MTL memory system and the object-analyzer pathway, plays an essential role in visual perception as well as memory. On this “perceptual-mnemonic” view, the perirhinal cortex operates as part of both the MTL and the object-analyzer pathway, as well as part of other cognitive systems.

- Second, different structures in the MTL make selective contributions to visual perception and memory. The perirhinal cortex is dedicated to processing information about objects, whereas the hippocampus is dedicated to processing information about places and paths, with

a very limited role in object-related information processing.

## PERIRHINAL CORTEX CONTRIBUTIONS TO PERCEPTION AND MEMORY

As noted above, visual processing for object identification is thought to be carried out by the visual object-analyzer pathway. This pathway consists of a series of anatomically linked cortical fields extending from the primary visual cortex, caudally, to the inferior temporal area TE, rostrally. Parallel, modality-specific cortical pathways are available for other sensory systems (e.g., somatic sensation and audition). The higher-order cortical fields for each sensory system, together with multimodal cortical regions (e.g., the orbital prefrontal cortex, which is important for gustatory and olfactory signals as well as visual signals, the posterior parietal cortex, and the superior temporal polysensory cortex) project into the perirhinal cortex (**Figure 2**), and, typically, these projections are reciprocated (Suzuki & Amaral 1994). Thus, the perirhinal cortex is in a position to construct higher-order visual and multimodal representations of objects.

Although the perirhinal cortex seems, on anatomical grounds, to be a prime candidate for providing a mechanism underlying the perception of objects, the prevailing theory concerning this part of the brain suggests otherwise. As outlined in the introduction, current neuropsychological theory holds that the MTL plays no role in the perception of complex visual stimuli. Because the perirhinal cortex is definitively part of the MTL, either the anatomical picture is misleading or the prevailing theory needs correction.

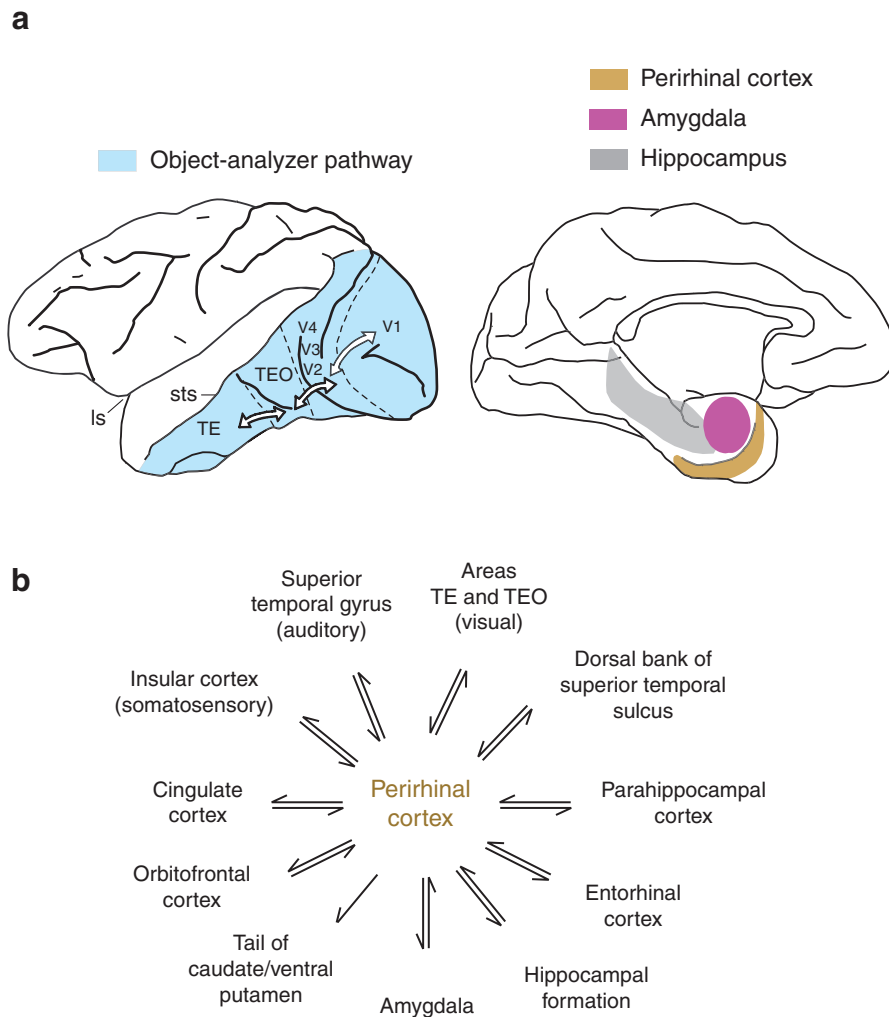
The evidence for the prevailing, memory-only theory rests on the finding that MTL damage affects the recall of information relatively long after the information is acquired but not immediately afterward. For example, the famous patient H.M., who became profoundly amnesic after receiving bilateral re-

moval of his medial temporal lobes for relief of intractable epilepsy, can retain information as long as it is held in a putative short-term memory store. This information is lost, however, after a minute or two has passed or whenever new information is brought into short-term memory (Corkin 2002, Scoville & Milner 1957). In formal tests of visual stimulus memory, subjects are often presented with a sample to be remembered, and later they receive a choice test, during which memory for the sample is evaluated. This test is called a delayed matching-to-sample task or, in another version, a delayed nonmatching-to-sample task. Although amnesic patients with damage to the perirhinal cortex accurately recognize sample objects when a short period of time intervenes between the sample and the memory test, the same patients show deficits when longer periods of time intervene (Buffalo et al. 1998).

One possible interpretation of this finding, and others like it, is that sensory and perceptual processing are fully intact in the absence of the MTL, but the memory of objects is selectively impaired (Buffalo et al. 1999). On this view, damage to the MTL produces a selective deficit—namely, rapid forgetting—but perception is completely normal. However, alternative interpretations are possible, and they provide a stronger and more comprehensive account of the empirical data.

## Studies in Nonhuman Primates

Evidence contrary to the memory-only view of MTL function came initially from studies in macaque monkeys. In one study using the matching-to-sample task, Eacott et al. (1994) first found that monkeys with combined damage to the perirhinal and entorhinal cortex showed a pattern of good performance with short delays between sample and test but poor performance relative to controls with longer delays between sample and test. This result is compatible with other findings obtained in monkeys with perirhinal cortex damage (Baxter & Murray 2001b, Buffalo et al. 1999,



**Figure 2**

(a) Lateral (*left*) and medial (*right*) views of the macaque cerebral cortex. The lateral view shows the location and extent of the visual object-analyzer pathway (*blue*) and some of the anatomical connections between cortical fields (*arrows*). The medial view shows the location and extent of the perirhinal cortex (same color as in **Figure 1**). The magenta and gray regions show the locations of the amygdala and hippocampus, respectively. Abbreviations: ls, lateral sulcus; sts, superior temporal sulcus; V1–V4, TEO, and TE, visual cortical areas. (b) Schematic diagram showing selected connections of the perirhinal cortex. Double-headed arrows indicate reciprocal connections.

Meunier et al. 1993, Nemanic et al. 2004, Zola-Morgan et al. 1989) and resembles that described above for human amnesic patients with MTL damage (Buffalo et al. 1998). The overall picture is one of rapid forgetting in monkeys that have sustained damage to the perirhinal cortex.

However, Eacott et al. (1994) also found a surprising impairment: When the visual perceptual demands were increased from the original stimulus set by making the stimuli smaller and removing color, the monkeys showed impairments even when no delay intervened between sample and test. This

## THE PMFC MODEL

The Perceptual–Mnemonic/Feature–Conjunction (PMFC) Model was developed to unify anatomical and physiological data regarding the organization of the inferior temporal cortex with neuropsychological findings on the effects of damage to this region. In contrast with other views that posit perirhinal cortex as part of a memory system separate and distinct from the ventral object-analyzer pathway, the PMFC model recognizes the contribution of the perirhinal cortex to both the object-analyzer pathway and the MTL. The perirhinal cortex may participate in other neural circuits, for example, with prefrontal cortex, independently of its interactions within the MTL (**Figure 2**).

To test the model, we built a simplified neural network model that reflects the hierarchical organization of the visual object-analyzer pathway. Lesions were made in the component of the network housing complex conjunctions of features, the one corresponding to perirhinal cortex. The model was used to simulate extant data (Bussey & Saksida 2002) and to predict the effects of lesions of perirhinal cortex. In acquisition of visual discriminations with varying degrees of feature ambiguity (see **Figures 3** and **4**), the neural network model accurately simulated the effects of lesions of perirhinal cortex in monkeys (Bussey et al. 2002, 2003).

result was obtained by using a modification of the standard matching-to-sample task, called simultaneous matching-to-sample, together with conditions examining performance on “0-second” delay. In the 0-second delay condition, the choices appeared when the sample stimulus disappeared from a video screen. In the simultaneous condition, both the sample and the choices were visible at the same time. Instead of exhibiting good performance at 0-second delays and simultaneous matching, which we would predict if perception was perfectly intact, the monkeys exhibited deficient performance. Thus, the monkeys that had sustained perirhinal and entorhinal cortex damage showed a perceptual deficit, as well as difficulties with memory. Later, Buckley & Gaffan (1997) found that monkeys with perirhinal cortex lesions learned concurrent visual discriminations with a small stimulus

set (e.g., 10 problems) at a normal rate, but they were impaired when acquiring a large stimulus set. This finding, too, suggested that a difficulty arose when there was a requirement to discriminate visually a large, indeterminate number of items from each other, a situation that would be perceptually demanding.

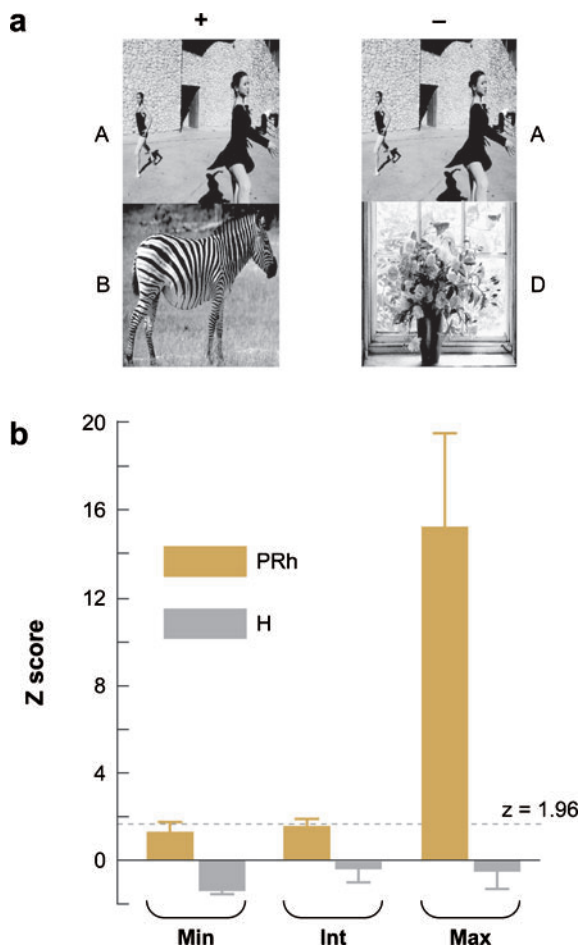
Thus, the supposedly pure “memory deficit” described by Buffalo et al. (1998) could, in fact, have been due to factors that their study did not take into account. What they found was that with long delays between the sample presentation and test, a memory deficit was revealed. Their finding indicates that the perirhinal cortex plays an important role in memory, but it says nothing about whether perirhinal cortex contributes to object perception, except under the relatively narrow conditions of their experiment. Because in our view a particular task (e.g., discrimination learning or delayed matching-to-sample) is unlikely to provide a specific measure of “perception” or “memory,” and because we judged it equally unlikely that one could neatly segregate perception and memory in the brain, we tested a different idea regarding perirhinal cortex function.

Anatomical and physiological data suggest that the object-analyzer pathway is composed of cortical fields containing hierarchically organized visual representations; neurons in caudal visual fields of the object-analyzer pathway represent simple visual features, whereas neurons in more rostral visual fields represent conjunctions of features (Desimone & Ungerleider 1989). Accordingly, we proposed that the perirhinal cortex, located at the most rostral and medial extent of the object-analyzer pathway, operates as a continuation of the ventral visual processing stream (Bussey & Saksida 2002, Murray & Bussey 1999). We further proposed that the perirhinal cortex would contain representations of complex conjunctions of features (see The PMFC Model). On this view, the perirhinal cortex participates in both perception and memory: It is important for perception

because it contains mechanisms enabling the representation of complex conjunctions of features; it subserves memory because it serves as a storage site of complex stimulus representations in both the short- and long-term.

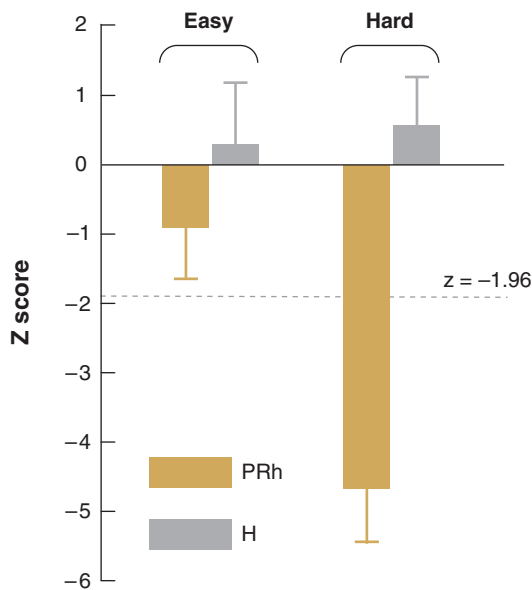
To test this idea, we designed a visual discrimination task for monkeys that would require them to use representations of complex conjunctions of features. We did this by using a problem in which combinations of features, rather than any individual feature, best predicted the correct item. In the context of discrimination learning, this can be arranged by having individual features appear as part of both the correct (S+) and incorrect (S-) objects in a pair. We have termed this property of discrimination problems *feature ambiguity*. An example of this kind of problem is AB+, CD+, BC-, AD-, in which the letters A, B, C, and D represent single features, the combination of two letters represents an object, and + and - indicate correct and incorrect, respectively. Concurrent presentation of the four possible permutations of correct and incorrect choices would yield a problem with the maximum amount of feature ambiguity, i.e., complete feature overlap between the correct and incorrect choices. In discrimination problems with this property, an individual feature is an unreliable predictor of whether a particular object is correct (rewarded); only a combination of features will guide correct responses (see **Figure 3a**).

To date, we have explicitly tested a role for macaque perirhinal cortex in representing complex conjunctions of features in four different experiments. In the first two experiments, monkeys were required to discriminate object pairs with varying degrees of feature ambiguity, and the rate of acquisition of the discrimination problems was measured. As predicted, we found that the greater the degree of feature ambiguity, the greater the magnitude of the impairment after perirhinal cortex lesions (Bussey et al. 2002, 2003) (see **Figures 3** and **4**). Because the two experiments used different methods to manipulate



**Figure 3**

Acquisition of four-pair concurrent visual discriminations with varying levels of feature ambiguity (also known as feature overlap). (a) All objects were compound stimuli constructed by adjoining two different complex grayscale images. The images shown here represent one of the four trial types (AB+ versus AD-) in the maximum feature ambiguity condition. Capital letters illustrate the way in which the conjoined images implement the conjunction of “features”; choice of the image on the left was rewarded (+) and choice of the image on the right was unrewarded (-); neither the letters nor the plus and minus signs appeared in the test presentation. In practice, the position of the correct and incorrect images on the screen followed a pseudorandom order. (b) Scores of two groups of monkeys; bars show the average of four sets of problems per condition. Min, discrimination problems involving minimum (little or no) feature ambiguity; Int, discrimination problems involving intermediate levels of feature ambiguity; Max, discrimination problems involving the maximum possible feature ambiguity. PRh, monkeys with bilateral perirhinal cortex lesions ( $n = 4$ ). H, monkeys with bilateral selective hippocampal lesions ( $n = 4$ ). Scores above the dashed line ( $z = 1.96$ ) indicate significant impairment relative to controls (data from Bussey et al. 2002 and Saksida et al. 2006).



**Figure 4**

Scores of two groups of monkeys on acquisition of single-pair visual discriminations with varying levels of feature ambiguity. All objects were grayscale images that were blended (or “morphed”) using commercially available software. For the bars labeled Easy, discrimination problems involved little or no feature ambiguity. For those labeled Hard, discrimination problems involved high levels of feature ambiguity. Bars show the average of five problems of each type. PRh, monkeys with bilateral perirhinal cortex lesions ( $n = 4$ ). H, monkeys with bilateral selective hippocampal lesions ( $n = 4$ ). Scores below the dashed line ( $z = -1.96$ ) indicate significant impairment relative to controls (data from Bussey et al. 2003 and Saksida et al. 2006).

feature ambiguity—constructed objects and blended objects, respectively—yet obtained similar results, the findings are likely to be general.

The third experiment examined monkeys’ performance when feature ambiguity was abruptly introduced to already-learned discriminations, rather than examining the rate of acquisition of new discrimination problems. Again, as predicted, monkeys with perirhinal cortex lesions were impaired relative to controls when tested under conditions of high feature ambiguity (Bussey et al. 2003, experiment 2; see **Figure 5**). These three experiments, taken together, indicate that perirhinal cortex is important for representing the constellation of features that comprise individual objects. Complex objects and

images of the type used here are known to activate perirhinal cortex neurons; according to our model the perirhinal cortex is not important for all conjunctions, only for conjunctions of a relatively high level of complexity.

The same monkeys with perirhinal cortex lesions were not impaired when required to discriminate objects with low feature ambiguity, nor were they impaired when required to acquire difficult color or size discriminations (Bussey et al. 2002, 2003). Consistent with these findings, researchers likewise found other groups of monkeys with perirhinal cortex lesions to be unimpaired when visual discriminations were made perceptually difficult by systematically varying hue and saturation in a color discrimination, by rotating stimuli, shrinking or enlarging the stimuli, and degrading the stimuli, among other manipulations. Although these manipulations increased the difficulty of the discriminations, as evidenced by an effect on performance, there was no added effect of perirhinal cortex damage (Buckley et al. 1997, Hampton & Murray 2002). Consequently, it appears that the perirhinal cortex is not important for just any type of perceptually difficult visual discrimination but is crucial only for discriminations that require resolution of feature ambiguity in complex visual stimuli and in which feature ambiguity is the factor that creates the difficult perceptual demands.

More recently, Saksida et al. (2007) carried out a fourth study to test whether perirhinal cortex in monkeys contributed to representing conjunctions of objects presented on a computer screen. In this study, unlike the earlier ones, we manipulated feature ambiguity at the object level, such that the task required monkeys to represent the conjunction of objects (transverse patterning). In this experiment, too, and consistent with an earlier report (Alvarado & Bachevalier 2005a), monkeys with perirhinal cortex lesions were severely impaired (Saksida et al. 2007, see **Figure 6**). By contrast, the same monkeys were unimpaired on a control task involving little or no feature ambiguity. The findings



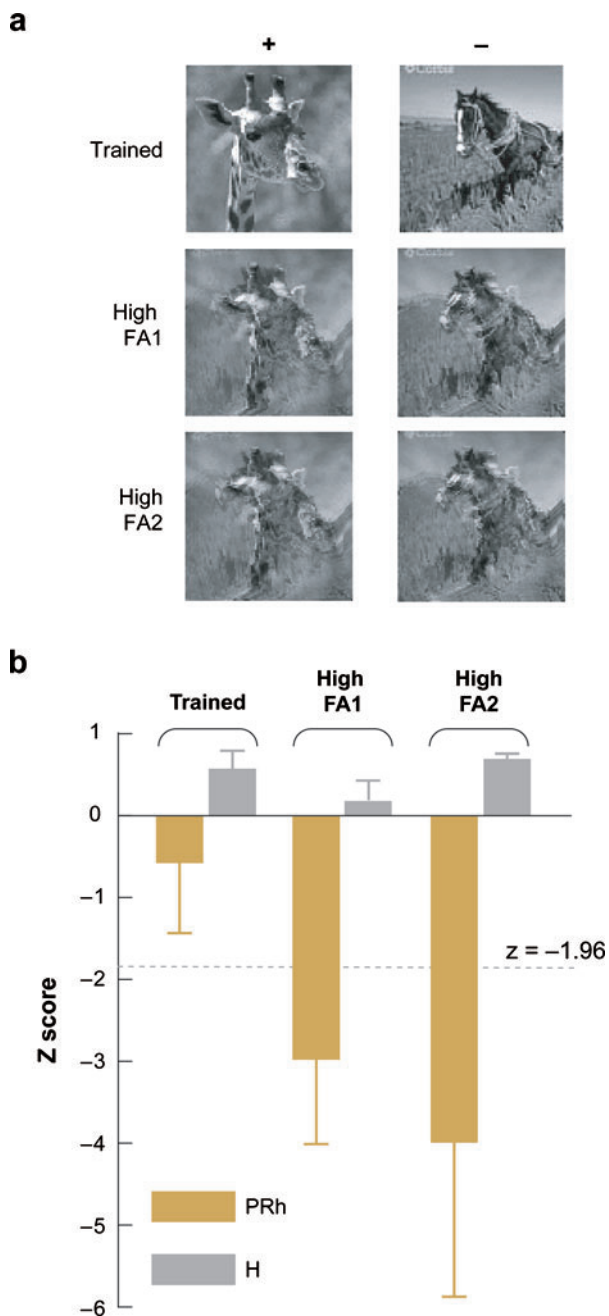
suggest the intriguing possibility that perirhinal cortex is important for representing any features that regularly occur together in a visual scene or that are repeatedly associated with reward, regardless of whether those features comprise an object.

Other studies carried out in macaque monkeys provide additional support for the idea that perirhinal cortex contributes to perception when complex conjunctive representations are required. Buckley and colleagues (2001) tested monkeys on a series of oddity tasks in which choices were simple geometric shapes, blocks of color, or different views of one object (rotated in 3 dimensions) combined with one view of a different object. In each case, the monkey's task was to choose the one item, of several presented, that differed from the others. Monkeys with perirhinal cortex lesions were impaired in performing judgments about different views of

complex objects but not in performing judgments about colors or shapes (Buckley et al. 2001). The oddity tasks possessed, on each trial, all the information required to make the oddity judgment. There was no requirement

**Figure 5**

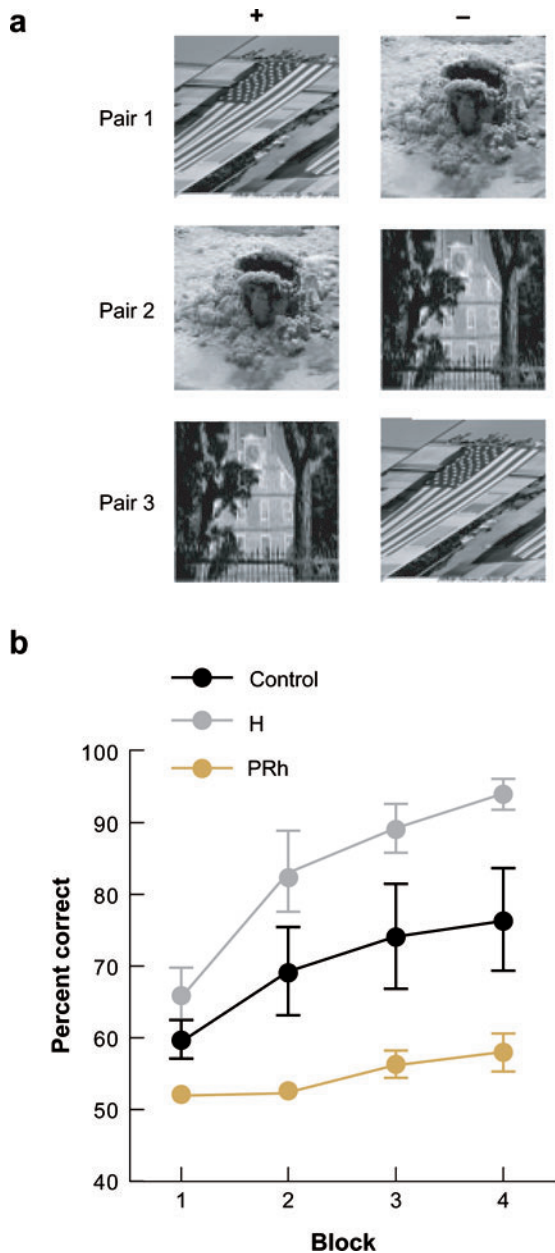
Performance scores of two groups of monkeys when feature ambiguity (FA) was introduced to an already-learned visual discrimination. (a) All objects were grayscale images that were blended (or "morphed") using commercially available software. Trained, initial visual discrimination problems involving little or no feature ambiguity (no blending); High FA1, same stimuli as in "Trained" condition with moderate levels of feature ambiguity introduced through blending; High FA2, same stimuli as in "Trained" condition with high levels of feature ambiguity introduced through greater blending. In this example, images on the left and right sides of each pair have been designated correct (rewarded, +) and incorrect (unrewarded, -), respectively. In practice, the location of the correct image (*left or right*) on the monitor screen followed a pseudorandom order. (b) All monkeys learned the initial discrimination problem on day 1. On day 2, discrimination problems for all three conditions were mixed within a session to create a performance test. PRh, monkeys with bilateral perirhinal cortex lesions ( $n = 4$ ). H, monkeys with bilateral selective hippocampal lesions ( $n = 4$ ). Scores below the dashed line ( $z = -1.96$ ) indicate significant impairment relative to controls (data from Bussey et al. 2003 and Saksida et al. 2006).



to hold information over a delay period and, hence, no overt visual memory component. Thus, the impairment after perirhinal cortex lesions on the oddity tasks provides yet additional evidence for a perceptual impairment rather than an impairment limited to memory functions, and moreover it is consistent with

the idea that perception is impaired only when complex, conjunctive representations are required.

The idea that perirhinal cortex contributes to perception has been criticized on grounds that measures of perception are confounded with measures of learning. For example, because rate of acquisition was the measure of interest in both the discrimination learning designs (Bussey et al. 2002, 2003) and the oddity design (Buckley et al. 2001), deficits after perirhinal cortex ablation could, in principle, be due to a difficulty with learning rather than a deficit in perceptual processing per se (Hampton 2005, Levy et al. 2005). Although this could be a valid concern in some circumstances, a common conceptual difficulty lies in understanding that, despite a long tradition of viewing discrimination tasks as assessments of memory in monkeys, both discrimination learning designs reviewed here (Bussey et al. 2002, 2003) carefully controlled for both the acquisition and memory components of the task. As in all discrimination tasks, the



**Figure 6**  
Acquisition of three-pair concurrent visual discrimination problems with a high level of feature ambiguity (the transverse patterning problem). (a) Representative pairs of images presented to the monkeys. In this example, images on the left and right sides of each pair have been designated correct (rewarded, +) and incorrect (unrewarded, -), respectively. Note, for instance, that the flag image is rewarded for pair 1 but not for pair 3. In practice, the location of the correct image (*left or right*) followed a pseudorandom order. (b) Curves show group mean percent correct responses across four 8-session blocks for two sets of problems. In this study, ambiguity presented at the object level; each object was correct (rewarded) when paired with one object but incorrect when paired with a different object. Control, unoperated control monkeys ( $n = 8$ ), PRh, monkeys with bilateral perirhinal cortex lesions ( $n = 4$ ). H, monkeys with bilateral selective hippocampal lesions ( $n = 4$ ). Relative to the controls, monkeys with selective hippocampal lesions and perirhinal cortex lesions were significantly facilitated and impaired, respectively (data from Saksida et al. 2007).

monkeys did have to remember items. Their clear and complete memory of those items, however, was amply demonstrated by their good performance with low levels of feature ambiguity (**Figure 5**, *top row of images*). Similarly, it remains difficult to see why, in the oddity paradigm for example, an impairment in memory—for either the stimuli or the oddity rule—should have manifested itself with complex stimuli and not with simple stimuli of equal perceptual difficulty. Indeed, the findings from the oddity task (Buckley et al. 2001) are especially incompatible with the idea that memory impairments account for what we consider perceptual deficits. The most parsimonious account is that the monkeys' poor performance resulted from a perceptual impairment. In addition, the experiment involving introduction of feature ambiguity to already-learned discriminations (Bussey et al. 2003, experiment 2) addressed this issue directly (**Figure 5**). Because no learning took place during the sessions in which perceptual judgments were assessed (Bussey et al. 2003, 2006), the impairment cannot be interpreted as one of learning. These data may provide the strongest evidence yet that perirhinal cortex contributes to perception, and they rule out accounts in which the deficits observed after complete removal of the perirhinal cortex are attributed entirely to mnemonic functions, including learning.

### Studies in Humans

As already indicated, the perirhinal cortex plays a critical role in visual memory in both human and nonhuman primates. The tests outlined above—delayed matching- and nonmatching-to-sample—are thought to measure a specific type of memory known as object (or stimulus) recognition. Thus, just as monkeys with damage to perirhinal cortex are impaired in object recognition, humans with extensive damage to MTL structures, including the perirhinal cortex, are deficient in object recognition (Buffalo et al. 1998, Holdstock et al. 2000). Physiological evi-

dence from both human and nonhuman primates also suggests a common mechanism underlying object recognition. Neurons in widespread regions of the monkey and human ventromedial temporal cortex, including perirhinal cortex, show less activity on the subject's second or subsequent viewing of an object relative to the first, an effect termed repetition suppression (Desimone 1996, Riches et al. 1991, Schacter & Buckner 1996, Wiggs & Martin 1998). Human functional imaging studies have gone on to show that activity in perirhinal cortex during initial object viewing predicts the ability of subjects to recognize those objects later (Davachi et al. 2003, Gonsalves et al. 2005).

Also in parallel with data from nonhuman primates, recent studies have implicated the human perirhinal cortex in functions beyond recognition memory. For example, Barense et al. (2005) tested patients on the same type of four-pair concurrent discrimination task that had been used in monkeys (Bussey et al. 2002). The patients they studied had sustained either selective hippocampal damage or combined damage to the hippocampus and other MTL regions including the perirhinal cortex (the MTL group). As was the case for monkeys with perirhinal cortex lesions, patients in the MTL group were severely impaired in the high feature ambiguity conditions. The performance of patients with selective hippocampal damage, however, was indistinguishable from that of controls. These findings held over four replications, with four different classes of feature-ambiguous stimuli (bars, beasts, bugs, and blobs), and therefore indicated that perirhinal cortex in humans is important for tasks that require the use of complex conjunctive representations to resolve visual feature ambiguity.

Lee et al. (2005b) tested the same patients studied by Barense et al. (2005) on visual discrimination of blended (or morphed) objects similar to those used in the study of Bussey et al. (2003) described above. The MTL patients were also impaired on these discriminations, but patients with selective hippocampal

damage were not. Finally, in another study, Lee et al. (2005a) found that these MTL patients were impaired on a version of the oddity task similar to one on which monkeys with perirhinal cortex lesions demonstrated impairment (Buckley et al. 2001). These studies suggest that perirhinal cortex in humans, as in monkeys, plays a role in perception.

Not all studies, however, have found such impairments. Levy et al. (2005) tested the amnesic patients E.P. and G.P., who had extensive damage to MTL structures including perirhinal cortex, on the same morph paradigm described above (Bussey et al. 2003, Lee et al. 2005b). Patients E.P. and G.P. were unimpaired on these tasks. One possible explanation for the discrepancy between the results of this study and that of Lee et al. (2005b) is that the patients studied by Levy et al. (2005) may not have been challenged sufficiently in terms of feature ambiguity. Indeed, control subjects in their “very hard” condition (experiment 2a) were still performing at nearly 90% correct, and their performance did not drop to the level of controls in Lee et al. (2005b) or to that of the monkeys in Bussey et al. (2003). Because an impairment in E.P. began to emerge in the “very hard” condition, one wonders whether, had a more perceptually demanding condition been included, a deficit would have been detected.

Recently, however, a study by Shrager et al. (2006) attempted to address these problems, again using similar methods to, and taking care to match their control performances with, those of Lee et al. (2005b). Although patients were impaired in one or two conditions, the patients mostly had little difficulty in solving the visual discriminations with high levels of feature ambiguity. Why did this study obtain different results from that of Lee et al. (2005b)? One suggestion offered by Shrager et al. (2006) is that the cortical damage in the two sets of patients is subtly different. However, the patients tested in the study of Shrager et al. had a large amount of damage (especially patient E.P.), yet none of them was impaired. Another explanation is similar to that men-

tioned above for the monkey studies, namely, that the impairment reported in the study of Lee et al. was one of learning, not perception. This situation could arise because the stimulus set used by Shrager et al. was larger than that used by Lee et al., and hence subjects in the Lee et al. study received more repetitions of stimuli and therefore had more opportunity to learn about specific stimuli. However, a performance analysis across trials showed that no learning was taking place in the subjects studied by Lee et al. (2005b), indicating that the poor performance of the patient group cannot be accounted for in terms of a learning impairment. In addition, such an account cannot easily explain the results of other studies showing impairments, for example, in the oddity tasks. Therefore, it remains uncertain why the findings of Shrager et al. (2006) differ so markedly from those of Lee et al. (2005b) and from other findings reported by the same group of investigators (Barens et al. 2005, Lee et al. 2005a), as well as from the nonhuman primate studies outlined in the previous section. Nevertheless, the weight of the evidence from humans and from monkeys suggests that the perirhinal cortex plays an important role in perception, specifically for complex conjunctions of the features that compose objects.

## **MULTIPLE FUNCTIONAL SUBDIVISIONS WITHIN THE MTL OF PRIMATES**

Having addressed one pillar of the prevailing theory of the MTL—that each of its components must function in memory but not in perception—we now address the other pillar: that each of the components of the MTL contributes to memory in a similar way. The empirical evidence presents a strong challenge to this theoretical view.

Although Squire et al. (2004) recently concluded that there was insufficient evidence to support separate functions for the hippocampus versus adjacent cortex of the MTL, the evidence from animal studies carried out in the 1990s was compelling, and recent evidence

has further strengthened the view that different functional subdivisions exist within the MTL. Here, we provide an update on this continuing controversy and begin by distinguishing three related propositions about the role of the various components of the MTL in memory, as assessed by visual recognition tests: (a) They all contribute to memory; (b) they all contribute in a roughly comparable way; and (c) they all contribute in a necessary way. The prevailing view accepts all three propositions, yet the weight of the evidence is to the contrary. Damage restricted to the hippocampus has either no effect or a very minor effect on object-recognition memory tests, as detailed below. Damage to the perirhinal cortex, by contrast, causes profound deficits on such tests. Thus, the second and third propositions can be rejected: The neuroanatomically distinct structures that comprise the MTL do not all contribute to object recognition, as measured by delayed nonmatching-to-sample tasks, in either a comparable or necessary way. The first possibility listed above, that they all contribute but in some facultative and relatively minor way, cannot be ruled out with lesion or neuroimaging methods.

### Studies in Nonhuman Primates

Several findings argue for functional dissociations within the MTL. The functional specializations involve processing of objects, which appears to be carried out by the perirhinal cortex and adjacent temporal neocortex, as opposed to processing of places and paths, which appears to be carried out by the hippocampal formation. At least two lines of evidence support a role for perirhinal cortex in object processing. First, in the case of recognition memory as measured by delayed nonmatching-to-sample, there is a positive relationship between the extent of the combined damage to perirhinal and entorhinal cortex and the magnitude of the recognition loss (Meunier et al. 1993). By contrast, a meta-analysis of the studies involving selective hippocampal lesions in monkeys (Baxter

& Murray 2001c) revealed an inverse relationship between the extent of damage to the hippocampus and the magnitude of the recognition loss. Thus, paradoxically, the greater the hippocampal damage, the smaller the memory impairment. There is, as yet, no complete explanation for this pattern of results. At the systems level, the data suggest the possibility that after partial damage to the hippocampus, the remainder of it interferes with processing in structures important for recognition memory such as the perirhinal and entorhinal cortex. In any event, the hippocampus can hardly be considered necessary for visual recognition if monkeys with complete hippocampal lesions performed the nonmatching-to-sample task as well as controls did, especially when 40 min can intervene between the presentation of the sample and the test (Murray & Mishkin 1998). In addition, factors that have been asserted to account for this lack of impairment in the study by Murray & Mishkin (e.g., two-stage surgeries, preoperative training) have been refuted both theoretically and empirically (Baxter & Murray 2001a). For example, in the handful of studies that have compared the effects of lesions carried out in one versus two stages, two-stage operations do not reliably produce a milder effect on behavior than do one-stage surgeries, a finding consistent with our own empirical evidence (discussed in Baxter & Murray 2001a,c).

Second, recent studies testing the contribution of the hippocampus to visual perception have revealed distinct differences between the hippocampus and perirhinal cortex. Specifically, when monkeys with selective hippocampal lesions were tested on the same kinds of perirhinal cortex-dependent, feature-ambiguous visual discriminations described above, they were unimpaired (Saksida et al. 2006). Thus, the perirhinal cortex but not the hippocampus is required to represent complex conjunctions of nonspatial features (**Figures 3–5**).

Taken together, the data from tests of visual recognition and visual discrimination are consistent with the idea that structures within

the MTL have dramatically different functions. Indeed, on one test of visual discrimination, acquisition by monkeys with selective hippocampal lesions was facilitated at the same time that acquisition by monkeys with perirhinal cortex lesions was severely impaired (Saksida et al. 2007, see **Figure 6**; compare Alvarado & Bachevalier 2005b). The finding of opposing effects of lesions of different structures within the MTL refutes the idea that the MTL structures work together in this kind of discrimination learning. Indeed, rather than working together in memory, as the prevailing view posits (Squire et al. 2004), the hippocampus and perirhinal cortex may in some circumstances be part of neural circuits that compete for response selection.

In studies comparing the roles of perirhinal cortex and hippocampus in object recognition and other types of object processing, the hippocampus had little or no role in the visual perception and memory of objects. However, relatively few studies in monkeys have directly compared the roles of perirhinal cortex and hippocampus in spatial processing. In a few instances, selective hippocampal lesions produced deficits in locating food sources in a large arena (Hampton et al. 2004, Lavenex et al. 2006) and in learning the location within a two-dimensional “spatial” scene that produces food reward delivery (Murray et al. 1998). In the latter task, combined damage to perirhinal and entorhinal cortex produced a deficit just as large as that observed after hippocampal damage, perhaps because the objects in the scene provided the context for spatially directed movements and because the perirhinal cortex is necessary for the perception of the object conjunctions that comprise a scene (see above). Selective hippocampal lesions also disrupt monkeys’ abilities to remember spatial locations on a test tray (Alvarado & Bachevalier 2005b, Beason-Held et al. 1999; compare Murray & Mishkin 1998). On a delayed nonmatching-to-location task administered in a manual test apparatus, a task in which object features provide

no help in responding to the correct location, monkeys with selective hippocampal lesions were impaired relative to controls, whereas monkeys with perirhinal cortex lesions were not (Alvarado & Bachevalier 2005a,b). Thus, the overall pattern of results suggests a predominant role for the hippocampus in spatial processing and a predominant role for the perirhinal cortex in object processing. Strong evidence for such a division of labor is also evident in humans, discussed next, and in rats, which is addressed in the penultimate section of this review.

Although we have emphasized a role for the hippocampus in processing spatial information, we do not mean to exclude a role for the hippocampus in object-related information processing. This role appears to lie in general pattern association for nonspatial information, perhaps involving timing (Brasted et al. 2003, Charles et al. 2004), and in humans, language, which may account for the often-discussed role of hippocampus in remembering events (episodic memory) and in mental time travel (autonoetic knowledge), the appreciation of oneself as an entity moving through both space and time (Aggleton & Brown 1999, Tulving 1983).

Finally, in monkeys, selective hippocampal lesions produce a reduction in the unlearned defensive responses to a potential predator, such as an artificial snake (Chudasama & Murray 2004). Damage to the adjacent amygdala cannot account for the deficit. This finding, taken together with the studies cited above, provides strong support for the view that the hippocampus plays a very different role than do other components of the MTL. It is essential for signaling potential environmental threats, including those from potential predators, a function that strays very far indeed from the concept of declarative memory.

## Studies in Humans

Studies in humans have also challenged the idea of functional homogeneity within the

MTL. Earlier studies focused on the possibility of different types of memory being subserved by different regions within the MTL. For example, Vargha-Khadem et al. (1997) reported three patients with developmental amnesia stemming from bilateral hippocampal damage. These particular patients exhibited severely impaired episodic memory with relatively intact semantic memory, which presumably could be mediated by other parts of the MTL. Other studies have found impaired recollection but intact object-recognition memory in patients with hippocampal damage, again pointing to functional subdivisions within the human MTL (e.g., Aggleton & Shaw 1996, Holdstock et al. 2002, Yonelinas & Levy 2002).

Additional evidence indicates that structures within the human MTL may be differentially involved in functions beyond memory, again echoing the findings from nonhuman primates. For example, Barense et al. (2005) found not only that patients with perirhinal cortex damage were impaired in high feature ambiguity visual discriminations, but also that patients with selective hippocampal damage were not impaired. Moreover, recent evidence supports the suggestion that the hippocampus may be involved in visual perception, as well—not for objects, but for spatial scenes. Lee et al. (2005b) found that patients with selective hippocampal damage were impaired on the visual discrimination of morphed scenes but not on the discrimination of morphed faces. Instead, only the MTL patients with additional damage in perirhinal cortex showed impairments on the morphed-face task. In another study, Lee et al. (2005a) tested these same patients with hippocampal damage on spatial and face versions of the oddity task. Patients were presented with three different images of the same room (from different views) and a fourth image of a different room. A similarly designed test of oddity employing different views of faces was used. Here, too, the patients with hippocampal damage were impaired only when the stimuli were spatial and not when

the stimuli consisted of faces. These findings, from two separate paradigms, converge with the evidence from nonhuman primates and provide further evidence for dissociations of function within the MTL. Specifically, these observations suggest a role for the hippocampus in the perception and representation of scenes.

Further support for this view has recently been derived from patients with dementia. Alzheimer's disease (AD) is associated with predominant hippocampal atrophy, whereas semantic dementia (SD) patients have greater perirhinal cortex damage (Davies et al. 2004). These two patient groups, together with appropriate controls, were tested on the scenes and faces versions of an oddity task. Consistent with the findings from the focal lesion studies outlined above, the AD patients were selectively impaired in oddity judgments for scenes, whereas the SD patients were selectively impaired in oddity judgment for faces (Lee et al. 2006b).

From these observations, it appears that stimulus material is a critical factor in determining whether and when various components of the MTL become involved in a given perceptual task. To assess whether stimulus type would also be a key dimension in nondeclarative memory, Graham et al. (2006) tested patients with selective hippocampal lesions on simple categorization and perceptual learning of both faces and virtual reality scenes. The patients demonstrated preserved categorization and perceptual learning of faces but abnormal performance on virtual reality scenes. These findings imply that stimulus type may be a more critical predictor of performance on memory tasks (declarative and nondeclarative) than previously thought. They also suggest that reports of good nondeclarative memory after MTL damage may, in some cases, simply reflect the use of stimuli that fail to tap the processes dependent on structures in this region, such as spatial processing in the case of the hippocampus (see also Chun & Phelps 1999).

Although no consistent pattern of findings in the functional imaging literature supports a strict division of labor within the MTL (see Henson 2005 for review), two trends are evident. First, functional imaging studies point to a role for the perirhinal cortex in the encoding of item information and a role for the hippocampus in encoding contextual information (e.g., Davachi et al. 2003, Ranganath et al. 2004). Second, several studies suggest a role for perirhinal cortex specifically in the processing of objects (Lee et al. 2006a, Pihlajamaki et al. 2004, Tyler et al. 2004). These findings are entirely consistent with those reviewed above and below.

The roles of both the perirhinal cortex and the hippocampus in the perception and memory of scenes deserve some comment. From the evidence in monkeys reviewed above, perirhinal cortex is likely necessary for intact perception and memory not only of single objects but also of the conjunctions of items that compose a visual scene. The hippocampus contributes to this function, as well, but in a different way. The hippocampus plays its largest role in assessing the relative locations of objects in a scene, including both currently viewed objects and those recalled from memory. The perirhinal cortex, by contrast, represents the conjunction of objects that appear together without respect to their locations in a scene (Brown & Aggleton 2001). Thus, one can appreciate how it might seem as though the perirhinal cortex and hippocampus contribute comparably to scene memory, much as the prevailing theory might suppose. These contributions, however, differ dramatically when examined in sufficient detail and with an understanding of the underlying cognitive processes and mechanisms involved. Lack of attention to such detail has, in our view, generated unnecessary controversy. In an effort to resolve the questions and controversies outlined above, several researchers have begun to focus their efforts on studying rodents, a topic we address next.

## RODENT “MTL”: HOMOLOGY AND ANALOGY WITH PRIMATES

Research on rodents has some advantages over work on nonhuman primates; chiefly, the cost of rodent experiments is a fraction of those carried out in nonhuman primates. This fact allows larger group sizes; more replications and variations of experimental designs; and a wider variety of neurosurgical, excitotoxic, neuropharmacological, and genetic manipulations. Thus, this work could resolve some of the difficulties encountered in research on the MTL of humans and nonhuman primates. We address the relevant rodent studies separately in this section, in part because the work is conducted so differently from a methodological perspective, in part because the data are among the most recent considered here, and in part because we know of no current review of this aspect of neuropsychology in rodents.

The brains of rodents and nonhuman primates display considerable anatomical and functional similarity. Although rodents do not have a clearly identifiable medial temporal “lobe,” they do have structures, such as the hippocampus and perirhinal cortex, that are homologous to parts of the MTL in primates (**Figure 1**). It is clear from comparative morphology that the perirhinal cortex and the hippocampus in rodents and primates descended from the last common ancestor of these two groups, and that this ancestor was fairly primitive in most of its mammalian traits. According to most molecular phylogenies, these lineages diverged  $\sim 112$  mya. The question is whether the perirhinal cortex and hippocampus in rodents and primates have similar functions and are thus analogous as well as homologous.

The rodent studies have not resolved anything unequivocally, of course: Comparable controversies exist for rodents—mainly rats—as for primates. Nevertheless, recent results from research on rats support all the ideas about MTL function outlined above, and



some of the findings are strikingly similar to those from nonhuman primates.

### Role of Perirhinal Cortex in Perception and Memory

Data from rodent studies support the idea that the perirhinal cortex houses complex conjunctive representations for the resolution of feature ambiguity. For example, in work that predates the studies in monkeys (Bussey et al. 2002) and humans (Barens et al. 2005), Eacott et al. (2001) showed that rats with perirhinal cortex lesions were impaired in the acquisition of feature-ambiguous visual discriminations, much like the result illustrated in **Figure 3** for monkeys. Similarly, Moran & Dalrymple-Alford (2003) reported that rats with perirhinal cortex lesions were impaired in acquiring a configural task, which involves discriminating multiple-feature stimuli. Their studies were carried out in a maze environment, yet these same rats demonstrated intact spatial memory. Norman & Eacott (2004) explicitly incorporated feature ambiguity into an object-recognition setting and showed that rats with perirhinal cortex lesions were impaired more under conditions of high feature ambiguity than low feature ambiguity, much like the result illustrated in **Figure 4** for monkeys. More recently, rats with perirhinal cortex were impaired on tests of object recognition under conditions of 0-second delay, but only when the objects used were perceptually similar (Bartko et al. 2007). Gilbert & Kesner (2003) have also reported findings consistent with the idea that perirhinal cortex in rats, as in monkeys, houses complex conjunctive representations for the resolution of feature ambiguity. By contrast, when very simple stimuli such as lights and tones are used, perirhinal cortex lesions in rats do not necessarily lead to impairments in configural learning (Bussey et al. 2000). This observation agrees with the idea that perirhinal cortex houses complex (but not simple) conjunctive representations and that perirhi-

nal cortex cannot be understood simply as the “conjunctive representation center” of the brain (Bussey & Saksida 2005). Moreover, the finding that perirhinal cortex lesions disrupt the acquisition of certain classically conditioned responses to complex stimuli (e.g., Campolattaro & Freeman 2006, Lindquist et al. 2004) reinforces the notion that it is the nature or complexity of the stimuli, as opposed to the sensory modality or experimental paradigm, that is important in determining whether a particular task is perirhinal-cortex dependent.

### Dissociable Functions within the Rodent “MTL”

Perhaps even more evidence exists for functional distinctions between the perirhinal cortex and hippocampus for rodents than for primates, but there is just as much controversy, as well. For example, as in primates, evidence in rats demonstrated that hippocampal damage does not impair the acquisition of perirhinal cortex-dependent feature-ambiguous discriminations. Just as lesions of the monkey hippocampus can facilitate certain feature-ambiguous discriminations (e.g., in transverse patterning, as shown in **Figure 6**), so fornix lesions in rats can facilitate performance on this task (Bussey et al. 1998).

As in human and nonhuman primates, investigators agree that the rodent perirhinal cortex is important for object memory and that the rodent hippocampus is important for spatial memory (see Bussey & Aggleton 2003 for a summary of these findings). The controversy that remains revolves around whether perirhinal cortex also plays a role in spatial memory and whether the hippocampus also plays a role in object memory.

With respect to the former issue, Bilkey and colleagues have consistently found impairments in spatial memory following perirhinal cortex lesions (Liu & Bilkey 1998a,b,c, 1999; see Aggleton et al. 2004 for a comprehensive review). These authors

concluded, however, that these impairments after perirhinal cortex damage probably resulted from the intrusion of nonspatial feature ambiguity into the task demands.

With respect to whether the rat hippocampus plays some role in object recognition in addition to its well-established role in spatial memory, Clark et al. (2000, 2001) reported that rats with hippocampal lesions were impaired on both a spontaneous object-recognition task and a delayed nonmatching-to-sample task. These findings confirm the view of Squire and colleagues from their primate work, but Winters et al. (2004) obtained a very different result. Winters et al. found a clear functional double dissociation between the hippocampus and perirhinal cortex. Specifically, Winters et al. found that rats with excitotoxic perirhinal cortex lesions were impaired on object recognition but not in spatial processing and, conversely, that rats with selective hippocampal lesions were impaired in spatial processing but not object recognition. Forwood et al. (2005) extended these observations by showing that rats with hippocampal lesions, which performed at only chance levels on a spatial memory task, performed as well as did controls on a test of object recognition with delays of 48 h. Thus, the issue of whether the hippocampus contributes to object memory remains controversial, and several ideas have been suggested to account for the discrepancy in results from different laboratories. Because Winters et al. (2004) and Forwood et al. (2005) used an object-recognition test designed to minimize spatial and contextual factors, we suggest that the hippocampus becomes important for object recognition when spatial and contextual factors become relevant to task performance. Similar suggestions have been offered to account for the mild impairments observed after hippocampal damage in monkeys (Nadel 1995, Nemanic et al. 2004). Such factors may be the source of the relatively mild impairments reported following hippocampal lesions during object-recognition tests conducted in an open field or

swimming pool (Clark et al. 2000, Prusky et al. 2004). However, the arena used in some studies reporting hippocampal impairments was relatively small, darkened, and contained few objects or landmarks visible from the arena (Clark et al. 2000), facts that argue against the idea that contextual cues contributed to performance. Broadbent et al. (2004) suggested another possible explanation for the different results. In their study, damage to 75% of the dorsal hippocampus in rats was required for impairments in object recognition to emerge. Accordingly, perhaps a certain percentage of hippocampal damage is necessary before object-recognition impairments can be observed. This explanation is unlikely to account for the absence of impairment reported by Winters et al. (2004) and Forwood et al. (2005), however, because the amount of hippocampal damage in these studies was extensive. Furthermore, the explanation is at odds with the analysis by Baxter & Murray (2001c) showing an inverse relationship between hippocampal damage and impairment on recognition memory in monkeys.

Finally, some rodent studies have gone beyond the primate studies, testing for possible dissociations within the hippocampus itself. As in monkeys, hippocampal damage in rats can produce impairments in the affective domain. In rats, damage to the ventral but not dorsal hippocampus produces behavioral changes that have been likened to anxiolytic effects, including increased ingestion of novel foods (or of familiar foods in a novel environment), increased tendency to enter open arms of an elevated plus maze, and a reduced neuroendocrine stress response to confinement in a bright chamber (Bannerman et al. 2002, 2003; Kjelstrup et al. 2002). In addition, ventral but not dorsal hippocampal lesions yield a reduction in unlearned defensive responses to cat odor (Pentkowski et al. 2006). These studies provide further evidence in favor of functional dissociations within the MTL and for the view that the hippocampus is important for functions other than declarative memory.

## CONCLUDING COMMENTS

The prevailing theory of the MTL holds that each of its components must function in memory but not perception, and that each of its components contributes to memory in a comparable way. Much recent evidence, presented above, suggests otherwise. Both the perirhinal cortex and hippocampus appear to mediate nonmnemonic processes, in addition to mnemonic ones. In addition, each component of the MTL has a specialized function, and some, such as the hippocampus, have subdivisions with different, specialized functions. For some tasks, especially relatively nonspecific tasks that incorporate a large number of cognitive processes, normal performance may require all parts of the MTL, but more refined analysis can reveal their specialized contributions.

Converging data from monkeys, humans, and rats show that the perirhinal cortex functions very differently from the hippocampus. The perirhinal cortex plays a crucial role in visual perception whenever complex (but not simple) conjunctions of features increase the demands on the system. Because the perirhinal cortex contributes to the storage of these representations in memory, it plays a key role in both the perception and the memory of objects. The hippocampus, by contrast, plays little role, if any, in perception or representation of conjunctions of visual features and, hence, contributes little to object identification. Instead it contributes mostly to the memory of places and paths and to the spatial layout of scenes. Preliminary evidence suggests that the hippocampus, like the perirhinal cortex, has both perceptual and mnemonic functions,

with a specialization for the hippocampus in the spatial domain. Thus, the perirhinal cortex and hippocampus may subserve aspects of object and spatial perception, respectively. The findings argue for a reevaluation of current views regarding the organization of memory.

In our view, the biggest challenge to the PMFC model outlined above is whether it can provide a unified account of the perceptual and mnemonic functions of the perirhinal cortex. If the PMFC framework is correct, then it should be able to account for the canonical memory impairments observed after perirhinal cortex damage—namely, impairments on object recognition memory—in terms of feature ambiguity. This is a stringent challenge, but a recent computational modeling study indicates that it is possible (Cowell et al. 2006). This extension of the PMFC model makes specific predictions that can be tested experimentally. For example, the model predicts that perirhinal cortex lesions should cause object-recognition memory impairments when a judgment of novelty can be made on the basis of the conjunctions of features but not on the basis of individual features alone. Such a finding would show particularly clearly that the same factor (i.e., feature ambiguity) that makes visual discriminations sensitive to perirhinal cortex damage is the factor that makes object recognition sensitive to such lesions. A related prediction is that the magnitude of the impairment should increase as the degree of similarity between the sample and novel objects increases. These predictions are currently being tested, and if they are borne out, the results would provide additional, strong support for the view outlined above.

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## Errata

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