Research report

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

Robert K. Lech a,b, *, Boris Suchan a,b

a Institute of Cognitive Neuroscience, Dept. of Neuropsychology, Ruhr University Bochum, Germany
b International Graduate School of Neuroscience, Ruhr University Bochum, Bochum, Germany

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

Article history:
Received 4 October 2013
Received in revised form 14 March 2014
Accepted 17 March 2014
Available online 24 March 2014

Keywords:
Visual perception
Discrimination
Recognition memory
fMRI
Medial temporal lobe

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.

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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].
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
Fig. 1. Example of stimulus displays from the discrimination task. Easy discriminations of all stimulus types are displayed on the left and hard discriminations on the right. Size oddity judgements of rectangles (bottom line) were used as a baseline condition for fMRI analysis.

Fig. 2. Example of stimuli from the encoding and recognition task. All stimuli in the encoding task were novel and trial unique. Stimuli in the recognition task consisted of new distractor pictures, old pictures from the encoding task, old targets from the discrimination task, and old non-targets from the discrimination task.
task were novel and trial unique, in order to prevent repetition suppression resulting from repeated presentation.

For the recognition task, which took place a week after the first session, subjects were instructed that they would have to recognize items from the first testing session. These were presented one at a time, intermixed with distractor pictures. Four types of pictures were used for both face and scene trials (36 each): New distractor pictures, familiar pictures from the encoding task, familiar targets from the discrimination task, and familiar non-targets from the discrimination task. The latter stimuli were included to examine a possible incidental encoding, but only pictures from the easy conditions were used, because the rotated stimuli from the hard condition would have been more difficult to recognize. All pictures in both sessions were presented for 4 s, with a variable inter-trial interval (ITI) ranging from 1 to 3 s. A fixation cross was presented during all ITIs.

2.4. Image acquisition

The experiment was performed using a Philips 3 T Achieva MRI scanner with a 32 channel SENSE head coil. A T1 weighted structural scan was acquired for every participant at the start of the first experimental session (220 slices, voxel size = 1 mm × 1 mm × 1 mm, TE = 3.8 ms, flip angle = 8°). T2* weighted echo-planar MR images (EPI) were acquired in all three experimental conditions in an ascending sequence of 30 slices (voxel size = 1.65 mm × 1.65 mm × 3 mm, TR = 2200 ms, TE = 35 ms). Five dummy images were acquired at the start of each session and discarded directly, to allow for MRI signal stabilization.

2.5. Data analysis

The functional and structural images were preprocessed using the latest release of SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8). The preprocessing included the following steps: Slice-time correction, realigning and unwarping, co-registering the EPIs with the structural scan, segmenting the structural scan into grey and white matter, and normalizing the EPIs to MNI space with DARTEL [39]. The unwarping procedure was used in order to reduce distortions caused by magnetic field inhomogeneities, which result from the participants’ movements. All images were resliced into 1 mm × 1 mm × 1 mm voxels, and finally smoothed with a Gaussian kernel of 3 mm full-width half-maximum (FWHM). Small voxel and smoothing kernel sizes were chosen in order to increase sensitivity in the investigated brain structures, which are relatively small in size. The preprocessed images then were submitted into a first level GLM analysis, where the blood oxygenation level dependency (BOLD) signal was modeled with the canonical hemodynamic response function. A high-pass filter at 128 s was used to remove low frequency drifts. For the discrimination task, seven regressors were defined, one for correct responses to each stimulus type (“easy baseline”, “hard baseline”, “easy faces”, “hard faces”, “easy scenes”, “hard scenes”), with an additional regressor for the presentation of the fixation cross. Contrasts for face and scene discrimination were defined by subtracting the correct “hard baseline” responses from the correct “hard face” or “hard scene” responses. The model for the recognition task included the following regressors: correct recognition, correct rejection, false alarms, and misses for face and scene stimuli, as well as a fixation regressor. Correct recognition was contrasted against correct rejections for both stimulus types. The fixation regressors were added in order to increase the amount of explained variance and were not used for further analysis. All resulting contrasts (face discrimination, scenes discrimination, face recognition, scene recognition) were then used for group inference in the second level analysis.

In the group-level random effects analysis, a within-subjects full factorial model with two factors was applied to the data from the discrimination and recognition task. The model included the factors “task” (discrimination; recognition) and “stimulus type” (faces; scenes). Main effects for both factors and interactions were used as contrasts of interest. Significant activation foci in the full factorial analysis were used to extract mean signal changes (in percent) with MarsBar software (http://marsbar.sourceforge.net/), and were then fed into paired t-tests.

All reported statistics refer to whole brain analyses. Due to a strong a priori hypothesis about the involvement of the MTL in visual perception, the statistical maps were initially analyzed using an uncorrected threshold of \( p < 0.001 \) with a minimum of 10 voxels per cluster [38,40]. To reduce type II errors while keeping type I errors low [41], a Monte Carlo simulation with 10,000 iterations was used [42–45], defining the threshold at \( p < 0.05 \), corrected for multiple comparisons. This simulation yielded a cluster extent threshold of 33 resampled voxels while assuming an individual voxel type I error of \( p = 0.001 \).

2.6. ROI analysis

For the localization of the resulting activations, bilateral ROIs were defined using hippocampal, parahippocampal, and perirhinal masks. The hippocampal and parahippocampal masks were taken from the Automated Anatomical Labeling Toolbox [46]. For the perirhinal mask, two perirhinal maps used in previous studies were additionally combined [10,47], resulting in a map derived from 28 subjects. Only activations in these structures were reported.

3. Results

3.1. Behavioral data

Repeated measures ANOVAs (with Greenhouse Geisser correction) were separately applied for discrimination and recognition tasks. For the discrimination task, reaction times (RTs) and accuracy (correct responses—false alarms) were analyzed with the factors stimulus (“faces”, “scenes”, and “baseline”) and difficulty (“easy”, “hard”). For RTs, the factors stimulus (\( F(2,32) = 12.375; p < 0.002 \)) and difficulty (\( F(1,16) = 332.365; p < 0.0001 \)), as well as the interaction of both (\( F(2,32) = 12.803; p < 0.0001 \)) yielded significant results. Paired t-tests indicated that the interaction was based on an overall increase of RTs in the “hard” condition in comparison to the easy condition. For easy discriminations, the RTs were slower for faces, as opposed to easy scenes and baseline stimuli (see Table 1). For accuracy, there were also significant effects for the factors stimulus (\( F(2,32) = 12.42; p < 0.0001 \)), difficulty (\( F(1,16) = 313.308; p < 0.0001 \)) and the interaction of both (\( F(2,32) = 11.331; p < 0.0001 \)), with the interaction being based on a reduced accuracy for “hard” baseline stimuli compared to the other stimuli.

For the recognition task, RTs were analyzed using the factors stimulus (faces, scenes) and response type (correct recognition, correct rejection, miss, false alarm). The analysis showed a main effect for the factor response type (\( F(2,32) = 7.765; p < 0.002 \)), with correct recognition ratings being faster than correct rejections, misses and false alarms (see Table 1). There was no main effect of the factor stimulus and no significant interaction of stimulus and response type. There was also no significant difference in accuracy between face and scene stimuli.

In order to assess if stimuli from the discrimination tasks were incidentally encoded, the number of recognized items and RTs from both discrimination and encoding task were compared. For this, stimuli from the discrimination task were separated into two categories, discrimination target and discrimination non-target.
A repeated measures ANOVA with the factors stimulus (faces, scenes) and encoding condition (explicit, discrimination target, discrimination non-target) revealed a main effect of the encoding condition for both correct responses ($F(2,32) = 5.693; p < 0.01$) and RTs ($F(2,32) = 51.116; p < 0.0001$), showing that implicitly encoded stimuli were remembered to a smaller degree and with an increase of the RT (see Fig. 3).

3.2. Imaging data

The full factorial analysis yielded in sum four activation clusters in the hippocampus and one cluster spanning the fusiform and parahippocampal gyrus (see Table 2 and Fig. 4).

Two clusters were found for the main effect of “task”, one for the contrast recognition > discrimination, located in the right posterior hippocampus (39 – 31 – 10; 47 voxels), and another one for the contrast discrimination > recognition in the left anterior hippocampus (−29 − 9 − 21; 40 voxels). One significant cluster was found for the main effect of “stimulus type”: The contrast faces > scenes yielded an activation cluster spanning across the right fusiform to the parahippocampal gyrus (25 − 39 − 14; 104 voxels). Two additional clusters showed significant activations for the interaction of the two factors, one in the left posterior hippocampus (−29 − 37 − 3; 10 voxels), and one in the right anterior hippocampus (35 − 14 − 14; 10 voxels), but only with a threshold of $p < 0.001$, uncorrected for multiple comparisons.

Surprisingly, no significant activations were found in the perirhinal cortex, even with an uncorrected threshold of $p < 0.001$ and a minimum cluster extent of 10 voxels. Furthermore, separate t-tests (easy faces, hardfaces, easy scenes, and hard scenes, all contrasted against the respective baseline discrimination in the first level) were calculated for the two tasks in order to investigate a possible masking of stimulus specificity by task-specific effects, still yielding no significant perirhinal activations. Additionally, the threshold was lowered to $p < 0.01$ to search for possibly weaker effects, but again, no significant activation of the perirhinal cortex was found. In order to further investigate stimulus specific effects, which were inconclusive in the full factorial analysis, the parahippocampal and fusiform gyrus were also used as ROIs in the separate t-tests. For the hard discrimination of faces, two large clusters were found in the left (−48 − 54 − 15; 712 voxels) and right (43 − 44 − 19, 916 voxels) fusiform gyrus. Three additional clusters were found for hard discriminations of scenes in the left (−22 − 43 − 7, 142 voxels) and right (31 − 45 − 6, 118 voxels; 32 − 33 − 15, 68 voxels) parahippocampal gyrus (see also Table 2).

The signal changes and paired t-tests for the interaction clusters revealed that both interactions were based on a difference between the activation for faces and scenes in the recognition task, while there was no significant difference between stimulus types in the discrimination task. While the left hippocampus showed a stronger activation for scenes and a deactivation for faces in the recognition task, the right hippocampus showed the opposite pattern, with a stronger activation for faces and a deactivation for scenes (Fig. 5). These results have to be interpreted carefully, since the interaction clusters did not reach the cluster extent threshold of 33 voxels. The mean signal changes in the hippocampal clusters, active for the main effect of “task”, did confirm the task-specific involvement of each cluster. The signal change in the fusiform and parahippocampal gyrus however showed a more differential involvement, with a stronger involvement in the recognition of faces and the discrimination of scenes.

**Fig. 3.** Mean reaction times and percentage of correct responses in the recognition task. Explicitly encoded items were recognized faster and with a higher accuracy than implicitly encoded items ($p < 0.05$). There was no difference between stimulus types or discrimination targets vs. non-targets. Error bars represent the standard error of the mean (SEM).

**Table 1**

|                      | Baseline | Faces | Scenes |
|----------------------|----------|-------|--------|
|                      | RT       | accuracy | RT       | accuracy | RT       | accuracy |
| Discrimination       |          |         |         |          |          |         |
| Easy discriminations | 1169(304)| 0.93 (0.12) | 1786 (403) | 0.94 (0.06) | 1244 (224) | 0.98 (0.02) |
| Hard discriminations | 2117(636) | 0.43 (0.14) | 2414 (311) | 0.09 (0.16) | 2505 (310) | 0.61 (0.10) |
| Recognition          |          |         |         |          |          |         |
| Correct recognition  |          |         |         |          |          |         |
| Misses               |          |         |         |          |          |         |
| Correct rejection    |          |         |         |          |          |         |
| False alarms         |          |         |         |          |          |         |

**Fig. 26.**
Table 2
Imaging results. Significant activations for main effects (p < 0.05 corr.) and interactions (p < 0.001) in the full factorial analysis. Additionally, significant clusters resulting from the separate t-tests of the discrimination task are listed. Each line represents one cluster.

| Task                                | MNI coordinates (x, y, z) | Cluster size | T-score | Anatomical structure                                      |
|-------------------------------------|---------------------------|--------------|---------|-----------------------------------------------------------|
| Recognition > discrimination        | 39 -31 -10                | 47           | 4.74    | Right posterior hippocampus                                 |
| Discrimination > recognition        | -29 -9 -21                | 40           | 4.61    | Left anterior hippocampus                                  |
| Faces > scenes                      | 25 -39 -14                | 104          | 4.54    | Right fusiform gyrus/parahippocampal gyrus                |
| Interactions                        | -29 -37 -3               | 10           | 5.26    | Left posterior hippocampus                                 |
|                                    | 35 -14 -14                | 10           | 4.37    | Right anterior hippocampus                                 |
| T-test hard scenes                  | -22 -43 -7                | 142          | 7.75    | Left parahippocampal gyrus                                |
|                                    | 31 -45 -6                 | 118          | 6.11    | Right parahippocampal gyrus                               |
|                                    | 32 -33 -15                | 68           | 5.62    | Right parahippocampal gyrus                               |
| T-test hard faces                   | 43 -44 -19                | 916          | 9.95    | Right fusiform gyrus                                      |
|                                    | -48 -54 -15               | 712          | 7.95    | Left fusiform gyrus                                       |

4. Discussion

The aim of this study was to further elucidate the different contributions of medial temporal lobe structures (especially the perirhinal cortex and the hippocampus) to visual discrimination and memory processing. A visual discrimination and a recognition task were directly compared in this fMRI study, using a within-subjects full factorial design. As expected, discriminations with a high feature ambiguity activated a region in the left hippocampus, but surprisingly for both faces and scenes, as could be shown in a contrast of discrimination versus recognition in a full factorial model. A cluster in the right hippocampus was activated during the recognition task, showing significant activation for the recognition of faces and scenes. The main effect of “stimulus type” yielded an activation cluster spanning from the right fusiform gyrus to the right parahippocampal gyrus. Signal changes revealed that this cluster was involved in both recognition of faces and discrimination of scenes. This differential involvement may have resulted from the large extent of the cluster, covering two different structures. Additional single t-tests confirmed the involvement of the fusiform gyrus in face discrimination and of the parahippocampal gyrus in scene discrimination. Furthermore, the two-way interaction with the factor “task” suggested differences in the processing of face and scene stimuli in the recognition task. Unexpectedly, there were no significant perirhinal activations for the discrimination or recognition of faces and scenes. This may be due to signal dropout in the MTL [48], which led to missing signal in parts of the perirhinal cortex. This is the most probable explanation, since even further analyses with separate t-tests for the two tasks as well as the lowering of the threshold for significant activations did not show any perirhinal activation clusters.

The present study provides further support for the growing body of evidence for an involvement of the MTL in the processing of visual stimuli [6, 7, 10, 11, 28–30], questioning the assumption that the MTL is a structure specialized only in memory processing [1, 23–26].

One common criticism regarding the involvement of the MTL in visual discrimination is the argument, that the measured activation supposedly reflects working memory demands of the discrimination task, since the hippocampus seems to be involved in certain kinds of working memory [32, 33]. These issues have been addressed by presenting the stimuli simultaneously and contrasting this experimental condition against a baseline condition, which uses the same kind of task and same number of stimuli, in order to control for working memory demands. The direct comparison of three-item displays (discrimination task) against one-item displays (recognition task) might be problematic in regards to differing working memory demands, but this issue was addressed by contrasting respective conditions in the first level analysis (hard discrimination > hard baseline and correct recognition > correct rejection for both faces and scenes). Possible effects of stimulus display size differences were subtracted, since both first level contrasts consisted of similar experimental conditions with the same amount of stimuli on the display.

Additionally, patient studies show that working memory deficits can be ruled out as an explanation for deficits in higher-order object perception. It has been shown that judging a single

Fig. 4. Significant activations from the full factorial model. For the discrimination task, “hard baseline” responses were subtracted from the correct “hard face” or “hard scene” responses. Correct recognition was contrasted against correct rejections for both stimulus types. All resulting contrasts were then submitted to the second level 2 x 2 full factorial analysis (task x stimulus type). Only the main factor “task” (p < 0.05 corr.) and the interaction of “task” and “stimulus type” (p < 0.001, k = 10) yielded significant activation in the hippocampus. One additional cluster in the fusiform gyrus (extending to the parahippocampal gyrus) showed significant activation for the main effect of “stimulus type”, in the contrast faces > scenes (p < 0.05 corr.).
object by the criterion (if it has a geometrically possible or impossible shape) is also impaired in a patient with MTL lesions [49].

Another possible explanation for MTL activation might have been the incidental encoding of the stimuli from the discrimination task. However, the behavioural results from the present study show that face and scene stimuli from the discrimination task were retrieved to a much smaller degree than stimuli that had to be learned explicitly in the encoding phase, despite being presented for the same amount of time. Also, although non-target stimuli were presented twice on the same screen, there was no significant difference to target stimuli in regard to reaction times or percentage of correct answers.

Furthermore, there is no clear functional specialization of the hippocampus, neither for the discrimination nor for the recognition task, as opposed to previous findings [9,17,18,19,40,50,51], since the hippocampus did process both stimulus types. Only a small difference for the recognition of faces and scenes in the left and right hippocampi was observable in the interaction clusters, but since these clusters would not survive a corrected threshold, these results have to be interpreted carefully. The lack of perirhinal activation may be due to signal dropout and does not suggest that this structure is not involved in mnemonic or visual processing, but the results from this study do not allow any speculation about its exact role. For future investigations it might prove useful to adapt scanning parameters that reduce the signal dropout in the MTL. Nevertheless, the phenomenological view, describing the hippocampus as being responsible for the processing of spatial stimuli and the perirhinal cortex for the processing of facial stimuli, seems to be insufficient to explain the observed activation pattern. Additionally, the absence of bilateral hippocampal activations for either

Fig. 5. Percent signal change (PSC) in clusters active for main effects and interaction contrasts. Analogue to the first level analysis, the baseline condition was subtracted from hard discriminations of faces and scenes for the discrimination PSCs. For recognition PSCs, the correct rejections were subtracted from correct recognition responses. This analysis confirmed the task-specific involvement of the two hippocampal clusters active for the main effect of “task”, as well as a differential involvement of the fusiform/parahippocampal cluster in the processing of different stimulus types. Furthermore, both interactions were based on a difference between the activation for faces and scenes in the recognition task, with no significant difference between stimulus types in the discrimination task. Error bars represent the standard error of the mean (SEM).
task should be interpreted carefully. These results could be possibly caused by a lack of statistical power and do not necessarily support the idea of a domain-general organization of the hippocampus.

The BIC model (binding of items and context) suggests an alternative view of the function of the MTL [52], arguing that the activation of specific MTL sub-regions depends on the type of information being processed and is not simply explainable by a one-to-one mapping. In this model, the hippocampus acts as the final point of a hierarchical processing, integrating items and their context, resulting in hippocampal activation for recollection memory. The BIC model would explain why there was no differential activation for face and scene stimuli in the hippocampus, since it would receive input from the other MTL structures (perirhinal and parahippocampal cortex) and integrate the information of the differing stimulus domains. The fusiform gyrus is not part of the BIC model. However, as a part of the ventral visual stream (especially the fusiform face area) it is heavily involved in the processing of faces [53,54] or, in a more general view, in building visual expertise for objects [55,56]. It is then followed by the perirhinal cortex, which may be regarded as the direct continuation of the ventral visual stream [57]. Overall the results are in line with the BIC model, assuming that the face/object-specific information that was passed on from the fusiform gyrus to the perirhinal gyrus did not yield any perirhinal activation due to signal loss.

There is further support for the assumption of the hippocampus possibly being a "convergence zone" that bridges representational gaps [58], with the perirhinal and parahippocampal cortex providing domain-preferential inputs [59]. As has been pointed out recently [38], MTL activation is heterogeneous and depends on many different factors, e.g. strategies, task requirements, and the type of processed information.

Multivariate pattern analysis revealed distinct representations of single memories in the hippocampus [60], suggesting that the subfields of the hippocampus may be involved in different aspects of formation and maintenance of representations. These results point to the direction that a much finer analysis of the MTL is needed to fully explain the observed activation clusters, since different parts of the hippocampus may be concerned with different processing types, as is implicated by our data.

5. Conclusions

In summary, the present study adds strong evidence to the body of research by directly comparing discrimination and recognition tasks in a within-subject full factorial fMRI design. It shows that the structures of the MTL, especially the hippocampus, are not only involved in the processing of long-term memory, but also in visual discrimination processes. These results support a perceptual-mnemonic theory of the MTL and question an exclusive participation of MTL structures in memory processing. They also show that there is a need for a model that is able to explain the various contributions of MTL structures to memory and perception. Only by controlling every aspect of a task and the information that is processed, alongside with a more detailed analysis of the contribution of smaller sub-regions, it will be possible to improve the understanding of the MTL. One way to achieve this may be to use a representational view of the MTL rather than artificially dividing functions into descriptive cognitive processes [61].

Acknowledgments

The present study was funded by a grant (Sonderforschungsbereich 874, CRC 874) from the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG) to Boris Suchan (Project B8). Robert K. Lech is supported by the International Graduate School of Neuroscience and the Ruhr-University Research School.

We thank Jonas Lins for his help with the programming of the discrimination task and Sabine Bierstredt for the preparation of the face stimuli. We would also like to thank all participants for taking part in this study.

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During impairments...