ANNUAL REVIEWS

Annual Review of Vision Science

Perception and Memory in the Ventral Visual Stream and Medial Temporal Lobe

Chris B. Martin[1] and Morgan D. Barense[2,3]

[1]Department of Psychology, Florida State University, Tallahassee, Florida, USA; email: cmartin@psy.fsu.edu

[2]Department of Psychology, University of Toronto, Toronto, Ontario, Canada; email: morgan.barense@utoronto.ca

[3]Rotman Research Institute, Baycrest Hospital, Toronto, Ontario, Canada

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Annu. Rev. Vis. Sci. 2023. 9:8.1–8.26

The *Annual Review of Vision Science* is online at vision.annualreviews.org

https://doi.org/10.1146/annurev-vision-120222-014200

Copyright © 2023 by the author(s).
All rights reserved

Keywords

memory, perception, medial temporal lobe, ventral visual stream, perirhinal cortex

Abstract

Perception and memory are traditionally thought of as separate cognitive functions, supported by distinct brain regions. The canonical perspective is that perceptual processing of visual information is supported by the ventral visual stream, whereas long-term declarative memory is supported by the medial temporal lobe. However, this modular framework cannot account for the increasingly large body of evidence that reveals a role for early visual areas in long-term recognition memory and a role for medial temporal lobe structures in high-level perceptual processing. In this article, we review relevant research conducted in humans, nonhuman primates, and rodents. We conclude that the evidence is largely inconsistent with theoretical proposals that draw sharp functional boundaries between perceptual and memory systems in the brain. Instead, the weight of the empirical findings is best captured by a representational-hierarchical model that emphasizes differences in content, rather than in cognitive processes within the ventral visual stream and medial temporal lobe.

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

INTRODUCTION

The notion of a modular mind is a core tenet of cognitive psychology. Early theorists relied on introspection to establish an ontology that reflected phenomenological distinctions among various aspects of cognition, such as memory, perception, and language (James 1890). Despite the challenges associated with drawing clear lines between psychological constructs, this parsing made empirical research on the mind possible. It established a common set of descriptions that facilitated communication across research groups, helped to define targeted research questions, contributed to the development of process-specific experimental paradigms, and provided a lens through which empirical results could be interpreted (Poldrack & Yarkoni 2016). In short, it made an immensely complex problem tractable. It also meant that research in cognitive psychology progressed along multiple parallel lines, each focused on a specific kind of cognition, with relatively limited crosstalk. Ultimately, evidence from behavioral and computational modeling research codified the idea that different kinds of cognition reflect fundamentally different kinds of domain-specific mental processes (Fodor 1983, Pylyshyn 1986, Tulving 1985a).

The tradition of carving cognition at its conceptual joints naturally shaped the research agenda in cognitive neuroscience (Fodor 1983). The discipline was fractured along the same ontological lines that divided cognitive psychology, and the pursuit of understanding a modular mind gave way to the pursuit of understanding a modular brain. Whether through neuropsychological investigations with patients or neuroimaging with neurologically healthy individuals, the formative period of cognitive neuroscience was characterized by attempts to map specific cognitive functions to discrete brain regions. Widely influential theories were predicated on the idea that different brain regions support different kinds of cognition (Cosmides & Tooby 1994, Kanwisher et al. 1996). One enduring idea that emerged from this process-based brain mapping tradition is that the cortical areas that support memory are distinct from those that support visual perception; the medial temporal lobe (MTL) constitutes a dedicated memory system that is distinct from the ventral visual stream (VVS) object processing hierarchy (Mishkin et al. 1983, Squire & Zola-Morgan 1991).

Intuitively, memory and perception feel like different aspects of cognition. One involves the apprehension of information outside of the mind, whereas the other involves a reawakening of previously encountered information that is stored inside the mind. This distinction can be a useful heuristic in the classroom and may even be sufficient to motivate an ontological delineation within cognitive psychology, but are the boundaries between memory and perception really so clear when it comes to the functional organization of the brain? Although our memories are complex and multimodal, they are often dominated by visual features, raising the question of whether processing visual information in memory reflects a neural architecture that is different from or common to that which supports visual perception.

The purpose of this review is to reanimate and update a discussion centered on the idea that the functional organization of the VVS and MTL is best captured by representational distinctions, rather than process-based distinctions. We focus on memory and visual perception to demonstrate the fact that a given brain region can enable multiple different kinds of cognition if the information to which it is preferentially tuned is task relevant (Bussey & Saksida 2007; Cowell et al. 2019; Graham et al. 2010; Lee et al. 2005a,b; Murray & Bussey 1999; Murray et al. 2007; Price & Friston 2005). For example, if a given brain region contains fully specified representations of objects, then this brain region will be recruited for both perceptual and mnemonic tasks should performance on these tasks require complex information about objects. This so-called representational perspective does not entirely dispense with the notion of a modular brain; instead, it suggests that the functional differences between modules are best thought of in terms of differences in kinds of information, rather than in kinds of processes. We illustrate this point through

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

consideration of findings from largely parallel lines of research on memory and visual perception conducted in humans and nonhuman animals. Specifically, we highlight evidence that reveals a role for structures in the VVS in supporting memory and a role for structures in the MTL in supporting visual perception.

Given the apparent diversity of its contributions to cognition, we place particular emphasis on the functional properties of the perirhinal cortex (PRC), a structure that sits at the interface of the VVS and the MTL. It enables mnemonic discrimination among categorized exemplars (Martin et al. 2013, 2018b; Kafkas et al. 2017), perceptual discrimination among visually similar objects (Barense et al. 2005, 2010, 2012; Baxter & Murray 2001; Buckley and Gaffan 1997; Eacott et al. 1994; Ferko et al. 2022; Inhoff et al. 2019; Lee et al. 2005a,b; O'Neil et al. 2009), semantic discrimination among conceptually similar objects (Kivisaari et al. 2012, Moss et al. 2005, Wright et al. 2015), and conceptual priming (Dew & Cabeza 2013, Heusser et al. 2013, Voss et al. 2009, Wang et al. 2010) and tracks cumulative lifetime experience with objects (Bowles et al. 2016, Duke et al. 2017). Its role in enabling these fundamentally different functions is not easily reconciled with a modular perspective of functional brain organization, at least not one based on classical distinctions between kinds of cognition.

As a starting point, we summarize theoretical models and synthesize relevant evidence that point to the VVS and the MTL as distinct perceptual and memory modules in the brain.

PERCEPTUAL PROCESSING IN THE VENTRAL VISUAL STREAM

Information leaving the primary visual cortex is channeled through two separate pathways (Goodale & Milner 1992, Mishkin et al. 1983). The dorsal pathway, also called the where or how pathway, is an occipitoparietal network of cortical areas that supports spatial cognition and the real-time transformation of visual input into motoric output. The ventral pathway, also called the what pathway, is an occipitotemporal network that supports the recognition of object identity by bridging visual input with information represented in long-term memory, including semantic and episodic knowledge. The fact that a visual stimulus changes rather dramatically over multiple timescales makes this process computationally very demanding. For example, when your dog Milo transitions from laying to running to rolling over, the visual information detected by the retina is radically different from one moment to the next, yet you have no trouble recognizing him as Milo despite these changes. This ability necessarily involves an abstraction of the stable and enduring qualities of a visual stimulus. To understand the relationship between visual perception and memory, we must first summarize the VVS mechanisms that support this abstraction and consider the historical perspective regarding the division between perception and memory.

The Neuroanatomy of Visual Object Recognition in the Ventral Visual Stream

It has long been known that the inferotemporal cortex makes critically important contributions to visual object recognition. Klüver & Bucy (1937) first noted that macaques with inferotemporal lesions were unable to discriminate between visually presented objects or associate them with previously learned behaviors. This pattern of impairment was replicable and highly specific in that lesions to the inferotemporal cortex affected recognition of objects but not perception of their spatial configurations (Pohl 1973). Building on these results, Mishkin et al. (1983) formalized the notion of ventral and dorsal visual pathways in a theoretical model that motivated a torrent of research, largely in nonhuman primates, that describes the connections among ventral stream regions in exquisite detail.

The projections from the striate cortex through the anterior temporal lobe were initially thought to form a serially organized anatomical hierarchy in which information moves rostrally

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

for additional processing (Felleman & Van Essen 1991, Riesenhuber & Poggio 1999). More recent theoretical conceptions of the ventral visual pathway highlight the fact that there are local and long-range feedforward and feedback connections that can account for categorical selectivity and top-down influences on visual perception (Kravitz et al. 2013). As it relates to mapping visual input onto representations stored in long-term memory, information flows from V1 to V2, to ventral aspects of V3 and V4, to area TEO, and finally to area TE. In monkeys, areas TEO and TE generally refer to the posterior and anterior inferotemporal cortex, respectively. Although it is difficult to directly compare brain areas in different species, it is assumed that area TE in monkeys corresponds to the lateral occipital cortex (LOC) in humans (Kourtzi & Kanwisher 2001, Orban et al. 2004). Of particular importance for this review, a major projection from area TE in macaques and the LOC in humans is to the PRC (Saleem & Tanaka 1996, Suzuki & Amaral 1994, Suzuki & Naya 2014), located on the ventromedial surface of the temporal lobe (**Figure 1**).

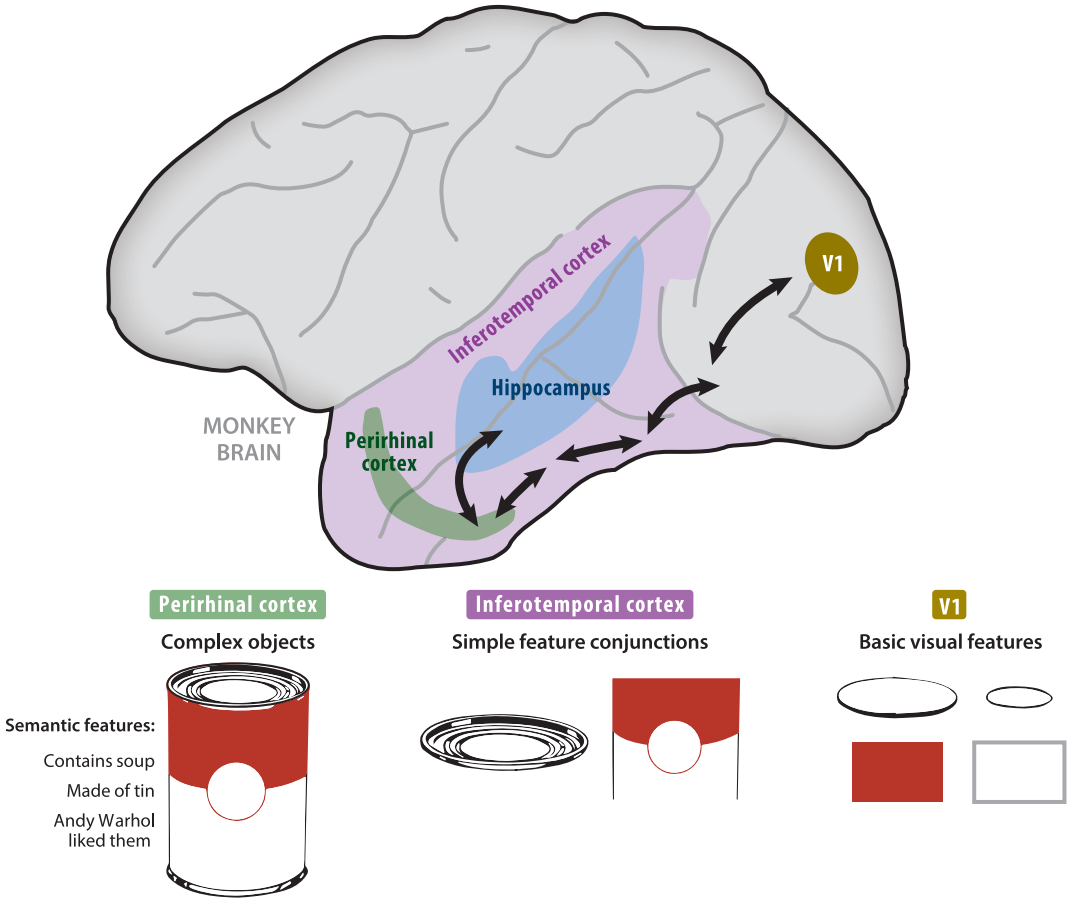

Figure 1

The ventral visual stream (VVS) object processing hierarchy in the rhesus macaque. The VVS originates in the primary visual cortex (V1; *gold*) and progresses along the ventral surface of the temporal lobe toward the perirhinal cortex (*green*). This pathway is organized hierarchically, such that regions in the posterior extent represent simple features, and more anterior regions represent increasingly complex information. A significant proportion of projections from the perirhinal cortex terminate in the hippocampus (*blue*), which represents high-dimensional content from both the ventral and dorsal visual streams. The hippocampus is thought to make important contributions to both episodic memory and spatial perception.

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Functional Properties of Object Recognition in the Ventral Visual Stream

The anatomical hierarchy in the occipitotemporal cortex can also be characterized as a functional hierarchy in which visual information is successively integrated into increasingly complex conjunctions of features (Barlow 1972). Within this framework, a given visual stimulus, such as an object or face, is represented by many neurons that respond to local features of a stimulus in low-level visual areas (e.g., V1) and relatively few neurons that respond to more holistic patterns in high-level visual areas (e.g., area TE). Thus, the conjunctive transformations that take place as information moves rostrally in the ventral visual pathway culminate in object-level representations that are encoded in a relatively small number of cells.

The idea of a representational hierarchy of increasing complexity is consistent with evidence from electrophysiological recordings in neurons along the rostral-caudal axis of the VVS. First, the receptive field size of individual cells increases moving anteriorly from V1 (Op De Beeck & Vogels 2000, Tanaka et al. 1991). Specifically, neurons in the striate cortex are activated when a visual stimulus occupies a very narrow part of the visual field, including the periphery, whereas neurons in area TE respond to stimulation of a much larger expanse of the visual field that almost always includes the fovea. The large receptive fields in the anterior inferotemporal cortex enable generalization across an object's features irrespective of where the object is in space. Second, the selectivity and complexity of neurons increases along the ventral visual pathway (Desimone et al. 1984, Gross et al. 1972, Quiroga et al. 2005). Neurons in V1 respond to simple features, such as a line in a particular orientation, that are common to many different stimuli. Conversely, neurons in the anterior inferotemporal cortex respond selectively to complex stimuli from within a given category, e.g., either faces or fruits but not both. Feedforward deep neural networks from computer vision have also revealed a gradient of complexity that does a reasonably good job of predicting corresponding differences in the complexity of object-evoked responses obtained using functional magnetic resonance imaging (fMRI) in humans and nonhuman primates (Cadieu et al. 2014, Güçlü & van Gerven 2015). Lastly, there is an increase in the degree of viewpoint and cue invariance along the ventral visual pathway (Hasselmo et al. 1989; Perrett et al. 1982, 1991; Rust & DiCarlo 2010). In the inferotemporal cortex, there appear to be at least two types of neuronal responses across multiple viewpoints. One subset of neurons expresses strong viewpoint dependencies, selectively firing in response to a given stimulus viewed at a particular angle. Another set of neurons expresses viewpoint invariance, selectively firing in response to a given stimulus irrespective of the viewing angle (Freiwald & Tsao 2010). This invariance extends to other optical transformations, including size, lighting, and color (Hietanen et al. 1992, Ito et al. 1995, Perrett et al. 1992). This pattern of results has been replicated in research conducted using fMRI in humans (Axelrod & Yovel 2012).

Large-Scale Perceptual Organization in the Ventral Visual Stream

As its name suggests, the VVS is traditionally described as a perceptual processing module. However, there are reliable differences in perceptual processing within this pathway. Lesion and neuroimaging research in humans and nonhuman primates has revealed several occipital and inferotemporal cortical regions that are biased toward processing stimuli from various biologically significant categories, including but not limited to objects and faces. The LOC has been linked to the processing of object shape in neurologically healthy participants (Grill-Spector et al. 2001, Kanwisher et al. 1997b). Findings from the seminal research conducted with patient D.F., an individual who has bilateral lesions in the LOC, support these neuroimaging results. Specifically, D.F.'s brain damage resulted in visual form agnosia, a condition characterized by an inability to consciously perceive shape (Goodale et al. 1991, James et al. 2003). Downstream of the LOC, the fusiform face area (FFA) responds preferentially to faces as compared to other categories of stimuli (Kanwisher

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

et al. 1997a, McCarthy et al. 1997, Nasr & Tootell 2012). A homolog of the FFA has also been identified in nonhuman primates (Tsao et al. 2006). Damage to the fusiform gyrus has been associated with a selective inability to discriminate between faces, likely due to impaired holistic face perception (Barton et al. 2002, Dalrymple et al. 2011, Moscovitch et al. 1997; see also Avidan et al. 2005, Steeves et al. 2006), and directly stimulating this region with surgically implanted depth electrodes selectively disrupts face perception (Parvizi et al. 2012). The origin of these category-specific perceptual clusters is not entirely clear, although it has been suggested that their selectivity reflects downstream consequences of retinal eccentricities in the striate cortex (Kravitz et al. 2013).

In addition to category-specific clustering of visual processing hubs, considerable evidence suggests that categorical information about visually presented objects is also represented within population codes that are distributed across the inferotemporal cortex both within and beyond specialized areas (Haxby et al. 2001, Kriegeskorte et al. 2008). The functional contributions of clustered and distributed categorical representations to object recognition remain a matter of debate; one promising suggestion is that clustered responses allow for rapid categorization, whereas distributed responses allow for discrimination among category exemplars (Grill-Spector & Weiner 2014).

Interactions Between Perceptual and Memory Modules

The evidence reviewed above suggests that the VVS contributes to object recognition by transforming simple visual features represented in its caudal extent into increasingly complex object representations in its rostral extent. Of course, establishing complex perceptual representations is only half of the recognition battle. On its own, information in the apex of the classically defined ventral visual pathway, i.e., the anterior inferotemporal cortex in humans and area TE in nonhuman primates, can enable discrimination between objects from different categories and, potentially, between sufficiently different exemplars from the same category. However, identifying a particular face as your mother or understanding that a coin can be exchanged for goods and services requires access to knowledge stored in long-term memory (Eradath et al. 2015, Inhoff & Ranganath 2015).

From a modular brain perspective, perception and memory are thought to be supported by distinct neural systems, the former in the VVS and the latter in the MTL (Mishkin et al. 1983, Squire & Zola-Morgan 1991, Tanaka 1997). Within this framework, it is assumed that the apical product of ventral stream perceptual processing projects to the MTL for mnemonic processing. In other words, memory begins where perception ends. Although the mechanistic nature of this cross-module exchange is not fully specified in relevant theoretical models, it is generally thought to take place at the level of the PRC, which is reciprocally connected to area TE in nonhuman primates and the inferotemporal cortex (including both the LOC and FFA) in humans (Lavenex et al. 2004, O'Neil et al. 2014, Ranganath & Ritchey 2012, Suzuki & Amaral 1994, Suzuki & Naya 2014). Moreover, given the reciprocal nature of the contact points between these different neural modules, it is also thought that mnemonic information coded in the MTL can exert top-down influence over ventral stream perceptual processing (Kravitz et al. 2013, Lehky & Tanaka 2016).

HISTORICAL PERSPECTIVES ON THE NEURAL BASIS OF MEMORY

Memory Systems

Memory is not thought to be a unitary construct in either the cognitive psychology or neuroscience traditions. For example, intuition alone tells us that the momentary persistence of the visual world that we experience after closing our eyes (i.e., iconic sensory memory) is a fundamentally different kind of memory than is knowing that the Eiffel Tower is in Paris (i.e.,

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

semantic memory). Although establishing widely agreed-upon definitions of the various subdivisions has proved challenging, Schacter & Tulving (1994) proposed criteria that have been broadly adopted to formalize the ontological boundaries between different kinds of memory. They suggest that memory systems serve different functions, abide by different principles, have different evolutionary and developmental histories, are supported by different neural substrates, and are associated with different kinds of mnemonic information. Against this background, evidence from well over 100 years of behavioral research in healthy populations and in individuals with brain damage, roughly 50 years of computational modeling, and 30 years of neuroimaging has resulted in a consensus regarding five memory systems: working memory; procedural memory; sensory memory, also known as the perceptual representation system; semantic memory; and episodic memory.

All of the memory systems noted above interact with perceptual outputs from the VVS. We focus specifically on semantic and episodic memory in this section due to the historical significance of their position within the modular view of brain function. Together, these memory systems constitute the declarative branch of long-term memory (Squire 1987) (**Figure 2**). Semantic memory refers to knowledge about the world that is culturally shared and acquired over a lifetime of experience (Tulving 1972). Information can be retrieved from semantic memory without reference to a particular learning episode. For example, you know that the Eiffel Tower is located in Paris, even if you have never visited France and cannot recall where or when you learned this factual knowledge. Episodic memory refers to memory for personally experienced events that are spatiotemporally unique, such as remembering the rainy spring day when you visited the Eiffel Tower (Tulving 1972). The phenomenology of episodic recollection can be likened to mental time travel (Tulving

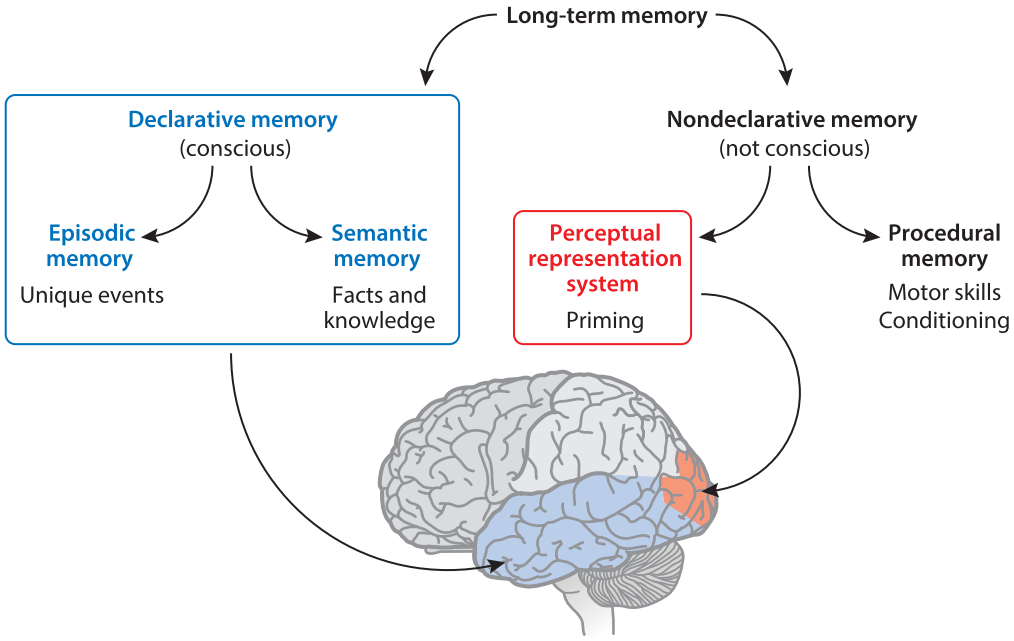

Figure 2

Traditional memory system taxonomy. The declarative memory system refers to memory for events (episodic) and facts (semantic). These memories can be consciously expressed and are traditionally thought to be dependent on the medial temporal lobe. The nondeclarative memory system refers to memories that influence behavior without conscious awareness. Priming, which is the subconscious influence that one stimulus has on the processing of another, is a form of nondeclarative memory that is traditionally thought to be dependent on a perceptual representation system in the ventral visual stream.

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

1985b). For example, you might be able to recollect climbing the steps of the Eiffel Tower and looking out over Paris in vivid detail. Decades of lesion research in humans and nonhuman primates, as well as more recent neuroimaging evidence, has primarily linked declarative memory to the functional integrity of the MTL.

The Medial Temporal Lobe as a Dedicated Declarative Memory System

The link between the MTL and declarative memory dates to seminal findings from the 1950s, in which a group of patients with intractable epilepsy, including the renowned patient H.M., underwent a radical and experimental treatment—bilateral MTL removal (Scoville & Milner 1957). This surgery left the patients profoundly amnesic, unable to acquire long-term memories for facts and events. Despite a striking inability to learn new facts and events, their memory deficit was remarkably isolated (Drachman & Arbit 1966, Penfield & Milner 1958, Scoville & Milner 1957, Wickelgren 1968). Patients showed severe anterograde amnesia, together with some retrograde amnesia for at least the immediate preoperative period, but they manifested no other obvious changes in perceptual abilities, intellect, or personality. Furthermore, all patients were able to hold relatively small amounts of information in their working memory for seconds or minutes, so long as they were not interrupted. The instant their attention was diverted to a new topic, however, the material was lost. In addition to their preserved working memory, patients with MTL lesions also showed spared knowledge that was based on rules or procedures (Corkin 2002). For example, MTL amnesics could acquire selected motor skills (e.g., mirror drawing) over a period of days, despite having no recollection of having carried out the task. Subsequent studies expanded the collection of preserved abilities in amnesia to include memory for skills, habits, and simple forms of conditioning, which eventually fell under the umbrella term of nondeclarative memory, a term referring to a collection of abilities that are unconscious and expressed through performance rather than conscious recollection (**Figure 2**).

This remarkable pattern of preserved and disrupted cognition became a cornerstone of cognitive neuroscience's prevailing paradigm, in which the brain is understood in terms of a modular organization of cognitive constructs that are mapped to specific brain regions or networks (Gazzaniga 2013). In their seminal paper, Squire & Zola-Morgan (1991) identified the main components of the MTL memory system to be the hippocampus and the adjacent, anatomically related entorhinal, perirhinal, and parahippocampal cortices (**Figure 2**). According to this viewpoint, declarative memory is a distinct brain function mediated by the MTL, and it is separable from other cognitive abilities, such as perceptual processing in the VVS (Squire & Wixted 2011).

Medial Temporal Lobe Anatomy and Connectivity

The MTL neocortex consists of the PRC, parahippocampal cortex, and entorhinal cortex, all of which are densely connected to the hippocampus, which is an evolutionarily older allocortical structure (**Figure 3**). A comprehensive picture of the structural and functional connectivity between these areas and the rest of the brain is well beyond the scope of this review; we highlight connections that are of particular relevance to the topic at hand. The PRC is a polymodal association area that receives a significant majority of its input from visual association areas in the ventral stream, namely areas TE and TEO in nonhuman primates and the LOC and fusiform gyrus in humans. It receives a smaller number of inputs from polymodal association areas, including the superior temporal sulcus and the anterior cingulate, and from the orbitofrontal cortex (Ranganath & Ritchey 2012, Suzuki & Amaral 1994, Suzuki & Naya 2014). It is reciprocally connected to all other structures in the MTL, with the strongest inputs from the parahippocampal cortex and

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

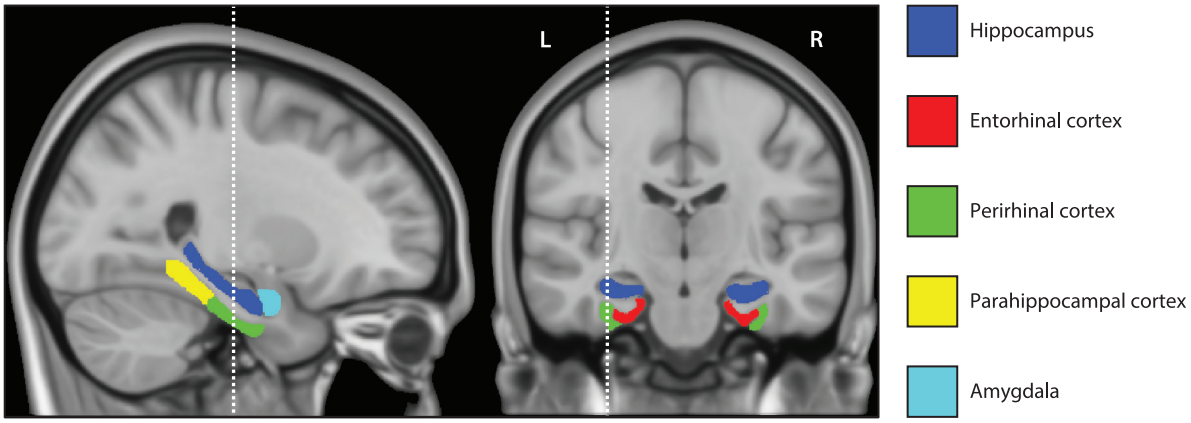

Figure 3

Medial temporal lobe anatomy, showing manually traced medial temporal lobe structures in both the left and right hemisphere.

the strongest projections extending to the hippocampus via the anterolateral entorhinal cortex (Insausti et al. 1987, Maass et al. 2015).

Whereas the PRC is primarily innervated by high-level visual regions in the ventral stream, the parahippocampal cortex receives its input from more posterior regions in the occipitotemporal cortex, including V3 and V4, and medial parietal areas that interface with the dorsal visual processing stream, such as the retrosplenial cortex (Kahn et al. 2008, Lavenex et al. 2002). The strongest projections from the parahippocampal cortex reach the hippocampus via the posteromedial entorhinal cortex (Maass et al. 2015). The hippocampus sits atop the MTL hierarchy, receiving VVS inputs from the PRC and dorsal visual stream inputs from the parahippocampal cortex (Lavenex & Amaral 2000). This pattern of connectivity makes the hippocampus uniquely capable of integrating information about objects from the ventral stream with spatial information from the dorsal stream (Eichenbaum et al. 2007).

Functional Specialization Within the Medial Temporal Lobe

Despite the popularity of the putative MTL memory system, there were several early findings from animal lesion studies that contradicted this view. Although tests of recognition memory were considered the gold standard for assessing amnesia in humans, monkeys with hippocampal lesions demonstrated normal or nearly normal recognition memory (Mishkin 1978, Murray & Mishkin 1984), and monkeys with rhinal lesions sparing the hippocampus showed severe recognition memory deficits (Murray & Mishkin 1986). Thus, it appeared that damage to the hippocampus was neither necessary nor sufficient to produce recognition memory deficits. The interpretation of these studies was complicated by the neuroanatomical complexity of the MTL and the pattern of fibers that pass through these deep brain structures. Specifically, the surgical approach used with this aspiration lesion technique resulted in damage to the underlying PRC, and subsequent work revealed that memory deficits originally attributed to hippocampal damage were in fact the result of damage to the PRC (Meunier et al. 1993). In fact, recent postmortem analysis of H.M.'s lesion revealed extensive damage to his rhinal cortex and that much of his hippocampus was intact (Annese et al. 2014). One meta-analysis of three monkey lesion studies revealed a surprising finding: Greater hippocampal damage was associated with better recognition memory performance (Baxter & Murray 2001), whereas more damage to the rhinal cortex led to worse recognition memory. These different MTL structures must therefore be contributing to memory in very different

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

ways. Some of the most prominent ideas regarding the division of labor between the hippocampus and other MTL structures are discussed below.

At the turn of the century, Vargha-Khadem et al. (1997) described an incredible group of amnesic cases who sustained selective hippocampal damage early in life. These individuals had profound deficits in episodic memory; they were unable to remember everyday events and performed poorly on laboratory-based tests of recall. Despite these impairments, they succeeded in mainstream schooling and attained average-range language competence, literacy, and general factual knowledge. This remarkable pattern of impaired episodic memory and intact semantic memory led to the suggestion that the parahippocampal cortex spared in these patients—specifically the PRC—was essential for semantic memory (Baddeley et al. 2001).

Around the same time, other distinctions were being drawn between memory processes. In a seminal review, Aggleton & Brown (1999) addressed the neural substrates of two distinct memory processes, recollection (the remembering of an event, associated with the retrieval of details tied to the specific time and place of that event) and familiarity (the feeling of knowing that something has been experienced in the past, without memory for the particular time and place in which it was experienced). This view proposed that the hippocampus, together with the fornix, mamillary bodies, and anterior thalamic nuclei, forms a system that supports recollection, whereas familiarity reflects an independent process that depends on a distinct system involving the PRC and the medial dorsal nucleus of the thalamus. These distinctions between hippocampally mediated recollection and PRC-mediated familiarity converge with distinctions drawn between episodic and semantic memory. Recollection is necessarily specific to an episode, whereas familiarity—like semantic memory—is not tied to any specific episode.

The complementary learning system is a network model that provides a computational explanation for the distinctions between hippocampal and PRC contributions to memory (McClelland et al. 1995, Norman & O'Reilly 2003). In this framework, the MTL neocortex (including the PRC) has a slow learning rate and uses overlapping distributed representations to extract the shared structure of events (e.g., generalities based on accumulated experience, such as the best strategy for parking a car). Thus, because it does not sufficiently differentiate the representations of different information, this cortex is unable to support recall of information that has only been encountered on one or two occasions. In contrast, the hippocampus learns rapidly, using pattern-separated representations to encode the details of specific events while minimizing interference (e.g., the memory for where the car is parked today is kept separate from the representation of where the car was parked yesterday).

Other prominent views of MTL function argue that the engagement of different MTL structures is best characterized by the type of information being processed (e.g., items, contexts, or the associations between items and their contexts), rather than the processes themselves. One theory posits that the hippocampus has a critical role in binding together arbitrarily related associations (termed relational memory), whereas MTL cortical structures maintain representations for individual items (Eichenbaum et al. 1994). This theory was subsequently developed into a binding of item and context model (Diana et al. 2007, Eichenbaum et al. 2007) that proposes that MTL subregions differ in terms of the information that they process and represent. More specifically, the PRC is thought to represent information about specific items (e.g., who and what). Conversely, the parahippocampal cortex is thought to represent information about the context of these items (e.g., where and when) and is well situated to do so given its dorsal visual stream inputs. The hippocampus represents the associations between these items and contexts. This framework has been extended within a theoretical model that positions the PRC as a core node in an extended anterior temporal network that supports memory-guided behavior via object recognition and evaluation (Ranganath & Ritchey 2012). This role contrasts with that of the parahippocampal cortex, which,

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

together with the retrosplenial cortex, constitutes a core hub in an extended posterior-medial network that supports contextual processing in memory (i.e., spatial and temporal features). The common thread across this family of theoretical models is the suggestion that each region has a functionally distinct role, but collectively, MTL regions support memory by linking item and context information.

Most recently, models of context and binding have been revised to incorporate information regarding the detail of the memory trace. In this perspective, the hippocampus is thought to be engaged in attentional, perceptual, or mnemonic tasks involving object-to-context binding when these representations are high in precision (Aly et al. 2013, Yonelinas et al. 2019). In these cases, precision is related to the resolution and dimensionality of the memory trace—a memory for an event highly similar in resemblance to a target event with many varying elements (e.g., color, shape, sound, context) is said to be high in precision (Cooper & Ritchey 2020, Richter et al. 2016).

In summary, the wealth of recent evidence suggests that different MTL structures make functionally dissociable contributions to memory, and as such, differing patterns of MTL damage will lead to distinct profiles of declarative memory impairment. These divergent outcomes have motivated the development of multiple theoretical positions that account for functional specialization across structures in the MTL. These models variably incorporate differences at the level of cognitive processes and representational content, and in some cases are constrained by functional and anatomical connectivity profiles, but always through the lens of memory. Development of a comprehensive and parsimonious model of MTL function must also accommodate empirical evidence that implicates its various structures in high-level visual perception.

REPRESENTATIONAL ACCOUNTS OF THE VENTRAL VISUAL STREAM AND MEDIAL TEMPORAL LOBE

Above, we review two widely influential perspectives on the neural bases of perception and memory. On the one hand, the ventral visual pathway has been characterized as a hierarchically organized swath of cortex that enables visual object perception. On the other hand, the MTL has been characterized as an interconnected set of structures that enables declarative memory. The prevailing historical view was that the VVS and MTL brain networks constitute complementary but distinct neural modules. However, this theoretical position cannot account for findings from an ever-expanding body of research that implicates MTL structures in high-level perceptual processing and VVS structures in mnemonic processing.

The discrepancy can, however, be reconciled within a theoretical framework that explains functional differences between the VVS and the MTL in terms of informational distinctions rather than process-based distinctions (Cowell et al. 2019, Gaffan 2001, Graham et al. 2010, Murray & Bussey 1999, Murray et al. 2007). In this view, the VVS is not necessarily a perceptual module, and the MTL is not necessarily a memory module. Instead, they are two points along a continuous processing hierarchy that represent visually apprehended information at different levels of complexity. As it relates to objects, then, the PRC constitutes the apex of the VVS, representing objects at their highest level of complexity—in terms of the complex conjunctions of features that comprise their visual, semantic, and perhaps multimodal attributes (Li et al. 2022). By dispensing with the notion that the psychological constructs of perception and memory are primary functional organizing principles in the occipitotemporal network, the representational-hierarchical framework predicts that a given region within the VVS-to-MTL hierarchy can support multiple different kinds of cognition. Whether it does is determined by the degree of representational complexity required to meet ongoing task demands. Perceptual discriminations between very different objects, such as a face and a fork, should be supported by representational differences reflected in low-level visual

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

areas in the posterior extent of the VVS. Conversely, if the task involves perceptual discrimination between two faces, then successful performance will reflect representational differences in high-level visual areas in the rostral extent of the VVS, such as the PRC. The same logic applies for memory-based discriminations: Memory for simple stimuli can be supported by posterior regions of the VVS, whereas memory for complex stimuli, or memory for stimuli embedded in a particular place and time, requires more complex representations in the MTL.

We next turn our attention to the empirical evidence that supports these predictions, which suggest a radical departure from the perspective of a modular brain that is neatly organized according to the psychological constructs based on the introspectively identifiable cognitive processes that emerged from early research in cognitive psychology.

EVIDENCE FOR MEDIAL TEMPORAL LOBE CONTRIBUTIONS TO OBJECT PERCEPTION

Research in Nonhuman Animals

One of the earliest indications that the PRC has a role outside declarative memory came from a study by Eacott et al. (1994). Macaques with targeted PRC lesions showed an object recognition deficit on a delayed match-to-sample task but no impairment on a simultaneous match-to-sample task (i.e., a perceptual comparison between two simultaneously presented stimuli). In other words, the animals performed well when memory demands were minimized and performance could be supported by perceptually based comparisons. Critically, however, when the perceptual load in the task was increased by decreasing the physical discriminability of the stimuli (i.e., making the objects more similar to one another), impairments emerged even in the simultaneous match-to-sample condition. This finding motivated a series of investigations that demonstrated that the role of the PRC extended beyond memory to include visual discrimination, provided that performance required access to perceptual representations that captured high-level, complex feature conjunctions (Buckley & Gaffan 1997, 1998).

To test more directly the hypothesis that the PRC supports high-level visual perception, Buckley et al. (2001) designed an oddity task that required a perceptual judgement to be made between simultaneously presented stimuli (i.e., which of six stimuli was the odd one out) (**Figure 4**). There were several conditions, which varied according to the demands that they placed on stimulus identification. For example, in one condition (termed the same-view condition), five identical views of one object, along with one view of another oddball object, were presented. In this condition, the oddball could easily be identified on the basis of discrimination between simple object features. In another condition (termed the different-view condition), five different views of the same object, together with one view of another oddball object, were presented. This task could not be discriminated on the basis of a simple feature. Control conditions required perceptual comparisons between stimuli that varied only along a single dimension, such as color, size, or shape. PRC lesions did not affect performance when discriminations could be solved on the basis of a single feature alone (i.e., same-view objects or the color, size, and shape conditions), even when these discriminations were made extremely difficult. Conversely, PRC lesions selectively impaired performance on more complex discrimination tasks, such as the different-view object condition.

Building on previous findings from lesion studies and results from computational modeling (Bussey & Saksida 2002), Bussey et al. (2002) assessed the performance of monkeys with PRC lesions on a series of concurrent discriminations in which the degree of feature overlap of the object stimuli was systematically varied. Importantly, as feature overlap increases across objects, single features are no longer informative, and a conjunction of features is required to identify the target object. PRC lesions caused no deficit in discriminations with minimum feature overlap,

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

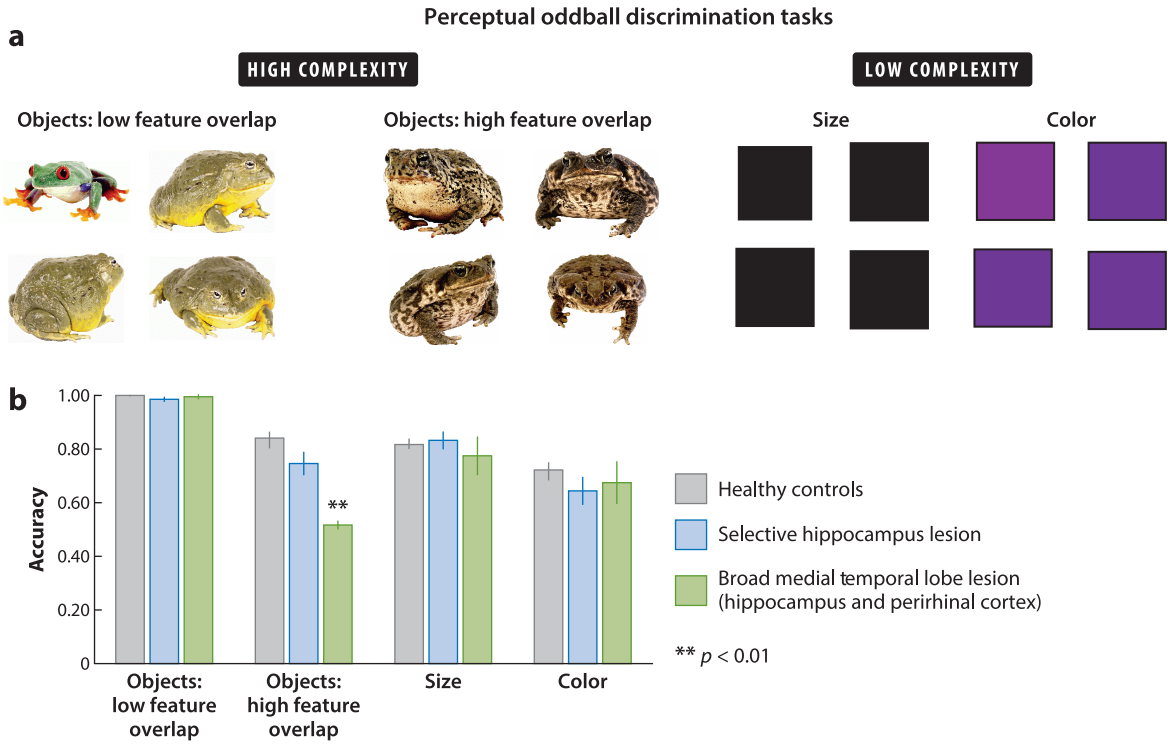

Figure 4

Perceptual discrimination impairments in humans with medial temporal lobe damage that includes the perirhinal cortex. (*a*) Perceptual oddball discrimination tasks. Participants were asked to identify the stimulus that is the odd one out within each four-item array. Conditions varied along two dimensions: object complexity and visual feature overlap. Oddballs in the high-complexity–low-feature-overlap condition could be accurately identified based on low-level perceptual differences. Oddballs in the high-complexity–high-feature-overlap condition could only be identified through consideration of feature conjunctions. Oddballs in the low-complexity tasks could be identified based on differences along a single dimension. (*b*) Patients with medial temporal lobe damage that included the perirhinal cortex were selectively impaired on the high-complexity–high-feature-overlap condition relative to healthy controls and individuals with medial temporal lobe damage restricted to the hippocampus. Figure created using data from Barense et al. (2007).

but as feature overlap increased, lesioned monkeys were increasingly impaired. Thus, irrespective of memory load, the degree of feature overlap—a visual property of the stimuli—proved to be the critical factor in determining the involvement of the PRC. This pattern of results was also obtained using a similar protocol in rodents (Bartko et al. 2007a,b). Moreover, this work has been extended to show that impoverished visual representations following PRC damage cause deficits not only in complex perceptual discrimination tasks, but also in the recognition of complex stimuli in the context of amnesia. For example, McTighe et al. (2010) showed that the classical deficit in object recognition memory seen in animals with PRC damage was attributed to an accumulation of feature-level interference, and removing such interference rescued memory (for corresponding results in humans, see Barense et al. 2012, Yeung et al. 2013).

Considered together, these findings suggest that impairments in visual discrimination reflect the fact that animals with damage to the PRC have impoverished conjunctive representations of complex stimuli, and the intact representations of simple features represented in more caudal VVS areas are insufficient to resolve feature-level interference in trials with high feature overlap across stimuli.

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Research in Humans

Despite the robust pattern of results obtained in research in animal models, initial efforts to identify perceptual deficits in humans with MTL damage were not successful (Levy et al. 2005, Shrager et al. 2006). These null results reinforced the widely held belief that the MTL forms a dedicated long-term declarative memory system (Kim et al. 2011, Knutson et al. 2012). However, a much clearer picture began to emerge when the experimental paradigms used in the animal research were directly adapted for use in individuals with MTL damage. Specifically, Barense et al. (2005) developed a concurrent object discrimination task using complex stimuli that systematically varied in terms of feature overlap across objects within each set. This approach revealed that patients with PRC damage, as compared to those with MTL damage restricted to the hippocampus, were profoundly impaired when a conjunction of features was required to identify the target object but not when targets could be identified by a single feature. Likewise, in a series of studies modeled after the animal literature, humans with PRC damage were impaired on odd-one-out and same-different discriminations when there was a high, but not when there was a low, degree of visual overlap between the objects (Lee et al. 2005a,b) (**Figure 4**). Just as in other species, their performance was intact when the objects differed along a single dimension, such as color, in a baseline task that was equated in overall difficulty. This pattern of results was replicated multiple times over, including in experiments that minimized mnemonic demands by using trial-unique stimuli (Barense et al. 2007, 2010; Erez et al. 2013) or classic perceptual tasks like figure-ground discrimination that can be performed quickly and automatically without awareness or working memory burden (Barense et al. 2012).

Finally, a series of neuroimaging studies in neurologically intact human participants provided evidence of a convergent role for the PRC in object perception. Consistent with observations following PRC lesions, when the perceptual task required discriminating between visually similar complex objects, perirhinal activity was increased relative to conditions that could be solved based on a single feature (Barense et al. 2010, 2011, 2012; Lee et al. 2008). Moreover, a novel application of fMRI multivariate pattern analysis showed that the PRC represented information specific to the conjunction of features comprising an object, over and above information regarding the features themselves (i.e., in terms of PRC coding, the whole was different from the sum of its parts). Moreover, this conjunctive coding was invariant to large changes in viewpoint across the objects. Together, the evidence from humans converges with that obtained in animals to suggest that the critical factor in determining the involvement of the PRC is whether the task—be it mnemonic or perceptual—requires objects to be discriminated on the basis of conjunctions of their features, rather than on single features alone. This is consistent with the notion that impairments following PRC damage are due to impoverished representations of complex stimuli, and the intact representations of simple features in earlier VVS regions are inadequate in contexts where there is a high degree of feature overlap (Bonnen et al. 2021).

Although it is beyond the scope of the current review, it is important to note that a parallel set of findings, obtained both in patient populations and with neuroimaging in cognitively healthy participants, implicates the hippocampus in this representational hierarchy, with a role in high-level scene perception (Aly et al. 2013; Lee et al. 2005a,b; Warren et al. 2011). Just as the PRC is essential for representing complex objects, the hippocampus is necessary for representing even more complex stimuli at a higher dimensionality, such as spatial scenes. This includes not only spatial information, but also unique, arbitrary associations between other relatively complex elements (e.g., temporal information, contextual information regarding the encoding context). This class of representational content not only would be important for complex spatial perceptual abilities, but would also form the informational bedrock underpinning our ability to remember a specific episode that happened at specific place and time. Thus, this theory provides

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

a parsimonious account for the essential role of the hippocampus in both episodic memory and spatial perception—both cognitive abilities call on the high-dimensional representational content thought to be the province of the hippocampus.

EVIDENCE FOR VENTRAL VISUAL STREAM CONTRIBUTIONS TO OBJECT MEMORY

Recognizing the prior occurrence of a stimulus is one of the most basic forms of declarative memory. This kind of recognition is necessarily predicated on experience-dependent brain changes that are often expressed as either increases or decreases in firing rates across successive repetitions of a visual stimulus. A considerable body of work has revealed precisely this kind of long-term sensitivity to stimulus familiarity in the PRC using invasive electrophysiological recordings in animals (Fahy et al. 1993, Xiang & Brown 1998) and fMRI in humans (Davachi et al. 2003, Henson et al. 2003, Montaldi et al. 2006) and in the context of biologically plausible computational models (Bogacz & Brown 2003, Cowell et al. 2006). Historically, these kinds of experience-dependent changes were not thought to take place in early visual areas, largely because stability is a desirable property of a low-level feature detector (Cooke & Bear 2015). Instead, early VVS structures were traditionally thought to support nondeclarative forms of memory, such as priming (**Figure 2**). However, an emerging body of research has indeed revealed neural expressions of familiarity detection, a form of memory that was previously thought to be dependent on the MTL, in the posterior extent of the VVS.

In a particularly compelling experiment, Frenkel et al. (2006) repeatedly presented visual gratings to head-restrained mice and found an orientation-specific enhancement of V1 responses that was selective to previously encountered stimuli. In other words, neurons well outside of the MTL expressed an electrophysiological response profile that reflected the recognition of a prior occurrence. Follow-up research using a similar experimental paradigm successfully linked these recognition memory signals in V1 to behavioral habituation, which in nonhuman species and preverbal infants has long been thought of as a canonical indicator of familiarity (Cooke et al. 2015). Perhaps most impressively, López-Aranda et al. (2009) revealed causal evidence for a role of V2 in supporting recognition memory in rats. Specifically, lesions that targeted layer 6 of V2 resulted in object recognition memory impairments. To rule out the possibility that these recognition memory deficits were caused by compromised representations in regions that are downstream of V2, such as the PRC and other structures in the MTL, the authors demonstrated that experimentally inducing an overexpression of the protein RGS-14 in layer 6 of V2 significantly improved recognition memory in the rodents. The same manipulation applied to structures in the MTL had no discernible effect on behavioral performance. Therefore, López-Aranda et al. (2009) showed that manipulations targeting a specific cellular layer of extrastriate area V2 can enhance or impair recognition memory independent of any corresponding functional changes in the MTL.

Incredibly, evidence for recognition memory signals in V1 response profiles can be observed not only for individual visual stimuli, but also for more complex sequences of stimuli (Gavornik & Bear 2014; for related results in monkey V4, see Eagleman & Dragoi 2012). Specifically, electrophysiological recordings show sensitivity in V1 to spatial and temporal violations in the sequence of previously encountered visual gratings. This effect has also been observed in human V1 using fMRI (Rosenthal et al. 2016). In addition to exhibiting differential responses to individual stimuli and sequences of stimuli, activity in mouse V1 also appears to predict upcoming visual stimuli in a spatially dependent manner and is sensitive to violations of those predictions (Fiser et al. 2016). Predictive coding in V1 has also been observed in humans (Ekman et al. 2017). Participants in this experiment were initially familiarized with sequenced stimuli, which were dots that flashed in succession at various locations on a screen. After learning, presenting participants with only the

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

beginning of each sequence triggered a cascade of V1 activity that was a recapitulation of the response to the entire sequence during learning. Thus, V1 is able to complete a previously learned pattern when kickstarted with a cue, which is a clear expression of a complex form of associative memory.

Research focused on fear conditioning in humans has also recently revealed a role for early VVS areas in the long-term representation of visual information. Whereas fear conditioning initially reflects learning supported by anterior aspects of the VVS, the long-term retention of the learned association between a visual stimulus and an aversive response is supported by information coded in V1 (You et al. 2021). As further evidence for experience-dependent plasticity in the primary visual cortex, activity patterns evoked by simple visual stimuli during the acquisition of conditioned fear memories become sparser as learning progresses (Yin et al. 2020). This kind of learning-related sharpening is precisely the kind of mechanism that has been suggested to underlie long-term memory representations in the PRC (Cowell et al. 2006).

Considered together, these data provide strong evidence that early visual areas support more than mere visual perception. Activity in the primary visual cortex captures information about prior experience with simple visual stimuli and with spatiotemporally unique sequences of simple visual stimuli. This pattern of results supports a key feature of representational-hierarchical accounts of VVS and MTL function, namely, that a given brain region in this pathway enables both memory and perception of visual information if the task demands resonate with the degree of representational complexity captured in that region.

COMPLEX REPRESENTATIONS ENABLE COMPLEX COGNITION

The evidence reviewed above blurs the functional neuroanatomical lines between perception and memory in the VVS and MTL. We argue that representational accounts of brain function have broader explanatory power than do modular perspectives that speak to the roles of the VVS and MTL in cognition. It is critically important, then, that our research efforts are aimed at developing a deep understanding of precisely what kind of information is represented in each brain region within the VVS-MTL hierarchy. With this goal in mind, we close our review with an examination of what is known about the representational properties of the PRC.

Strong empirical evidence has linked activity in the PRC to performance on difficult mnemonic (Kafkas et al. 2017; Martin et al. 2013, 2018a), perceptual (Barense et al. 2005, 2010, 2012; Baxter & Murray 2001; Buckley & Gaffan 1997; Eacott et al. 1994; Ferko et al. 2022; Inhoff et al. 2019; Lee et al. 2005a,b; O'Neil et al. 2009), and semantic (Kivisaari et al. 2012, Moss et al. 2005, Wright et al. 2015) discrimination tasks. Together, these findings suggest that the PRC represents multiple fundamentally different kinds of information pertaining to objects, possibly integrating high-level perception with knowledge about recent experience with specific exemplars, as well as category-level semantic knowledge that allows us to understand the meaning and significance of a given stimulus (Clarke & Tyler 2015). What, then, is the representational format of this highly complex, multidimensional information? Moreover, if the PRC has the capacity to capture all of these different kinds of high-level object features, then how is task-relevant information selected across varying contexts? The importance of these questions becomes clear when considering the fact that perceptual, episodic, and semantic information have relevance for and guide rather different kinds of behavior. For example, knowing that dogs have four legs and a tail has no relevance in the context of a task that requires perceptual discrimination between multiple different dogs, or for an episodically based discrimination between a recently encountered dog and one that you have not seen before.

We suggest that the PRC supports complex object-oriented cognition through a dynamic reshaping of its representational structure that aligns task-relevant features with context-specific

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

demands. For example, information about recency is prioritized in the context of a recognition memory task, information that reflects your knowledge about a category of objects is prioritized in the context of a semantic task, and high-level perceptual information is prioritized in the context of a visual discrimination task. This proposal is supported by evidence from a recent fMRI experiment that examined the representational structure of semantic information about objects in the PRC (Martin et al. 2018b). The experimenters used a carefully developed stimulus set in which visual and conceptual features varied independently across objects (e.g., hairdryer–comb, which are conceptually similar but visually distinct; hairdryer–electric drill, which are visually similar but conceptually distinct). Participants were asked to evaluate these object concepts during fMRI scanning across two task contexts that emphasized retrieval of either visual information from semantic memory (e.g., the prototypical shape of an object) or conceptual information from semantic memory (e.g., whether an object is living). Results from a pattern similarity analysis of fMRI data revealed that the PRC was the only region in the entire brain that reliably captured the visual and conceptual similarity structure of this special stimulus set irrespective of task demands (**Figure 5**). In other words, activity patterns in the PRC simultaneously reflected the visual similarity between the hairdryer and the comb and the conceptual similarity between the hairdryer and the gun. Despite both kinds of information being always detectable, task-relevant features more strongly shaped the representational structure of activity in the PRC. Specifically, visual

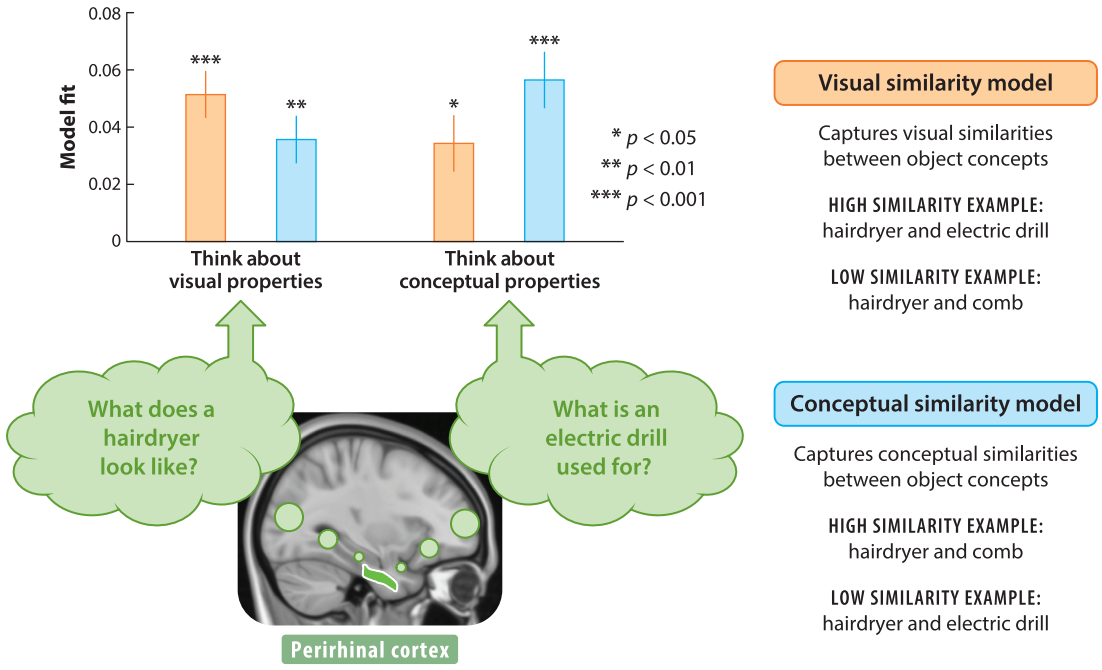

Figure 5

Context-specific reorganization of multidimensional object information in the perirhinal cortex (PRC). PRC patterns during visually or conceptually oriented task contexts capture the visual and conceptual similarities among object concepts. While participants were asked to think about either the way a hairdryer looks or what it is used for, activity in the PRC captured the high visual similarity between a hairdryer and an electric drill, as well as the high conceptual similarity between a hairdryer and a comb. Importantly, PRC representations were flexibly reshaped to reflect task-relevant information most strongly. For example, the visually based link between hairdryer and electric drill was most prominent in the visual task context, whereas the conceptually based link between hairdryer and comb was most prominent in the conceptual task context. Figure created using data from Martin et al. (2018b).

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

semantics came to the fore when participants thought about how object concepts typically look, and conceptual semantics came to the fore when they contemplated object meaning. This pattern of results suggests that the PRC has the capacity to integrate multiple fundamentally different kinds of information and that its representational structure is flexibly modulated by task demands. Ultimately, at the level of the PRC, it may not be possible to fully disentangle perceptual and semantic processing, and a better approach is to think about the nature of the object representation in which this information is integrated. These integrated representations provide the informational bedrock for interpretations of the sensory cacophony present in everyday experience, allowing us to interact appropriately with the objects in our world.

CONCLUDING REMARKS

Embracing the notion of a modular mind allowed the field of cognitive psychology to mature and flourish as a well-defined empirical discipline. This idea cast a long shadow on cognitive neuroscience, which has traditionally focused on mapping different aspects of cognition to discrete brain regions, a focus that is particularly evident in the near-canonical belief that the VVS supports visual perception and the MTL supports declarative memory. In this article, we review a large body of evidence that challenges this framework and instead suggests that the functional properties of the VVS and MTL can be best understood through a lens that magnifies the importance of representational distinctions, rather than process-based distinctions. In support of this view, we highlight findings that reveal roles for low-level perceptual areas in the VVS in memory and for structures within the MTL in high-level perception. If we hope to develop theoretical and computational models of the brain that generalize across task contexts and have broad explanatory power across species and levels of analysis, it will be critical that, as a field, we focus our efforts on advancing our understanding of how a given cortical area represents the visual world both in the present moment and in memory.

SUMMARY POINTS

1. Research in cognitive neuroscience has traditionally sought to map specific kinds of cognition to specific brain regions. This is exemplified by the widely held belief that the ventral visual stream (VVS) is a specialized module that supports visual perception, whereas the medial temporal lobe (MTL) is a specialized module that supports long-term declarative memory. However, considerable evidence suggests that functional specialization in the VVS and MTL cannot be captured by a distinction between perception and memory.
2. The representational-hierarchical framework offers an alternative to the modular view of the VVS and MTL. In this account, the functional differences between the VVS and the MTL are cast in terms of informational distinctions, rather than process-based distinctions. Thus, the VVS is not necessarily a perceptual module, and the MTL is not necessarily a memory module. Instead, they are two points along a continuous processing hierarchy that represent visually apprehended information at different levels of complexity.
3. Research in rodents, nonhuman primates, and humans indicates that MTL damage causes perceptual discrimination impairments irrespective of memory demands. More specifically, perceptual deficits can be revealed in tasks that require perceptually based comparisons among complex stimuli that have a high degree of feature overlap. Damage

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

in the perirhinal cortex (PRC) affects object perception, whereas damage in the hippocampus affects scene perception. MTL lesions do not affect performance on simple perceptual discrimination tasks, suggesting that the MTL represents high-level feature conjunctions of complex stimuli.

4. A rapidly expanding body of research suggests that recognition memory can be supported by information represented in the posterior extent of the VVS. Indeed, activity in V1 and extrastriate cortical areas discriminates between recently encountered and novel objects and between previously learned and novel sequences of events. Manipulating activity in these early visual areas can selectively improve or impair recognition memory performance in rodents.
5. The PRC, which may be the apex of the object processing hierarchy that bridges V1 and the MTL, supports multiple different kinds of object-oriented cognition, including perceptual, episodic, and semantic discrimination. This flexibility reflects its unique capacity for representing objects within a multidimensional code that captures multiple different kinds of features. Neuroimaging research in humans suggests that these multidimensional representations are dynamically reshaped by task demands to prioritize behaviorally relevant information.

FUTURE ISSUES

1. Are the memory signals that can be detected in early visual areas established during initial encoding, or are they the product of a postencoding consolidation process that transforms mnemonic information from an MTL-dependent state to an MTL-independent state? Consistent with the notion that early visual areas have a role in initial encoding, upregulation of activity in the rodent extrastriate cortex can dramatically improve long-term recognition memory for objects, whereas the same manipulation applied to the MTL did not affect long-term retention (López-Aranda et al. 2009).
2. Future research should aim to develop a deeper understanding of the kinds of memory that can be supported by early visual areas. Is the mnemonic information coded within the primary visual cortex, for example, ever available for phenomenological awareness? If so, what retrieval conditions or support would give rise to such awareness?
3. Object representations become increasingly complex as information is transformed moving rostrally along the VVS. However, whether this complexity reflects the successive integration of information represented at lower levels remains an open question. Does object information become inextricably intertwined as it ascends this hierarchical pathway, or do functionally segregated feature channels (e.g., shape, color) merely converge as they approach the apex?
4. Do the functional dynamics that enable the PRC to link conceptual information with visual information differ depending on whether the visual information is perceived in real time or retrieved from long-term memory? Previous neuroimaging research in humans has revealed a unique role for the PRC in simultaneously representing conceptual and visual semantic knowledge about objects (e.g., what something is used for and how it typically looks) when mnemonic retrieval is prompted using words as stimuli

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

(Martin et al. 2018a). It is unclear, however, whether this structure also simultaneously represents conceptual and visual information when pictures of category exemplars are used as stimuli.

5. We suggest that flexible, object-oriented cognition is supported by a dynamic shaping of representational content in the PRC that prioritizes task-relevant information (**Figure 5**). What are the neural mechanisms that drive these representational changes? One possibility is that these transient alterations reflect a complex interaction between a system of high-level representation in the PRC and a cognitive control system in the prefrontal cortex. Consideration of functional connectivity across multiple task contexts may provide insight into this issue.
6. Can our ever-deepening understanding of the functional properties of the PRC be leveraged in applied contexts? The rhinal cortex is among the first brain regions to be affected by the neuropathological changes that drive cognitive impairment in Alzheimer's disease (Braak & Braak 1991). The development of cognitive behavioral tasks that are sensitive to the functional integrity of these regions may directly translate to noninvasive early detection tools.
7. How, if at all, do high-level object representations in the PRC influence the way we physically interact with the world? Although memory and perceptual processing evolved to support complex and adaptive behavior, the relationship between complex information in the VVS and motor control remains underspecified. Additional insights regarding the roles of perceptual and mnemonic processing in the PRC may be obtained through measurements of mouse tracking and/or motion tracking in the context of object discrimination tasks.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

Aggleton JP, Brown MW. 1999. Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behav. Brain Sci.* 22(3):425–44

Aly M, Ranganath C, Yonelinas AP. 2013. Detecting changes in scenes: The hippocampus is critical for strength-based perception. *Neuron* 78(6):1127–37

Annese J, Schenker-Ahmed NM, Bartsch H, Maechler P, Sheh C, et al. 2014. Postmortem examination of patient H.M.'s brain based on histological sectioning and digital 3D reconstruction. *Nat. Commun.* 5:3122

Avidan G, Hasson U, Malach R, Behrmann M. 2005. Detailed exploration of face-related processing in congenital prosopagnosia: 2. Functional neuroimaging findings. *J. Cogn. Neurosci.* 17(7):1150–67

Axelrod V, Yovel G. 2012. Hierarchical processing of face viewpoint in human visual cortex. *J. Neurosci.* 32(7):2442–52

Baddeley A, Vargha-Khadem F, Mishkin M. 2001. Preserved recognition in a case of developmental amnesia: implications for the acquisition of semantic memory? *J. Cogn. Neurosci.* 13(3):357–69

Barense MD, Bussey TJ, Lee ACH, Rogers TT, Davies RR, et al. 2005. Functional specialization in the human medial temporal lobe. *J. Neurosci.* 25(44):10239–46

Barense MD, Gaffan D, Graham KS. 2007. The human medial temporal lobe processes online representations of complex objects. *Neuropsychologia* 45(13):2963–74

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Barense MD, Groen IIA, Lee ACH, Yeung L-K, Brady SM, et al. 2012. Intact memory for irrelevant information impairs perception in amnesia. *Neuron* 75(1):157–67

Barense MD, Henson RN, Graham KS. 2011. Perception and conception: temporal lobe activity during complex discriminations of familiar and novel faces and objects. *J. Cogn. Neurosci.* 23(10):3052–67

Barense MD, Henson RNA, Lee ACH, Graham KS. 2010. Medial temporal lobe activity during complex discrimination of faces, objects, and scenes: effects of viewpoint. *Hippocampus* 20(3):389–401

Barlow HB. 1972. Single units and sensation: a neuron doctrine for perceptual psychology? *Perception* 1(4):371–94

Bartko SJ, Winters BD, Cowell RA, Saksida LM, Bussey TJ. 2007a. Perceptual functions of perirhinal cortex in rats: zero-delay object recognition and simultaneous oddity discriminations. *J. Neurosci.* 27(10):2548–59

Bartko SJ, Winters BD, Cowell RA, Saksida LM, Bussey TJ. 2007b. Perirhinal cortex resolves feature ambiguity in configural object recognition and perceptual oddity tasks. *Learn. Memory* 14(12):821–32

Barton JJS, Press DZ, Keenan JP, O'Connor M. 2002. Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology* 58(1):71–78

Baxter MG, Murray EA. 2001. Opposite relationship of hippocampal and rhinal cortex damage to delayed nonmatching-to-sample deficits in monkeys. *Hippocampus* 11(1):61–71

Bogacz R, Brown MW. 2003. Comparison of computational models of familiarity discrimination in the perirhinal cortex. *Hippocampus* 13(4):494–524

Bonnen T, Yamins DLK, Wagner AD. 2021. When the ventral visual stream is not enough: a deep learning account of medial temporal lobe involvement in perception. *Neuron* 109(17):2755–66.e6

Bowles B, Duke D, Rosenbaum RS, McRae K, Köhler S. 2016. Impaired assessment of cumulative lifetime familiarity for object concepts after left anterior temporal-lobe resection that includes perirhinal cortex but spares the hippocampus. *Neuropsychologia* 90:170–79

Braak H, Braak E. 1991. Neuropathological stageing of Alzheimer-related changes. *Acta Neuropathol.* 82(4):239–59

Buckley MJ, Booth MCA, Rolls ET, Gaffan D. 2001. Selective perceptual impairments after perirhinal cortex ablation. *J. Neurosci.* 21(24):9824–36

Buckley MJ, Gaffan D. 1997. Impairment of visual object-discrimination learning after perirhinal cortex ablation. *Behav. Neurosci.* 111(3):467–75

Buckley MJ, Gaffan D. 1998. Perirhinal cortex ablation impairs visual object identification. *J Neurosci* 18(6):2268–75

Bussey TJ, Saksida LM. 2002. The organization of visual object representations: a connectionist model of effects of lesions in perirhinal cortex: model of perirhinal cortex. *Eur. J. Neurosci.* 15(2):355–64

Bussey TJ, Saksida LM. 2007. Memory, perception, and the ventral visual-perirhinal-hippocampal stream: thinking outside of the boxes. *Hippocampus* 17(9):898–908

Bussey TJ, Saksida LM, Murray EA. 2002. Perirhinal cortex resolves feature ambiguity in complex visual discriminations: perirhinal cortex and feature ambiguity. *Eur. J. Neurosci.* 15(2):365–74

Cadieu CF, Hong H, Yamins DLK, Pinto N, Ardila D, et al. 2014. Deep neural networks rival the representation of primate it cortex for core visual object recognition. *PLOS Comput. Biol.* 10(12):e1003963

Clarke A, Tyler LK. 2015. Understanding what we see: how we derive meaning from vision. *Trends Cogn. Sci.* 19(11):677–87

Cooke SF, Bear MF. 2015. Visual recognition memory: a view from V1. *Curr. Opin. Neurobiol.* 35:57–65

Cooke SF, Komorowski RW, Kaplan ES, Gavornik JP, Bear MF. 2015. Visual recognition memory, manifested as long-term habituation, requires synaptic plasticity in V1. *Nat. Neurosci.* 18(2):262–71

Cooper RA, Ritchey M. 2020. Progression from feature-specific brain activity to hippocampal binding during episodic encoding. *J. Neurosci.* 40(8):1701–9

Corkin S. 2002. What's new with the amnesic patient H.M.? *Nat. Rev. Neurosci.* 3(2):153–60

Cosmides L, Tooby J. 1994. Beyond intuition and instinct blindness: toward an evolutionarily rigorous cognitive science. *Cognition* 50(1–3):41–77

Cowell RA, Barense MD, Sadil PS. 2019. A roadmap for understanding memory: decomposing cognitive processes into operations and representations. *eNeuro* 6(4):ENEURO.0122-19.2019

Cowell RA, Bussey TJ, Saksida LM. 2006. Why does brain damage impair memory? A connectionist model of object recognition memory in perirhinal cortex. *J. Neurosci.* 26(47):12186–97

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Dalrymple KA, Oruç I, Duchaine B, Pancaroglu R, Fox CJ, et al. 2011. The anatomic basis of the right face-selective N170 IN acquired prosopagnosia: a combined ERP/fMRI study. *Neuropsychologia* 49(9):2553–63

Davachi L, Mitchell JP, Wagner AD. 2003. Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. *PNAS* 100(4):2157–62

Desimone R, Albright T, Gross C, Bruce C. 1984. Stimulus-selective properties of inferior temporal neurons in the macaque. *J. Neurosci.* 4(8):2051–62

Dew ITZ, Cabeza R. 2013. A broader view of perirhinal function: from recognition memory to fluency-based decisions. *J. Neurosci.* 33(36):14466–74

Diana RA, Yonelinas AP, Ranganath C. 2007. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends Cogn. Sci.* 11(9):379–86

Drachman DA, Arbit J. 1966. Memory and the hippocampal complex: II. Is memory a multiple process? *Arch. Neurol.* 15(1):52–61

Duke D, Martin CB, Bowles B, McRae K, Köhler S. 2017. Perirhinal cortex tracks degree of recent as well as cumulative lifetime experience with object concepts. *Cortex* 89:61–70

Eacott MJ, Gaffan D, Murray EA. 1994. Preserved recognition memory for small sets, and impaired stimulus identification for large sets, following rhinal cortex ablations in monkeys. *Eur. J. Neurosci.* 6(9):1466–78

Eagleman SL, Dragoi V. 2012. Image sequence reactivation in awake V4 networks. *PNAS* 109(47):19450–55

Eichenbaum H, Otto T, Cohen NJ. 1994. Two functional components of the hippocampal memory system. *Behav. Brain Sci.* 17(3):449–72

Eichenbaum H, Yonelinas AP, Ranganath C. 2007. The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.* 30:123–52

Ekman M, Kok P, de Lange FP. 2017. Time-compressed preplay of anticipated events in human primary visual cortex. *Nat. Commun.* 8:15276

Eradath MK, Mogami T, Wang G, Tanaka K. 2015. Time context of cue-outcome associations represented by neurons in perirhinal cortex. *J. Neurosci.* 35(10):4350–65

Erez J, Lee ACH, Barense MD. 2013. It does not look odd to me: perceptual impairments and eye movements in amnesic patients with medial temporal lobe damage. *Neuropsychologia* 51(1):168–80

Fahy FL, Riches IP, Brown MW. 1993. Neuronal activity related to visual recognition memory: long-term memory and the encoding of recency and familiarity information in the primate anterior and medial inferior temporal and rhinal cortex. *Exp. Brain Res.* 96(3):457–72

Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex* 1(1):1–47

Ferko KM, Blumenthal A, Martin CB, Proklova D, Minos AN, et al. 2022. Activity in perirhinal and entorhinal cortex predicts perceived visual similarities among category exemplars with highest precision. *eLife* 11:e66884

Fiser A, Mahringer D, Oyibo HK, Petersen AV, Leinweber M, Keller GB. 2016. Experience-dependent spatial expectations in mouse visual cortex. *Nat. Neurosci.* 19(12):1658–64

Fodor JA. 1983. *The Modularity of Mind: An Essay on Faculty Psychology*. Cambridge, MA: MIT Press

Freiwald WA, Tsao DY. 2010. Functional compartmentalization and viewpoint generalization within the macaque face-processing system. *Science* 330(6005):845–51

Frenkel MY, Sawtell NB, Diogo AC, Yoon B, Neve RL, Bear MF. 2006. Instructive effect of visual experience in mouse visual cortex. *Neuron* 51(3):339–49

Gaffan D. 2001. What is a memory system? Horel's critique revisited. *Behav. Brain Res.* 127(1–2):5–11

Gavornik JP, Bear MF. 2014. Learned spatiotemporal sequence recognition and prediction in primary visual cortex. *Nat. Neurosci.* 17(5):732–37

Gazzaniga MS. 2013. Shifting gears: seeking new approaches for mind/brain mechanisms. *Annu. Rev. Psychol.* 64:1–20

Goodale MA, Milner AD. 1992. Separate visual pathways for perception and action. *Trends Neurosci.* 15(1):20–25

Goodale MA, Milner AD, Jakobson LS, Carey DP. 1991. A neurological dissociation between perceiving objects and grasping them. *Nature* 349(6305):154–56

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Graham KS, Barense MD, Lee ACH. 2010. Going beyond LTM in the MTL: a synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia* 48(4):831–53

Grill-Spector K, Kourtzi Z, Kanwisher N. 2001. The lateral occipital complex and its role in object recognition. *Vis. Res.* 41(10–11):1409–22

Grill-Spector K, Weiner KS. 2014. The functional architecture of the ventral temporal cortex and its role in categorization. *Nat. Rev. Neurosci.* 15(8):536–48

Gross CG, Rocha-Miranda CE, Bender DB. 1972. Visual properties of neurons in inferotemporal cortex of the Macaque. *J. Neurophysiol.* 35(1):96–111

Güçlü U, van Gerven MAJ. 2015. Deep neural networks reveal a gradient in the complexity of neural representations across the ventral stream. *J. Neurosci.* 35(27):10005–14

Hasselmo ME, Rolls ET, Baylis GC. 1989. The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behav. Brain Res.* 32(3):203–18

Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P. 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293(5539):2425–30

Henson RNA, Cansino S, Herron JE, Robb WGK, Rugg MD. 2003. A familiarity signal in human anterior medial temporal cortex? *Hippocampus* 13(2):301–4

Heusser AC, Awipi T, Davachi L. 2013. The ups and downs of repetition: modulation of the perirhinal cortex by conceptual repetition predicts priming and long-term memory. *Neuropsychologia* 51(12):2333–43

Hietanen JK, Perrett DI, Oram MW, Benson PJ, Dittrich WH. 1992. The effects of lighting conditions on responses of cells selective for face views in the macaque temporal cortex. *Exp. Brain Res.* 89(1):157–71

Inhoff MC, Heusser AC, Tambini A, Martin CB, O'Neil EB, et al. 2019. Understanding perirhinal contributions to perception and memory: evidence through the lens of selective perirhinal damage. *Neuropsychologia* 124:9–18

Inhoff MC, Ranganath C. 2015. Significance of objects in the perirhinal cortex. *Trends Cogn. Sci.* 19(6):302–3

Insausti R, Amaral DG, Cowan WM. 1987. The entorhinal cortex of the monkey: II. Cortical afferents. *J. Comp. Neurol.* 264(3):356–95

Ito M, Tamura H, Fujita I, Tanaka K. 1995. Size and position invariance of neuronal responses in monkey inferotemporal cortex. *J. Neurophysiol.* 73(1):218–26

James TW, Culham J, Humphrey GK, Milner AD, Goodale MA. 2003. Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. *Brain* 126(11):2463–75

James W. 1890. *The Principles of Psychology*, Vol. I. New York: Henry Holt Co.

Kafkas A, Migo EM, Morris RG, Kopelman MD, Montaldi D, Mayes AR. 2017. Material specificity drives medial temporal lobe familiarity but not hippocampal recollection: familiarity-based recognition in the MTL. *Hippocampus* 27(2):194–209

Kahn I, Andrews-Hanna JR, Vincent JL, Snyder AZ, Buckner RL. 2008. Distinct cortical anatomy linked to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. *J. Neurophysiol.* 100(1):129–39

Kanwisher N, Chun MM, McDermott J, Ledden PJ. 1996. Functional imaging of human visual recognition. *Brain Res. Cogn. Brain Res.* 5(1–2):55–67

Kanwisher N, McDermott J, Chun MM. 1997a. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17(11):4302–11

Kanwisher N, Woods RP, Iacoboni M, Mazziotta JC. 1997b. A locus in human extrastriate cortex for visual shape analysis. *J. Cogn. Neurosci.* 9(1):133–42

Kim S, Jeneson A, van der Horst AS, Frascino JC, Hopkins RO, Squire LR. 2011. Memory, visual discrimination performance, and the human hippocampus. *J. Neurosci.* 31(7):2624–29

Kivisaari SL, Tyler LK, Monsch AU, Taylor KI. 2012. Medial perirhinal cortex disambiguates confusable objects. *Brain* 135(12):3757–69

Klüver H, Bucy PC. 1937. "Psychic blindness" and other symptoms following bilateral temporal lobectomy in Rhesus monkeys. *Am. J. Physiol.* 119:352–53

Knutson AR, Hopkins RO, Squire LR. 2012. Visual discrimination performance, memory, and medial temporal lobe function. *PNAS* 109(32):13106–11

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Kourtzi Z, Kanwisher N. 2001. Representation of perceived object shape by the human lateral occipital complex. *Science* 293(5534):1506–9

Kravitz DJ, Saleem KS, Baker CI, Ungerleider LG, Mishkin M. 2013. The ventral visual pathway: an expanded neural framework for the processing of object quality. *Trends Cogn. Sci.* 17(1):26–49

Kriegeskorte N, Mur M, Ruff DA, Kiani R, Bodurka J, et al. 2008. Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron* 60(6):1126–41

Lavenex P, Amaral DG. 2000. Hippocampal-neocortical interaction: a hierarchy of associativity. *Hippocampus* 10(4):420–30

Lavenex P, Suzuki WA, Amaral DG. 2002. Perirhinal and parahippocampal cortices of the macaque monkey: projections to the neocortex. *J. Comp. Neurol.* 447(4):394–420

Lavenex P, Suzuki WA, Amaral DG. 2004. Perirhinal and parahippocampal cortices of the macaque monkey: intrinsic projections and interconnections. *J. Comp. Neurol.* 472(3):371–94

Lee ACH, Buckley MJ, Pegman SJ, Spiers H, Scahill VL, et al. 2005a. Specialization in the medial temporal lobe for processing of objects and scenes. *Hippocampus* 15(6):782–97

Lee ACH, Bussey TJ, Murray EA, Saksida LM, Epstein RA, et al. 2005b. Perceptual deficits in amnesia: challenging the medial temporal lobe "mnemonic" view. *Neuropsychologia* 43(1):1–11

Lee AC, Scahill VL, Graham KS. 2008. Activating the medial temporal lobe during oddity judgment for faces and scenes. *Cereb. Cortex* 18(3):683–96

Lehky SR, Tanaka K. 2016. Neural representation for object recognition in inferotemporal cortex. *Curr. Opin. Neurobiol.* 37:23–35

Levy DA, Shrager Y, Squire LR. 2005. Intact visual discrimination of complex and feature-ambiguous stimuli in the absence of perirhinal cortex. *Learn. Mem.* 12(1):61–66

Li AY, Ladyka-Wojcik N, Qazilbash H, Golestani A, Walther DB, et al. 2022. Multimodal object representations rely on integrative coding. bioRxiv 2022.08.31.504599. **https://doi.org/10.1101/2022.08.31.504599**

López-Aranda MF, López-Téllez JF, Navarro-Lobato I, Masmudi-Martín M, Gutiérrez A, Khan ZU. 2009. Role of layer 6 of v2 visual cortex in object-recognition memory. *Science* 325(5936):87–89

Maass A, Berron D, Libby LA, Ranganath C, Düzel E. 2015. Functional subregions of the human entorhinal cortex. *eLife* 4:e06426

Martin CB, Douglas D, Newsome RN, Man LL, Barense MD. 2018a. Integrative and distinctive coding of visual and conceptual object features in the ventral visual stream. *eLife* 7:e31873

Martin CB, McLean DA, O'Neil EB, Köhler S. 2013. Distinct familiarity-based response patterns for faces and buildings in perirhinal and parahippocampal cortex. *J. Neurosci.* 33(26):10915–23

Martin CB, Sullivan JA, Wright J, Köhler S. 2018b. How landmark suitability shapes recognition memory signals for objects in the medial temporal lobes. *NeuroImage* 166:425–36

McCarthy G, Puce A, Gore JC, Allison T. 1997. Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci.* 9(5):605–10

McClelland JL, McNaughton BL, O'Reilly RC. 1995. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychol. Rev.* 102(3):419–57

McTighe SM, Cowell RA, Winters BD, Bussey TJ, Saksida LM. 2010. Paradoxical false memory for objects after brain damage. *Science* 330(6009):1408–10

Meunier M, Bachevalier J, Mishkin M, Murray E. 1993. Effects on visual recognition of combined and separate ablations of the entorhinal and perirhinal cortex in rhesus monkeys. *J. Neurosci.* 13(12):5418–32

Mishkin M. 1978. Memory in monkeys severely impaired by combined but not by separate removal of amygdala and hippocampus. *Nature* 273(5660):297–98

Mishkin M, Ungerleider LG, Macko KA. 1983. Object vision and spatial vision: two cortical pathways. *Trends Neurosci.* 6:414–17

Montaldi D, Spencer TJ, Roberts N, Mayes AR. 2006. The neural system that mediates familiarity memory. *Hippocampus* 16(5):504–20

Moscovitch M, Winocur G, Behrmann M. 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *J. Cogn. Neurosci.* 9(5):555–604

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Moss HE, Rodd JM, Stamatakis EA, Bright P, Tyler LK. 2005. Anteromedial temporal cortex supports fine-grained differentiation among objects. *Cereb. Cortex* 15(5):616–27

Murray EA, Bussey TJ. 1999. Perceptual-mnemonic functions of the perirhinal cortex. *Trends Cogn. Sci.* 3(4):142–51

Murray EA, Bussey TJ, Saksida LM. 2007. Visual perception and memory: a new view of medial temporal lobe function in primates and rodents. *Annu. Rev. Neurosci.* 30:99–122

Murray E, Mishkin M. 1984. Severe tactual as well as visual memory deficits follow combined removal of the amygdala and hippocampus in monkeys. *J. Neurosci.* 4(10):2565–80

Murray E, Mishkin M. 1986. Visual recognition in monkeys following rhinal cortical ablations combined with either amygdalectomy or hippocampectomy. *J. Neurosci.* 6(7):1991–2003

Nasr S, Tootell RBH. 2012. Role of fusiform and anterior temporal cortical areas in facial recognition. *NeuroImage* 63(3):1743–53

Norman KA, O'Reilly RC. 2003. Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. *Psychol. Rev.* 110(4):611–46

O'Neil EB, Cate AD, Kohler S. 2009. Perirhinal cortex contributes to accuracy in recognition memory and perceptual discriminations. *J. Neurosci.* 29(26):8329–34

O'Neil EB, Hutchison RM, McLean DA, Köhler S. 2014. Resting-state fMRI reveals functional connectivity between face-selective perirhinal cortex and the fusiform face area related to face inversion. *NeuroImage* 92:349–55

Op De Beeck H, Vogels R. 2000. Spatial sensitivity of macaque inferior temporal neurons. *J. Comp. Neurol.* 426(4):505–18

Orban GA, Van Essen D, Vanduffel W. 2004. Comparative mapping of higher visual areas in monkeys and humans. *Trends Cogn. Sci.* 8(7):315–24

Parvizi J, Jacques C, Foster BL, Withoft N, Rangarajan V, et al. 2012. Electrical stimulation of human fusiform face-selective regions distorts face perception. *J. Neurosci.* 32(43):14915–20

Penfield W, Milner B. 1958. Memory deficit produced by bilateral lesions in the hippocampal zone. *Arch. Neurol. Psychiatry* 79(5):475–97

Perrett DI, Hietanen JK, Oram MW, Benson PJ. 1992. Organization and functions of cells responsive to faces in the temporal cortex. *Philos. Trans. R. Soc. Lond. B* 335(1273):23–30

Perrett DI, Oram MW, Harries MH, Bevan R, Hietanen JK, et al. 1991. Viewer-centred and object-centred coding of heads in the macaque temporal cortex. *Exp. Brain Res.* 86(1):159–73

Perrett DI, Rolls ET, Caan W. 1982. Visual neurones responsive to faces in the monkey temporal cortex. *Exp. Brain Res.* 47(3):329–42

Pohl W. 1973. Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys. *J. Comp. Physiol. Psychol.* 82(2):227–39

Poldrack RA, Yarkoni T. 2016. From brain maps to cognitive ontologies: informatics and the search for mental structure. *Annu. Rev. Psychol.* 67:587–612

Price CJ, Friston KJ. 2005. Functional ontologies for cognition: the systematic definition of structure and function. *Cogn. Neuropsychol.* 22(3–4):262–75

Pylyshyn ZW. 1986. *Computation and Cognition: Toward a Foundation for Cognitive Science*. Cambridge, MA: MIT Press

Quiroga RQ, Reddy L, Kreiman G, Koch C, Fried I. 2005. Invariant visual representation by single neurons in the human brain. *Nature* 435(7045):1102–7

Ranganath C, Ritchey M. 2012. Two cortical systems for memory-guided behaviour. *Nat. Rev. Neurosci.* 13(10):713–26

Richter FR, Cooper RA, Bays PM, Simons JS. 2016. Distinct neural mechanisms underlie the success, precision, and vividness of episodic memory. *eLife* 5:e18260

Riesenhuber M, Poggio T. 1999. Hierarchical models of object recognition in cortex. *Nat. Neurosci.* 2(11):1019–25

Rosenthal CR, Andrews SK, Antoniades CA, Kennard C, Soto D. 2016. Learning and recognition of a non-conscious sequence of events in human primary visual cortex. *Curr. Biol.* 26(6):834–41

Rust NC, DiCarlo JJ. 2010. Selectivity and tolerance ("invariance") both increase as visual information propagates from cortical area V4 to IT. *J. Neurosci.* 30(39):12978–95

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)

Annu. Rev. Vis. Sci. 2023.9. Downloaded from www.annualreviews.org
Access provided by University of Toronto Library on 05/03/23. For personal use only.

Saleem KS, Tanaka K. 1996. Divergent projections from the anterior inferotemporal area TE to the perirhinal and entorhinal cortices in the macaque monkey. *J. Neurosci.* 16(15):4757–75

Schacter DL, Tulving E. 1994. What are the memory systems of 1994? In *Memory Systems*, ed. DL Schacter, E Tulving, pp. 2–38. Cambridge, MA: MIT Press

Scoville WB, Milner B. 1957. Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatry* 20(1):11–21

Shrager Y, Gold JJ, Hopkins RO, Squire LR. 2006. Intact visual perception in memory-impaired patients with medial temporal lobe lesions. *J. Neurosci.* 26(8):2235–40

Squire LR. 1987. *Memory and Brain*. Oxford, UK: Oxford Univ. Press

Squire LR, Wixted JT. 2011. The cognitive neuroscience of human memory since H.M. *Annu. Rev. Neurosci.* 34:259–88

Squire LR, Zola-Morgan S. 1991. The medial temporal lobe memory system. *Science* 253(5026):1380–86

Steeves JKE, Culham JC, Duchaine BC, Pratesi CC, Valyear KF, et al. 2006. The fusiform face area is not sufficient for face recognition: evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia* 44(4):594–609

Suzuki WA, Naya Y. 2014. The perirhinal cortex. *Annu. Rev. Neurosci.* 37:39–53

Suzuki WL, Amaral DG. 1994. Perirhinal and parahippocampal cortices of the macaque monkey: cortical afferents. *J. Comp. Neurol.* 350(4):497–533

Tanaka K. 1997. Mechanisms of visual object recognition: monkey and human studies. *Curr. Opin. Neurobiol.* 7(4):523–29

Tanaka K, Saito H, Fukada Y, Moriya M. 1991. Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *J. Neurophysiol.* 66(1):170–89

Tsao DY, Freiwald WA, Tootell RBH, Livingstone MS. 2006. A cortical region consisting entirely of face-selective cells. *Science* 311(5761):670–74

Tulving E. 1972. Episodic and semantic memory. In *Organization of Memory*, ed. E Tulving, W Donaldson, pp. 381–403. Cambridge, MA: Academic Press

Tulving E. 1985a. How many memory systems are there? *Am. Psychol.* 40(4):385–98

Tulving E. 1985b. Memory and consciousness. *Can. Psychol. Psychol. Can.* 26(1):1–12

Vargha-Khadem F, Gadian DG, Watkins KE, Connelly A, Van Paesschen W, Mishkin M. 1997. Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* 277(5324):376–80

Voss JL, Hauner KKY, Paller KA. 2009. Establishing a relationship between activity reduction in human perirhinal cortex and priming. *Hippocampus* 19(9):773–78

Wang W-C, Lazzara MM, Ranganath C, Knight RT, Yonelinas AP. 2010. The medial temporal lobe supports conceptual implicit memory. *Neuron* 68(5):835–42

Warren DE, Duff MC, Tranel D, Cohen NJ. 2011. Observing degradation of visual representations over short intervals when medial temporal lobe is damaged. *J. Cogn. Neurosci.* 23(12):3862–73

Wickelgren WA. 1968. Sparing of short-term memory in an amnesic patient: implications for strength theory of memory. *Neuropsychologia* 6(3):235–44

Wright P, Randall B, Clarke A, Tyler LK. 2015. The perirhinal cortex and conceptual processing: effects of feature-based statistics following damage to the anterior temporal lobes. *Neuropsychologia* 76:192–207

Xiang J-Z, Brown MW. 1998. Differential neuronal encoding of novelty, familiarity and recency in regions of the anterior temporal lobe. *Neuropharmacology* 37(4–5):657–76

Yeung L-K, Ryan JD, Cowell RA, Barense MD. 2013. Recognition memory impairments caused by false recognition of novel objects. *J. Exp. Psychol. Gen.* 142(4):1384–97

Yin S, Bo K, Liu Y, Thigpen N, Keil A, Ding M. 2020. Fear conditioning prompts sparser representations of conditioned threat in primary visual cortex. *Soc. Cogn. Affect Neurosci.* 15(9):950–64

Yonelinas AP, Ranganath C, Ekstrom AD, Wiltgen BJ. 2019. A contextual binding theory of episodic memory: systems consolidation reconsidered. *Nat. Rev. Neurosci.* 20(6):364–75

You Y, Brown J, Li W. 2021. Human sensory cortex contributes to the long-term storage of aversive conditioning. *J. Neurosci.* 41(14):3222–33

Review in Advance first posted on April 17, 2023. (Changes may still occur before final publication.)