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# Components of Recognition Memory: Dissociable Cognitive Processes or Just Differences in Representational Complexity?

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**ABSTRACT: Many current theoretical views within the literature on recognition memory—a representative sample of which is provided by the present special issue—advocate the dissociation of recognition memory into two cognitive processes: familiarity-based recognition, and recollection/recall. Furthermore, these processes are proposed to be mediated by distinct and dissociable anatomical regions, usually the perirhinal cortex and hippocampus, respectively. In this article, we describe a representational-hierarchical view that provides an account of cognition, including mnemonic and perceptual processing, within a brain pathway we term the ventral visual-perirhinal-hippocampal stream. According to this view cognition, perception, memory, and indeed amnesia may be understood by considering the content and organization of stimulus representations in the brain. Taking this view leads us to question the idea of cognitive modules for introspectively derived notions such as familiarity and recollection. We begin by reviewing the representational-hierarchical framework, explain how it has been used to account for object recognition memory in perirhinal cortex, and review the rationale for extending this framework to the hippocampus. We then discuss whether the principles of the representational-hierarchical framework can be used to understand recollection and familiarity in terms of stimulus complexity, and use these principles to reconsider some of the evidence for neuroanatomical, dual-process models of recognition memory.** **© 2010 Wiley-Liss, Inc.**

**KEY WORDS: recognition memory; stimulus representations; modular; visual perception; perirhinal cortex**

## INTRODUCTION

Most current neural theories of recognition memory adhere to the notion that familiarity and recollection are mediated by distinct neural systems, namely medial temporal lobe (MTL) cortex (especially perirhinal cortex) and hippocampus, respectively (e.g., Brown and Aggleton, 2001; Norman and O'Reilly, 2003; Aggleton and Brown, 2006; Haskins et al., 2008). Such a view fits squarely within the dominant paradigm in cognitive neuroscience of attempting to map psychologically defined modules onto anatomical regions of the brain.

Through the use of computational models and neuropsychological experiments, we have argued against the use of cognitive processing modules to explain the function of brain regions, focusing especially on a brain pathway we term the ventral visual-perirhinal-hippocampal stream. In the theoretical framework we propose, the effects of brain damage in these regions on cognition can be explained in terms of the hierarchically organized visual representations contained within them. The effects of brain damage to any part of this pathway are explained in terms of compromised representations at the level of features, objects or spatio-temporal context, depending on where the brain damage is located. That is, when the representations necessary for normal performance of a task are damaged, task performance will be impaired. Thus we account for lesion-induced impairments without appeal to multiple, separate cognitive processes or systems.

Our view provides a framework for understanding why damage to structures such as perirhinal cortex causes deficits in a number of cognitive domains, including object recognition memory and visual perceptual discrimination (Bussey and Saksida, 2002; Bussey et al., 2002, 2003; Cowell et al., 2006, 2010b; Bartko et al., 2007a,b; Murray et al., 2007). For example, the effects of lesions in the anterior and posterior ventral visual stream (VVS) on visual discrimination tasks have been widely interpreted as evidence for a dissociation between perceptual and mnemonic function in these two regions, but our simulation studies demonstrated that these findings could be reinterpreted in terms of the representations required for the solution of the tasks (Cowell et al., 2010b). Further, and of greatest relevance to the present special issue, we have suggested that the representational-hierarchical framework may be naturally extended to account for the role of the hippocampus in recognition memory (Cowell et al., 2006; Bussey and Saksida, 2007). In particular, we have suggested that the hippocampus can be characterized as an additional station in the ventral visual-perirhinal stream, which provides conjunctive representations of very high complexity (at the level of spatio-temporal context). We propose that these hippocampal representations are critical to multiple cognitive functions, including recognition memory, perceptual discrimination, categorization and so on, just as representations upstream of the hippocampus (in perirhinal cortex and inferotemporal cortex) may be necessary for multiple cognitive functions, in a manner that depends on the representational demands of the task.

To date, we have not explicitly addressed tasks presumed to tap recollection such as source memory and

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associative recognition with computational simulations. However, the natural extension of our theory would attempt to account for such data without positing a distinction between perirhinal cortex and the hippocampus in terms of cognitive processes. In the current article we explore the potential utility of trying to understand recognition memory in terms of the representational complexity required for the task at hand, rather than in terms of separate cognitive modules dedicated to distinct processes of familiarity and recollection. We begin by reviewing the representational-hierarchical framework and in particular how it has been used to account for object recognition memory in perirhinal cortex. We then consider the rationale for extending this framework to the hippocampus. Next, we discuss whether the principles of the representational-hierarchical framework can be used to understand recollection and familiarity in terms of stimulus complexity, and use these principles to reconsider some of the evidence for neuroanatomical, dual-process models of recognition memory. Finally, we examine the parallels between our proposals and the arguments of a recent 'memory strength' account of recognition memory (Squire et al., 2007), which finds support in a large body of evidence from cognitive psychology (Wixted, 2007), and is not wedded to the notion of anatomically separate modules for familiarity and recollection. We also emphasize critical differences between our view and theirs. We conclude with the suggestion that, although tentative, our account may offer some interesting food for thought in relation to an alternative interpretation of the recognition memory literature.

## THE REPRESENTATIONAL-HIERARCHICAL VIEW

In this section, we provide an overview of the representational-hierarchical framework and explain how it has been used to account for object recognition memory in perirhinal cortex. In addition, we outline the implications of this view for hippocampal function. Much of the evidence in favor of this theory has also been reviewed elsewhere, for example in Bussey and Saksida (2005a,b, 2007), Cowell et al. (2010a), Murray et al. (2007), and Saksida and Bussey (2010).

### A Role for Perirhinal Cortex in Both Perception and Memory

A wealth of data from neuropsychological studies in monkeys indicates that perirhinal cortex is critical to object recognition memory (Zola-Morgan et al., 1989; Meunier et al., 1993; Eacott et al., 1994; Murray and Mishkin, 1986, 1998). This body of data has been used to support the widely held view that perirhinal cortex plays a critical role in declarative memory, and declarative memory only, as part of a putative medial temporal lobe memory system that is damaged in amnesia (Squire and Zola-Morgan, 1991; Squire et al., 2004). Eacott et al. (1994) suggested that perirhinal cortex might have a role in perception, evidenced by the impairment of animals with perirhinal lesions on both zero-delay object recognition and simultaneous matching-to-sample. Buckley et al. followed this up with further lesion studies demonstrating that perirhinal cortex is critical for visual discrimination under certain circumstances (Buckley and Gaffan, 1997; Buckley et al., 2001; Bussey et al., 2002, 2003); these authors suggested that perirhinal cortex is important for "object identification". Gradually, a new framework has begun to emerge in which researchers have questioned the traditional "multiple memory systems" view of perirhinal cortex function (Gaffan, 2002; Bussey, 2004). The first instantiation of the representational-hierarchical view that we describe in the present article is an account of perirhinal cortex function that was formulated to make sense of a puzzling set of findings concerning the effects of perirhinal cortex lesions on visual discrimination behavior (Bussey and Saksida, 2002). Data from studies using animals with damage to perirhinal cortex indicated that these animals were impaired at learning to discriminate between pairs of visual stimuli under certain conditions (Eacott et al., 1994; Buckley and Gaffan, 1997, 1998a,b), but it was not initially clear what properties of a discrimination task were required to induce dependence on perirhinal cortex. To resolve this puzzle, Bussey and Saksida (2002) proposed that perirhinal cortex can be thought of as part of the VVS. Specifically, the inconsistent effects of perirhinal lesions on visual discrimination can be explained by considering the hierarchical organization of stimulus representations in the ventral visual-perirhinal stream. In the Perceptual-Mnemonic Feature-Conjunction (PMFC) model of Bussey and Saksida (2002), simple features are represented in more posterior regions of the hierarchy and progressively more complex conjunctions of these features are represented in later, anterior stations, reaching the level of a "whole object" in perirhinal cortex. The PMFC model is a simple connectionist network that instantiates the hierarchy of stimulus representations in two layers, corresponding to "pos-

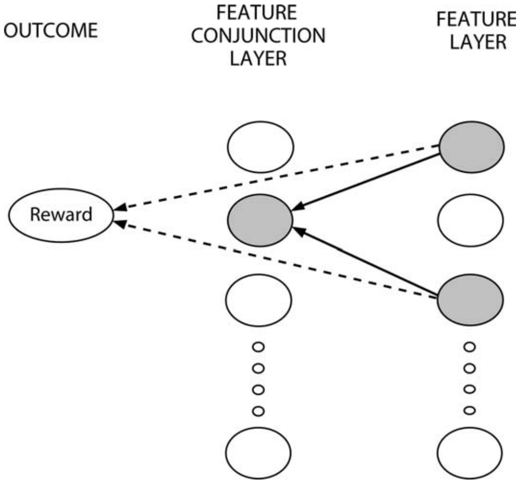

**FIGURE 1. The PMFC model of Bussey and Saksida (2002). The network contains two layers of units, the feature layer and the feature conjunction layer, and an outcome node representing events (e.g., reward). Each node in the feature layer represents a single element of a stimulus. Each node in the feature conjunction layer represents a unique conjunction of features. The feature conjunction layer corresponds to perirhinal cortex (PRh) and the feature layer corresponds to more caudal regions of the ventral visual stream.**

terior VVS" and "perirhinal cortex" (Fig. 1). It suggests that perirhinal cortex lesions cause impairments in visual discrimination because they remove the conjunctive representations of complex stimuli, and the remaining representations of simple features are insufficient for discrimination of visual objects, under certain conditions. Thus, the PMFC model claims that the effects of perirhinal cortex lesions on visual discrimination are due to compromised representations, and as such it suggests that perirhinal cortex has a role in perceptual discrimination.

An illustration of the basic principles of the PMFC model is provided by an experimental paradigm known as the biconditional task. In this visual discrimination learning task, subjects are required to discriminate between pairs of objects that are composed of features in such a way that the features appear equally often as part of rewarded and unrewarded stimuli. Formally, the stimuli are composed following the scheme: AB+, CD+, BC−, AD−, where a letter indicates half of a stimulus, a pair of letters indicates a whole stimulus, and ± indicates whether the stimulus is consistently rewarded or unrewarded. In this task, the individual halves of the stimuli cannot be used to predict reward; only the conjunctions of the stimulus halves are useful in solving the discrimination. Bussey and Saksida (2002) termed this property of visual discriminations "feature ambiguity," and proposed that its resolution requires the use of object-level conjunctive representations in perirhinal cortex.

Studies in monkeys have revealed that perirhinal cortex lesions can indeed cause impairments in the acquisition of the biconditional discrimination (Buckley and Gaffan, 1998a; Bussey et al., 2002). The PMFC model's ability to account for these findings was demonstrated using a simulation in which the network was trained to discriminate between two pairs of stimuli constructed according to the biconditional scheme. Stimulus halves, or features, were represented by distinct units on the "posterior VVS" layer of the model, whereas conjunctions of those features were represented by units in the "perirhinal cortex" layer of the model. Representations on both layers were allowed to enter into association with reward during training, in which the stimuli were repeatedly presented to networks and consistently rewarded or unrewarded. Intact networks served as a control group, while networks with the "perirhinal cortex" layer removed simulated the effect of perirhinal cortex lesions. Networks in both groups were trained on the biconditional pairwise concurrent discrimination task until either criterion was reached or a maximum of 500 blocks of training had been administered. Removing the "perirhinal cortex" layer of the network had a devastating effect on the acquisition of the biconditional discrimination, as is shown in Figure 2.

Thus, the contribution of perirhinal cortex to visual discrimination is seen to be critical when the task requires representations of the conjunctions of complex features that are, individually, ambiguous. This hypothesis has since been supported by a number of experiments, using various manipulations of feature ambiguity, in monkeys (Bussey et al., 2002), rats (Bartko et al., 2007b) and humans (Barense et al., 2005). In the next section, we demonstrate how this hypothesis can be extended to provide a mechanistic account of the role of perirhinal cortex in object recognition memory.

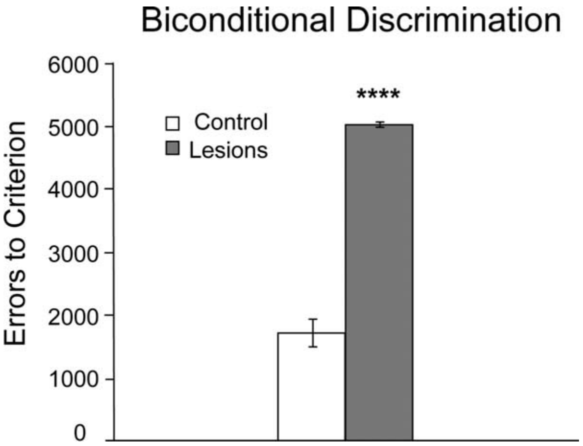

**FIGURE 2. Acquisition of a biconditional discrimination by the PMFC model of Bussey and Saksida (2002). Error bars represent ± SEM. ****$P < 0.0001$ vs. Control.**

## Perirhinal Cortex and Object Recognition Memory

The initial formulation of the representational-hierarchical view explained the role of perirhinal cortex in visual discrimination learning. However, the canonical effect of perirhinal cortex lesions is an impairment in object recognition memory (Zola-Morgan et al., 1989; Gaffan and Murray, 1992; Meunier et al., 1993; Mumby and Pinel, 1994; Aggleton et al., 1997; Buckley et al., 1997; Baxter and Murray, 2001; Malkova et al., 2001; Winters et al., 2004). Since the PMFC model purports to be an account of perirhinal cortex function, we investigated whether the framework could be extended to address the role of this structure in object recognition memory. We developed the connectionist network to offer a mechanistic account of the effects of perirhinal cortex on recognition memory, still based upon the assumption that perirhinal cortex contributes to cognition via representations of the complex conjunctions of visual features possessed by objects (Cowell et al., 2006). Just as in the model's account of visual discrimination learning, perirhinal representations are proposed to play a critical role in memory when it is difficult to solve a task using the representations of simple features alone. The connectionist model was modified from Bussey and Saksida (2002), principally by introducing the possibility of development of the stimulus representations with experience, which provides an index of the amount of exposure the network has had to the stimulus. The model demonstrated an account of three canonical findings from the object recognition memory literature: (1) that impairments following perirhinal cortex lesions are worsened by increasing the delay between the study phase and the test phase, (2) that perirhinal cortex lesions cause greater impairments as the length of the list of to-be-remembered items is increased, and (3) that perirhinal cortex lesions do not cause impairments in the recognition of objects that have been repeatedly presented.

The model of object recognition memory is shown in Figure 3. Stimulus representations in the model are organized according to the same hierarchy that was assumed by the original

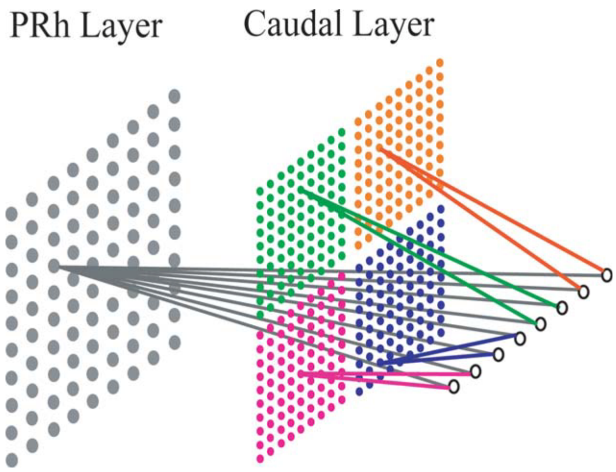

**FIGURE 3. The object recognition memory model of Cowell et al. (2006). As in the PMFC model, simple features are represented on the "caudal" layer and conjunctions of those features are represented on the perirhinal ("PRh") layer. Stimulus inputs are shown on the far right; each stimulus has eight "dimensions," which are paired into four, two-dimensional "features". The caudal layer represents the four features in four separate regions, whereas the PRh layer combines the four features into a single conjunction to give a representation of the whole stimulus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]**

PMFC model: simple features are represented individually in the posterior, or "caudal" layer, and complex conjunctions of those features are represented in the anterior, perirhinal layer. Note that in this model, as in the network of Bussey and Saksida (2002), we make the simplifying assumption that each layer of the model contains units at just one level of complexity, in terms of the number of features combined into a conjunction. Of course, in the brain, each "layer" or "station" in the VVS will possess a degree of heterogeneity in terms of the level of complexity to which the individual neurons respond. For example, if a given layer tends to predominantly represent conjunctions of four features, it will nonetheless also represent some conjunctions of five features, or three features; as such, the degree of overlap, at any given level, between the representations of two similar objects that share many features is not as "all-or-none" as our simplified scheme implies. In the object recognition model, the mechanism for recognition memory relies upon the development of stimulus representations during a study or "encoding" phase. Each layer of the model is instantiated as a two dimensional grid, in which stimulus representations self-organize, that is, they develop through experience. We simulate recognition memory by presenting a stimulus to the network for a short period of time, during which the network repeatedly "samples" the stimulus, such that its representation within the model becomes increasingly sharpened. Upon presentation of the same stimulus during a test phase, the sharpened representation of the "familiar" stimulus may be distinguished from an untuned representation of a "novel" stimulus, allowing the network to "choose" the more familiar stimulus, just as animals do in a recognition memory task. This mechanism is very similar to the index of familiarity used by Norman and O'Reilly (2003).

The model explains the delay-dependent deficit in recognition memory seen in animals with perirhinal cortex lesions by appeal to an interference account of forgetting. That is, we assume that during the delay between encoding and test, a subject experiences many visual stimuli, both real and imagined; we simulate this by briefly presenting many stimuli to the model. Critically, we also assume that commonly encountered visual objects possess many features in common such as simple lines, shapes, textures, and colors, such that these features will occur repeatedly and become highly familiar. However, the unique conjunction of a particular set of features that makes up an individual object occurs rarely, if at all, during a delay, and so does not become familiar. During the "test" phase of a recognition memory simulation, we require networks to discriminate between a novel and a familiar object. If a delay has intervened since the "study" phase, the features of the novel object will appear familiar on the caudal layer of the model, because they were repeatedly presented—and therefore encoded—as part of other objects that were experienced during the delay. In contrast, the unique conjunction of the novel object that is represented on the perirhinal layer of the model is not affected by the interference, since the probability of the exact conjunction that specifies the novel object being experienced during the delay is very low. Therefore, following a delay, the discrimination between novel and familiar stimuli can be made effectively on the basis of the perirhinal cortex representations, but not on the basis of caudal layer feature representations. The longer the delay, the greater the repetition of the commonly occurring features that compose complex objects, and the more sharply tuned the feature representations in caudal regions become, producing greater impairments in recognition memory in the absence of perirhinal cortex (Fig. 4). Thus, the

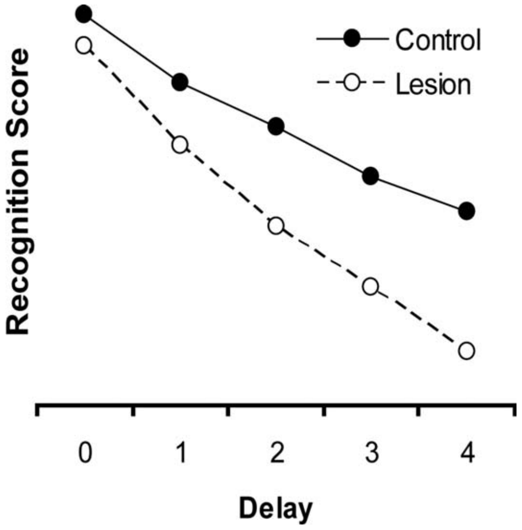

**FIGURE 4. Recognition memory performance across a delay, simulated using the object recognition model shown in Figure 3. Networks in the "Lesion" group were subject to removal of the PRh layer; networks in the "Control" group remained intact. See text, and Cowell et al. (2006), for details of simulations.**

specific role of perirhinal cortex in recognition memory can be seen to be very similar to its role in visual discrimination: representations in perirhinal cortex are required when the information about individual features provided by more posterior brain regions is ambiguous with respect to the task demands.

The model can also account for the finding that perirhinal cortex lesions cause greater impairments as the length of the list of to-be-remembered items is increased. Analogous to the interference assumed during a delay, as animals are required to encode a greater number of complex objects, the features that compose those objects are more likely to occur repeatedly. After encoding a long list of objects possessing shared features, an animal forced by damage in perirhinal cortex to rely upon caudal feature representations will be unable to distinguish familiar objects from novel items, because the features of all objects will appear familiar.

The third observation accounted for by the model is the absence of impairments following perirhinal cortex lesions when the stimuli used to test object recognition memory are repeatedly presented, such that after a few trials, both novel and familiar stimuli are highly familiar. In a typical repeated items recognition memory task, two visual objects are presented to the subject repeatedly, with the designation of "novel" and "familiar" varied randomly from trial to trial. That is, the label "novel" simply comes to mean "presented in a study phase less recently." In the model, this effect emerges naturally from the development of stimulus representations: with repeated presentations, both the novel and familiar objects become well encoded on both the caudal and perirhinal layers. When required to distinguish between them on the basis of familiarity, neither perirhinal nor caudal representations are helpful in solving the task, since both the "novel" and "familiar" stimulus representations appear familiar. This is in line with the data from Eacott et al. (1994), who showed that perirhinal cortex lesions did not impair repeated-items object recognition. However, unlike our networks, both control and lesioned monkeys in this study were able to solve the task at short delays, which prompts the question: where in the brain could this task solution be computed? The answer may lie in an analogy with the trial-unique version of the task. In normal trial-unique object recognition, interference during the delay period renders the features ambiguous (in terms of familiarity) through their repeated presentation, such that solving the task requires the representations of unique feature conjunctions in perirhinal cortex. In repeated-items recognition, not only are the individual features familiar, but whole objects too become equally familiar through their repeated presentation, leading to a problem that might be termed "object ambiguity". In Cowell et al. (2006) we argued that object ambiguity in a repeated-items recognition task requires higher level conjunctions than are found in perirhinal cortex for its solution; conjunctions of the type that would be found downstream of perirhinal cortex, in the hippocampus, where relational information such as the "where" and "when" of events is uniquely represented (Eichenbaum et al., 1996; Squire et al., 2004). Consistent with this hypothesis, Rawlins et al. (1993) reported that lesions of the hippocampus or fornix in rats impair performance of a repeating-items delayed matching-to-sample. In addition, Charles et al. (2004) found that monkeys with fornix transections were impaired on a recognition memory task in which they were required to judge the relative recency of two stimuli. Note that these findings do not necessitate the assumption of a brain module for computing recency. A more parsimonious explanation is that repeating-items recognition tasks merely provide an additional degree of ambiguity that must be resolved by additional, even more complex conjunctive representations.

In addition to accounting for much extant data on object recognition memory, the model makes several novel predictions. According to the model, the functional role of perirhinal cortex is best described in terms of the type and complexity of the stimulus representations it contains. Thus, whether perirhinal cortex is important for a given task is determined by the stimulus material used, and how that material is presented (along with other task factors, discussed below). For example, according to the model, perirhinal cortex lesions should cause impairments in object recognition memory not just after a study-test delay (presumed to place a greater load on memory), but also at zero delay, if the stimuli are manipulated such that the novel and familiar objects share many features (a manipulation presumed to place a greater demand on perceptual discrimination ability). The model predicts that, in the absence of perirhinal cortex, the representations of features in the caudal layer will provide a poor solution to the task, because any features of the novel object that are shared with the familiar object will appear familiar. This prediction was confirmed with a study of spontaneous object recognition behavior in rats, in which stimuli were constructed of LEGO to enable explicit control of the level of similarity between objects (Bartko et al., 2007a). In the "perceptually similar" condition, stimuli were expressly constructed so that novel/familiar stimulus pairs shared a number of features; in the "perceptually dissimilar" condition, novel/familiar pairs were composed of LEGO pieces in such a way that they could be distinguished on the basis of simple features alone. The experimental data supported the prediction of the model: rats with perirhinal cortex lesions were impaired in the "perceptually similar" condition, but not the "perceptually dissimilar" condition, relative to control rats.

A second novel prediction of the model concerns the effects of interfering material on object recognition memory. In the model, forgetting in amnesia is assumed to occur via interference, such that repeatedly occurring features become sharply tuned and thus appear familiar, which causes impairments in recognition memory when novel objects are composed of those features. To simulate a delay, we assumed the presence of interfering activity in visual cortex. It follows from this account that the interpolation of interfering material between the study and test phases of an object recognition task should induce greater forgetting in animals with perirhinal lesions, in a manner that depends on the interfering stimulus material used. The model predicts that if the interfering stimuli share features with the novel objects in the test phase, then perirhinal impairments will be greater than if the interfering stimuli are dissimilar to the novel objects. Bartko et al. (in press) carried out a test of this prediction in rats, comparing the spontaneous object recognition performance of a control group with perirhinal lesioned animals. Novel and familiar stimuli were always constructed of LEGO, but there were two levels of interference: "dissimilar" (predicted to cause low interference) and "similar" (predicted to cause high interference). In the "dissimilar" condition, animals were presented with visual stimuli that were dissimilar to the novel and familiar stimuli: they were laminated picture cards showing two-dimensional photographs of objects. In the "similar" condition, animals were shown interfering items made of LEGO, which shared many features with the LEGO objects used as "familiar" and "novel" items. As predicted by the model, lesioned rats were impaired in the similar, but not the dissimilar, interference condition.

## A Note on Levels of Analysis

Our view of the ventral visual-perirhinal-hippocampal stream is couched at the anatomical systems level, and although we have said this many times before, it is worth repeating again for the sake of clarity. Our approach is to question the prevalent cognitive neuroscience assumption that putative psychological processes such as short-term memory, long-term memory, or perceptual discrimination can be mapped neatly onto anatomical regions of the brain. We do not make specific claims about lower levels of analysis, for example at the neural or neural network level. So, within a given anatomical region one could find mechanisms—long-term plasticity mechanisms, for example—that are important for the persistence of a given representation, but which may not be necessary for, say, a perceptual same/different judgment between two simultaneously presented stimuli. Indeed, such dissociations of mechanism have been reported, and in perirhinal cortex as well. Barker et al. (2006) showed that infusion of an NMDA receptor antagonist into perirhinal cortex impaired recognition memory after a long, but not a short delay. And most interestingly, infusion of a selective kainate receptor antagonist produced the opposite pattern: amnesia after a short (20 min) but not a long (24 h) delay. For our part, we have found that M1 muscarinic receptor antagonism within perirhinal cortex can impair both perceptual discrimination and memory across a delay, whereas M2 receptor antagonism produces only the latter effect, suggesting a similar dissociation of mechanism (Bartko et al., 2008). These results suggest separate short- and long-term plasticity mechanisms within perirhinal cortex (and almost certainly elsewhere as well). Such findings are not in the least incompatible with our anatomical-systems-level view. What we would suggest, however, is that such mechanisms do not dissociate along anatomical lines, such that all stations within the ventral visual-perirhinal-hippocampal stream may share similar lower-level mechanisms. The strong version of our view is that relative complexity of representations is sufficient to account for the result of brain damage to these regions.

## Extending the Representational-Hierarchical View Upstream From Perirhinal Cortex

The representational-hierarchical view, in its account of both visual discrimination learning and object recognition memory, explains the role of perirhinal cortex in terms of the complex conjunctive representations presumed to reside there. In both experimental paradigms, perirhinal cortex is critical for cognitive function when the task cannot be solved on the basis of simple features alone. However, we do not view perirhinal cortex as the only region containing configural representations. Rather, the representations in a particular region of the VVS are configural only relative to those in more posterior regions upstream of them; concomitantly, the representations in each region are "elemental" relative to those in more anterior regions downstream. The assumption is that visual configural representations residing in perirhinal cortex are different from those in more posterior regions of the VVS only by virtue of their complexity. Thus, we predict that perirhinal cortex is important for resolving feature ambiguity arising at the level of whole objects (i.e., when stimuli can be distinctly represented only by complex conjunctions) but that discrimination problems using very simple stimuli will not be impaired following perirhinal cortex lesions, because the representations required for solving such a task are presumed to reside in regions posterior to perirhinal cortex. Indeed, we have found that perirhinal cortex lesions do not impair color or size discriminations in monkeys or humans (Bussey et al., 2003; Lee et al., 2005a,b).

Thus, the representational-hierarchical view provides an account not only of the effects of perirhinal cortex damage on cognition, but also of the effects of lesions elsewhere in the ventral visual-perirhinal-hippocampal stream. The effects of brain damage to any part of the processing pathway are explained in terms of compromised representations of features, objects or spatio-temporal context, depending on where the brain damage is located. When the representations necessary for solving a task are damaged, task performance will be impaired. The level of complexity of the stimulus representations necessary for solving a given task is determined by several factors, such as the stimulus material used, the task instructions and the task design, which, in combination, determine the representational demands of the task.

The importance of task design is illustrated by several of the examples above, for example the biconditional task, or trial-unique vs. repeating items delayed nonmatching to sample. We examined the importance of the combination of stimulus material and task design to investigations of object processing in a recent paper that extended the representational-hierarchical view in a posterior direction (Cowell et al., 2010b). In this study, we used connectionist simulations to revisit and reinterpret the results of an important and influential body of literature from the 1960s and '70s, in which the function of the VVS was examined in monkeys (e.g., Iwai and Mishkin, 1968; Cowey and Gross, 1970; Gross et al., 1971; Wilson et al., 1972; Blake et al., 1977). These studies used visual discrimination learning tasks in combination with lesions of either posterior or anterior areas of the VVS. The tasks typically fell into two categories: either they were presumed to tap mnemonic function because they required monkeys to learn multiple pairwise discriminations between complex objects concurrently (which imposed a high load on memory), or they were considered to be perceptual tasks because fewer pairwise discriminations were involved and the to-be-discriminated stimuli were simpler (and hence thought to test purely visual discrimination function). Often, the studies revealed a double dissociation between the behavioral effects of damage to posterior and anterior regions on the two types of task. Such dissociations were interpreted as evidence for a functional distinction across these brain regions, with memory carried out in anterior areas and perception in posterior areas. However, one common trait prevailed across all of these studies: the stimuli used in the "mnemonic" tasks were complex—e.g., whole objects—whereas the stimuli used in the "perceptual" tasks were simple—e.g., two-dimensional outlines of simple shapes rendered in black and white. In Cowell et al. (2010b) we simulated these studies using an extended version of the PMFC model, in which we added additional layers of stimulus representation to the network in order to enable the simulation of lesions in both posterior and anterior regions of the VVS. Simulations with the extended PMFC model demonstrated that a double dissociation typical of the monkey studies described above could be reproduced without assuming separate processes in distinct functional modules for perception and memory (see Fig. 5). In the same way that lesions in perirhinal cortex in the original PMFC model produced impairments in visual discrimination of complex stimuli, lesions in the posterior layers of the network, where simple stimulus representations are found, produced impairments in visual discrimination of simple stimuli. Therefore, according to the representational-hierarchical view, the area of VVS critical for a given visual discrimination task depends on the level of complexity of conjunctive representations required to disambiguate the stimuli used in that task. If animals are required to discriminate simple patterns possessing simple conjunctions of few visual features, the simple conjunctions represented in posterior regions are critical for good performance. Conversely, if animals must discriminate whole objects possessing complex conjunctions of many visual features, representations in anterior regions such as perirhinal cortex are needed to solve the task efficiently.

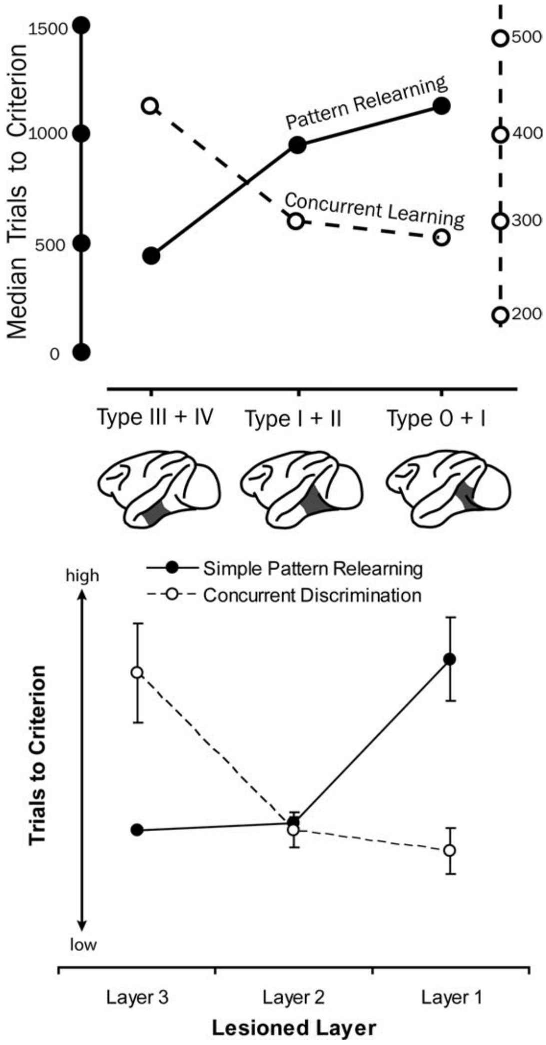

**FIGURE 5. Upper Panel: acquisition of visual discriminations by monkeys in two tasks used by Iwai and Mishkin (1968). *X*-axis indicates the placement of the brain lesion in each group; *Y*-axis indicates the median number of trials taken by monkeys to reach criterion. The "Pattern Relearning" task involved the discrimination of a single pair of simple stimuli (the outline of a square versus a plus sign). The "Concurrent Discrimination" task required monkeys to learn eight object-pair discriminations, concurrently. Animals with posterior lesions were relatively impaired on the Pattern Relearning task, whereas animals with anterior lesions were relatively impaired on the Concurrent Discrimination task. Lower Panel: Simulation data generated by the extended PMFC model on the two tasks of Iwai and Mishkin (1968); see Cowell et al. (2010b) for details. Figure modified from Iwai and Mishkin (1968) and Cowell et al. (2010b).**

A neuroimaging study by Tyler et al. (2004) provides an excellent example of the influence of the task instructions on the brain regions recruited to solve the task. The authors presented color pictures of objects and asked subjects to name the object at either a specific level (e.g., rhinoceros, hammer) or a domain level (e.g., living or man-made). According to the representational-hierarchical view, domain level naming should require access to information about the general properties of an object, which can be gleaned from global features, and thus the task need engage only posterior regions of inferior temporal cortex. In contrast, producing a specific name for an object should require a "fine-grained" representation containing more detailed information, which must be extracted from specific conjunctions of features, and thus engagement of both posterior regions of IT and perirhinal cortex should be observed. The results of Tyler et al. (2004) were in line with this account: naming objects on a specific level generated bilateral activation in the entire posterior to anterior extent of the fusiform gyrus including the occipital cortex; domain level naming activated posterior regions of occipital cortex and fusiform gyrus bilaterally, but the activation did not extend as far in the anterior direction as in specific level naming. Only specific level naming produced significant activation of perirhinal cortex. In addition, Tyler et al. (2004) tested the abilities of two herpes simplex encephalitis patients, with bilateral anterior temporal lobe damage, on a picture-naming study comparable to that used in the neuroimaging study. The patients were considerably impaired at naming at the specific level, but very accurate at naming at the domain level. Thus, both neural activity and the effects of brain damage were shown by this study to vary as a function of task demands.

Moreover, the study presented by Cowell et al. (2010b) demonstrates explicitly the continuous nature of the representational-hierarchical view. When an animal learns a particular visual discrimination, the model predicts that if the optimal stage in the VVS for solving the discrimination is damaged, discrimination performance should be severely impaired. The closer a brain lesion falls to the processing stage best able to resolve ambiguity in the to-be-discriminated stimuli, the worse will be the resultant discrimination performance. In summary, the representational-hierarchical view holds that no brain region within the stream is constrained to perform only one cognitive function, and no cognitive function is constrained to occur in only one brain region. A given brain region can be important for a given task—be that putatively a "memory" or a "perception" task—depending on the stimulus representations that it contains. We extend these predictions not just to visual discrimination performance along the ventral visual-perirhinal stream, but also to priming, categorization, short-term memory (see Warren et al., 2010) and recognition memory. In our view, none of these functions is likely to be strictly localized to a single, specific region.

## Extending the Representational-Hierarchical View Downstream From Perirhinal Cortex

In the continuous account of object processing outlined above, each stage in the representational hierarchy underlies the capacity for visual discrimination or recognition memory of the stimulus representations it contains. At each station in the pathway, recognition memory or visual discrimination is no longer supported when the representations do not comprise conjunctions complex enough to solve the task. Extrapolating this scheme in an anterior direction, the hippocampus sits at the top of the hierarchy of representations, where it is well positioned to represent the unique conjunction of an object with time, space, and context. The idea that the contribution of the hippocampus to cognition emerges from its ability to combine object representations with other information in the environment is in line with the current consensus that the hippocampus represents complex, "episodic" or relational information, including knowledge of "where" and "when" (Eichenbaum et al., 1996; Squire et al., 2004). Although we have, at the present time, performed no explicit simulations of hippocampal processing with any of the neural network implementations of the representational-hierarchical view, we speculate here about how extension of our computational framework could account for the role of the hippocampus in recognition memory.

We have already seen how the extension of the hierarchy to the hippocampus is important for explaining, for example, repeated items nonmatching-to-sample (Eacott et al., 1994; Cowell et al., 2006): perirhinal cortex-level complex object representations are ambiguous with respect to reward when objects are repeatedly presented, therefore, hippocampal-level contextual representations are required to resolve the object-level ambiguity inherent in the task. However, if the representational-hierarchical view applies to the hippocampus just as it applies to perirhinal cortex and regions upstream, then a prediction is that the higher-level conjunctive representations housed in the hippocampus contribute not just to recognition memory but also to other cognitive functions, most notably perceptual discrimination. In two recent studies (Clelland et al., 2009; McTighe et al., 2009) rats or mice were trained to discriminate locations on a computer screen that varied in their distance apart. Animals with damage to dorsal hippocampus, or with a knockdown of neurogenesis in the dentate gyrus (DG), were impaired on this task when the locations were close together, but not when they were far apart. The task in each case was identical; the factor that determined the effects of hippocampal dysfunction was perceptual similarity. Thus, these data suggest that the hippocampus may be critical for spatial perceptual discrimination, in addition to its well-established role in memory.

An additional strand of evidence for the role of hippocampus in perceptual discrimination comes from a series of human studies on scene perception by Lee et al. (2005a,b) which found that patients with selective damage to hippocampus were impaired at the discrimination of spatial scenes. In a further study, Lee et al. (2007) tested patients with Alzheimer's disease, who are known to have greater damage in hippocampus than in other MTL areas, and patients with Semantic Dementia, who typically have greater pathology in perirhinal cortex than in other MTL regions. The Alzheimer's patients were impaired on scene, but not face discriminations, relative to healthy subjects, whereas the Semantic Dementia patients performed worse than controls on face, but not scene discriminations. This double dissociation reinforces the suggestion that both perirhinal cortex and hippocampus are involved in perceptual discrimination, but that their differential involvement is determined by the level in the stimulus representation hierarchy at which they operate.

In a further "oddball" study by Lee et al. (2005a,b), participants were asked to choose the oddball stimulus from an array in a series of tasks testing their ability to discriminate color, shape, faces, objects, and spatial scenes. Patients with MTL lesions including perirhinal cortex were impaired at making oddity judgments for faces and spatial scenes, whereas patients with damage restricted to the hippocampus were impaired at making oddity judgments only for spatial scenes. In a similar study assessing oddity judgments in patients with Alzheimer's Disease and patients with Semantic Dementia (Lee et al., 2006), Alzheimer's Disease patients were impaired at judging oddity for scenes, but not faces, presented from different views, whereas Semantic Dementia patients were impaired at judging oddity for faces, but not scenes, presented from different views. As before, these findings are easily accounted for by the representational-hierarchical framework.

In addition to a role for the hippocampus in the perceptual discrimination of spatial scenes, Graham et al. (2006) have presented evidence that hippocampus is important for other cognitive functions besides declarative memory. In this study, patients with selective bilateral hippocampal lesions were impaired relative to controls on the categorization of visually presented spatial scenes, and in perceptual learning about spatial scenes. Critically, these patients did not show impairments in categorization or perceptual learning for face stimuli. In line with the representational-hierarchical view, the data suggest that the hippocampus may play a role in many cognitive functions, in a manner that depends on the representational demands of the task.

## Summary

In this section we have described data from a variety of tasks and explained how the representational hierarchical can account for them in a nonmodular manner. In the next section, we will review tasks designed to test recollection and familiarity, and consider how data interpreted as evidence for modules for these two functions may also be accounted for by a nonmodular view, in terms of the organization of stimulus representations.

## THE REPRESENTATIONAL-HIERARCHICAL VIEW AND DUAL PROCESS THEORIES OF RECOGNITION MEMORY

Most current models of the neuroanatomical organization of recognition memory seem to agree that perirhinal cortex (or MTL cortex) is important for the discrimination of novel objects from familiar objects. This is commonly interpreted as evidence that MTL cortex provides a signal for familiarity, or knowing that something has occurred before (Mandler, 1980). This idea has been championed most strongly by Brown and Aggleton (1999, 2001), and more recently adopted as a central assumption by many other theories (Norman and O'Reilly, 2003; Fernandez and Tendolkar, 2006; Eichenbaum et al., 2007). In addition, the hippocampus is seen as being critical for the process of recollection, or knowing where and under what circumstances something has occurred. This idea is consistent with the dual process view of recognition memory that is popular within the field of cognitive psychology, for example, the dual process high-threshold/signal detection theory (DPSD) of Yonelinas (1994). The DPSD cognitive model posits that two distinct processes underlie recognition memory decisions, namely familiarity and recollection. Recollection under the DPSD model is assumed to be a high-threshold, "all-or-none" process, in which an item either evokes recollection, giving rise to a high-confidence judgment of recognition, or the item evokes no recollection at all. When recognition fails, the subject is assumed to resort to familiarity, a mnemonic process said to be mutually exclusive with, and secondary to, recollection. The DPSD model assumes that familiarity is continuous and can be modeled by a signal detection process. In this scheme, all stimulus items possess a certain level of familiarity, with the population of items being composed of two distributions—"old" (encoded targets) and "new" (unfamiliar distracters)—that may overlap along the familiarity axis. Recognition decisions based upon familiarity are made by means of a fixed criterion; any item falling above the criterion is declared "old" and any item falling below it is declared "new". The DPSD model has been extremely influential in the field of recognition memory, not least because many neuroanatomical models use similar assumptions to separate the contributions of familiarity and recollection to empirical recognition data, in the search for neural correlates of these processes (Yonelinas et al., 1998; Rugg and Yonelinas, 2003; Aggleton and Brown, 2006; Wixted, 2007).

The representational-hierarchical account of object recognition memory is consistent with the idea that object representations in perirhinal cortex can provide an index of familiarity upon which recognition judgments may be based (Cowell et al., 2006; see discussion above). However, we do not presume that perirhinal cortex is the only region to compute familiarity. For example, in line with the idea that upstream VVS regions may contribute to recognition memory, Voss et al. (Voss et al., 2008; Voss and Paller, 2009) have reported that, under certain conditions, the accuracy of recognition memory judgments can be dissociated entirely from the hallmarks of explicit memory processes, such as high confidence in the response and enhancement by encoding with full attention. These functions are traditionally associated with medial temporal lobe structures at the anterior end of VVS. Instead, these studies suggested, with both behavioral and electrophysiological evidence, that repetition-induced perceptual fluency in occipital regions may have provided a reliable and valid memory cue; such a mechanism is very much in line with the familiarity signal produced by the "sharpening" of stimulus representations in both the perirhinal cortex layer and caudal VVS layer of our model.

Not only do we suggest that the putative familiarity signal may be computed in regions outside of perirhinal cortex, we also reject the assumption that it must be complemented by a cognitively and neuroanatomically distinct process of recollection. Indeed, the logical extension of the representational-hierarchical view would be that the distinction between recollection and familiarity may be accounted for not in terms of separate processes in separate neuroanatomical regions, but in terms of the stimulus representations maintained within those regions. For example, hippocampal stimulus representations possess a rich representational content including spatial, contextual or relational information (Eichenbaum et al., 1996; Squire et al., 2004) that may be necessary for making recognition memory judgments often attributed to a "recollection" process, such as source memory responses and retrieval of paired associates.

Therefore, we consider the possibility that differences between the contributions of perirhinal cortex and hippocampus to cognition may be best understood in terms of the types of stimulus representations that these structures maintain. On this view, it is possible that a difference in neural architecture between perirhinal cortex and hippocampus may be required in the representational hierarchy we propose, in order to augment the capacity of the processing stream as it transitions from representing single objects to representing complex episodic events and scenes—a transition that demands a dramatic increase in the dimensionality of stimulus space. In sum, our preliminary thesis is that, although the subjective phenomena of recollection and familiarity exist, these notions may not be rooted in differential psychological processes that map cleanly onto the structures of perirhinal cortex and the hippocampus. Instead, we attempt to define the contribution of these two regions to recognition memory in terms of the type and complexity of representations they contain. In this section, we illustrate our proposal by suggesting a reinterpretation of some recognition memory findings from the perspective of the representational-hierarchical view.

### Recognition Memory Tasks: Different Cognitive Functions or Different Representational Demands?

There is the potential for misinterpretation of lesion effects when the cognitive demands of behavioral tasks are not well characterized. As discussed in the context of visual discrimination learning, above, factors including task design, the stimulus material used in a task, and the task instructions can have a profound effect on the engagement of different brain regions. We suggest that this is because these factors can have a profound effect on representational demands. In the monkey visual discrimination tasks simulated by Cowell et al. (2010b), for example, networks required representations at a level of complexity appropriate for the stimuli and task design; in Tyler et al. (2004), the instructions in the two tasks required subjects to use different stimulus representations (even though the physical stimulus material being presented to subjects was the same in both tasks) in order to extract a different type of information. As a result, different brain regions were recruited in different task conditions.

Similar issues can arise in studies of recognition memory, where familiarity and recollection are presumed to be separable via the use of tasks that differentially engage the two cognitive processes. A typical paradigm for the collection of recognition memory data is a "source memory" task, in which subjects are presented with a list of study items each presented in one of two different formats. For example, items might be read aloud in either a male or a female voice, or presented on a computer screen at either the top or the bottom, or printed in red ink vs. blue ink, and so on. At test, subjects are required to indicate whether an item was on the study list (an "old/new" decision) and, if judged to be "old", from which source the item was produced (male/female, top/bottom, red/blue). It is assumed that an old/new judgment can be made on the basis of familiarity or recollection, whereas accurate source memory may rely only upon recollection (Jacoby, 1991; Yonelinas, 1999; Elfman et al., 2008). However, from the perspective of the representational-hierarchical framework, the mapping of these tasks onto distinct cognitive functions is potentially confounded by a difference in the representational demands of the two tasks. In the case of old/new judgments, it is sufficient that the moderately complex feature-conjunctions that constitute an object be recognized as previously encoded in order to carry out the task. In the case of the source memory task, possessing a "familiar" representation of the object-level conjunction is insufficient: the subject must have a representation that combines the item with the spatio-temporal or multi-modal context in which it was presented—a feat that most would agree depends on hippocampal processing. Indeed, in line with this analysis, Diana et al. (2007) suggest that item encoding in perirhinal cortex can be contrasted with item-and-context binding in hippocampus, in other words, different representational demands. At the same time, however, these authors describe the cognitive processes in terms of familiarity and recollection processes. We suggest that there is no need to invoke new processes when the representational demands already distinguish the tasks and give a plausible explanation of the differential involvement of perirhinal cortex and hippocampus. In our view, any differential engagement of perirhinal cortex and hippocampus by tasks such as source memory may be explained in terms of representational demands, without invoking distinct cognitive systems. Indeed, it would seem that the onus is on proponents of dual-process theories to show why invoking an explanation in terms of psychological process is necessary, when the very definition of recollection as involving context readily provides a more parsimonious account in terms of representational demands.

A second example of a potential confound between representational demands and cognitive processes is provided by the popular remember-know paradigm. Subjects are asked to indicate whether recognized items are remembered (accompanied by recollection of the encoding episode) or simply known (accompanied by a feeling of familiarity in the absence of information about specific details), with the assumption that "remember" responses engage a recollection process whereas "know" responses rely upon familiarity judgments. The canonical example of such a dissociation is provided by Mandler's (1980) "butcher on the bus" analogy, in which the face of the butcher encountered on the bus merely elicits a nonspecific feeling of familiarity until recollection of specific information (e.g., the context of the butcher's shop and the occasion of one's weekly shopping trip) occurs. In this example, recollection of the specific details requires a richer, more complex representation of the conjunction of face information with temporal, spatial and contextual details of the butcher's shop. The necessary face representation is likely available in anterior temporal lobe cortex (Kriegeskorte et al., 2007), whereas a complex conjunctive representation that integrates the spatial, temporal, and contextual details is presumably present only in the hippocampus (Eichenbaum et al., 1996; Squire et al., 2004; Diana et al., 2007). One reason perirhinal cortex is thought to be particularly important for familiarity is that it houses "unitized"—that is, conjunctive—representations (Yonelinas, this issue). We hope it is clear from the summary above that there is no reason to assume that perirhinal cortex is the only region that houses unitized representations; indeed the idea that conjunctive representations exist throughout the VVS is the "standard view" (Riesenhuber and Poggio, 1999). The perirhinal-unitization idea is that man + apron + hat forms a unitized representation of butcher. By this logic, however, it seems that butcher + butchershop, the representation we activate when we "recollect", should also be considered a unitized representation. And the same argument can be extended further, such that a very simple stimulus—orientation + horizontal motion, for example, known to be represented in very early regions of the visual system—is also considered a unitized representation. Without an explanation of why the perirhinal case constitutes unitization and the other cases do not, it might appear that the covert logic being employed in the dual process account is that because perirhinal cortex underlies familiarity, it must uniquely contain unitized representations—an argument that seems somewhat circular.

One conclusion that may be drawn from the foregoing interpretation of dissociations in the effects of perirhinal and hippocampal lesions is that the representational-hierarchical view suggests that both regions may be involved in making familiarity judgments. That is, the account is not consistent with a view of perirhinal cortex as the sole module for familiarity. We assess some of the evidence for that proposition in the next section.

## Evidence From Repetition-Sensitive Responding in Recognition Memory Tasks

As previously mentioned, interest in the distinction between recollection and familiarity was heightened when Aggleton and Brown (1999) proposed a neuroanatomical basis for these two processes. According to this view, the recollection process is carried out by the hippocampal-diencephalic system, which comprises the hippocampus, fornix, mamillary bodies, anterior thalamus, and retrosplenial cortex and the familiarity process is putatively subserved by an anatomically distinct system in medial temporal lobe cortex, including the perirhinal cortex and related structures (Mumby et al., 1995; Aggleton and Shaw, 1996; Maguire, 2001; Warburton et al., 2001; Aggleton and Brown, 2006; Carlesimo et al., 2007; Tsivilis et al., 2008).

An important line of evidence put forward by Aggleton and Brown to support the idea that perirhinal cortex is critical for detection of familiarity comes from the "repetition-sensitive responding" properties of some perirhinal neurons (Desimone, 1996; Brown and Xiang, 1998). This term refers to the observation that a neuron responds more strongly to the first presentation of a stimulus than to subsequent presentations of the same stimulus. Approximately a quarter of neurons in perirhinal cortex show repetition-sensitive behavior (Brown and Xiang, 1998), and Aggleton and Brown (1999, 2006) (Brown and Aggleton, 2001) have argued that this population of neurons in particular is critical for the detection of familiarity.

The representational-hierarchical view accounts for repetition sensitive responding in perirhinal cortex by suggesting that this neural mechanism forms part, but not the whole, of the code for familiarity discrimination. In the model of object recognition (Cowell et al., 2006), the mechanism for encoding an object in perirhinal cortex involves the sharpening of its representation. In the brain this would correspond to many neurons dropping out of the representation, but a few becoming more active in response to the encoded stimulus. That is, similar to other models of recognition memory (e.g., Norman and O'Reilly, 2003), the model suggests that enhancement of some neural responses as well as reduction in other neural responses is part of the code for familiarity, and indeed enhancement in a subset of neocortical neurons is found, empirically (Miller and Desimone, 1993; Rainer and Miller, 2000; Rainer et al., 2004).

Subsequent to the proposal of Aggleton and Brown (1999, 2006; Brown and Aggleton, 2001) that repetition-sensitive neurons are critical for the detection of familiarity, perhaps because of the widespread assumption (not necessarily strictly adhered to by Aggleton and Brown) that perirhinal cortex participates in a dedicated declarative memory system, perirhinal cortex has been treated to a certain extent as though it were a module for familiarity, and so has been studied in this regard to the exclusion of other regions (see Squire et al., 2007, for review). However, our view—given that the mechanism for encoding a visual stimulus as familiar in our model is simulated in the same way throughout the VVS—would suggest that familiarity judgments are not made on the basis of perirhinal cortex (or MTL) representations alone. Rather, familiarity judgments can, in principle, be made throughout the VVS. Indeed, an important corollary of the model's familiarity mechanism is the claim that repetition-sensitive responding should occur throughout the ventral visual-perirhinal-hippocampal stream in a stimulus-dependent manner.

Interestingly, there is considerable evidence for this proposition. For example, Brown and Xiang (1998) review the wealth of electrophysiological data indicating that repetition-sensitive responding is found throughout the inferior temporal cortex, and possibly in more posterior visual cortical areas. More recently, Vidyasagar et al. (2010) reported repetition-sensitive responding in areas V1, V2/V3, and area MT using oriented Gabor patches as stimuli in an fMRI study. Others have found repetition-sensitive effects in hippocampus when novel pictures of visual scenes (Stern et al., 1996) or other stimuli with a critical spatial component are used (Rolls et al., 1989; Feigenbaum and Rolls, 1991; Rolls and Omara, 1995). And indeed, Brown and Xiang (1998) spend a considerable amount of time discussing differences in response properties across different brain regions in the context of their potential utility as a familiarity signal. However, for the most part this body of data has not been focused on within the context of recognition memory. We suggest here that it might be interesting to consider these data in light of the representational-hierarchical view, in which the observation of repetition-sensitive responding throughout the VVS is interpreted as evidence for a mechanism for encoding visual stimuli in way that enables familiarity judgments throughout the entire pathway. Brown, Warburton and Aggleton (this issue) also suggest that a consideration of repetition-sensitive responding outside perirhinal cortex may be important for a full understanding of recognition memory.

An additional prediction of our framework is that repetition-sensitive responding should be seen in perirhinal cortex for object-level stimuli and in more posterior areas for simpler stimulus material. It is interesting, therefore, to consider the fact that the stimuli that are typically used in assays of familiarity are most often at the object level, and hence we would expect the effects of familiarity encoding in conventional tasks to be seen mainly in perirhinal cortex. Indeed, our view would suggest that there may well be a gradation in the extent of repetition-sensitive responding along the ventral-visual-perirhinal stream, due to an increase in the uniqueness of representations with progression from early visual areas to the anterior temporal lobe. Posterior regions of the VVS contain representations of stimulus features that are commonly occurring, and therefore—as in the mechanism for delay-dependent forgetting in the absence of perirhinal cortex—these representations suffer from greater interference than unique object representations in anterior regions. That is, the feature representations spend more time in a "recently encoded" state, and so the process of sharpening (see Grill-Spector et al., 2006), presumed in the model to be the underlying cause of observed repetition sensitive phenomena, may be less often witnessed. And indeed, this very uniqueness and the resulting relative lack of interference between representations may be a critical underlying reason that object-level stimulus representations are the most useful representations for computation of a signal of familiarity.

## Evidence From Animal Lesion and Imaging Studies of Recognition Memory

One of the major planks in the argument for perirhinal cortex as the specific locus of a signal for familiarity comes from studies of recognition memory in animals. It is well established that performance on object recognition tasks, in rats, is impaired by perirhinal cortex lesions. Therefore it is widely agreed that perirhinal cortex is important for the recognition of individual objects. Other researchers have used tasks that are direct analogues of the object recognition tasks, but which test spatial recognition (Jackson-Smith et al., 1993; Conrad et al., 1996; Sanderson et al., 2007). Using such tasks, these authors have found that rats with hippocampal lesions or receptor subunit deletions in hippocampus are impaired, relative to controls. Therefore it seems clear that the hippocampus is important for the recognition of places, in tasks analogous to object recognition.

In interpreting the effects of lesions on object and place recognition tasks, both a dual process account and the representational-hierarchical view would agree that perirhinal cortex is critical for the recognition of objects and the hippocampus is critical for the recognition of places. Where the two accounts differ is the way in which task performance is interpreted in terms of cognitive processes. The representational-hierarchical view claims that the critical difference between object and place recognition tasks is in terms of the representational demands of the task: in object recognition, representations of individual objects must be discriminated in terms of their prior occurrence, in place recognition it is different places that must be discriminated in terms of their prior occurrence. Therefore the object recognition findings indicate that representations in perirhinal cortex are critical for the familiarity discrimination of individual objects, and the place recognition findings indicate that the hippocampus is critical for the familiarity discrimination of places, which requires complex conjunctive representations of items and their spatial relations. This view is more or less identical to the interpretation Kesner (1999) has given to these data. A similar representational account also seems to be more appropriate for imaging studies such as that carried out by Wan et al. (1999). In this study, as noted by the authors, and in line with the representational-hierarchical framework, stimulus material was critical to the engagement of the different brain regions: areas within the hippocampus, but not perirhinal cortex, were differentially activated by novel and familiar spatial arrangements, whereas perirhinal cortex was instead differentially activated by novel vs. familiar items. Accounting for such data in terms of spatial vs. nonspatial content seems much more parsimonious than supposing that the recognition of familiar spatial arrangements, but not the recognition of familiar items, involves a recollective process.

## Contrasting the Representational-Hierarchical View With the Complementary Learning Systems Model

The complementary learning systems (CLS) account of Norman and O'Reilly (2003) is a computationally explicit dual process model of recognition memory, in which MTL cortex computations underlie familiarity judgments and computations in hippocampus underlie recollection. Although the Cowell et al. (2006) computational model of recognition memory superficially bears some strong resemblances to the CLS framework, the two models are distinguished by some fundamental differences.

In both the "MTL cortex" layer of the Norman and O'Reilly (2003) model and the perirhinal layer of the Cowell et al. (2006) network, object representations are encoded via a sharpening mechanism such that a highly tuned representation signals that an object is familiar. In Norman and O'Reilly, the computations in MTL neocortex make the region well-suited for performing pattern generalization, since a key feature of the MTL cortex component of the model is that similar stimuli have similar representations. This is contrasted in the model with the hippocampal mechanism, which performs pattern separation by pulling apart the representations of similar stimuli through the use of sparse representations. Despite the apparent similarities, the perirhinal layer of the model presented by Cowell et al. (2006) functions in a very different way from the "MTL cortex" layer in Norman and O Reilly (2003). In Cowell et al., the principal computational role of the perirhinal layer is more akin to pattern separation than pattern generalization. This is because of the assumption in Cowell et al. (2006) that objects are made up of discrete features, which are drawn from a pool that is limited in size. Eight possible input dimensions can each take on one of four values; this leads to a very large number of possible objects, but those object representations are nonetheless separated on the perirhinal cortex layer. The scheme of object representations leads to a much smaller number of distinct visual representations on the caudal layer, since here they are constrained to be represented as four separate "features", where a feature is a simple conjunction of two input dimensions. We represent object similarity in terms of shared features, which causes overlap in the representations on the caudal layer of the model (where features are represented individually) but not in the perirhinal layer, where a difference of just one feature is enough to give an object a totally new identity and evoke a distinct representation at the whole-object level. Thus, in the recognition memory simulations we have presented, perirhinal cortex performs pattern separation and representations in the caudal layer of the model provide a measure of the similarity between objects (pattern generalization). However, we note that this is the case only because all simulations were of object recognition memory. At this level of stimulus complexity, perirhinal cortex separates the stimuli, and all preceding layers of the VVS represent stimulus similarity. If the representational-hierarchical view were used to simulate place recognition, perirhinal cortex would become the locus of pattern generalization, and the hippocampus would be required for pattern separation.

In sum, in the representational-hierarchical view, the issue of which region performs pattern separation and which performs pattern generalization is determined by the level of stimulus complexity required by the task at hand, rather than by fixed functional roles of different brain structures (see also Kesner and Rogers, 2004). In algorithmic terms, throughout the stream, if "area n" performs separation, then "area n-1" performs generalization. So we would not expect that separation is performed only in the hippocampus and that MTL cortex performs only generalization. Rather than assuming distinct processes in the hippocampus and MTL cortex, we rely upon only an assumption of differences in the complexity of stimulus representations in the two regions, to account for functional differences.

We note that the CLS view, insofar as it shares assumptions with O'Reilly and Rudy (2001), also allows for the formation of conjunctive representations in MTL neocortex and does not claim that the hippocampus is the only site where conjunctive representations may be learned (O'Reilly and Norman, 2002); as such, MTL neocortex could in some cases contribute to pattern separation, and therefore the CLS view does not strictly assign fixed functional roles to MTL neocortex and hippocampus. However, the CLS framework claims that conjunctive representations in neocortex are learned in a slow, task-driven fashion, rather than automatically. Moreover, in O'Reilly and Rudy (2001), the development of conjunctive representations in neocortical regions occurs specifically when novel re-combinations of familiar features are required to solve the task, and is achieved by error-driven learning. Therefore the MTL neocortical processing that is assumed by the CLS framework contrasts with that assumed by our framework, in which conjunctive representations develop in an unsupervised and automatic manner, simply by virtue of the inputs to the region. Not only this, but the CLS view makes the explicit assumption of distinct cognitive processing mechanisms in the hippocampus vs. the MTL neocortex.

Therefore, for object recognition memory, there is a fundamental difference in the two frameworks' characterization of the role of perirhinal cortex: in our view, the contribution of perirhinal cortex depends critically on its ability to discriminate object-level conjunctions possessing shared features (pattern separation); in the CLS view, this pattern separation process is attributed to hippocampus. However, when considering tasks other than trial-unique object recognition, our view is consistent with the CLS framework. For example, the role of MTL neocortex assumed by the two models is very similar in repeated-items object recognition, perceptual discrimination of places, scenes and spatial configurations, and memory for complex episodic events involving "what," "where," and "when".

These similarities notwithstanding, the models of Norman and O'Reilly (2003) and Cowell et al. (2006) derive from opposing fundamental assumptions. The former model begins with the assumption that the hippocampus and perirhinal cortex use separate neural and cognitive mechanisms; the distinction between recollection and familiarity then emerges from the processing algorithms assumed in each component of the model (see also Elfman et al., 2008). The latter model emerges from a very different framework, in which stations both downstream and upstream of perirhinal cortex putatively operate according to similar underlying mechanisms, and functional differences emerge because of the way that information is represented at each station, specifically, because the complexity of conjunctions increases up the hierarchy. We would argue that the assumption of differences in representation is more parsimonious than an assumption of completely different modes of processing.

## CHALLENGES TO DUAL PROCESS MODELS OF RECOGNITION MEMORY: "MEMORY STRENGTH" AND "REPRESENTATIONAL COMPLEXITY"

Above we examined how some of the evidence in favor of dual process models of recognition memory can be reinterpreted within the single-process framework of the representational-hierarchical account. This is a novel approach, but not unique in its reexamination of the utility of the concepts of familiarity and recognition to understanding recognition memory (Wixted, 2007; Malmberg, 2008). Wixted (2007) has suggested that psychological measures of recognition memory can be best accounted for by a signal detection process operating on a single, continuous 'memory strength' variable. This view of the cognitive mechanisms of recognition memory has certain parallels with the representational-hierarchical view. The model that Wixted advocates suggests that while the processes of familiarity and recollection, at least subjectively, may exist, they are not confined to one brain region and nor do they operate in an independent and mutually exclusive manner. Rather, processes such as familiarity, recollection—and indeed other cognitive dimensions such as the perception of recency or frequency—are said to contribute jointly to a single perceived memory signal, and it is the strength of this signal that is taken into account when making recognition memory decisions.

Squire et al. (2007) have argued that many prior studies attempting to separate recollection and familiarity processes have instead separated strong from weak memories. This confound has occurred because there is a strong correlation between the strength of a memory and the ability to "recollect" that memory, as measured by tests such as associative recognition, the remember-know procedure and source memory. Squire et al. suggest that the frequent mapping of strong memories onto hippocampus and weak memories onto perirhinal cortex may be caused by different functions relating neural responses to the fMRI signal in these two regions.

The representational-hierarchical view also suggests a novel characterization of the functional distinction between hippocampus and perirhinal cortex, which, like the suggestion of Squire et al. (2007), is in line with the notion that a single mnemonic variable underlies recognition memory decisions. In our view, the hippocampus is most useful for recognition memory of stimulus material that involves rich representational content, such as the space, time and context of an event. In contrast, the perirhinal cortex is most useful for recognition memory of objects. If, as is often the case, recollection is defined in terms of the ability to retrieve spatio-temporal contextual details (such as source memory), then our view would support a division of recollection and familiarity across hippocampus and perirhinal cortex. However, our account does not require the assumption of separate processes in order to account for the data. Moreover, the representational-hierarchical view, unlike neuroanatomical dual process models, is not subject to the criticisms of Squire et al. (2007) that the evidence for separable neural substrates of familiarity and recollection is better explained by a memory strength hypothesis. Our framework can account naturally for the suggestion that strong memories are more often associated with the hippocampus and weak memories with perirhinal cortex, if one assumes that memory strength often (but not invariably) increases when richer content is incorporated into a representation, such as the context that is provided by hippocampal representations.

The foregoing compatibilities notwithstanding, there remain several key differences between the representational-hierarchical view and the account put forward by Squire et al. (2007). A critical difference is the reliance of our view on the type and content of representations in each brain region: under this account, the role of any brain region is determined by the representational demands of the task, and since labels for processes such as "recollection" and "familiarity" are avoided, we do not seek to test our model by searching for the neural signatures of these processes in either the hippocampus or the perirhinal cortex. A consequence of this difference is that the representational-hierarchical view predicts that the representational demands are critical to the involvement of different brain regions in recognition memory, but the "memory strength" hypothesis does not. Indeed, Squire et al. (2007) emphasize the similarities between perirhinal cortex and hippocampus in, for example, object recognition memory, whereas we emphasize functional double-dissociations between these two structures (Winters et al. 2004). A further distinction between the two accounts is that Squire and colleagues have consistently argued that recognition memory is mediated solely by structures within the MTL (Squire and Zola-Morgan, 1991; Squire et al., 2004), whereas the representational-hierarchical view explicitly predicts that recognition memory for certain stimulus materials should be carried out outside of MTL structures (Saksida, 2009), a prediction that was recently supported by the finding that cells in V2 contribute to recognition memory (Lopez-Aranda et al., 2009). A related distinction is that the representational-hierarchical view argues that structures such as the perirhinal cortex and hippocampus may have a role in perception and other nonmnemonic cognitive functions (much of the evidence for which was discussed above), whereas Squire and colleagues do not subscribe to this notion, arguing instead that the MTL is specialized for declarative memory (Buffalo et al., 1999; Squire et al., 2004; Shrager et al., 2006).

## CONCLUSIONS

In this paper, we have presented a representational-hierarchical model of cognition in the ventral visual-perirhinal-hippocampal stream. The model has been shown to account for many findings in the literature, including some very paradoxical ones. The strong version of this view questions anatomical modularization on the basis of psychological notions such as familiarity or recollection. Instead we assume that each region in the stream is able to contribute to a variety of cognitive processes depending on the representations it contains. The natural extension of this view accounts for recognition memory without appeal to distinct cognitive or neuroanatomical modules for recollection and familiarity. We do not deny the existence of the subjective experiences of familiarity and recollection, but we question the utility of these concepts for advancing our understanding of the neuroanatomical organization of recognition memory and the cognitive processes that may underlie it.

Evidence has been presented by others, throughout this issue and elsewhere, associating the hippocampus with the phenomenological experience that occurs when a memory is recollected in full, that is, including its spatio-temporal context. We have suggested that the simple reason that the hippocampus is usually involved during recollection as so defined is because it contains representations of spatio-temporal context. Put another way, the butcher on the bus is ambiguous, until the hippocampus resolves the "object-level ambiguity," by virtue of its higher-level spatio-temporal conjunctive representations (see discussion of "object ambiguity" above). But if conjunctive representations, and resolution of ambiguity, happen throughout the ventral visual-perirhinal-hippocampal stream, why then is primarily the hippocampus associated with the experience of recollection? We would argue that this is because of the way our world is constructed: our subjective experience of recollection tends to be in terms of spatio-temporal contexts, which are represented in the hippocampus. And because of this, the experience of recollection involves the hippocampus for filling in the spatio-temporal contextual details of a memory, that is, the dominant role of the hippocampus in recollection is due to the stimulus representations that it maintains.

However, we have been arguing that regions throughout the ventral visual-perirhinal-hippocampal stream are important for any cognitive function that requires the representations maintained in the region. Therefore, on this view, shouldn't regions throughout the ventral visual-perirhinal-hippocampal stream be important for both familiarity and recollection, depending on the stimulus representations required? Perhaps they are. Consider the following two scenarios, relating to familiarity and recollection, respectively.

Have you ever walked into a room and found it overwhelmingly familiar, yet not known why? This seems to be a universal experience. Since a room is a place, maybe this feeling of familiarity is mediated by the hippocampus. This possibility is supported by evidence from amnesics with selective hippocampal damage who show deficits in scene, but not face, recognition memory (e.g., Cipolotti et al., 2006; Bird et al., 2007; Taylor et al., 2007). It also mirrors the finding from animals, described above, that hippocampal lesions impair tests of place recognition analogous to the object recognition tests that have been taken as evidence for familiarity processes in perirhinal cortex. Thus, the hippocampus may be involved in feelings of familiarity as well as recollection.

Consider a second thought experiment. Let us first agree that a miniature model car is not a spatio-temporal context: it is an item, an object. A man collects hundreds of miniature model cars. One day, walking outside his house, he finds a tiny piece of bent metal. He is sure it is familiar, that he has seen it before. He has a feeling of familiarity. But where does he know it from? Then he remembers—it is the fender from his model Ferrari! With this remembrance comes flooding in all of the details of this object, he "sees" the tiny car in his mind's eye. He has the subjective feeling or experience of recollection. Since the car is an object, and not a spatio-temporal context, this feeling of familiarity is presumably mediated by regions outside the hippocampus, such as perirhinal cortex. This possibility is supported by the finding of intact recollection of faces (as measured using ROC analyses) in patients with focal hippocampal damage (e.g., Bird et al., 2007; Bird et al., 2008) and by evidence from brain imaging (see Awipi and Davachi, 2008). Thus, regions outside the hippocampus may be involved in feelings of recollection as well as familiarity. It seems to us that experiments manipulating feelings of familiarity and recollection, along with spatial and nonspatial material, could help distinguish the representational from the processing view.

So perhaps familiarity doesn't only occur for single items. And perhaps recollection can happen at lower levels of representation than a full "episodic" event. Maybe the experience of recollection is simply the positive experience of the resolution of ambiguity, at whichever level it occurs. And maybe in real life this resolution simply tends to happen less often with lower-level feature and object representations, and more often with higher-level, spatio-temporal, and contextual representations.

We hope that these preliminary thoughts on recognition memory, coming from a representational-hierarchical perspective, have provided readers with some useful and interesting food for thought.

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