Research report

Involvement of the human medial temporal lobe in a visual discrimination task

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HIGHLIGHTS

- We examine the involvement of MTL structures in visual discrimination.
- We directly compare recognition and visual discrimination tasks in an fMRI study.
- We find significant hippocampal activation for the discrimination of pictures with high feature ambiguity, as well as for the recognition of stimuli.

ARTICLE INFO

ABSTRACT

Recent imaging and lesion studies suggest that the human medial temporal lobe (including the hippocampus and the perirhinal cortex), which is traditionally believed to be of central importance for memory processing, is also involved in processing and discrimination of complex visual stimuli. The aim of this study was to use functional magnetic resonance imaging in healthy subjects to further elucidate the contributions of different medial temporal lobe structures to perceptual and mnemonic processing of faces and scenes, by directly comparing the activation in a visual discrimination and a recognition task (one week after encoding). A within-subjects full factorial analysis revealed significant hippocampal activation for both discrimination and recognition task, with no differential activations for the processing of faces or scenes. No perirhinal activation was found in either of the experimental conditions. These results support a perceptual-mnemonic theory of the medial temporal lobe, while questioning a simple mapping of different functions to single structures like hippocampus and perirhinal cortex.

1. Introduction

The structures of the medial temporal lobe (MTL) are traditionally believed to be specialized for declarative/relational learning and memory [1] and hence are labeled the "medial temporal lobe memory system" [2]. The underlying theoretical view describes the structures of the MTL, including the hippocampus with its adjacent perirhinal, entorhinal and parahippocampal cortices, as being exclusively involved in mnemonic processes, but not in other cognitive processes such as perception [1,3–5].

Recent research has proposed an "emergent memory account" [6] or a "perceptual-mnemonic theory" [7] for the MTL and assumes that the perirhinal cortex is a rostral extension of the ventral visual stream (VVS) [8,9] and therefore involved in the processing of visual stimuli [10,11].

Research from the past two decades provides considerable evidence for the participation of MTL structures in the processing of complex visual stimuli, mainly related to the discrimination of objects or of spatial stimuli with "high feature ambiguity" [12]. The first studies were conducted on non-human primates [12–14], since the perirhinal cortex of monkeys has numerous connections to visual sensory areas [15,16]. However, an increasing number of studies deals with human subjects.

Patients with MTL lesions, including hippocampus and perirhinal cortex, fail in visual discrimination tasks for specific stimuli, depending on the location of the lesion [9,17–19]. Patients with selective hippocampal damage display impaired visual discrimination of morphed scenes, but not for the discrimination of morphed faces, in contrast to patients with extensive MTL lesions, who are impaired in discriminating scenes and faces [18]. Additionally, patients with perirhinal lesions show deficits for the visual discrimination of complex objects [9].

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These findings suggest that there is a double dissociation of the putative perceptual functions of the hippocampus and the perirhinal cortex, with parallels to the well-established memory functions of these areas [20]. Based on the fact that the hippocampus is an allocortical structure that evolved very early in vertebrate history [21], it seems highly unlikely that the neocortical (and therefore anatomically highly dissimilar) perirhinal cortex has identical or similar functions (see also [22]).

However, other studies with similar designs [23–26] could not show any visual discrimination deficits resulting from hippocampal or perirhinal damage. These contrary results could partly arise from differences in lesion assessment, assuming that patients with perceptual deficits could be impaired due to lesions that extend beyond the MTL [27].

The results obtained in patient studies have also been supported by functional neuroimaging in healthy human subjects. Several studies could demonstrate hippocampal and perirhinal activation for mnemonic and perceptual tasks [10,28–30]. Barense et al. [30] could demonstrate perirhinal cortex activation for the discrimination of faces and artificial objects (so-called "greebles") and posterior hippocampal activation for scene and face processing. Besides, there also seems to be an effect of familiar (famous faces and real world objects) versus unfamiliar (novel faces and artificial objects) stimuli, with increased activation in perirhinal cortex and hippocampus for familiar stimuli [31].

Another concern that has been raised about the interpretation of the results as being based on a perceptual role of the MTL is the problem that studies examining visual discrimination use stimulus arrays consisting of multiple pictures that are presented simultaneously. It has been argued that deficits could be explained by an involvement of MTL structures in working memory processes [32,33], Amnesic patients with long-term memory deficits can also show short-term memory impairments [34,35]. However, working memory for relational information can be intact in patients with MTL damage [36].

The matter remains highly controversial and is in urgent need of further research to build a comprehensive model of the functions of the human medial temporal lobe. The present study aimed to directly compare perceptual and memory processing within the MTL of healthy subjects in a within-subjects full factorial design. Functional imaging techniques were used for both mnemonic and perceptual tasks, while previous studies have employed recognition tasks only outside of the scanner. Subjects performed a visual discrimination and a recognition task on two sessions. Incidental encoding was investigated by measuring the total number of remembered items from the visual discrimination. Based on previous findings, we expected hippocampal and perirhinal activation for the recognition task. We also expected a contribution of the MTL to the processing of stimuli with high feature ambiguity, resulting in significant activation in "hard" conditions of the discrimination task. For both tasks we expected the perirhinal cortex to be active for the processing of faces and the hippocampus for the processing of scenes. We also expected a contribution of the fusiform gyrus and the parahippocampal gyrus to the processing of faces and scenes, respectively. This should shed more light on the involvement of the MTL structures in mnemonic and perceptual processing and on the question if there is an overlap of these functions in the MTL.

2. Materials and methods

2.1. Ethics statement

The study received ethical approval by the local Ethics Committee of the Medical Faculty of the Ruhr University Bochum, which conforms to the Declaration of Helsinki.

2.2. Participants

Twenty right-handed and neurologically healthy subjects (10 male and 10 female subjects; mean age: 23.06 years; range: 18–29) participated in this study. Three subjects had to be excluded, two because a very low number of recognized items and one because of excessive movement in the scanner. All participants gave informed written consent after a detailed explanation of the procedure.

2.3. Experimental design

The experiment took place in two sessions inside an MRI scanner. The first session consisted of a visual discrimination task and an encoding task. For the second session, which was carried out exactly one week later, participants had to perform a recognition task. The experiment was performed using Presentation® software (Neurobehavioral Systems, Inc., Albany, CA, USA) and MRI video goggles with a resolution of 800×600 pixels, registering the answers with a keypad suitable for MRI.

For the discrimination task, 180 greyscale pictures of each faces, scenes, and black rectangles were employed in separate blocks in an oddity task [29]. Three stimulus types (rectangles, faces, scenes) and two difficulty conditions ("easy" and "hard") were employed (Fig. 1), resulting in six blocks with 36 trials each. Three pictures were shown simultaneously to minimize working memory demands. Subjects had to indicate by key press which picture was the "odd-one-out". Pictures from the "easy" condition were easily distinguishable by single features, so that the MTL would not be needed in their processing. Pictures from the "hard" condition had a high feature ambiguity, resulting in a higher discrimination difficulty, which is supposed to recruit MTL structures.

Scene stimuli for the "hard" condition were created using a previously employed panoramic technique [37], with a "sliding window" (for a detailed procedure see [38]), resulting in stimulus triplets with varying overlap (with 75% or 90% overlap between the pictures). The target stimulus for the "hard" scene discrimination task was defined as the stimulus with the smallest overlap in regards to the other two pictures. Face stimuli for the "hard" condition were created by taking pictures from different viewing angles ($-60°$, $-30°$, $0°$, $30°$, $60°$), with an additional masking of the hair for increased difficulty. The size oddity judgements of the black rectangles were used as a baseline in the fMRI analysis.

In the "easy" condition of this task, only two different pictures (two different frontal view faces or scenes) were used, with one of them being presented at two random positions and the other one (the "odd-one-out") being presented at the third remaining position. In the "hard" condition, panoramic pictures with different viewing angles were used. For the subsequent first level analysis of the fMRI data, a baseline condition was included, in which black rectangles with varying size had to be discriminated. In the "hard" condition, the size differences between the rectangles were much smaller ("easy" stimuli differed in a range from 5 to 10 pixels, "hard" stimuli from 30 to 40). Besides, their positions were jittered randomly to a small degree so that the edges did not line up, again to increase discrimination difficulty. A piloting, which was performed before the experiment, ensured similar error rates in the "easy" and "hard" condition for all three stimulus types. The presentation of easy and hard conditions was balanced across all subjects and stimulus types, in order to prevent a training effect.

Immediately afterwards, in the second part of the first session, subjects had to study and encode 36 face and 36 scene stimuli for the recognition task in the second session (Fig. 2). The participants were instructed that there would be a memory test for the items from the encoding task. To increase the depth of processing, subjects also had to indicate if they evaluate the pictures as positive or negative. All pictures used in the encoding and discrimination