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Review

The medial temporal lobe: Memory and beyond

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HIGHLIGHTS

- We discuss the contributions of hippocampus and perirhinal cortex to recollection and familiarity.
- We present the effects of objective stimulus manipulation on recollection and familiarity ratings.
- Recent studies, dealing with perceptual-mnemonic theory of the medial temporal lobe, are reviewed.

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ABSTRACT

The structures of the medial temporal lobe, e.g., the hippocampus, entorhinal cortex, perirhinal cortex, and parahippocampal cortex, are known to be essential for long-term memory processing and hence are labeled the medial temporal lobe memory system. Nevertheless, the exact contributions of each structure and the involvement in different cognitive processes remain controversial. This article discusses recent findings dealing with recognition memory and a long lasting involvement of the hippocampus and perirhinal cortex in episodic memory, based on functional imaging and lesion studies. Furthermore, a new paradigm employing objective manipulations of recollection and familiarity is presented, showing no anatomical distinction for these two processes, as opposed to studies using subjective ratings. Additionally, results regarding an involvement of the medial temporal lobe in visual processing are presented, in general supporting the visual-mnemonic theory. The discussed findings show that many questions regarding the functional organization remain unsolved, and that we are in need of further research to create a comprehensive model of the medial temporal lobe. For this, we might need to give up the distinctions into different cognitive processes and start to investigate the different types of representations that are processed by the medial temporal lobe.

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1. Introduction

Since the classical case of patient H.M. [1], who underwent a bilateral removal of the hippocampus (with lesions extending to adjacent structures like the entorhinal cortex and the medial temporal pole), the medial temporal lobe (MTL) has been functionally linked to long-term memory. The prevailing theoretical view, the medial temporal lobe memory system, ascribes purely

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mnemonic functions to a subset of structures of the MTL. These structures include the hippocampus, the entorhinal and perirhinal as well as the parahippocampal cortices [2,3]. The main function of these structures has been associated with declarative memory for facts, events and relations [4]. Within this system, at least two further functional subdivisions have been discussed in the literature. Recollection is a process in which subjects can consciously retrieve previously learned information including its temporal and spatial context, with a high degree of certainty. This process is thought to be processed by the hippocampus. Familiarity on the other hand is the feeling of knowing some contents without further information about the context and with less certainty, and it is thought to be functionally related to the perirhinal cortex [5,6]. Different approaches yield additional evidence for spatial memory being mediated by the parahippocampal cortex [7], whereas associative/relational memory is associated with the hippocampus [8,9]. Anatomically, the perirhinal cortex is strongly connected with inferior temporal regions of the ventral visual processing stream, whereas the parahippocampal cortex has stronger connections to the dorsal visual stream as well as to the auditory association cortices [10,11].

This short review will focus on selected publications dealing with the functional organization of the medial temporal lobe and the interactions of visual processing and the encoding and retrieval of new information. The topics recognition memory and perception in the MTL have been both discussed controversially. Moreover, they seem to share certain similarities, like the assumption that there is a functional division of those processes within the MTL, with differing neural correlates. It remains unclear if familiarity and recollection are part of the same process [9,12], and how exactly items and context are being processed by the different MTL structures [13–15]. Besides conducting functional imaging studies using fMRI, we also examined patients with lesions to characterize the patterns of specific memory functions.

2. Recollection, familiarity, and their separation over time

Based on a two component model for recognition memory, recollection and familiarity can be distinguished experimentally [13,16,17]. A number of models of recognition memory have been proposed, and it has been discussed controversially whether this distinction reflects different processes and whether these two components are mediated by different anatomical structures, with the hippocampus being responsible for recollection and the perirhinal cortex being responsible for familiarity [4,18]. It is also under debate if these structures do show a long lasting involvement in episodic memory. The multiple trace theory asserts that the hippocampus is required for retention and retrieval of episodic memories over extended periods of time [18,19], while others argue that the role of the hippocampus is time-limited, with a gradual transfer of storage from the hippocampus to neocortical regions (consolidation theory, see [4]). Little is known about the changes in the neural correlates of familiarity memory over time, but it is assumed to fade quickly [20]. Supporting evidence for the anatomical separation of familiarity and recollection processes has been found by investigating patients with ischemic damage to the right hippocampus [21]. These patients demonstrated an isolated impairment in recollection with intact familiarity, supporting the notion that familiarity and recollection are mediated by distinct structures of the MTL.

In a prospective study [22], we investigated the differential involvement of the hippocampus and the perirhinal cortex in recollection and familiarity processes over a time period of six weeks. After an initial encoding of 183 colored images of everyday life objects, a subset was presented in combination with new distractor images. Retrieval was performed immediately, as well as three and six weeks after encoding. Subjects had to indicate whether they recognized an item and in a second step, whether they specifically remembered having seen this particular item or whether it seemed merely familiar (familiarity/recollection rating). Results support the idea of two distinct processes mediated by distinct areas, with the hippocampus showing activations for recollection ratings and the perirhinal cortex showing deactivations for familiarity ratings. Additionally we could demonstrate that this pattern persists for a period of up to six weeks [22]. Overall, these results yield evidence for an anatomical and a long lasting temporal separation of these two types of recognition memory and further support the multiple trace theory [18]. Nevertheless, there has been contrary evidence that has shown no differential involvement of the hippocampus for familiarity or recollection [23,24]. It has been suggested that evidence for a differential involvement might often be confounded with effects of memory strength [12,25,26].

3. Objective stimulus manipulations and their effect on familiarity and recollection

The typical recollection/familiarity distinction is often assessed in a recognition memory paradigm, using the remember/know task. Results illustrate different types of recognition for items that have been encoded before. The responses in such tasks are subjective, as the participants decide whether they saw the item before and whether they code it as familiarity or recollection memory. But what if the items were manipulated in an objective way? Could familiarity be induced when the formerly encoded item was manipulated during recognition? Faces are easy to manipulate using the so called morphing technique. One face can be morphed into a second one and the overlap or the morphing steps can be varied automatically by the morphing software package. The attempts to use the same approach for landscapes do not result in a satisfactory image, since the borders of parts of the landscapes remain blurred. To overcome these problems a new approach has been developed in our lab using a “moving window” [27]. This moving window was used to extract various excerpts of one image which differ with respect to their degree of overlap. This approach was used to create landscape stimuli that have a comparable percentage of overlap, similar to morphed images. The morphing technique provides the possibility to determine the exact ratio of the mixture of two images; the subjective, perceived overlap had to be determined in a calibration procedure. This enabled us to manipulate familiarity in an objective way and investigate its relationship with subjective memory strength. Results suggest that the perceived percentage of morphing differed between both approaches. Additionally it varied for faces and landscapes. The final experiment was conducted using the calibrated morphing steps to manipulate the recognition contents with respect to their original (encoded) information.

Subjects were scanned during encoding and retrieval of the formerly learned faces and landscapes. Two types of parametrical modulators were used for the analysis, with responses as subjective modulators and the morphing steps of a picture as an objective modulator. Encoding related activation has been found bilaterally in the hippocampus for faces and landscapes. Retrieval of morphed faces and manipulated landscapes was related to activation increase in the amygdala for faces and a decrease of activation in the hippocampus for scenes. In an additional analysis, the different morphing steps as well as the different response confidence ratings were both included in the analysis, taking both approaches into account. Again, recognition of faces was accompanied by activation increase in the hippocampus. Successful recognition of landscapes was also related to an activation increase and also a decrease in the hippocampus bilaterally. These results do not show activation