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Research report

The hippocampus plays a role in the recognition of visual scenes presented at behaviorally relevant points in time: Evidence from amnestic mild cognitive impairment (aMCI) and healthy controls

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ABSTRACT

When people perform an attentionally demanding target task at fixation, they also encode the surrounding visual environment, which serves as a context of the task. Here, we examined the role of the hippocampus in memory for target and context. Thirty-five patients with amnestic mild cognitive impairment (aMCI) and 35 healthy controls matched for age, gender, and education participated in the study. Participants completed visual letter detection and auditory tone discrimination target tasks, while also viewing a series of briefly presented urban and natural scenes. For the measurement of hippocampal and cerebral cortical volume, we utilized the FreeSurfer protocol using a Siemens Trio 3 T scanner. Before the quantification of brain volumes, hippocampal atrophy was confirmed by visual inspection in each patient. Results revealed intact letter recall and tone discrimination performances in aMCI patients, whereas they showed severe impairments in the recognition of scenes presented together with the targets. Patients with aMCI showed bilaterally reduced hippocampal volumes, but intact cortical volume, as compared with the controls. In controls and in the whole sample, hippocampal volume was positively associated with scene recognition when a target task was present. This relationship was observed in both visual and auditory conditions. Scene recognition and target tasks were not associated with executive functions. These results suggest that the hippocampus plays an essential role in the formation of memory traces of the visual environment when people concurrently perform a target task at behaviorally relevant points in time.

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1. Introduction

According to the traditional method of experimental psychology, investigators use a target task that captures the central focus of attention (James, 1890). Recently, it has been demonstrated that images that are exposed together with targets of an unrelated task are better recalled than images that are presented with behaviorally irrelevant distractors or alone (Lin et al., 2010; Swallow and Jiang, 2010). A possible explanation is that attention boosts not only the target task but also the encoding of its background context. For example, Swallow and Jiang (2010) presented a series of photographs of natural and urban scenes with a distractor or a target and asked participants to remember these images. Concurrently with the scene encoding task, participants pressed a key when a colored square appeared in the middle of the images, an odd auditory tone was exposed, or a red "X" embedded among other colored letters were detected. Surprisingly, the target task did not disturb scene encoding. In contrast, participants displayed better memory for scenes presented together with the target task than for scenes presented with irrelevant distractors (Swallow and Jiang, 2010).

Lin et al. (2010) asked the participants to complete an attentionally demanding letter detection or auditory tone discrimination target task, while also viewing a series of briefly presented natural and urban scenes. When there was no target task, memory recall for the scenes was at chance level. However, participants remembered the scenes surprisingly well when they were presented concurrently with a target task at fixation. Lin et al. (2010) concluded that visual scenes outside the spatial focus of attention are encoded at behaviorally relevant points in time, although this task is not suitable for disentangling encoding and retrieval.

Swallow and Jiang (2010) called this phenomenon the attentional boost effect. However, its mechanism has not been clarified. There are at least three potential explanations (Swallow and Jiang, 2011). The first possibility is a simple attentional cuing effect. In target detection tasks, behaviorally relevant events elicit an attentional orienting response, which enhances not only the target event, but also the processing of stimuli that are presented concurrently with the target (Duncan, 1980). The second possibility implies that the target generates a reward signal (Seitz and Watanabe, 2009), and following the rules of reinforcement learning, scenes that are presented with targets may be reinforced because they signal the rewarding event. The third possibility is a perceptual grouping mechanism, assuming that if scenes and targets are bound together as a single perceptual object, then enhanced attention to one part of it (i.e., to the target) will also lead to increased attention to the other part of the object, in this case, the scene (Driver and Baylis, 1989). However, Swallow and Jiang (2011) demonstrated that these three mechanisms could not fully explain the attentional boost effect in a simple and parsimonious manner. First, targets and context images must overlap in time for the enhancement of memory (targets appearing 100 msec before or 100 msec after the image without temporal overlap do not facilitate memory of the contextual image), but they need not be synchronized (no need of common onset for target and context image, which is an important grouping cue). This suggests that perceptual grouping cannot fully explain the effect. Second, the overlap of the target and context image is not sufficient; focused attention to targets did not enhance memory for task-irrelevant images when participants are asked to ignore background scenes, which suggests that focused attention to target does not boost background scene encoding under all circumstances and it can be intentionally inhibited (Swallow and Jiang, 2011).

Swallow and Jiang (2011) suggested that grouping might occur after perceptual processing when the item is bound to the context in memory (see also Polyn and Kahana, 2008). According to the item-in-context theory, the medial temporal lobe, including the hippocampal formation, is essential for the encoding of objects in their appropriate context (Dickerson and Eichenbaum, 2010; Eichenbaum et al., 2007). In the above-described paradigm, the target may refer to the item, and the background scene may represent the context. In the present study, we explored the role of the hippocampus in the encoding and retrieval of targets and background scenes. We used two complementary approaches. First, we examined the relationship between hippocampal volume and scene recognition performance in healthy volunteers. Second, we investigated scene recognition in patients with amnestic mild cognitive impairment (aMCI) who exhibit marked hippocampal atrophy and declarative memory impairments (Collie and Maruff, 2000; Gauthier et al., 2006; Petersen et al., 1999; Shi et al., 2009). The main hypothesis was that the atrophy of the hippocampal region in aMCI disrupts the integration of target and scene and primarily affects context encoding (Dickerson and Eichenbaum, 2010). In addition, given that some patients with aMCI show deficits in attention and executive functions (Kramer et al., 2006; Levy-Gigi et al., 2011; Price et al., 2010), we also investigated the relationship between executive and attentional functions and performance on the target task. This is an important control condition because if patients fail to recall the target, scene recognition deficits can be the result of generalized cognitive dysfunctions and not a specific item-context binding deficit. Finally, we tested the perception and short-term recall of single scenes in aMCI in order to exclude the possibility that patients are not able to reconstruct and retrieve briefly presented complex visual information.

2. Materials and methods

2.1. *Participants*

Thirty-five individuals with aMCI and 35 healthy controls participated in the study (Table 1). We used the Mayo Clinic Alzheimer's Disease Research Center criteria for the diagnosis of aMCI (Knopman et al., 2003; Petersen et al., 1999): "A. The presence of a new memory complaint, preferably corroborated by an informant; B. Objective evidence of impairment of short-term memory (for age); C. Normal general cognitive functions; D. No substantial interference with work, usual social activities, or other activities of daily living; E. No dementia." (Knopman et al., 2003) Exclusion criteria included history of neurological or psychiatric disorders, head trauma,

Table 1 – Demographic and neuropsychological characteristics of the participants.

	Control ($n = 35$)	aMCI ($n = 35$)
Gender ratio (male/female)	21/14	21/14
Age (years)	63.2 (9.6)	63.8 (10.0)
Education (years)	14.9 (3.0)	14.7 (2.9)
RAVLT[a]	50.0 (4.0)	41.9 (5.5)
Boston Naming Test	52.7 (3.6)	50.9 (4.3)
Semantic fluency[b]	20.0 (4.2)	17.8 (4.3)
One-touch Stockings of Cambridge, mean proportion of prefect solutions[c]	0.69 (0.12)	0.59 (0.12)
One-touch Stockings of Cambridge, mean number of attempts for perfect solution[d]	1.5 (.7)	2.1 (1.2)
Perception of single scenes, % correct	95.1 (1.3)	95.9 (1.4)

Data are mean (standard deviation). Significant differences are marked with alphabets.
a $t(68) = 7.1$, $p < .001$.
b $t(68) = 2.18$, $p = .03$.
c $t(68) = 3.29$, $p = .002$.
d $t(68) = -2.39$, $p = .02$.

substance misuse, and medications affecting central nervous system functions. None of the patients with aMCI displayed delusions, hallucinations, depression, anxiety, irritability/lability, aggression/agitation, euphoria, apathy, disinhibition, aberrant motor behavior, sleep disturbance, eating/appetite change, and stereotypical behavior, as measured with the Neuropsychiatric Inventory (Cummings et al., 1994; Nyatsanza et al., 2003). For the assessment of declarative memory, semantic memory, and executive functions, we used the Rey Auditory Verbal Learning Test (RAVLT), the Boston Naming Test, and the semantic fluency test (Lezak, 1995). In addition to these standard tests, we investigated executive functions with the One-touch Stockings of Cambridge task (Owen et al., 1995). During this test, two sets of three stockings are presented on a touch-screen, each set containing three colored balls. The task is to rearrange the balls in the bottom display so that the position of balls matches that in the top of the screen. Participants are requested to calculate the minimum number of moves to obtain the solution. The dependent measures are the mean proportion of correct solutions and the mean number of attempts for correct solution (Owen et al., 1995).

Each participant underwent a structural brain magnetic resonance imaging (MRI) investigation (for methodological details, see later). First, we excluded patients with vascular lesions or cortical atrophy. Second, following the method of Myers et al. (2002, 2003), only aMCI patients with confirmed and marked hippocampal atrophy were included in the study. Two independent expert neuroradiologists confirmed the absence of vascular lesions, cortical atrophy, and the presence of hippocampal atrophy. The aim was to investigate aMCI patients who most closely resemble selective human amnesia due to the damage of the medial temporal lobe.

The study was carried out in accordance with the Declaration of Helsinki and was approved by the institutional ethics committee. After a complete description of the study, we obtained a written informed consent from each participant.

2.2. *Structural brain imaging*

We utilized the FreeSurfer protocol using a Siemens Trio 3 T scanner (Martinos Center for Biomedical Imaging, Boston, MA, USA; http://surfer.nmr.mgh.harvard.edu; version: v5.1.0, Dell XPS workstation). Briefly, we applied a multiecho FLASH sequence with a 1 mm^3 isotropic resolution (256 × 256 matrix, 176 sagittal slices with a thickness of 1 mm, TR 2530 msec, TI 1100 msec, TE 1.64/3.5/5.36/7.22 msec, bandwidth 651 Hz, non-selective excitation at 7°). Image processing included the removal of non-brain tissue with a hybrid watershed/surface deformation procedure, automated Talairach transformation, and segmentation of white and gray matter (Fischl et al., 2004; Segonne et al., 2004; see also Gronenschild et al., 2012). We measured the volume of the hippocampi and the cerebral cortex, normalized to the intracranial volume.

2.3. *Rapid serial visual presentation and target detection tasks*

We presented the stimuli on a VP2765-LED-27" monitor (ViewSonic, Walnut, CA; refresh rate: 60 Hz, resolution: 1920 × 1080 pixel, viewing distance: 50 cm, output luminance: 65 cd/m^2, size: 28°). The photographs of urban and natural scenes were from the LabelMe Natural and Urban Scenes database (Oliva and Torralba, 2001) (http://cvcl.mit.edu/database.htm) and a previously used stimulus set (Antal et al., 2000). Participants were not familiarized with the photographs before the experiment. Each scene was presented only once.

We used the modified method of Lin et al. (2010). Each experimental trial consisted of a rapid serial presentation of 16 scenes (exposure time: 133 msec/scene, interstimulus interval: 367 msec). This presentation rate (two images/sec) does not allow attentional blink (Lin et al., 2010). Attentional blink is not altered in MCI (Perry and Hodges, 2003), and in a pilot study, we found no attentional blink when the temporal parameters of the Lin et al. (2010) study were used in elderly participants with or without aMCI (Szamosi and Kéri, unpublished observations).

2.3.1. *Scenes with visual targets*

A gray square (size: 1°) was presented in the center of some scenes. The square contained white target letters or black distractor letters (type: Calibri, font size: 20) (Fig. 1). Both target and distractor letters appeared in the center of two–two nonconsecutive scenes. The remaining 12 scenes did not contain letters. We asked the participants to remember the target letters and to ignore the distractor letters. After each trial, the task was to type the target letter, and then we presented two scenes ("A" and "B") for 3000 msec. One of these scenes was from the presented sequence (serial positions 7–14), and the other was not included in the trial. We requested the participants to indicate which of the two scenes appeared in the sequence by pressing key "A" or "B" on the computer keyboard (Fig. 1). The test scene, which was from the presented sequence, could be a stimulus originally

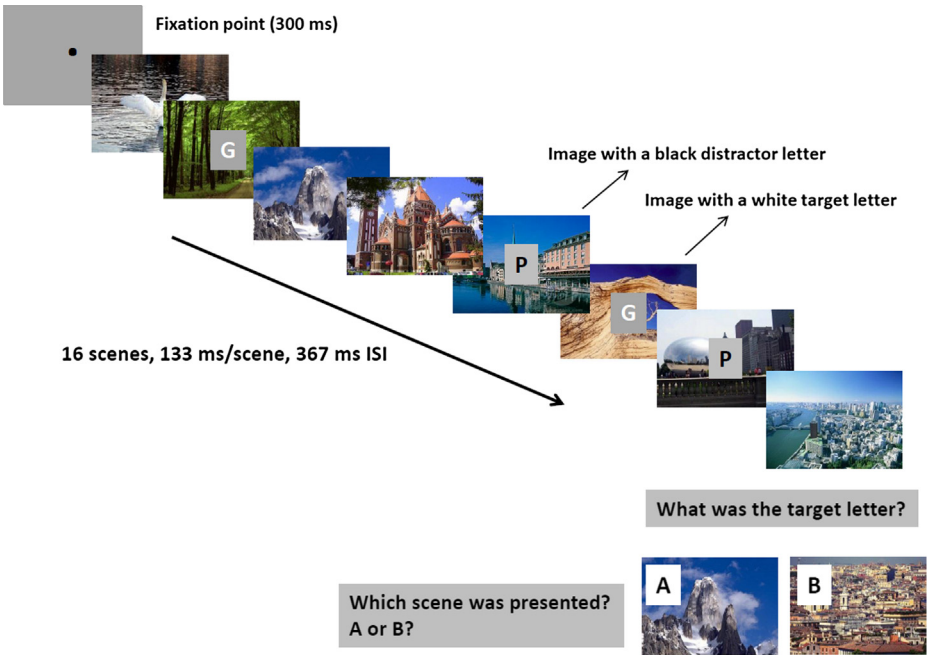

Fig. 1 – Illustration of a trial consisting of a sequence of scenes. Two scenes were presented with white target letters that should be remembered, and two scenes contained black distractor letters that should be omitted. Following the trial, participants first typed the target letter and then chose from the two test scenes. In the auditory condition, target and baseline tones were presented with the scenes, and participants were asked to indicate whether the pitch of the target tones was lower or higher than that of the baseline tones. After the tone discrimination task, participants chose from the two test scenes, as in the case of visual targets. ISI – interstimulus interval.

exposed with a target letter, a distractor letter, or a scene without letter. There were 300 intermixed trials in 10 blocks of 30 trials. When scenes with targets were the test stimuli in the recognition task, the scenes with targets were always from serial positions 7–14 in the sequence, that is, the two target stimuli appeared in this phase of the sequence. The same was true for the other two types of stimuli to be tested. Short breaks interleaved the trial blocks. Before the test, each volunteer participated in a training session, which consisted of 30 trials.

2.3.2. *Scenes with auditory targets*

In this task, we paired each scene with a brief auditory tone (50 msec). Baseline tones (260 Hz, 40 dB) were paired with 14 scenes. Target tones were presented together with two nonconsecutive scenes. The frequency of the target tones was different from that of the baseline tones: 130 Hz (low pitch) or 520 Hz (high pitch). Following the scene-tone sequence, we asked the participants to indicate whether the pitch of the target tones was lower or higher than that of the baseline tones (key "A" for high, key "B" for low). Following the pitch discrimination task, we administered a scene recognition task, as described in the letter detection procedure. There were 10 blocks of 20 trials, which included 100 trials testing the recognition of scenes paired with baseline tones and 100 trials for scenes paired with target tones.

The method of the present study differed from the original paradigm of Lin et al. (2010). First, we included targets and distractors within one experiment, and there were two targets and two distractors in contrast to a single target (Lin et al., 2010). Our aim was to minimize the likelihood that perceptual novelty (i.e., a single white letter embedded in a series of 16 stimuli) elicited attentional boosting. Second, we used a two-alternative forced choice scene recognition test, as opposed to a "Yes/No" binary decision test (Lin et al., 2010), in order to avoid possible impulsive responses, leading to a high level of false alarm rate.

2.4. *Single trial short-term memory for scenes*

The stimulus presentation time and delay duration were identical to those in the main experiments. In this perceptual and short-term memory control condition, a single scene was presented for 133 msec without letters or tones. After an interval (367 msec), we presented two scenes ("A" and "B") for 3000 msec. One of these scenes was presented before and the other was new. The task was to indicate which of the two scenes was presented by pressing key "A" or "B" on the computer keyboard. There were 10 trials using stimuli that were not included in the rapid serial visual presentation tasks. The perceptual control task was conducted before the main experiment.

2.5. *Data analysis*

We used STATISTICA 9 software (StatSoft Inc., Tulsa) for data analysis. Before comparing patients with aMCI and controls, we ran Kolmogorov–Smirnov tests to evaluate the normality

of data distribution. Demographic variables, letter detection/tone discrimination performance, and brain volumes were compared with two-tailed *t* tests. Repeated-measures analyses of variance (ANOVAs) were applied to compare scene recognition performances in the case of different stimulus types. We used *F* tests for planned comparisons and Scheffé's tests for post hoc comparisons. We calculated Pearson's product moment correlation coefficients between scene recognition and hippocampal volume. We also conducted analyses of covariance (ANCOVAs) to evaluate the relationship among scene recognition, diagnosis, and hippocampal volume. The level of statistical significance was set at $\alpha < .05$.

3. Results

3.1. *Demographics, background neuropsychology, and perception of single scenes*

Patients with aMCI and controls did not differ in age, education, and gender ratio. There was a marked between-group difference in the RAVLT, whereas it was less pronounced in the case of semantic fluency and Boston Naming Test. Patients with aMCI also displayed impaired performances on the One-touch Stockings of Cambridge test, whereas they showed intact perception and short-term memory of single scenes (Table 1).

3.2. *Letter recall and tone discrimination*

Fig. 2 depicts letter recall and tone discrimination performance in patients with aMCI and healthy controls. There were no significant differences between the two groups (*t* test, $p > .2$).

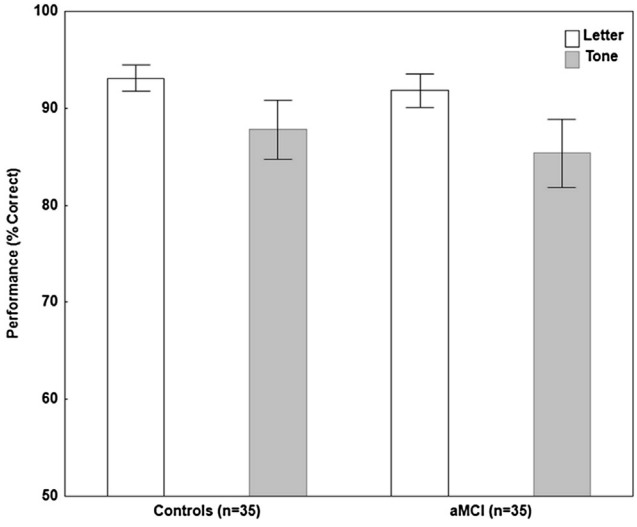

Fig. 2 – Letter recall and tone discrimination performance in healthy controls and patients with aMCI. There was no significant difference between the two groups. Error bars indicate 95% confidence intervals.

3.3. *Scenes presented with letters*

Fig. 3 depicts the results from the scene-letter experiment. The group (aMCI *vs* controls) by stimulus type (scenes alone, scenes with target letter, scenes with distractor letters) ANOVA revealed significant main effects of group [$F(1,68) = 17.78$, $p < .001$, $\eta^2 = .21$] and stimulus type [$F(2,136) = 84.87$, $p < .001$, $\eta^2 = .55$]. There was a significant two-way interaction between group and stimulus type [$F(2,136) = 40.26$, $p < .001$, $\eta^2 = .37$]. Planned comparisons with *F* tests indicated that healthy controls improved their scene recognition performance in the target letter condition relative to scenes alone [$F(1,68) = 125.69$, $p < .001$] and scenes with distractor letters [$F(1,68) = 136.97$, $p < .001$]. A similar effect was observed in individuals with aMCI, although it was much less pronounced [scenes with target letters *vs* scenes alone: $F(1,68) = 4.05$, $p < .05$; scenes with target letters *vs* scenes with distractor letters: $F(1,68) = 5.15$, $p < .05$]. In patients with aMCI, scene recognition performance was above chance level only in the target letter condition (*t* test, $p < .05$). Scheffé's tests indicated that healthy controls performed better than aMCI patients only when scenes were presented with targets ($p < .001$). In the other conditions (scenes alone and scenes with distractors), the two groups did not differ ($p > .1$) (Fig. 3).

3.4. *Scenes presented with tones*

Fig. 4 depicts the results from the scene-tone experiment. The group (aMCI *vs* controls) by stimulus type (scenes with baseline tones and scenes with target tones) ANOVA revealed significant main effects of group [$F(1,68) = 28.12$, $p < .001$, $\eta^2 = .29$] and stimulus type [$F(1,68) = 67.0$, $p < .001$, $\eta^2 = .50$]. There was a significant two-way interaction between group

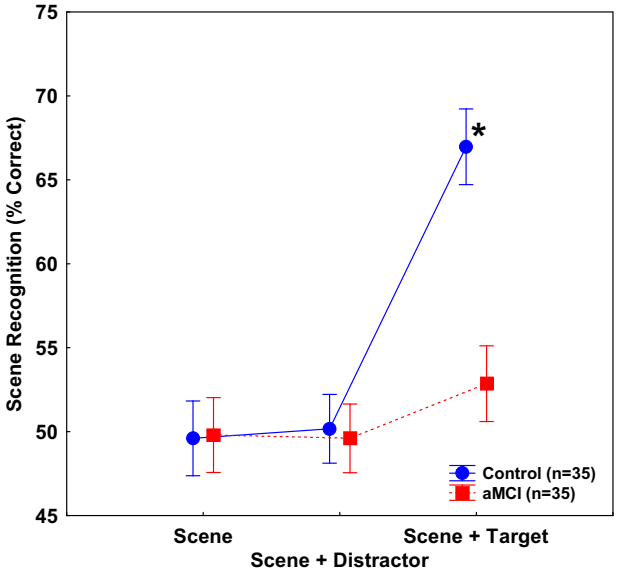

Fig. 3 – Recognition performance in the case of scenes presented alone, with distractor letters, and with target letters. In the target condition, patients with aMCI exhibited lower performance relative to controls (*$p < .001$, Scheffé's test). Error bars indicate 95% confidence intervals.

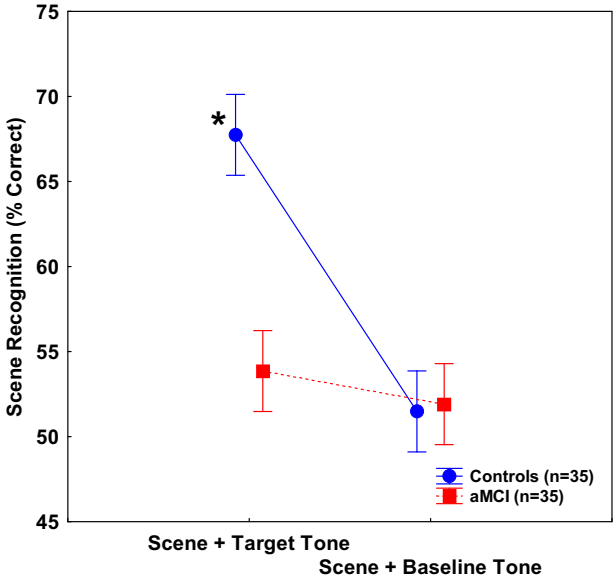

Fig. 4 – Recognition performance in the case of scenes presented with target tones and baseline tones. In the target condition, patients with aMCI exhibited lower performances relative to controls (*$p < .001$, Scheffé's test). Error bars indicate 95% confidence intervals.

and stimulus type [$F(1,68) = 41.46$, $p < .001$, $\eta^2 = .38$]. F tests revealed that healthy controls displayed higher levels of scene recognition in the target tone condition relative to the baseline [$F(1,68) = 106.61$, $p < .001$]. This effect was not significant in patients with aMCI ($F < 2$, $p > .2$), but the patients performed above chance level when scenes were presented with target tones (t test, $p < .05$). Scheffé's tests indicated that controls showed higher levels of recognition relative to aMCI patients when scenes appeared with target tones ($p < .001$). In the case of baseline tones, the performance of aMCI patients and controls did not differ ($p > .1$) (Fig. 4).

3.5. *Hippocampal volume, scene recognition, and background neuropsychology*

As expected, patients with aMCI showed bilateral hippocampal atrophy relative to controls, but there was no significant cortical volume loss (Table 2). In healthy controls, we found significant positive correlations between the right, left, and total hippocampal volume and recognition performance when scenes were exposed together with target letters and target tones (scenes with target letters, right: $r = .71$, $p < .001$, left: $r = .39$, $p < .05$, total: $r = .58$, $p < .001$; scenes with target tones, right: $r = .62$, $p < .001$, left: $r = .51$, $p < .005$, total: $r = .60$, $p < .001$).

Table 2 – Hippocampal and cortical volume (mm^3) in patients with aMCI and healthy controls.

	aMCI ($n = 35$)	Controls ($n = 35$)
Right hippocampus[a]	2467.7 (514.2)	3545.5 (380.4)
Left hippocampus[b]	2414.6 (482.8)	3462.6 (380.5)
Cerebral cortex	428,105.8 (68,802.4)	444,236.0 (74,025.7)

Data are mean (standard deviation). Significant differences are indicated by alphabets.
a $t(68) = 9.97$, $p < .001$.
b $t(68) = 10.1$, $p < .001$.

In patients with aMCI, the correlations between hippocampal volume and scene recognition did not reach the level of statistical significance ($-.2 < r < .3$, $p > .05$). When we analyzed the two groups together, we observed similar correlations to that reported in the control group ($rs > .65$, $p < .001$). Figs. 5 and 6 depict the correlations between total hippocampal volume and scene recognition in patients with aMCI and controls.

We conducted an ANCOVA with scene recognition performance as the dependent variable, diagnosis (aMCI *vs* controls) as the categorical predictor, and total hippocampal volume as the continuous predictor. In the case of scenes with target letters, this analysis revealed significant main effects of diagnosis [$F(1,67) = 9.77$, $p < .005$, $\eta^2 = .13$] and total hippocampal volume [$F(1,67) = 12.96$, $p < .005$, $\eta^2 = .16$]. Similarly, in the case of scenes with target tones, there were significant main effects of diagnosis [$F(1,67) = 9.81$, $p < .005$, $\eta^2 = .13$] and total hippocampal volume [$F(1,67) = 8.33$, $p < .05$, $\eta^2 = .11$].

In controls and patients with aMCI, hippocampal volume did not correlate with recognition performance when scenes were presented alone or with distractors, and it did not correlate with target tasks (letter recall and tone discrimination) ($-.2 < r < .2$, $p > .1$). Cortical volume did not correlate with the behavioral measures ($-.1 < r < .1$, $p > .1$). Scene recognition performance for different types of stimuli (target, distractor, scenes alone) and target task performance did not correlate with background neuropsychological test scores, including executive functions and RAVLT ($-.2 < r < .2$, $p > .1$).

4. Discussion

We found a differential deficit in the target detection and scene recognition task: individuals with aMCI had intact performance for targets, but they performed poorly on scene recognition in both target and non-target trials. These results suggest that the memory trace of contextual information (scenes), in which an attentionally demanding central task (letter detection) is embedded, may be more vulnerable for hippocampal pathology, an essential feature of aMCI, than the representation of the central task. We confirmed this finding in healthy volunteers: in their case, the volume of the hippocampus positively correlated with the recognition of scenes presented with targets, but not with memory for target letters or tones. There was no significant cortical volume loss in aMCI, and cortical volume did not correlate with task performance. Finally, the same pattern of performance was observed regardless of target task modality (letter or sound), which indicates a similar role of the hippocampus in scene encoding in the case of visual and auditory targets (Macaluso, 2010).

The difference in hippocampal volume between controls and aMCI patients, however, did not fully predict scene recognition performance. It is likely that in aMCI other factors also contribute to scene recognition deficits (e.g., attentional impairment not detected by the background

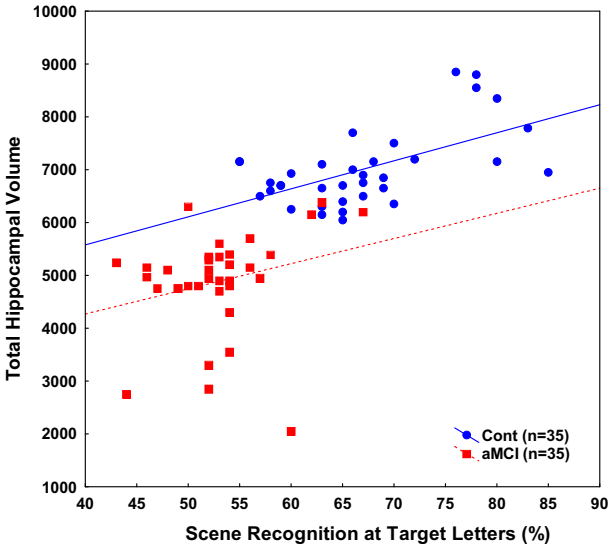

Fig. 5 – Correlation between total hippocampal volume (mm^3) and recognition performance when scenes were presented with target letters in controls (Cont) and patients with aMCI.

neuropsychological tests) (Taya et al., 2012), and beyond volume loss more specific pathological processes affecting the hippocampal formation are also implicated (Small et al., 2011).

The dissociation between target and scene memory should be interpreted with caution because of the different psychometric properties. The target task was in the central focus of attention involving in-depth processing, and participants achieved a high level of performance. Focused attention may reduce interference effects, which is critical in early memory decline in aMCI (Dewar et al., 2012). In contrast, in the case of scenes there were lower performances and higher variances relative to the target task. Finally, it is an oversimplification to claim that a single circumscribed brain area is responsible for scene recognition. Instead, a widely distributed neuronal network may be involved in which the hippocampus plays a key role (Cabeza et al., 2011; Chun and Johnson, 2011; Sestieri et al., 2010).

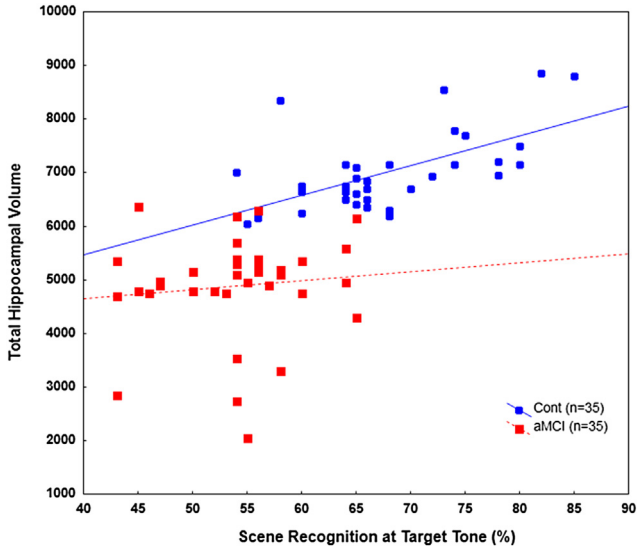

Fig. 6 – Correlation between total hippocampal volume (mm^3) and recognition performance when scenes were presented with target tones in controls (Cont) and patients with aMCI.

We also found that patients with aMCI successfully recognized single scenes even under a rapid presentation condition in the absence of a target. However, they displayed severe impairments in the serial presentation condition when memory traces were either lost rapidly over time or displaced by further traces of scenes (i.e., interference). In other words, the hippocampus may encode scenes at all times, but after a rapid serial presentation, these memory traces cannot be recalled on a subsequent test unless they are presented together with a target receiving an extra encoding boost.

A possible explanation for the results is that the deficit we observed is a consequence of executive and attentional dysfunctions in aMCI. However, we did not find any correlation between scene recognition and executive functions. In the case of target letters, patients may use non-hippocampal mediated explicit rehearsal to maintain the single target, which is a simple and familiar stimulus. In contrast, the medial temporal lobe may be crucial for the short-term retention of complex and unfamiliar scenes (Olson et al., 2006; Rose et al., 2012). However, it is not likely that aMCI patients have a general deficit in spatial processing and scene construction, a role that has been attributed to the hippocampus (e.g., Lee et al., 2005; Mullally et al., 2012; O'Keefe and Nadel, 1978), because they showed intact perception of single briefly presented scenes and exhibited a mild but significant attentional boost effect in the case of visual targets.

The present results are in accordance with the item-in-context model of the hippocampus. According to this theory, which focuses on the functional specialization of the medial temporal lobe, the perirhinal cortex is responsible for the processing of objects, the parahippocampal cortex represents the context, and the hippocampus places objects into an appropriate context (Davachi, 2006; Diana et al., 2007; Dickerson and Eichenbaum, 2010; but see Watson et al., 2012). When attention is paid to the target, it may increase the attentional spotlight and useful field of view (thus not just orienting, but also the spatial extent of the information that is perceived), and therefore the hippocampus receives more input.

Howard et al. (2011) recently provided compelling evidence for a double dissociation between hippocampal and parahippocampal functions. These authors showed that the hippocampus is particularly pertinent in the identification of novel changes in the spatial relationship between objects and their surrounding context (Howard et al., 2011). Previously, we showed that patients with hippocampal atrophy fail to reverse reward–punishment associations related to the context but not to the central item (Levy-Gigi et al., 2011). Here, we went further and demonstrated that the hippocampus is also essential in memory for background context when there is an attentionally demanding task related to the central item. This context representation (scene recognition in the target condition) is also impaired in survivors of life-threatening traumas,

which may be the result of hippocampal dysfunction (Levy-Gigi and Kéri, 2012). This model assumes that for the successful encoding and retrieval of the context (scene), it must be bound to the attentionally weighted target item. In healthy individuals, larger hippocampal volume may be associated with more efficient target-scene binding, leading to a higher level of scene recognition. In this respect, a limitation of the current design is that the memory test did not in fact probe target-scene binding, but only retention of targets and scenes separately. In addition, further studies are warranted to characterize the differential role of medial temporal lobe subregions in this process and its regulation by attentional processes.

There are several other lines of evidence suggesting that the hippocampus is implicated in the representation of complex visual images. Kreiman et al. (2000) showed that neurons in the human hippocampus selectively respond to visual images during perception and imagination. In the framework of the model of Rolls et al. (2008), the hippocampus is an extension of the ventral visual stream, which is responsible for the processing of complex visual objects and scenes. As a self-organizing learning network, the hippocampus is essential for spatial scene representation (Bussey and Saksida, 2007; Rolls et al., 2008).

The results of this study may have relevance for translational neuroscience. Evidence suggests that short-term visual memory impairment may be a preclinical marker of Alzheimer's disease (Parra et al., 2010). If hippocampal pathology can be tackled more successfully by tasks in which visual context is encoded at behaviorally relevant points in time, as compared with attentionally demanding central tasks, the current rapid serial visual presentation paradigm may be suitable for the detection of early stages of aMCI and other memory disorders (Dickerson and Eichenbaum, 2010; Hughes et al., 2011).

In conclusion, hippocampal atrophy in individuals with aMCI and smaller hippocampal volume in healthy volunteers are associated with less efficient visual scene recognition when the scene serves as a context for attentionally demanding memory tasks. Performance on the attentionally demanding task is spared in aMCI and does not correlate with hippocampal volume in healthy volunteers. These results suggest that the hippocampus may be involved in memory processes related to the context at behaviorally relevant points in time.

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