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Object memory and perception in the medial temporal lobe: an alternative approach

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The medial temporal lobe (MTL) includes several structures — the hippocampus, and the adjacent perirhinal, entorhinal and parahippocampal cortices — that have been associated with memory for at least the past 50 years. These components of the putative ‘MTL memory system’ are thought to operate together in the service of declarative memory — memory for facts and events — having little or no role in other functions such as perception. Object perception, however, is thought to be independent of the MTL, and instead is usually considered to be the domain of the ventral visual stream (VVS) or ‘what’ pathway. This ‘textbook’ view fits squarely into the prevailing paradigm of anatomical modularisation of psychological function in the brain. Recent studies, however, question this view, indicating that first, the MTL is functionally heterogeneous, and second, structures in the MTL might have a role in perception. Furthermore, the specific contributions of the individual structures within the MTL are being elucidated. These new findings indicate that it might no longer be useful to assume a strict functional dissociation between the MTL and the VVS, and that psychological functions might not be modularised in the way usually assumed. We propose an alternative approach to understanding the functions of these brain regions in terms of what computations they perform, and what representations they contain.

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Introduction

The medial temporal lobe (MTL) includes several structures — the hippocampus, and the adjacent perirhinal, entorhinal and parahippocampal cortices [1,2**] — that have been associated with memory for at least the past 50 years, following the discovery of the profound effects of MTL resection on memory in the patient H.M. [3]. Such findings, along with the development of animal models of

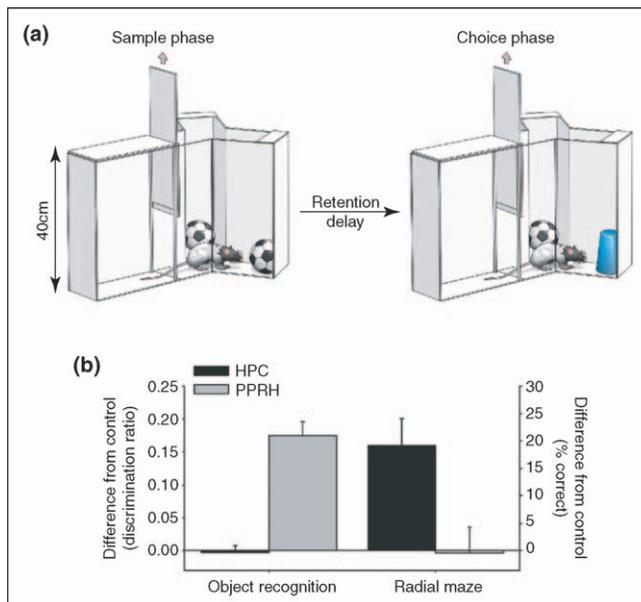
MTL amnesia, led eventually to the development of a framework in which memory was divided into two broad categories: declarative memory, or memory for facts and events, and non-declarative memory (e.g. perceptual learning, priming, skills and habits, classical conditioning and non-associative learning). Object perception is thought to be independent of the MTL, and instead is usually considered to be the domain of the ventral visual stream (VVS) or ‘what’ pathway [4]. Current statements of this view of memory organization can be found in the work of Squire and co-workers [2**,5].

The task that we have been set is to discuss recent advances in our understanding of object (visual) memory and perception in the MTL focussing on the years 2004–2005. As far as possible, therefore, the studies reviewed here are restricted to these two years. The questions on which we focus are those currently at the forefront of research in this area: is the MTL functionally homo- or heterogeneous? Is the MTL important for memory only, or does it have a role in perception? And, if the MTL does have a role in perception, what are the specific contributions of the individual subregions? Recent studies have yielded some exciting and controversial findings, and have questioned the assumption of a sharp functional distinction between the MTL and the VVS. We offer suggestions as to the implications of these findings, and how we might best make further progress in this area.

Is the medial temporal lobe functionally homo- or heterogeneous?

The prevailing, ‘textbook’ view of MTL function is that structures within this system operate together in the service of long-term declarative memory [2**]. Several researchers have, however, suggested a view of functional heterogeneity and independence within the MTL, according to which the hippocampus and perirhinal cortex serve distinct and doubly dissociable functions [6–9]. This view has been supported by studies showing single and double dissociations between perirhinal cortex and hippocampus or fornix lesions on object recognition and spatial memory, respectively. The reported double dissociations have, however, all involved fornix lesions as a method for inducing hippocampal dysfunction, and fornix lesions might not be functionally equivalent to hippocampal lesions [10]. In addition, and perhaps more importantly, the fornix is not considered to be part of the MTL memory system [11]. More recently, Winters *et al.* [12*] tested rats with excitotoxic lesions of perirhinal (plus postrhinal) cortex and hippocampus on object recognition using an apparatus designed to minimise putative spatial–

Figure 1



Evidence for heterogeneity within the MTL. (a) Winters *et al.* [12^{*}] demonstrated a double dissociation between the effects of excitotoxic lesions of the hippocampus and peri- postrhinal cortex using a spontaneous object recognition task carried out in a modified apparatus designed to minimize the potentially confounding influence of spatial-contextual and locomotor factors, as it has been suggested that the hippocampus becomes important for object recognition when spatial or contextual factors become important. (b) A clear functional double dissociation was observed: animals with hippocampal damage were impaired relative to animals with perirhinal cortex damage and controls on a spatial memory task, whereas rats with perirhinal damage were impaired relative to the hippocampal and control groups in object recognition. Mean difference scores were calculated for each lesion group by subtracting performance on each task from the mean control group performance levels on that task. Abbreviations: HPC, rats with hippocampal lesions; PPRH, rats with perirhinal (plus postrhinal) cortex lesions. Copyright 2004 by the Society for Neuroscience, reprinted with permission.

contextual and locomotor confounds. A very clear double dissociation was found (see Figure 1). Furthermore Forwood *et al.* [13], using the same apparatus, found that rats with hippocampal lesions were no different from controls in their ability to remember objects after delays as long as 48 h, the longest delay, to our knowledge, that has been used with rats. It was suggested that the hippocampus becomes important for object recognition when spatial-contextual factors become relevant to task performance. It is conceivable that such factors are related to relatively mild impairments that are reported in hippocampal-lesioned rats during object recognition tests conducted in an open field or swimming pool apparatus [11,14]. Broadbent *et al.* [15], however, suggested that a certain percentage of hippocampal damage is necessary (e.g. 75% for the dorsal hippocampus) before object recognition impairments can be observed. It is unclear, however, how this could explain the absence of impairment shown

by Winters *et al.* and Forwood *et al.* [12^{*},13], because the amount of hippocampal damage in these studies was extensive. Similar dissociations within the MTL have been reported in recent imaging studies; Pihlajamaki *et al.* [16], for example, found differential activation in structures within the MTL in response to changes in object identity and spatial configurations of objects.

Thus the evidence, in our opinion, points quite clearly to heterogeneity of function within the putative MTL system. Indeed, the MTL contains both neocortical (e.g. perirhinal cortex) and allocortical (hippocampus) structures, the former having evolved late in vertebrate history and the latter having evolved very early. These structures, moreover, are anatomically highly dissimilar, and so it seems rather unlikely that they would have identical or perhaps even similar functions (for a complete discussion see Murray and Wise [17^{*}]). In addition, the above studies confirm the well established role of the hippocampus in spatial cognition, and indicate that the perirhinal cortex in particular is crucial for object recognition. Indeed, other recent studies have shown that the perirhinal cortex is important for all stages of object recognition memory — encoding, consolidation and retrieval — and indicate how different glutamate receptors contribute differently to these stages [18,19]. Other recent studies have investigated the role in object recognition of cholinergic and GABAergic systems [20–22] in addition to intracellular systems [23]. These studies did not use cell-body lesions but found impairments in object recognition after selective and subtle manipulations within perirhinal cortex, confirming that circuitry within perirhinal cortex *per se* is important for object recognition; that is, that lesions of perirhinal cortex do not affect object recognition simply because they cut off information from other regions such as the hippocampus.

In the following section, we review studies that provide further evidence of dissociations between perirhinal cortex and hippocampal function. They also address the question of whether MTL structures might be important for more than long-term declarative memory and, specifically, whether they might be important for perception.

Is the medial temporal lobe important for memory only, or does it have a role in perception? And if the medial temporal lobe does have a role in perception, what are the specific contributions of the individual subregions?

Some background

Early studies using an object recognition paradigm pointed to a role for perirhinal cortex in visual perceptual function [24]. Further studies indicated that perirhinal cortex is important not just for object recognition but also for visual discrimination learning and memory [25–27]. When taken together, however, the pattern across these

studies was puzzling, because subjects were impaired in some visual discriminations but not in others. To explain these results, several authors [26,28] suggested a role for perirhinal cortex in object identification, which can be thought of as requiring ‘the knowledge that a particular object is the same across the different instances in which it is experienced’ [29]. Shortly thereafter, we developed the ‘Perceptual–Mnemonic/Feature–Conjunction’ (PMFC) neural network model of object identification (See Box 1) [30,31]. According to this model, the effects of perirhinal cortex damage on visual discriminations can be explained by assuming that perirhinal cortex has visual information processing properties similar to other regions within the VVS, and that the perirhinal cortex is the final station in this pathway. We proposed that the apparently inconsistent effects of lesions within this region could be understood by considering the hierarchical organization of representations in the VVS. Specifically, the aspect of this hierarchy that is crucial to the account of perirhinal cortex function is the emergence of increasingly complex conjunctions of features with progression rostrally. The model further assumes a high degree of specificity of the representations in perirhinal cortex (the idea that ‘the whole is greater than the sum of the parts’ [30]). Subsequent electrophysiological studies have provided support for this assumption [32], and have confirmed the existence of highly specific complex visual representations throughout the MTL [33]. Without such specific complex conjunctive representations, the subject must rely on representations of simple features (components of stimuli) in caudal regions of the VVS to attempt to solve visual discriminations. If the features do not provide an easy solution to a problem — for example, if features are rewarded when they are part of one object but not when they are part of another — subjects with damage in perirhinal cortex can be impaired. We have introduced the term ‘feature ambiguity’ to try to capture this idea verbally. The neural network model was able to simulate extant data on the effects of lesions in perirhinal cortex [30], and made predictions that were subsequently tested in experiments with macaque monkeys. One study used a set of concurrent discriminations in which the number of objects to be discriminated was held constant while the amount of feature ambiguity varied; monkeys with perirhinal cortex lesions were impaired in the higher feature-ambiguity conditions only [34]. Another study showed that these monkeys were also impaired at solving single-pair discriminations but only when the discriminanda shared many features [35]. These monkeys were not impaired on equally difficult control conditions, such as colour and size discriminations. (For a review of these studies see Bussey *et al.* [36••].) We therefore proposed that “The effects of lesions in perirhinal cortex . . . are due not to the impairment of a particular *type* of learning or memory—for example, stimulus-reward or stimulus-response, declarative or procedural—but to compromising the representations of visual stimuli” [30]. Thus, accord-

Box 1 The PMFC model.

The PMFC model was developed in an attempt to make sense of the puzzling finding that although damage to perirhinal cortex can lead to impairments in pair-wise visual discriminations, it does so only under certain circumstances. We began to think about the perirhinal cortex, not only as part of a mnemonic system in which perirhinal cortex works in concert with the hippocampus, but also as part of the ventral visual stream (VVS) or ‘what’ pathway. Much neurophysiological evidence suggests that the representations in the VVS are organised hierarchically, simple features being housed in more caudal regions, and increasingly more complex conjunctions of features being housed in more rostral regions. Perirhinal cortex, according to this view, houses perhaps the most complex conjunctive representations, at a level of complexity close to that of real-world objects. We proposed that effects of perirhinal cortex lesions on visual discriminations are due to damage to these complex conjunctive representations. This is in contrast to other views that assume perirhinal cortex to be part of a memory system separate and distinct from the VVS perceptual system. To test the theory, we built a simplified neural network model that embodies these principles. Lesions were made in the component of the network corresponding to perirhinal cortex, and the resulting effects compared with previously reported effects of lesions in perirhinal cortex in monkeys. The model was able to simulate accurately the effects of lesions of perirhinal cortex [30].

Although we first simulated extant data, the real test of the model was to allow it to make novel predictions that we could then test experimentally. We designed tasks for monkeys that would require them to use representations of complex conjunctions of features. We did this by using visual discrimination problems in which combinations of features, rather than any individual feature, predicted the correct item. In the context of discrimination learning, this can be arranged by having individual features appear as part of both correct and incorrect objects. The number of features that were ambiguous in this way was varied, resulting in visual discrimination tasks with differing degrees of feature ambiguity. These studies provided further support for the model: monkeys with perirhinal cortex lesions were impaired on visual discriminations with higher, but not lower, amounts of feature ambiguity [34,35].

As outlined in the main text, further experiments in monkeys, rats and humans have found support for this view. However, it is important to note that although these experiments have, in the first instance, examined the effects of perirhinal cortex lesions, our view is not that the perirhinal cortex is the only region of the brain housing conjunctive representations. Indeed, the model is based on the idea of a hierarchy of representations throughout the VVS. We hypothesise that the region of the VVS–MTL that is most important for the solution of a particular task is the one which contains the representations that are optimal for that task (this idea contrasts with the psychological–modular view, which assumes that particular brain regions carry out particular psychological functions). Recent imaging studies provide support for this idea (see main text). An important next step in extending and testing this model is to see how well it can account for damage in other regions of the VVS.

ing to this view, which regions in the perirhinal cortex–VVS are recruited for a task depends on what stimulus representations are useful for that task.

Memory and perception in the medial temporal lobe: the past two years

Several studies published in the past two years have taken us much further forward in addressing these issues of representation, and the different contributions individual MTL structures might make to perception. Studies in

human patients have been particularly revealing. We summarize these results below according to their implications for understanding the functions of perirhinal cortex and the hippocampus.

Perirhinal cortex

Barens *et al.* [37] tested two groups of patients; the first had selective hippocampal damage and the second had combined hippocampal damage and parahippocampal damage that included perirhinal cortex (the ‘MTL group’), on the same type of four-pair concurrent discrimination task used in Bussey *et al.* [34] and described briefly above. Whereas patients in the MTL group were severely impaired in the high feature ambiguity conditions, the performance of patients with selective hippocampal damage was indistinguishable from that of controls. These findings held over four replications, with four different classes of feature-ambiguous stimuli. The findings of Barens and co-workers provide further evidence of dissociability of function within the MTL, and indicate that, as in monkeys, perirhinal cortex and not the hippocampus contains conjunctive representations for the resolution of nonspatial feature ambiguity.

Lee *et al.* [38] tested the same patients studied by Barens and co-workers on complex (face) morph discriminations similar to those used in the study of Bussey *et al.* [35] described briefly above. Again, the MTL patients were impaired on these discriminations, but patients with selective hippocampal damage were not (see Figure 2). In another study, the MTL patients were shown to be impaired on an ‘oddy’ task in which subjects make perceptual judgements as to which of several faces was the ‘odd one out’ [39]. Performance on this task has been shown to be impaired in monkeys with perirhinal cortex lesions [40]. These studies by Lee *et al.* [38,39] suggest that perirhinal cortex in humans, as in monkeys, has a role in perception.

The hippocampus

The fact that the perirhinal cortex might have a role in perception suggests that memory and perception cannot be neatly organized into anatomically separate regions of the brain. This is a significant advance in our understanding; the current paradigm assumes that such functions are strictly modularised. The perirhinal cortex performs its perceptual–mnemonic function at an anatomical interface between regions thought to be important for perception and memory, that is, the VVS and hippocampus. But recent evidence supports the suggestion that even the hippocampus might have a role in perception — not for objects, but for spatial scenes. Lee *et al.* [38] found that patients with selective hippocampal damage were impaired in the visual discrimination of morphed scenes (Figure 2). These patients were not impaired, however, on the morphed face discriminations that were impaired in MTL patients. In another experiment, Lee *et al.* [39]

found that these same hippocampal patients were impaired in the perceptual oddity task — but only when the stimuli were spatial (virtual reality rooms). Again, the performance of the face oddity task was not impaired in these patients, but was impaired in the MTL patients. These findings provide further evidence for dissociations of function within the MTL, and, most strikingly, for a role for the hippocampus in the perceptual discrimination of scenes.

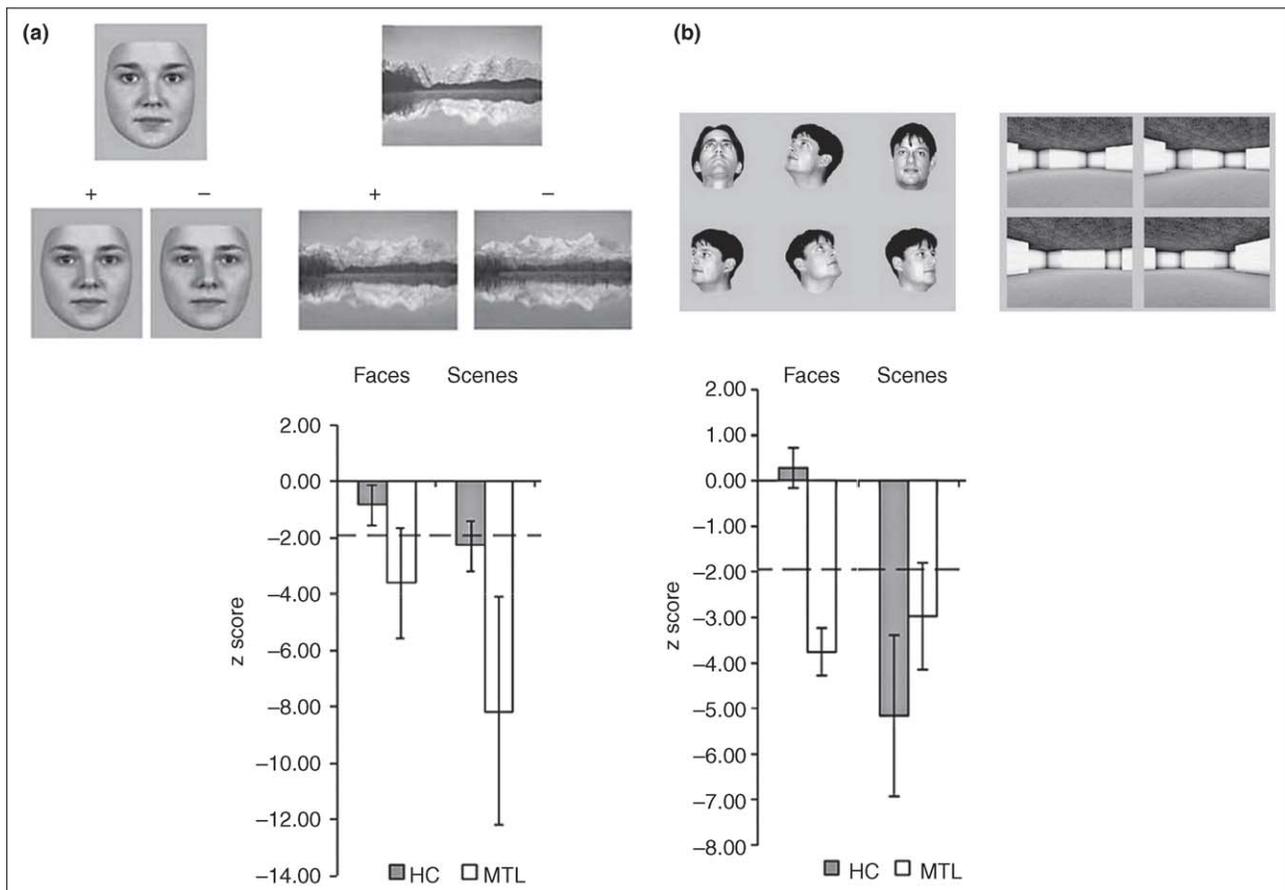
The suggestion that the MTL structures might have a role in perception is, as one might expect, highly controversial (see, for example, reference [41]). Indeed, others [42] have reported no such perceptual impairments in their MTL patients. Such studies, however, have been criticized on several grounds, including the suggestion that they did not manipulate perceptual difficulty in a way that might be expected to recruit perirhinal cortex [36•,43•]. The perception of spatial scenes has not yet been tested by an independent laboratory. Clearly, the suggestion that the human MTL, and in particular the hippocampus, is involved in spatial perception will strike many as radical, and thorough investigation will be required before the idea can finally be accepted, or rejected.

Conjunctive representations beyond the medial temporal lobe

The above findings support the view that the perirhinal cortex and hippocampus have roles in perception, and that the perirhinal cortex houses conjunctive representations that are useful for the resolution of feature ambiguity. Our view is not, however, just about perirhinal cortex or the hippocampus, and does not posit that perirhinal cortex is the ‘conjunctive representation centre’ of the brain. Indeed, visual conjunctive representations are assumed to reside throughout the VVS. Thus, the VVS need not always be considered separately from the MTL, but perhaps is better thought of as continuous with it. This continuous representational system is not devoted to a particular type of memory or perception. Instead, which regions of this ‘system’ are recruited for a particular task depends on the representations required by the task. Two imaging studies from the past two years illustrate this idea nicely.

Tyler and co-workers [44•] conducted an event-related fMRI study in which they presented pictures of common objects for subjects to name at two levels of specificity — basic and domain (see Figure 3). Tyler and co-workers hypothesized that basic-level naming would require fine-grained discrimination between similar objects, and thus, as in the feature-ambiguous discrimination tasks in the monkey and human studies described above, should recruit complex conjunctive representations in anterior temporal regions possibly including MTL structures. By contrast, domain-level naming would require access to a

Figure 2

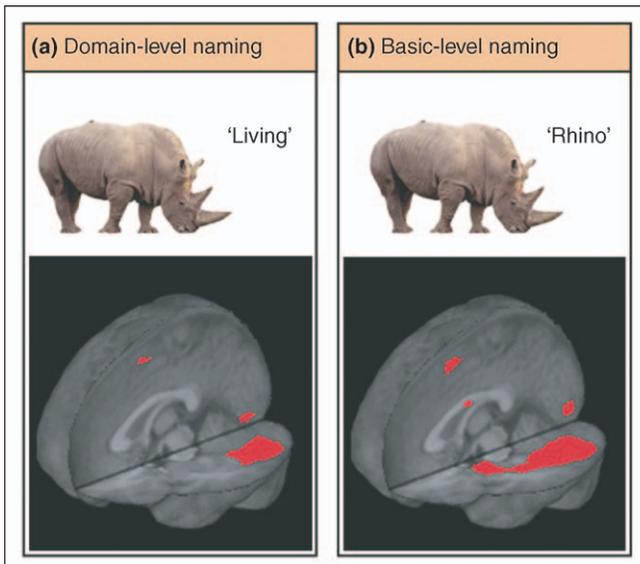


Evidence that MTL structures might have perceptual functions. In this pair of studies by Lee *et al.* [38,39], visual discrimination was investigated in amnesic subjects. Patients with selective hippocampal damage could discriminate feature-ambiguous faces, but were significantly poorer at discriminating scenes. By contrast, patients with medial temporal lobe damage including perirhinal cortex were significantly impaired at discriminating both faces and scenes. **(a)** Data from morphed picture discriminations [38]. The subjects were instructed to select the picture that they perceived to contain a greater proportion of the original correct stimulus. The original target item was continually present on the computer screen, thereby eliminating any explicit mnemonic component. **(b)** 'Odd-one-out' discrimination [39]. In this study, subjects were asked to select the odd stimulus from an array of several images. Stimuli consisted of faces, objects, colours, and scenes in the form of virtual reality rooms. On each trial, patients were presented with four images on the screen and were required to select the odd stimulus. Three of the faces were the same face viewed from different angles, whereas the fourth consisted of a different face. Three of the scenes were of the same virtual reality room viewed from different vantage points, whereas one was a view of a different room. Trial unique stimuli were used, with no stimulus being shown more than once in each condition. Data from (a) and (b) are presented as in [43**]. Scores beyond the dashed line ($z = -1.96$) indicate significant impairment. Abbreviations: HC, patients with selective hippocampal damage; MTL, patients with combined hippocampal damage and parahippocampal damage that included perirhinal cortex. Copyright 2004 by Wiley and Elsevier, reprinted with permission.

coarser grained representation of objects housed in posterior regions of the VVS. The results bore this prediction out (see Figure 3). Note that the different activations were found in the two conditions even though subjects were viewing the same stimulus materials, thus suggesting that the regions recruited were those that house the representations necessary for the task. In addition, the anterior areas activated correlated with damage in patients with basic naming impairments [44*]. A further study reports that objects that are similar to each other and are, therefore, more difficult to discriminate from each other activate anterior regions of the system, whereas objects that are dissimilar do not. Moreover,

patients with damage in these anterior regions, including perirhinal cortex, show a similar behavioural pattern [45]. A similar categorical naming task has been imaged by Rogers *et al.* [46], whose interpretation of the results was similar, suggesting that activation of a particular region depends not on the stimulus, but on the process required for the task. Our interpretation would differ slightly in that we would in this case emphasize not process, but representation. In our view, what distinguishes the different neocortical regions in the VVS is not the processes (computations) carried out in these regions, which will be similar as these regions share similar cortical circuitry. What differs between regions are the representations

Figure 3



Activation of VVS-MTL in a picture-naming task. Tyler and co-workers [44*] asked whether object processing activates different regions of the VVS-MTL to different degrees depending on the level of detailed information that must be extracted from a stimulus to perform a naming task. They predicted that a task that requires access to a more coarse-grained representation of an object should activate posterior regions of the VVS. A task that requires more detailed information for finer-grained discriminations, however, should activate more anterior regions of the VVS possibly including the MTL. This figure illustrates significant activations for naming the same pictures at (a) a domain level and (b) at a basic level, superimposed on a T1 image. Basic-level naming generated bilateral activation in the entire posterior-to-anterior extent of the VVS. Domain-level naming engaged posterior regions of occipital cortex and fusiform gyrus bilaterally, but did not extend as far anteriorly as activation resulting from basic level naming. Note that the different activations were found in the two conditions even though subjects were viewing the same stimulus materials, suggesting that the regions recruited were those that house the representations necessary for the task.

stored in these regions. These different representations are useful for different tasks. As in the monkey and human studies described above, in the case of tasks requiring discrimination of complex stimuli, complex conjunctive representations are often most useful, and so more anterior regions will have the highest activation levels.

Conclusions: an alternative approach

For several years, the field of neurobiology of memory has been dominated by a 'multiple memory systems' view, according to which different memory systems, including a separate 'perceptual representation system' [47], are segregated into dedicated modules in the brain. Indeed, this has for some time been the paradigm to which work in this area has been expected to conform. However, the utility of this framework has been questioned [48–50]. Indeed, the 2004–2005 studies reviewed above, and the computa-

Box 2 Some outstanding questions.

1. Our model and the animal and human experiments outlined above suggest that conjunctive representations in perirhinal cortex resolve feature ambiguity in complex visual discriminations. How do the conjunctive representations in perirhinal cortex support object recognition memory? Norman and Eacott [51], for example, reported that rats with perirhinal cortex lesions were impaired when feature ambiguity was increased in an object recognition setting. Such findings suggest a common mechanism underlying both object recognition and discrimination, consistent with our account. What remains to be demonstrated, however, is how the PMFC model can account for findings such as set-size effects [24] and delay-dependent impairments in object recognition.

2. The present article is about 'objects', that is, entities in the visual modality. But the MTL structures including perirhinal cortex receive multimodal information. Is this a critical difference determining the functions of the MTL structures and caudal regions of the VVS? What is the relationship between this perirhinal multimodality and semantic memory (see question 5 below)?

3. A small 2-D photograph of a mountain range appears to be processed as a 'place'. Why?

4. We have suggested that object perception and memory impairments following perirhinal damage can be understood in terms of nonspatial ambiguity. Can the spatial perceptual and memory impairments following hippocampal damage be understood in terms of 'spatial ambiguity'? A review by White [52] discusses ambiguity in spatial maze tasks. Could the hippocampus have a role in resolving 'spatial ambiguity' in perceptual tasks? See Buckley *et al.* [53] for work addressing this issue.

5. Is there a relationship between the hippocampal–scene, perirhinal–object dissociations within the MTL discussed here and the organization of episodic and semantic memory in the brain [6]? Perhaps the hippocampus is involved in both episodic memory and spatial cognition, because episodes are set in scenes. Alternatively, the hippocampus could perform computations that are useful for both episodic memory and spatial cognition. Perirhinal cortex, however, seems to handle context-independent knowledge about objects, leading Murray and Bussey [31] to suggest that "the perirhinal cortex is the core of a system specialized for storing knowledge about objects, analogous to a semantic memory system in humans." Some of the results described above, such as those of Tyler *et al.* [44*], tentatively support this idea. In addition, volumetric studies have revealed predominant involvement of perirhinal cortex compared with that of other MTL regions in patients with 'semantic dementia' [54], and performance on a range of semantic tests correlated with perirhinal volume [54]. Furthermore, preliminary results suggest that performance of patients with semantic dementia resembles that of patients (and of monkeys) with perirhinal cortex damage on the morphed-faces task described above [43*]. Indeed, this finding completes a double-dissociation with the finding of impaired discrimination of morphed scenes by patients with Alzheimer's disease [43*]. Such findings suggest that the object–place dissociations map onto semantic–episodic dissociations, but are by no means conclusive.

6. Can the PMFC model be extended to account for the effects of damage in regions throughout the VVS?

7. Now that we are beginning to improve our understanding of the organization of perception and memory in the VVS–MTL at the anatomical level, we can 'drop down a level' to ask: what are the mechanisms underlying these functions? Recent work, some of which has been reviewed in the main text, has elucidated some components of a putative mechanism underlying object recognition, but this enquiry is really only just beginning, and much more must be done. Of particular importance, now that it appears that the same brain regions might mediate both perception and memory, is the question of whether the lower-level mechanisms of these functions are similar.

tional, animal and human studies leading up to these new findings, are not compatible with this paradigm, and suggest that we might need to reconsider some fundamental assumptions. We would like to question the prevailing programme of trying to map psychological constructs such as ‘perception’, ‘semantics’, ‘categorisation’, and other notions onto anatomical modules in the brain. Evolution did not design the brain according to psychological categories that we have just recently invented, although neuroscience would be much easier had she done so. Instead of restricting ourselves to this way of thinking, we suggest attempting to understand the functions of brain regions in terms of what computations they perform, and what representations they contain. These computations and representations will depend on the circuitry within a region, and the information the region receives. The overall contribution of a region to behaviour–cognition will also depend, of course, on a region’s efferent connections. In the case of the VVS–MTL, we would emphasize the hierarchical organization of representations, culminating in complex object-level representations in the perirhinal cortex and spatial (and perhaps temporal) representations in the hippocampus. These representations are probably useful for all sorts of things — perception, memory, and categorization at different levels of specificity — the regions that are useful for a task being those that perform useful computations and contain useful representations.

Some outstanding questions are outlined in [Box 2](#).

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