

Untangling memory from perception in the medial temporal lobe

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An active debate in the learning and memory literature centers on the question of whether the perirhinal cortex, part of the medial temporal lobe (MTL), plays its major role in declarative/relational learning and memory or if it also makes an important contribution to high-level perception, similar to the functions of the adjacent visual area TE. Here I consider evidence from neuroanatomical and neurophysiological studies and argue that the perirhinal cortex has distinct and dissociable structure and function from area TE, making its major contribution to declarative/relational learning and memory. I propose additional neurophysiological studies that could help differentiate between these two debated roles of the perirhinal cortex: memory alone or memory plus high-level perception.

Two theories of medial temporal lobe (MTL) function

Brain areas throughout the entire ventral visual pathway from area V1 to area TE as well as the structures of the MTL all respond in a selective fashion to visual stimuli [1–3] and exhibit a wide range of different forms of plasticity [4–6]. Although both ventral visual stream and MTL areas share these two broad characteristics, one prominent view argues for a clear differentiation of function between these two regions. This view is supported by a broad range of neuropsychological studies as well as experimental lesion studies [7] and indicates that the MTL is primarily engaged in declarative/relational memory with little or no contribution to perception (MTL memory system view; **Box 1**) [8,9]. Ventral visual areas including visual area TE are thought to be primarily involved in visual perception as well as other non-declarative forms of plasticity, including procedural and perceptual learning as well as representation of long-term visual memories.

An alternative view supported by findings from neuropsychological studies in humans, experimental lesion studies as well as computational models [10], emphasizes the functional similarities between the structures of the ventral visual pathway and the MTL and suggests that the structures of the MTL should be considered more as a functional continuum with the areas of the ventral visual pathway (Perceptual–Mnemonic view; **Box 1**) [11]. Although different levels of this continuum are thought to contain different visual representations, they are also thought to share other key functions including the ability to form “conjunctive representations” [11,12]. The flash point of the disagreement between these two views centers

on the question of the functions of the perirhinal cortex: a part of the MTL that is located at the boundary between the ventral visual pathway and the rest of the MTL. Whereas the MTL memory system view argues that the major function of the perirhinal cortex is in the service of declarative/relational memory, the Perceptual–Mnemonic view argues that the perirhinal cortex plays important roles in both memory and high-level visual perception [7,10,13]. To bring a new perspective on this debate, in this article, I consider experimental findings from neuroanatomical studies and behavioral neurophysiology studies focused on the perirhinal cortex and visual area TE, which is considered the highest level of the ventral visual processing pathway. I argue that data from both these approaches support the idea that the perirhinal cortex and area TE exhibit distinct and dissociable structure and function, inconsistent with some of the key predictions of the Perceptual–Mnemonic view. Moreover, I argue that neurophysiological evidence indicates that what has been interpreted as a perceptual deficit following perirhinal lesions could be better understood as an associative learning and memory deficit. I propose neurophysiological experiments that could help differentiate between these two interpretations.

Evidence from neuroanatomical studies

Cytoarchitectonics

Cytoarchitectonics, or the study of laminar organization of cell bodies, can be helpful in defining and distinguishing between different brain areas. Detailed analyses of the major cytoarchitectonic characteristics of the perirhinal cortex and area TE do not indicate an incremental change from one area to the next as specified by the Perceptual–Mnemonic view, but instead they indicate a clear shift from classic neocortical features in area TE to more rudimentary allocortical-like features in the perirhinal cortex [14]. Area TE is a neocortical area characterized by a thick layer II, prominent granule cells in layer IV and small cells in deep layers V and VI (**Figure 1**). These are the same basic cytoarchitectonic features present in early visual areas (**Figure 1**) [15]. By contrast, the entorhinal cortex, part of the MTL, is a prototypical allocortical brain area with a more rudimentary organization distinguished by large darkly staining cells that organize themselves in irregular clumps in layer II, a complete absence of cells in layer IV and large darkly staining cells that make up deep layers V and VI (**Figure 1**) [16]. The question that arises is what are the cytoarchitectonic features of the perirhinal cortex, an area that sits between the entorhinal cortex and area TE.

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Box 1. Recent evidence supporting the Perceptual–Mnemonic and MTL memory system points of view

The MTL memory system view is anchored by the original description of human amnesia as a selective impairment in memory that does not affect perception [40] and since that time it has gathered support over many years of research from both neuropsychological and experimental studies in animals [13].

Most recently, many of the primary research studies that have addressed this debate have been done by groups attempting to explore the putative perceptual functions of the perirhinal cortex. For example, one recent study reported that human subjects with MTL damage, that included perirhinal cortex, exhibited significant impairments on the most difficult object “odddity” tasks in which subjects selected the odd stimulus from an array of similar stimuli [41]. These findings were interpreted as positive evidence for a role of the perirhinal cortex in perception. By contrast, Shrager *et al.* [42] reported that a different set of patients with MTL lesions that included the perirhinal cortex were unimpaired on a series of discrimination learning tasks and trial unique visual discrimination tasks requiring difficult perceptual discriminations. It has been proposed that the group of the MTL- damaged patients tested by Barense *et al.* [41] could have had significantly more lateral temporal lobe/visual cortex damage than the group studied by Shrager *et al.* [42] and that the different lesion extents could underlie these conflicting results [7]. Another recent study reported that bilateral

lesions of the perirhinal cortex in monkeys resulted in impairment on configural discrimination problems and suggested that these findings were consistent with the idea that the perirhinal cortex contains configural representation of visual stimuli [43]. However, because animals were trained on these problems after the lesion was made, it remains unclear if the observed deficit was due to impairment in configural learning, complex stimulus representations or both. A recent series of studies in rodents reported that rats with bilateral perirhinal lesions were impaired on single trial recognition memory tasks, consistent with the idea that these animals have visual perceptual deficits [37,38]. However, because the object stimuli being discriminated were large relative to the rat, it is possible that the animal was using a form of working memory to hold the key to differentiating features of the large objects because it sampled multiple objects during the exploration period. These recent findings and alternative interpretations illustrate both the challenges in disambiguating perceptual from mnemonic functions in lesion studies as well as the contentious state of the current field. For these reasons it will be important to turn towards a wider range of experimental approaches to address this question including both anatomical and neurophysiological approaches. Computational models that take into account the known physiological responses will also be useful in this regard.

The perirhinal cortex exhibits all the major allocortical characteristics of the entorhinal cortex including irregular clumps of darkly staining cells in layer II, a poorly defined layer IV and large darkly staining cells in deep layers V and VI (Figure 1) [14]. These data do not indicate a gradual blending of cytoarchitectonic features between areas, but a more abrupt shift from neocortical area TE to the allocortical-like perirhinal cortex. Data from tract tracing studies also support this view [17,18].

Patterns of cortical connectivity

Two major differentiating features distinguish the global connections of the perirhinal cortex from those of area TE

(Figure 2). The first is the range of sensory modalities that project to these areas. Many studies have defined area TE as the highest level of the ventral visual processing pathway because of its massive projections from other upstream visual areas [17,19,20]. By contrast, the perirhinal cortex receives input not only from visual areas (including a prominent direct input from area TE) but also direct input from somatosensory areas as well as other polymodal association areas including regions on the fundus and dorsal bank of the superior temporal sulcus and a major input from the parahippocampal cortex [18]. The second major differentiating feature between perirhinal cortex and area TE is their interconnections with the

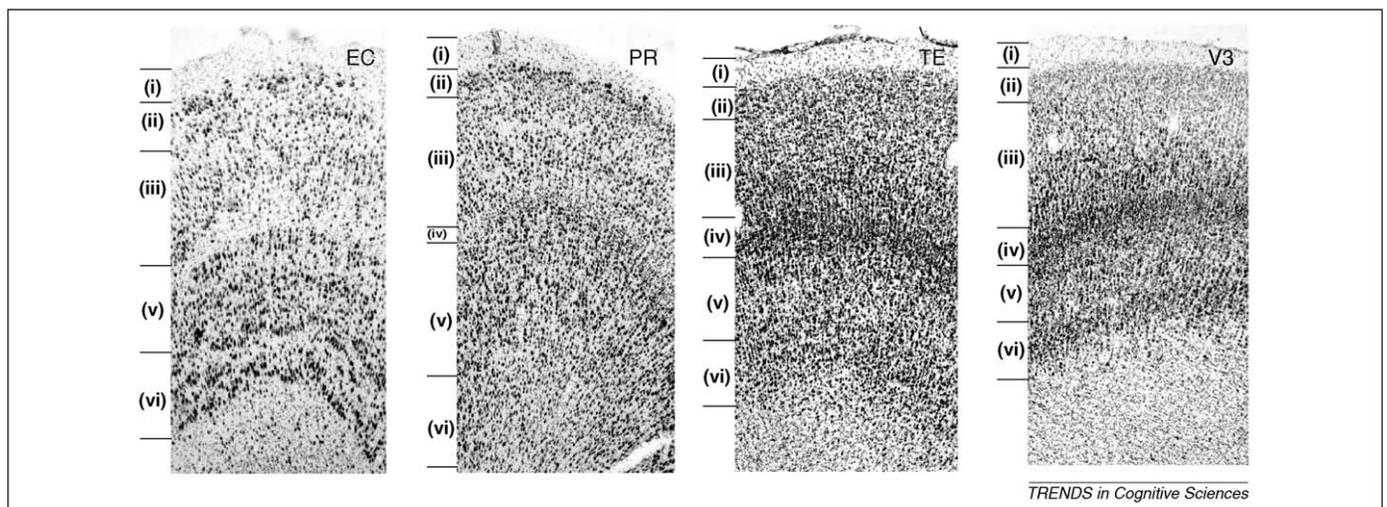


Figure 1. Cytoarchitectonic organization of the entorhinal cortex, perirhinal cortex, area TE and V3. Photomicrographs of Nissl-stained sections through various cortical areas showing the changes in cytoarchitectonic organization from allocortical areas (entorhinal cortex) to classic neocortical areas (visual area V3). The leftmost panel shows the intermediate subdivision of the entorhinal cortex (EC). The entorhinal cortex is a classic allocortical region with irregular clumps of darkly stained cells in layer II, a sparsely populated layer III, no granule cells in layer IV and deep layers V and VI made up of large, darkly stained cells. The middle left panel shows a section through area 36 of the perirhinal cortex (PR). Similar to the entorhinal cortex, area 36 also contains characteristic irregular clumps of darkly stained cells in layer II and large darkly stained cells throughout layers V and VI. The perirhinal cortex also contains a weak and sparsely populated layer IV. The middle right panel shows a section through visual area TE. In contrast to the perirhinal cortex, area TE exhibits a much more laminar organization with small lightly stained cells in layer II, a much thicker and more densely packed layer IV and deep layers made up of smaller cells than those seen in the allocortical areas. The right panel shows a section through another prototypical neocortical area V3, from a section situated at the level of the calcarine sulcus (–35.1 mm from Bregma). Area V3, similar to other early visual cortical areas including areas V1 and V2, is made up of small, lightly stained cells in layer II, a very thick and densely populated layer IV with an overall highly laminar organization.

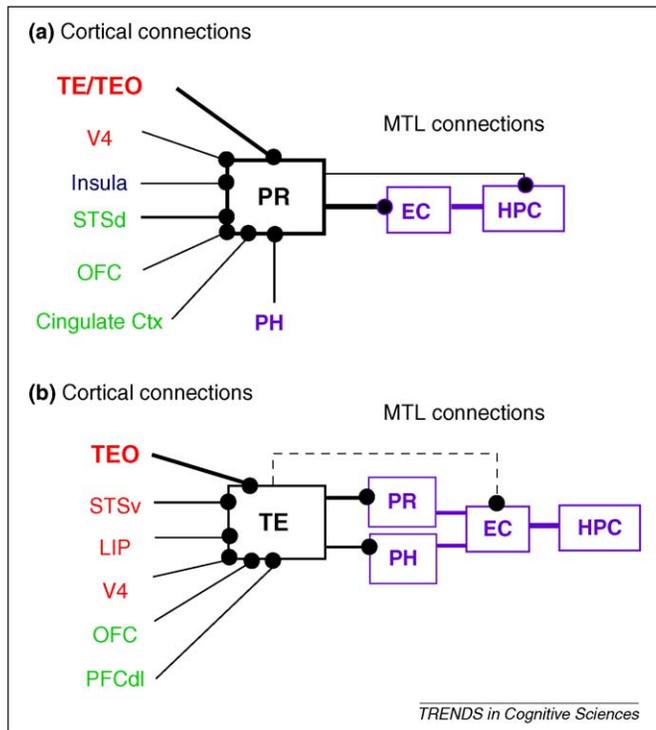


Figure 2. Major cortical and MTL connections of the perirhinal cortex and area TE. (a) Connections of the perirhinal cortex (PR). Left side of the panel lists the major cortical inputs to the perirhinal cortex. Visual areas are color coded in red, somatosensory areas in blue and polymodal association areas are shown in green. MTL areas and their interconnections are shown in purple. The size of the lettering and thickness of the lines illustrates the relative density of the projections. The right side of the figure illustrates the interconnections of the perirhinal cortex with the entorhinal cortex (EC) and hippocampus (HPC), the major components of the hippocampal formation. (b) Connections of visual area TE. Left side of the panel shows the major inputs to visual area TE. Note that all major cortical inputs to area TE arise from other visual areas except those polymodal inputs from the orbitofrontal cortex (OBF) and the dorsolateral portions of the prefrontal cortex (PFCdl). The right side of the panel shows the projections of area TE into the MTL. Although TE projects to both the PR and parahippocampal (PH) cortices, its projections to the EC are limited (indicated by the dashed line) and it has no direct projections to the HPC. Other abbreviations: V4, visual area V4; Cingulat Ctx, cingulate cortex area 23; STSd, dorsal bank of the superior temporal sulcus; STSv, ventral bank of the superior temporal sulcus; LIP, area LIP of the posterior parietal cortex; PH, parahippocampal cortex areas TH and TF.

hippocampal formation (i.e. the hippocampus and entorhinal cortex). Whereas the perirhinal cortex has powerful direct projections to the entorhinal cortex [21,22], as well as direct interconnections with area CA1 of the hippocampus [23–25], area TE has only limited direct projections to the entorhinal cortex [26,27] and no direct input to area CA1. Taken together, the connectional and cytoarchitectonic data support the view that perirhinal cortex is not part of a continuum of the ventral visual pathway, but instead is a unique polymodal association area with strong structural and connectional ties to the rest of the hippocampal formation.

Evidence from behavioral neurophysiology

Although few studies have directly compared the neurophysiological properties of perirhinal and TE neurons on the same task, the available data indicate that these areas exhibit distinct forms of neural plasticity. Naya, Miyashita and their colleagues compared the responses of neurons in the perirhinal cortex and area TE during the performance of a long-term visual paired-associate (VPA) task after

Box 2. The VPA task

Associative memory is defined as memory for the relationship between two or more items. We use this form of memory on a daily basis and it includes our ability to learn the name of someone we have just met (e.g. name–face associative learning/memory). A classic way to tap associative memory in monkeys is with the use of the VPA task. In this task, monkeys are not associating names with faces, but visual stimuli with other unique visual stimuli. Figure 1 presents an illustration of the types of stimuli and individual trials employed in this task.

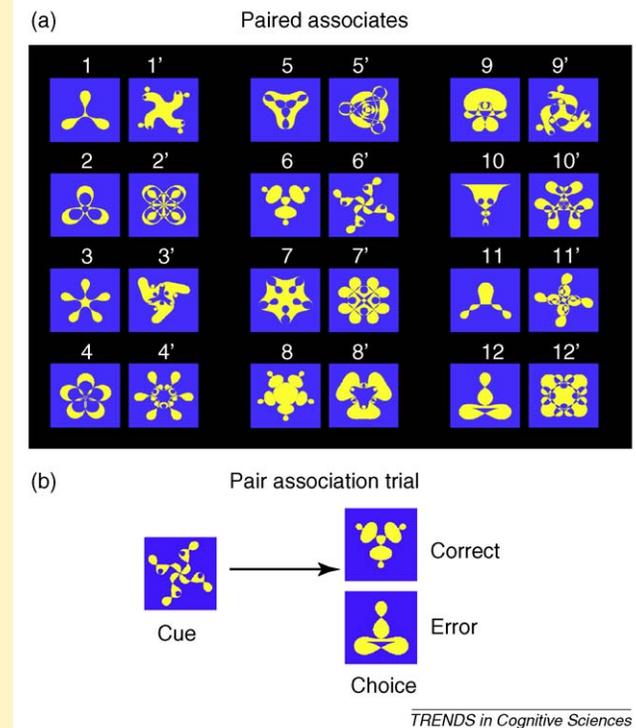


Figure 1. The VPA task. (a) In the studies discussed in [44] and [29], 12 pairs of Fourier descriptors (1-1' and 12-12') were used as stimuli. (b) This panel shows the sequence of individual trials. Cue stimuli were presented at the center of a video monitor. Choice stimuli were presented randomly in two of four positions on the video monitor. One of the choice stimuli was the paired associate of the cues (Correct-pair 6 and 6') and the other choice stimulus is a distracter (Stimulus 12). Reproduced with permission from Sakai and Miyashita [44] and Naya et al. [29].

animals had learned to associate two unrelated visual objects in long-term memory (Box 2) [28,29]. A similar proportion of neurons in the perirhinal cortex and area TE responded selectively to the complex visual images used in this task, but differed dramatically in their representation of the learned long-term associations [29]. Whereas 33% of the visually responsive perirhinal neurons signaled the learned associations with highly correlated responses to the pairs of stimuli that had been associated in long-term memory (pair coding signals; Figure 3a), only 5% of the visually responsive cells in area TE showed such responses. Analysis of the retrieval signal seen during the delay period of this same task indicated that the perirhinal cortex initiates the retrieval signal whereas area TE serves as a relay station for the retrieved information (Figure 3b) [28].

Consistent with previous lesion studies [30], several neurophysiological studies have reported that perirhinal neurons participate in new associative learning, changing

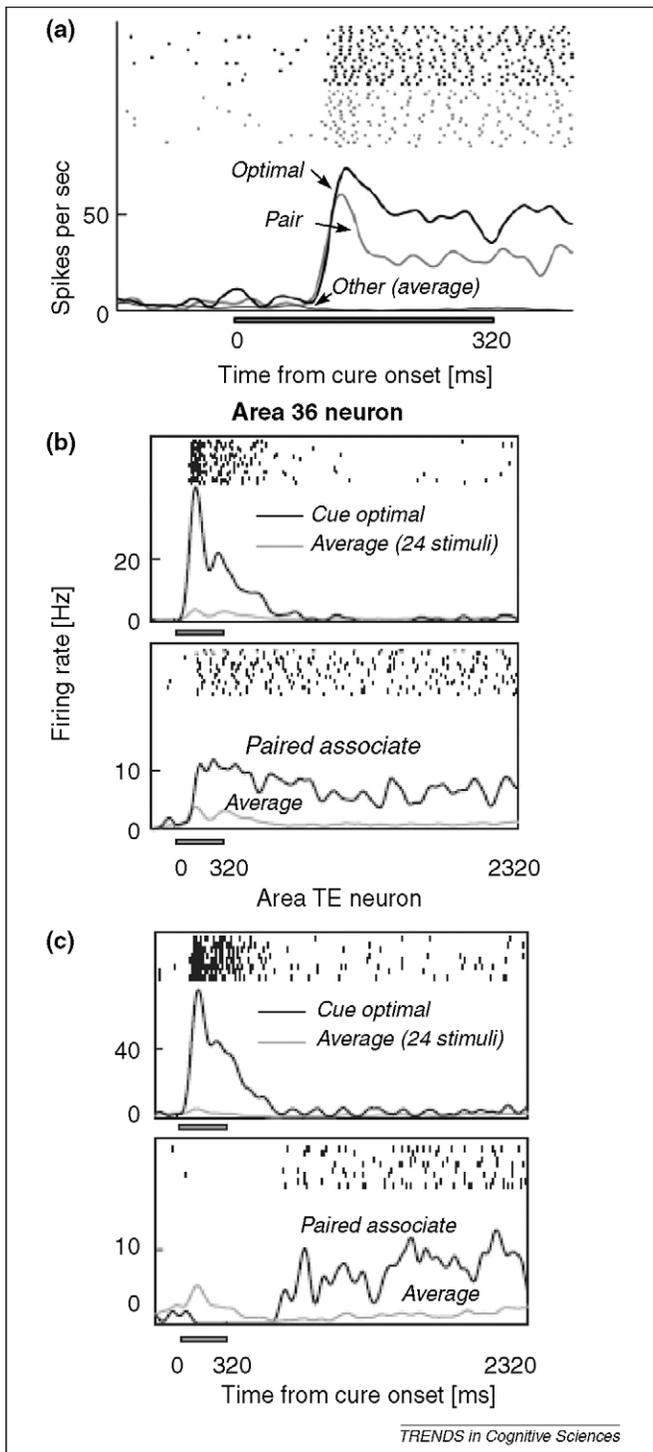


Figure 3. Long-term associative memory and retrieval signals in the perirhinal cortex. **(a)** Illustration of a pair-coding cell in the perirhinal cortex showing its stimulus-selective responses to the optimal stimulus (stimulus that elicits the highest response; thick black line) and the pair stimulus (the paired associate of the optimal stimulus; gray line) during the VPA task (Box 2). The thin black line denotes the average response to the other trials (other). The horizontal bar indicates the cue presentation period. **(b)** Illustration of neuronal activity related to memory retrieval (pair recall neuron) in the perirhinal cortex. Black lines indicate responses to the cue-optimal stimulus (upper panel) or its paired associate (lower panel). Gray lines show the mean responses to all 24 stimuli. Stimulus-selective delay activity following the paired-associate presentation was closely coupled with a strong and early cue response to its paired associate (lower panel). **(c)** Illustration of neural activity related to memory retrieval in area TE (all conventions the same as (b)). Similar to the perirhinal cortex, TE neurons responded to the cue optimal stimulus robustly. However, the response to its paired associate was significantly delayed within the trial related to the signal seen in the perirhinal cortex. Reproduced with permission from Naya *et al.* ((a) [29]) and Naya *et al.* ((b) [28]).

their firing rate and stimulus-selective responses dynamically in parallel with the animal's behavioral learning curve (Figure 4) [6,31]. Unfortunately, the same dynamic learning signals have not been examined in area TE during new associative learning. Several studies report shifts in stimulus selectivity in area TE after difficult-to-learn visual discriminations [4,32,33] however, the dynamics of these shifts in selectivity have not been examined [34]. Although the literature comparing learning signals across the perirhinal cortex and area TE is far from conclusive, the available data support the view that these areas exhibit distinct functions. The perirhinal cortex exhibits fast associative learning [6,31], long-term associative representation [29] and associative retrieval signals [28]. By contrast, area TE provides sensory signals into the perirhinal cortex [28] and signals well-learned complex visual stimuli with increased selectivity [4,32,33].

Using neurophysiological findings to differentiate between the MTL memory system and Perceptual-Mnemonic views

One prediction supported by the neurophysiological findings is that the perirhinal cortex is necessary in a task that requires associative learning, memory or retrieval. Although this prediction will ultimately need to be tested using lesion/inactivation studies, it provides an alternative explanation for the perirhinal lesion effects that have been interpreted as evidence for a perceptual function of the perirhinal cortex. Previous studies show that perirhinal lesions impair the ability to learn complex discriminations with high feature overlap [35–38], including trial unique learning situations [37]. However, because normal animals could have solved these discriminations by using their perirhinal cortex to associate the differentiating visual features of the individual stimuli in memory [6,30], impaired associative learning and not impaired perception could underlie the observed learning deficit. By contrast, in simple discrimination tasks, visual stimuli processed by area TE can be directly associated with reward, not requiring the additional visual associative functions of the perirhinal cortex. Neurophysiological recordings showing perirhinal neurons that change their firing rate selectivity in parallel with learning during high feature overlap discriminations would support an associative learning interpretation. This learning signal would be first seen in the perirhinal cortex and then propagate to area TE. By contrast, if the perirhinal cortex was crucial for the perception of these complex stimuli, one would predict highly selective responses to these stimuli even before learning occurred. The observation that the perirhinal cortex can associate a wide range of stimuli in memory [6,30] including simple visual stimuli [39] leads to the suggestion that the perirhinal cortex could be required in all situations requiring new associations to be learned dynamically irrespective of the complexity of the visual stimulus. Although both views predict that the perirhinal cortex would exhibit learning/memory signals during a simple color-color conjunction/association task, only the Perceptual-Mnemonic view predicts that the crucial area for such coding would be found in the visual area one step higher in the hierarchy from the area in which the stimuli can be

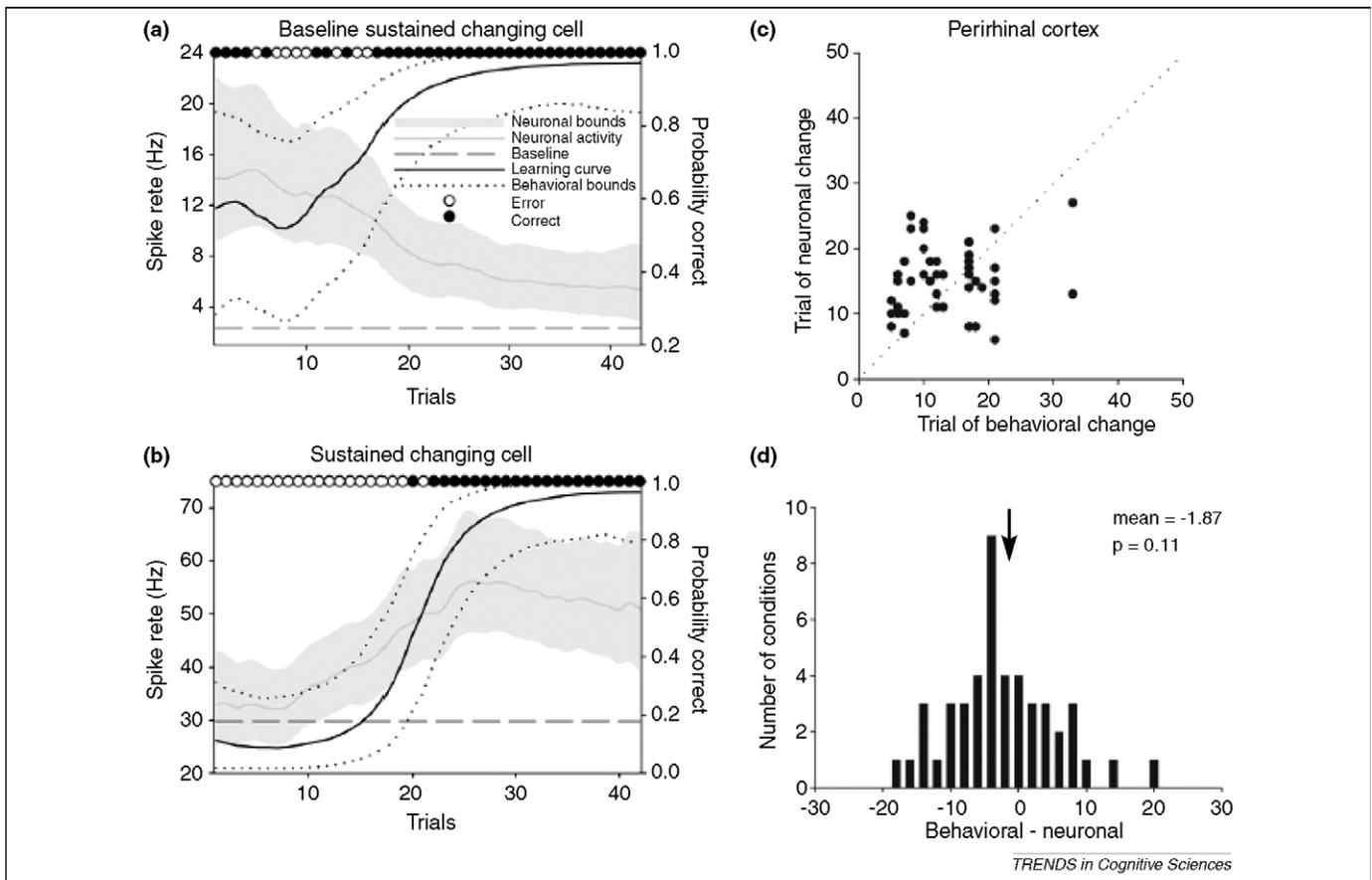


Figure 4. Associative learning signals in the perirhinal cortex. (a) and (b) illustrate the dynamic changes in neural activity seen in the perirhinal cortex as a function of learning. (a) shows a baseline sustained changing cell that signals learning by decreasing its firing rate to baseline levels of activity in parallel with learning. By contrast, the sustained changing cells signal new learning with increases in their neural activity that parallel the animal's behavioral learning curve. (c) shows the distribution of trial number of behavioral change plotted against the trial number of neural change. Conditions where learning lags behind changes in neural activity appear below the unity line and conditions where learning leads changes in neural activity appear above the unity line. The histogram (d) shows the number of conditions with particular lead/lag values. Positive differences between behavioral and neural change values indicate condition when learning lagged behind changes in neural activity. These findings show that perirhinal neurons change their activity dynamically in parallel with new associative learning. Reproduced with permission from Yanike *et al.* [6].

resolved (i.e. in area TE for simple color stimuli). By contrast, the MTL memory system view predicts that the associative learning, memory and retrieval signal would be dependent on the perirhinal cortex. These neurophysiological predictions provide a novel way to test the putative role of the perirhinal cortex in memory versus perception.

Conclusions and future directions

I have argued that, consistent with the MTL memory system view, data from neuroanatomical and neurophysiological studies support the idea that the perirhinal

cortex and area TE have distinct and separable functions. Whereas the perirhinal cortex acts in the service of declarative/relational learning and memory, area TE is involved primarily in higher order visual perceptual functions. It will be important to continue considering both anatomical and physiological approaches as we work to understand the important question of the functional relationship between the MTL and the areas of the ventral visual processing pathway (Box 3).

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Box 3. Questions for future research

- What is the pattern and dynamics of neuronal responses in area TE during the learning of new associations?
- What is the pattern and dynamics of neuronal responses in TE and the perirhinal cortex during incremental discrimination learning tasks?
- Do perirhinal and TE neurons exhibit similar abilities to conjoin stimuli in memory (i.e. conjunctive representation of Bussey and Saksida, 2007 [11])?
- How do the perirhinal cortex and area TE interact during new learning, consolidation and retrieval of associative memories?

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