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Distinct visual perspective-taking strategies involve the left and right medial temporal lobe structures differently

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This study assesses the role of the human medial temporal lobe (MTL) structures in the coordination of spatial information across perspective change and, in particular, in visual perspective taking—namely the capacity to know what another individual is seeing on the visual scene. Fourteen patients with unilateral temporal lobe resection and 21 control subjects performed two tasks, called 'object location memory' and 'viewpoint recognition', respectively. In the object location memory task, subjects had to memorize the position of a target object in the environment from an initial viewpoint. They were then shown the same environment from a new viewpoint and had to indicate whether or not the target object had moved. In the viewpoint recognition task, subjects had to imagine the perspective of an avatar from the initial viewpoint and then decide whether or not the new viewpoint was that of the avatar. The results showed a double dissociation, with left MTL patients being impaired in the object location memory task but not in the viewpoint recognition task and right MTL patients being impaired in the viewpoint recognition task but not in the object location memory task. Furthermore, based on multiple regression analyses between performance and the volumes of the different MTL structures, we discuss the specific involvement of the left temporopolar cortex and of the right hippocampus in different kinds of visual perspective taking.

Keywords: perspective taking; spatial memory; social cognition; temporopolar cortex; hippocampus

Abbreviations: LTL = left temporal lobe; MTL = medial temporal lobe; RTL = right temporal lobe; WAIS-R = Wechsler Adult Intelligence Scale-Revised

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Introduction

The capacity to know where another individual is directing attention in space and what he or she is seeing on the current visual scene, which we refer to as 'visual perspective taking' in the present study, provides critical information for monitoring social interactions. It is likely a prerequisite to understand another's intentions, actions and emotional reactions, as well as to adapt one's own behaviour to the current situation (Frith and Frith, 2006). One major question is therefore to comprehend how an individual is able to switch from a first-person perspective to a third-person perspective and what mechanisms and brain structures underlie this ability. In the present study, we focused on the role played in visual perspective taking by the medial temporal lobe (MTL), which includes the hippocampus, the entorhinal cortex, the perirhinal cortex, the parahippocampal cortex, as well as the temporopolar cortex, which is often described as antero-medial rather than strictly MTL but will be considered here as part of MTL structures.

Many studies suggest that the MTL structures are involved in object location memory across perspective change and that this spatial function is lateralized on the right in humans. For instance, it has been shown that, when the task is to memorize the locations of several objects in an array and to retrieve them from a new perspective, patients with right MTL damage are impaired, whereas patients with left MTL damage are not (e.g. Kosslyn *et al.*, 1989; Morris *et al.*, 1996; Abrahams *et al.*, 1997; Nunn *et al.*, 1999;

Holdstock *et al*., 2000; Parslow *et al*., 2005). Such results have often been presented as proof that the right human MTL is specifically involved in allocentric (as opposed to egocentric) spatial memory, of which cognitive maps are a well-known example (Tolman, 1948; O'Keefe and Nadel, 1978).

In an allocentric reference frame, spatial locations are, by definition, coded relative to the surrounding environment but independently of the position and orientation of the observer and apart from any viewpoint on the current scene (Klatzky, 1997). Accordingly, allocentric processing is likely to be essential for memory of spatial layouts across perspective change and evidence for this has been found in various behavioural studies. For example, increased accuracy was found when object location memory was probed from a novel viewpoint aligned with environmental landmarks (McNamara *et al*., 2003) or with the walls of the testing room (Mou and McNamara, 2002) compared to misaligned viewpoints. Using a paradigm adapted from Wang and Simons (1999), Burgess *et al*. (2004) also found that subjects were significantly better at remembering the array of object locations when it was oriented consistently with respect to a single external visual cue than when it was not.

Interestingly, some authors have emphasized that the number of locations to remember could also be a crucial factor to explain the involvement of the right MTL structures in object location memory across perspective change (Bohbot *et al*., 1998; Burgess, 2002; King *et al*., 2005; Parslow *et al*., 2005). For instance, when subjects have to retrieve a unique location from a viewpoint different from the one adopted at encoding, neither right nor left damage to the hippocampus induces impairment (Bohbot *et al*., 1998; King *et al*., 2002). However, a patient with bilateral MTL damage restricted to the hippocampi performed at chance level as soon as there was more than one object location to recall (King *et al*., 2002). More recently, Parslow *et al*. (2005) showed that patients with right but not left MTL damage were impaired in a similar perspective change paradigm when the array to remember contained six objects but not when it contained only four objects.

Despite the large number of neuropsychological studies investigating the role of MTL structures in object location memory across perspective change, none of them, to our knowledge, has directly assessed the involvement of the hippocampus and adjacent cortices in visual perspective taking. However, studies using functional brain imaging techniques (Creem *et al*., 2001; Zacks *et al*., 2003; Vogeley *et al*., 2004) have suggested that visual perspective taking is usually associated with increased activity in parietal areas, which are known to underlie egocentric spatial representations (Andersen *et al*., 1985; Berthoz, 1997; Vallar *et al*., 1999; Galati *et al*., 2000), but not with MTL activation. One important difference between visual perspective taking and simple object location memory across perspective change is that, in visual perspective taking, the next viewpoint is primed by another observer (or at least by an arrow). One explanation for the absence of MTL activation in the studies quoted above is therefore that being primed encourages egocentric spatial processing and allows performing the task without any need of allocentric processing ('egocentric/allocentric' hypothesis): the subjects would make a mental translocation of their own viewpoint to the position of the other, while updating the locations of the elements of the environment in their egocentric reference frame. However, according to the literature reviewed above, another explanation is that the environments used in these studies were too simple and that the number of locations to be manipulated across viewpoints was too small to involve the MTL structures ('numerical' hypothesis).

The present study aimed to distinguish between these two hypotheses and, more generally, to directly investigate the involvement of the human MTL structures in visual perspective taking. Two tasks inspired by Amorim (2003) were used in unilaterally MTL-damaged patients: the object location memory task and the viewpoint recognition task. In the object location memory task, subjects were asked to memorize the location of a target object (a lamp) in a complex virtual environment from an initial viewpoint and to indicate, from a new viewpoint, if the lamp had changed its position in the environment. In order to assess whether having the opportunity to anticipate the new viewpoint at time of encoding could influence the performances of MTL-damaged patients, an avatar was visible from the initial viewpoint in half of the trials, whose position could be used by subjects to anticipate the viewpoint depicted after perspective change (priming versus no-priming condition). In the viewpoint recognition task, the avatar was always visible from the initial viewpoint and subjects were asked to imagine what the avatar was seeing. After a perspective change, subjects had to indicate whether or not the new perspective was the one adopted by the avatar. According to the 'egocentric/allocentric' hypothesis, patients with lesions to the right MTL were expected to be impaired in the no-priming condition of the object location memory task, which requires allocentric coding of the lamp location, but neither in the priming condition of the same task nor in the viewpoint recognition task, which could all be solved using egocentric spatial processing. In contrast, according to the 'numerical' hypothesis, patients with lesions to the right MTL were expected to be impaired in the viewpoint recognition task, which required the manipulation of a large number of landmark locations across perspective change, but not in the object location memory task, which consisted in memorizing only one unique location with respect to the environment. No particular expectation has been formulated concerning performance of the left MTL patients.

Material and Methods

Participants

A total of 14 patients and 21 control subjects took part in the study. All patients had undergone unilateral temporal lobe surgery for the relief of intractable epilepsy at the Salpêtrière hospital,

Table 1 Characteristics of control group and of LTL and RTL patient groups

	Control ($n = 21$) Mean (SD)	LTL ($n = 7$) Mean (SD)	RTL ($n = 7$) Mean (SD)
Gender	15M/6F	3M/4F	5M/2F
Age (years)	35 (2)	36 (8)	40 (13)
Seizure onset (years)	–	9 (6)	9 (9)

SDs are given between brackets. Age of seizure onset ranged from 1 to 17 years in the LTL group and from 2 to 27 years in the RTL group.

Table 2 Neuropsychological test scores for patients with RTL and LTL resection

Neuropsychological Tests	RTL ($n = 7$) Mean (SD)	LTL ($n = 7$) Mean (SD)
WAIS-R[a] (Full-scale IQ)	99.4 (11.1)	95.4 (11.4)
Auditory-verbal span	6.2 (1.0)	6.1 (1.1)
Visuo-spatial span	6.0 (0.6)	6.1 (1.1)
RAVLT[b] (max. 15)		
First recall	6.0 (1.4)	5.4 (1.3)
Fifth recall	12.0 (1.8)	10.9 (2.3)
Delayed recall	10.4 (3.4)	7.1 (3.4)
Rey Figure (max. 36)		
Copy	27.6 (2.9)	28.4 (1.4)
Delayed recall	12.6 (5.0)	16.9 (6.0)

[a]Wechsler Adult Intelligence Scale-Revised (WAIS-R, Wechsler, 1989).
[b]Rey Auditory Verbal Learning Test (RAVLT, Rey, 1964).
SDs are given between brackets.

Paris, France, at least 6 months before. At the time of testing, they had been seizure free for at least 6 months. Two groups of patients were distinguished: seven left temporal lobe (LTL) patients and seven right temporal lobe (RTL) patients. Language functions were lateralized in the left hemisphere in all patients, as confirmed by the intracarotid amobarbital injection procedure (Wada and Rasmussen, 1960). Control subjects were all right handed and had no history of neurological disease, head injury, neurosurgery problems or psychiatric disorders. All participants gave informed consent to be tested after the nature and possible consequences of the experiment had been explained to them. The study was approved by the local ethics committee (CCPPRB 120-98). Patient and control groups did not differ significantly in terms of age [$F(2,32) = 0.74$, $P = 0.49$] (Table 1). All the patients had a full-scale IQ above 80 on the Wechsler Adult Intelligence Scale-Revised (WAIS-R) and the mean IQs of both the LTL and the RTL group were within the normal range. Neuropsychological data regarding to both LTL and RTL patient groups are provided in Table 2. Note that IQ measurement was part of a standard clinical neuropsychological assessment for all the patients that underwent surgical treatment of their epilepsy but that it has not been done for control subjects.

Surgical procedure and MRI volumetric analysis

Surgery undergone by the patients consisted of a standard unilateral *en bloc* resection (Falconer, 1971) of MTL structures, including the amygdala, the hippocampus, the temporal pole, the entorhinal, perirhinal and to a lesser extent the parahippocampal cortices (Fig. 1). None of the patients suffered from lesions outside the MTL structures. For each patient, T_1-weighted imaging was performed on a 1.5-T MR unit using a standard head coil and tilted coronal 3D magnetization-prepared rapid acquisition gradient-echo sequence with the following parameters: 14.3/6.3/1 (TR/TE/excitation); inversion time, 250; flip angle, 12°; field of view, 240 mm; matrix, 256 × 192. This resulted in 124 contiguous T_1-weighted partitions with a 1.5-mm section thickness oriented perpendicular to the long axis of the hippocampus. Each acquisition was transferred to an independent workstation (Advantage Windows, AW 4.1, GE Medical System, Milwaukee, WI, USA) and the volumes of the different structures of both resected and non-resected MTLs (i.e. left and right hippocampi as well as left and right temporopolar, entorhinal, perirhinal and parahippocampal cortices) were measured using the 3D option software imaging package (Volume Analysis, GE Medical System, Milwaukee, WI, USA). Each anatomical structure was manually delineated according to the landmarks defined in our previously protocol (see Noulhiane *et al.*, 2006, for a full description of the method).

The mean volume for each anatomical structure and each group of patients are presented in Table 2. For each patient, the volume of each structure was compared to the corresponding mean volume in a control population (Noulhiane *et al.*, 2006). The results of these comparisons, expressed as mean *Z*-scores over patients, are also shown in Table 2. It appears that the surgical resection resulted in significant volume reduction of all structures but the parahippocampal cortex. In contrast, when considering the non-resected side of the brain, the analyses did not show any volume difference between the control population and the patients groups.

In order to assess whether the resection was similar in both LTL and RTL groups, one repeated measures ANOVA was conducted, with resection (resected side versus non-resected side) and structure (temporopolar cortex versus perirhinal cortex versus entorhinal cortex versus parahippocampal cortex versus hippocampus) as within-subject factors, group (LTL patients versus RTL patients) as a between-subjects factor and the volume of MTL structures as the dependent variable. The results showed a main effect of resection [$F(1,12) = 966.50$, $P < 0.0001$] but neither a main effect of group [$F(1,12) = 0.15$, $P = 0.71$] nor an interaction between the group and resection factors [$F(1,12) = 1.69$, $P = 0.22$], suggesting that, on average, the MTL resection was significant as well as equivalent in both LTL and RTL patients. Furthermore, there was an interaction between the resection and structure factors [$F(4,48) = 65.62$, $P < 0.0001$]. Tukey *post hoc* analyses revealed that the resection, in terms of volume, was significant for each single anatomical structure ($P < 0.0005$) except the parahippocampal cortex ($P > 0.05$), suggesting, as already mentioned from *Z*-scores, that the surgery spared (at least partially) the parahippocampal cortex.

Stimuli and apparatus

The virtual model of an architectural environment as well as the picture stimuli were generated using 3Dstudio MAX® and Character Studio® with a 24-mm lens (≈74 × 59° simulated FOV). The experiment was generated and monitored using ERTS-VIPL™, a PC-compatible software package that allows development and performance of psychological experiments (Beringer, 1994).

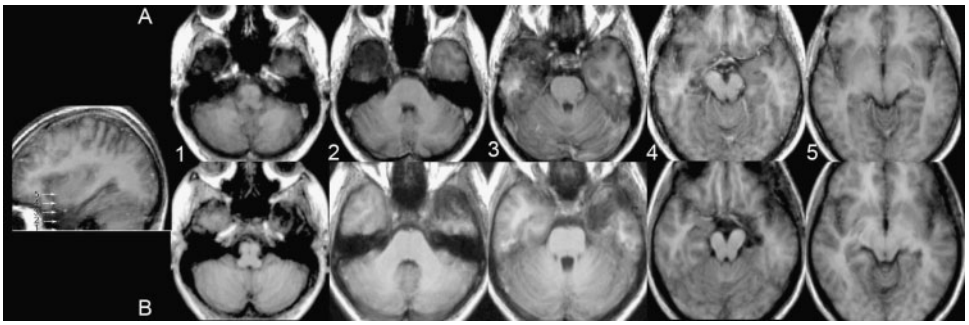

Fig. 1 Using the SPM software normalization routines (SPM5, http://www.fil.ucl.ac.uk/spm), a linear spatial normalization of individual anatomical volumes to the MNI-Talairach space were estimated to provide an overlap of lesions over the RTL (**A**) and LTL (**B**) patient groups.Five series of MRI slices were selected (see the sagittal plane and axial slices: 1–5 in a caudo-rostral direction, step: 15 mm) to display a 3D view of the resection in each patient group. In the two patient groups, the resection included the temporal pole, the amygdala, the hippocampus and various amounts of the adjacent cortices (entorhinal, perirhinal and parahippocampal cortices).

Fig. 2 Survey perspective of the virtual architectural environment used in the experiment. The camera and target (lamp) positions used to generate the stimuli are presented. An avatar location is instantiated.

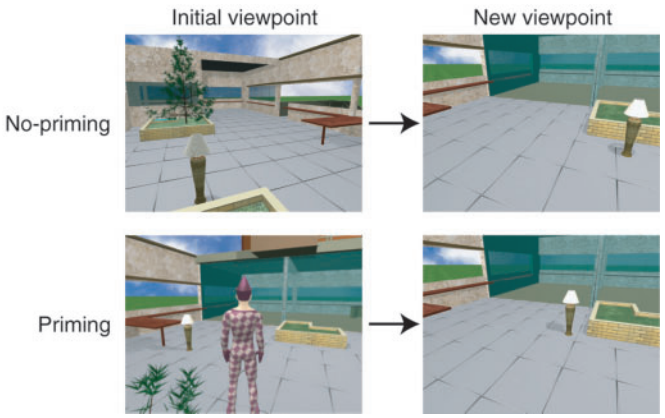

Fig. 3 Illustration of the object location memory task. After examining an initial view for 5 s, observers switched perspective and indicated from the new viewpoint if the lamp had changed its position. In the priming condition, observers were primed by the avatar occupying their future location in the environment. In the no-priming condition, no avatar was present in the scene and the new viewpoint was unpredictable. The upper and lower examples show non-primed (135° viewpoint change) and primed (0°) trials, respectively.

The different virtual camera and target (a lamp standing on the floor) positions used to generate the stimuli are illustrated in Fig. 2. Sixteen cameras were placed along two concentric circles, the centre corresponding to the middle of the virtual room. The eight 'initial viewpoint' cameras were distributed at 45° intervals in a circle with a radius of 3.60 m. The eight 'new viewpoint' cameras were distributed at 45° intervals in a circle with a radius of 1.80 m, each being aligned with an 'Initial viewpoint' camera. It is worth noting that the difference between the initial and new viewpoints with respect to the distance to the centre of the camera configuration was the same in all trials whatever the condition and therefore did not constitute a confounding variable. All the cameras were positioned at the avatar eye-level, and directed towards the centre of the camera configuration. The eight target positions were distributed in the same circle as the 'new viewpoint' cameras, every 45° (each target equidistant between each pair of adjacent cameras).

Procedure and design

Object location memory task

Subjects were seated in front of a monitor. In order to familiarize them with the environment before the experiment started, they were shown five times a short movie consisting of a 360° tour of the virtual room. The object location memory task consisted of 32 trials without any feedback, preceded by four training trials (not included in the data analysis). Each trial was designed as follows. The subject memorized the position of the lamp from an initial viewpoint displayed for 5 s, followed automatically by a new viewpoint on the visual scene (Fig. 3). The task was to indicate, from the new viewpoint, if the lamp had moved in the environment during the perspective change. Each new viewpoint was displayed until the subjects gave their answer (change versus no-change) or for a maximum of 30 s (in the event of no answer). The time window of 30 s was chosen long enough to minimize the number of 'no answer' for want of time. A computer keyboard was used to record responses. Participants triggered each trial by pressing the space bar.

Subjects were informed of the distinction between two conditions. In the no-priming condition, the new viewpoint was unpredictable from the initial viewpoint. In the priming condition, the new viewpoint was primed via an avatar: subjects were explicitly

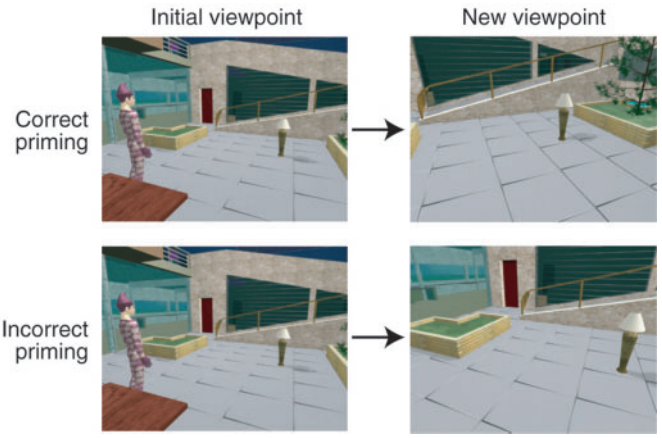

Fig. 4 Illustration of the viewpoint recognition task. After examining an initial view for 5 s, observers indicated if the new viewpoint was the one they expected according to the priming by the avatar, i.e. if the new viewpoint was the perspective adopted by the avatar. The upper and lower examples show correctly (45° viewpoint change) and incorrectly (90°) primed trials, respectively.

instructed that, when an avatar was visible from the initial viewpoint (50% of the trials), they could anticipate the new viewpoint since it corresponded to that of the avatar.

In half of the trials (50% of the non-primed trials and 50% of the primed trials), the lamp position was changed across viewpoint change; it moved to its next possible clockwise or counterclockwise position.

In order to prepare the stimuli, initial and new viewpoints were chosen from among those possible, with the constraints that the lamp should always be clearly visible, and that the viewpoint angular difference (difference in degrees between the initial and new viewpoints) was either 0°, 45°, 90° 135° or 180° (irrespective of direction). The design was totally counterbalanced for the viewpoint angular differences, the directions of perspective change and the conditions.

Viewpoint recognition task

In this task, subjects were seated in front of the same monitor and shown the same virtual environment as in the object location memory task. The procedure was the same as in the object location memory task. Each of the 32 trials was designed as follows. An avatar was visible from an initial viewpoint displayed for 5 s and subjects were asked to imagine and memorize what the avatar was seeing. Then, a new viewpoint on the visual scene was automatically displayed and the task was to judge if this new viewpoint was identical to the one adopted by the avatar, which was no longer visible (Fig. 4). A computer keyboard was used to record responses. Participants triggered each trial by pressing the space bar.

Subjects were informed of the distinction between two conditions. In the correct priming condition, the new viewpoint was the one primed, namely the one adopted by the avatar before the perspective change. In the incorrect priming condition, the new viewpoint was different from the one primed, and corresponded to the camera 45° to the left or right of the primed viewpoint.

For both correctly and incorrectly primed trials, the position of the lamp changed in the same way as in the object location memory task in half of the trials and not in the other half (Fig. 4). However, unlike the object location memory task, subjects were explicitly told to ignore the lamp and to answer irrespective of any change in the lamp position.

In order to prepare the stimuli, initial and new viewpoints were chosen from among those possible, with the constraints that the avatar should always be clearly visible, and that the viewpoint angular difference (difference in degrees between the initial and new viewpoints) was either 0°, 45°, 90° 135° or 180° (irrespective of direction). The design was totally counterbalanced for the viewpoint angular differences, the directions of perspective change and the conditions.

Perspective change

Each change from the initial to the new viewpoint can be theoretically broken down into two 'displacements': a translation from the circle of initial viewpoint cameras to the circle of new viewpoint cameras, and a rotation according to the angular viewpoint change of the trial (0°, 45°, 90°, 135° or 180°). It should be emphasized that the translation 'displacement' was the same in all trials whatever the angular viewpoint change. Therefore, even when the angular viewpoint change was equal to 0°, the passage from the initial to the new viewpoint entailed a real perspective change on the visual scene, making pure snapshot visuo-spatial memory insufficient to retrieve the lamp position or to recognize the avatar viewpoint.

Results

Object location memory task

In order to analyse the data of the object location memory task, a four-way ANOVA was conducted with group (control versus LTL versus RTL) as a between-subjects factor and priming (no-priming versus priming), lamp displacement (steady lamp versus moving lamp) and viewpoint angular difference (0°, 45°, 90°, 135°, 180°) as within-subject factors. The dependent variable was accuracy (percentage of correct answers).

The results showed a main effect of viewpoint angular difference [$F(4,128) = 9.61$, $P < 0.0001$], suggesting that the greater this difference (from 0° to 180°) the less accurate were the subjects (from 96% to 78% correct, respectively). However, this effect of viewpoint angular difference varied significantly with priming [$F(4,128) = 4.55$, $P < 0.005$], accuracy ranging from 94 to 81% in the priming condition and from 98 to 76% in the no-priming condition. This significant interaction between viewpoint angular difference and condition induced a higher variance of performance in the no-priming condition than in the priming condition, which reflects that the main effect of angular viewpoint difference (i.e. the greater the viewpoint angular difference the less accurate) is more important in the no-priming condition than in the priming condition. Consistent with this view, an additional analysis testing the hypothesis of a linear effect of viewpoint angular difference on accuracy showed a clear linear trend in performance

in the no-priming condition [$F(1,32) = 29.31$, $P < 0.0001$], whereas this trend was only marginally significant in the priming condition [$F(1,32) = 3.88$, $P = 0.06$]. Thus, even if there was no main effect of priming [$F(1,32) = 1.61$, $P = 0.21$], it seemed that the presence of the avatar reduced the dependence of accuracy on viewpoint angular difference.

The results also showed a main effect of group [$F(2,32) = 3.55$, $P < 0.05$; see Fig. 5]. More precisely, *post hoc* comparisons (Tukey test) showed that LTL patients (81% correct) were slightly but significantly ($P < 0.05$) less accurate than control subjects (90% correct), while RTL patients provided intermediate performances (85% correct) that did not differ either from control subjects ($P = 0.27$) or from LTL patients ($P = 0.74$).

Interestingly, a significant interaction between group, priming and viewpoint angular difference [$F(8,128) = 2.03$, $P < 0.05$] provided further information about the differences between the three groups of subjects. Trend analyses performed separately for each group revealed that, in control subjects and RTL patients, the average linear trend observed in the no-priming condition [$F(1,20) = 12.01$, $P < 0.05$ and $F(1,32) = 12.31$, $P < 0.05$, respectively] was no longer significant in the priming condition [$F(1,32) = 0.34$, $P = 0.57$ and $F(1,32) = 0.00$, $P = 1.00$, respectively], whereas in LTL patients, this linear trend was significant in both the no-priming and priming conditions [$F(1,32) = 7.60$, $P < 0.001$ and $F(1,32) = 7.15$, $P < 0,05$, respectively) (Fig. 6)].

Finally, there was no main effect of lamp displacement [$F(1, 32) = 2.22$, $P = 0.15$] but a significant interaction between lamp displacement and priming [$F(1, 32) = 4.54$, $P < 0.05$]. More precisely, *post hoc* analyses (Tukey test) showed that 'steady lamp' trials were more error-prone

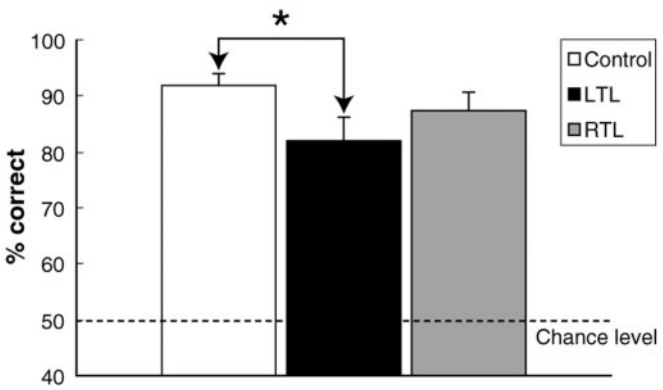

Fig. 5 Main effect of group on accuracy in the object location memory task. LTL (left temporal lobe) patients were significantly impaired relative to control subjects. RTL (right temporal lobe) patients differed neither from control subjects nor from LTL patients. Asterisk indicates a statistically significant difference ($P < 0.05$).

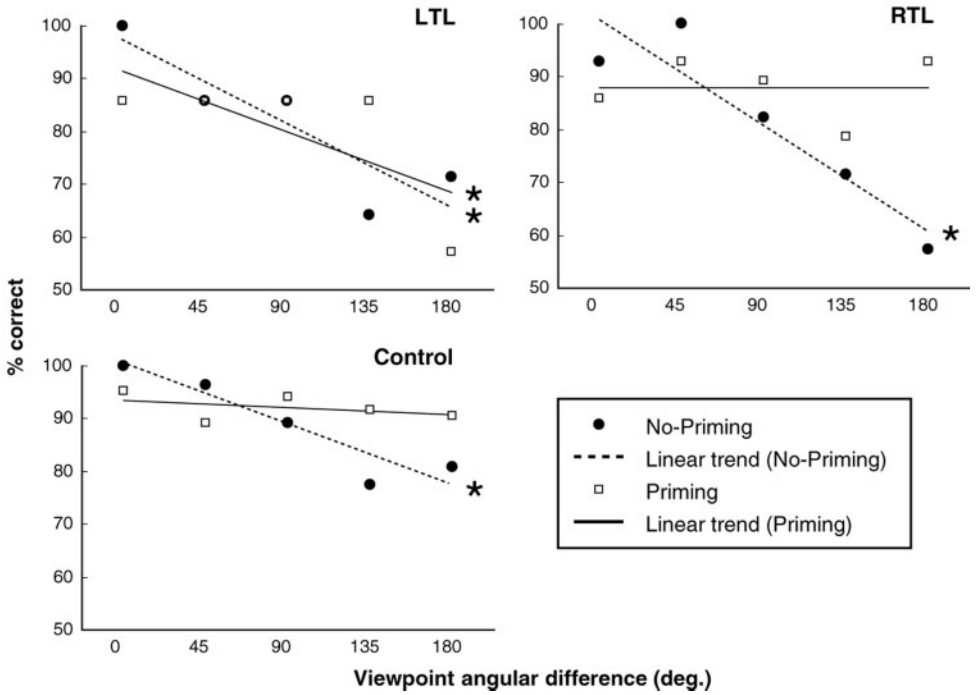

Fig. 6 The effect of viewpoint angular difference on accuracy in the object location memory task for each of the three groups of subjects. This figure illustrates the significant interaction between viewpoint angular difference, priming and group in the object location memory task. Trend analyses performed separately for each group revealed that, in control subjects and RTL (right temporal lobe) patients, the linear trend observed in the no-priming condition was no longer significant in the priming condition, whereas in LTL (left temporal lobe) patients, this linear trend existed in the no-priming condition and remained significant in the priming condition. Asterisk indicates a significant linear trend, i.e. a significant linear relation between performance and viewpoint angular difference.

than 'moving lamp' trials in the no-priming condition ($P<0.05$), while there was no such difference in the priming condition ($P=0.95$).

Viewpoint recognition task

In order to analyse the data of the viewpoint recognition task, a repeated measures ANOVA was conducted with group (control versus LTL versus RTL) as a between-subjects factor and priming (correct priming versus incorrect priming), lamp displacement (steady lamp versus moving lamp) and viewpoint angular difference (0°, 45°, 90°, 135°, 180°) as within-subject factors. The dependent variable was accuracy (percentage of correct answers).

There was no significant main effect of group [$F(2,32)=2.51$, $P=0.10$]. However, the results showed a significant main effect of priming [$F(1,32)=62.74$, $P<0.001$] as well as a significant interaction between priming and group [$F(2,32)=7.02$, $P<0.005$]. *Post hoc* analyses (Tukey test) showed that, whatever the group, subjects were less accurate in the incorrect priming condition than in the correct priming condition ($P<0.05$). In addition, the results summarized in Fig. 7 showed that, in the incorrect priming condition, RTL patients were much less accurate than control subjects (44% correct versus 74% correct, $P<0.01$), whereas there was no significant difference between these two groups in the correct priming condition (93% correct versus 87% correct, $P=0.99$). LTL patients (63% correct and 90% correct in the incorrect and correct priming conditions, respectively) did not differ significantly either from control subjects ($P=0.72$ and $P=0.99$, respectively) or from RTL patients ($P=0.40$ and $P=0.99$, respectively).

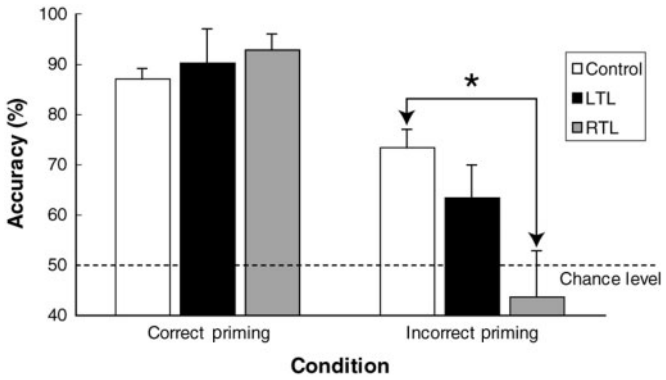

Fig. 7 Significant interaction between group and priming factors in the viewpoint recognition task. RTL patients were significantly impaired relative to control subjects in the incorrect priming condition, but not in the correct priming condition. LTL patients did not differ significantly either from control subjects or from RTL patients.

Finally, there was neither a main effect of lamp displacement [$F(1,32)=1.60$, $P=0.22$] nor an interaction between group and lamp displacement [$F(2,32)=0.22$, $P=0.80$]. And overall, the viewpoint angular difference did not affect the accuracy of viewpoint recognition judgements [$F(4,128)=1.73$, $P=0.15$].

Regression analyses

In order to address the question of the relative contribution of the various MTL structures as well as of temporopolar cortices to visual perspective taking, we conducted multiple regression analyses as described by Crane and Milner (2005). Each of the 10 anatomical measures (remaining volumes of hippocampus, entorhinal cortex, perirhinal cortex, parahippocampal cortex and temporopolar cortex on both resected and non-resected sides) were first regressed against the four behavioural measures (performances at the primed and non-primed trials of the object-location recognition task, performances at the correctly and incorrectly primed trials of the viewpoint recognition task) separately for RTL and LTL patients. The resulting squared correlation coefficients shown in Table 4 were subsequently used in multiple regression analyses, for each patients group, to construct the better model to predict each of the four behavioural measures. A forward selection procedure was used: the first anatomical measure that was included in the model was the one with the highest squared correlation coefficient, the second anatomical measure to be included was the one with the second highest squared correlation coefficient and so on. At each step of the procedure, in order to retain one anatomical measure as an additional independent variable in the model, it was decided that a change in the squared correlation score of at least 10% was necessary and that the

Table 3 Mean volumes (mm^3) of the medial temporal lobe structures of the resected (A) and non-resected (B) sides in the RTL and LTL groups

	Temporopolar cortex	Perirhinal cortex	Entorhinal cortex	Hippocampus	Parahippocampal cortex
(A) Resected side					
RTL group	150 (380)	274 (324)	63 (110)	300 (231)	1674 (403)
LTL group	101 (268)	483 (255)	296 (198)	329 (206)	1984 (252)
(B) Non-resected side					
RTL group	3447 (879)	2863 (424)	1571 (331)	4700 (451)	2423 (620)
LTL group	3270 (1120)	2936 (681)	1420 (265)	4714 (626)	2387 (297)

Note that the resected side corresponds to the right side for the RTL group and to the left side for the LTL group. SDs are given between brackets. +Z-scores.

Table 4 Squared correlation coefficients for the anatomical measures against the performance measures in LTL and RTL patients

Anatomical structure	Object location memory		Viewpoint recognition	
	No-priming	Priming	Correct priming	Incorrect priming
LTL patients				
Left temporopolar cortex	0.117	0.850	0.139	0.248
Right temporopolar cortex	0.554	0.118	0.002	0.122
Left perirhinal cortex	0.034	0.064	0.085	0.268
Right perirhinal cortex	0.625	0.528	0.061	0.000
Left entorhinal cortex	0.419	0.284	0.000	0.132
Right entorhinal cortex	0.644	0.559	0.101	0.007
Left hippocampus	0.012	0.001	0.156	0.000
Right hippocampus	0.475	0.153	0.056	0.000
Left parahippocampal cortex	0.047	0.047	0.001	0.002
Right parahippocampal cortex	0.170	0.067	0.251	0.391
RTL patients				
Left temporopolar cortex	0.001	0.103	0.066	0.138
Right temporopolar cortex	0.380	0.147	0.051	0.252
Left perirhinal cortex	0.694	0.090	0.584	0.276
Right perirhinal cortex	0.102	0.183	0.212	0.071
Left entorhinal cortex	0.241	0.710	0.089	0.113
Right entorhinal cortex	0.180	0.693	0.055	0.261
Left hippocampus	0.049	0.201	0.042	0.022
Right hippocampus	0.422	0.551	0.168	0.771
Left parahippocampal cortex	0.194	0.164	0.047	0.001
Right parahippocampal cortex	0.352	0.161	0.281	0.248

incremental *F*-score should be significant (at the 0.05 probability level). All the models reported below correspond to the final solution of this forward selection procedure.

The best model for the performance at primed trials of the object location memory task included only the left temporopolar cortex in RTL patients [$F(1,5) = 28.25$, $r^2 = 0.85$, $P < 0.005$] and both left and right entorhinal cortices in LTL patients [$F(2,4) = 12.77$, $r^2 = 0.86$, $P < 0.05$].

The best model for the performance at the non-primed trials of the object location memory task included only the right entorhinal cortex in RTL patients [$F(1,5) = 9.04$, $r^2 = 0.64$, $P < 0.05$] and the left perirhinal cortex as well as the right hippocampus in LTL patients [$F(2,4) = 12.77$, $r^2 = 0.80$, $P < 0.05$].

The best model for the performance at the correctly primed trials of the viewpoint recognition task included only the left perirhinal cortex in LTL patients [$F(1,5) = 7.01$, $r^2 = 0.58$, $P < 0.05$]. There was no significant model in RTL patients.

Finally, the best model for the performance at the incorrectly primed trials of the viewpoint recognition task included only the right hippocampus in LTL patients [$F(1,5) = 16.79$, $r^2 = 0.77$, $P < 0.01$]. There was no significant model in RTL patients.

Because several studies have showed that the age of seizure onset may influence the intensity and type of consequences of the epilepsy on cognitive functions (e.g. Dikmen *et al.*, 1975; Upton and Thompson, 1997; Hermann *et al.*, 2002), we also addressed the question of the influence of the age of seizure onset on visual perspective performances. Each of the four behavioural measures (performances at the primed and non-primed trials of the object-location recognition task, performances at the correctly and incorrectly primed trials of the viewpoint recognition task) was regressed against the age of seizure onset separately for RTL and LTL patients. None of these regressions was significant ($P > 0.05$).

Discussion

The aim of this study was to assess the role of the human MTL structures in visual perspective taking. Patients with unilateral temporal lobe resection sparing the parahippocampal cortex, as well as control subjects, performed two different tasks. In the object location memory task, they had to memorize the position of one target object in the environment from an initial viewpoint. They were then shown the same environment from a new viewpoint and had to indicate whether or not the target object had moved. In the viewpoint recognition task, subjects had to imagine the perspective of an avatar from the initial viewpoint and then had to decide whether or not the new viewpoint was the one adopted by the avatar. Our main finding was a double dissociation, with left MTL patients being impaired in the object location memory task but not in the viewpoint recognition task and right MTL patients being impaired in the viewpoint recognition task but not in the object location memory task.

Functional lateralization of MTL

The fact that RTL patients were impaired in the viewpoint recognition task but not in the object location memory task supports the idea of an involvement of the right MTL structures in visual perspective taking. Moreover, it supports the 'numerical' hypothesis formulated in the Introduction section, which suggests that the absence of MTL activation, and in particular of right MTL activation, in fMRI studies investigating visual perspective taking (Creem *et al.*, 2001; Zacks *et al.*, 2003; Vogeley *et al.*, 2004) is due to the use of too simple experimental environments, with too few locations to be coordinated across perspective change. Consistent with this hypothesis, Burgess (2002) suggested that the role of the right MTL, and in particular of the right hippocampus, in perspective change paradigms would be in fact to incorporate the different locations to be manipulated in a single abstracted

and allocentric configuration, allowing the cognitive load due to egocentric spatial updating to be reduced. According to this author, this chunking of spatial information would be particularly useful when the viewpoint is shifted within a rich environment, in which there are many landmark locations to remember.

In contrast with the results in RTL patients, the fact that LTL patients were impaired in both priming and no-priming conditions of the object location memory task but not in the viewpoint recognition task suggests that the left MTL structures are preferentially involved when only a small number of locations have to be remembered across perspective change. Interestingly, the double dissociation found in the present study can be interpreted within the framework of the hypothesis by Kosslyn of brain functional lateralization, which suggests that the human right hemisphere is involved in the processing of coordinate visuo-spatial information, with the left hemisphere rather playing a role in the processing of categorical information (Kosslyn, 1987; Kosslyn *et al.*, 1989). On the one hand, categorical processing would be optimal for coding a small number of locations but would become inefficient for important numbers. On the other hand, coordinate processing would be optimal for coding a large number of locations, but would be too expensive in terms of cognitive demands compared with categorical processing when only few locations have to be remembered.

Changing strategy in object location memory

In the object location memory task, the results showed that LTL but not RTL patients were impaired relative to control subjects. Consistent with this finding, Schmidt *et al.* (2007) recently reported in a functional brain imaging study using the same task (no-priming condition only) and the same environment, that object location memory was associated with activation in the left but not the right parahippocampal gyrus. In the present study, the absence of interaction between the group and the priming factors suggests that being primed did not help the LTL patients to better perform the object location memory task. Nevertheless, there was a significant interaction between group, priming and viewpoint angular difference, which needs to be discussed.

On the one hand, the performance in the non-primed trials varied linearly according to the viewpoint angular difference in the three groups of subjects: the greater the angle between the initial and test viewpoints, the less accurate were the subjects. Consistent with the literature about mental rotation and perspective change (e.g. Shepard and Metzler, 1971; Cooper and Shepard, 1973; Easton and Sholl, 1995; Diwadkar and McNamara, 1997; Shelton and McNamara, 1997; Farrell and Thomson, 1998; Wraga *et al.*, 2000; Amorim, 2003), this suggests that, in order to solve the task, subjects (whatever the group) first memorized the position of the lamp from the initial viewpoint and then, at the time of testing, performed spatial transformations (spatial updating) in order to align the initial and test viewpoints before giving their answer.

On the other hand, in the primed trials, the linear effect of the angular difference between the initial and test viewpoints was abolished in both control subjects and RTL patients but remained significant in LTL patients. In a previous study using the same paradigm with only control subjects, Amorim (2003) explained this effect of priming by arguing that the avatar allowed the subjects to perform spatial updating before perspective change, i.e. before the time of testing. However, another interpretation is that, when the avatar could be used to anticipate the test viewpoint, both control subjects and RTL patients changed their strategy to solve the task, whereas LTL patients did not, or at least did not in the same way.

Consistent with the idea of a change of strategy across conditions, the performance of RTL patients was correlated with the volume of the right entorhinal cortex in the non-primed trials but was significantly correlated with the volume of the left temporopolar cortex in the primed trials. By contrast, the performance of LTL patients was correlated with the volume of the left perirhinal cortex and of the right hippocampus in the non-primed trials and with the volume of both left and right entorhinal cortices in the primed trials.

The perirhinal cortex seems to be a critical region for object identification (Gaffan and Parker, 1996; Buffalo *et al.*, 1998; Wan *et al.*, 1999; see also the review by Brown and Aggleton, 2001), while the entorhinal cortex, which receives inputs from both the perirhinal and parahippocampal cortices (Insausti *et al.*, 1987; Suzuki and Amaral, 1994) has been shown to be involved in object location memory in monkeys (Charles *et al.*, 2004) as well as in humans (Owen *et al.*, 1996; Sommer *et al.*, 2005). It is therefore not surprising that we found significant correlations between performances in our object location memory task and the volumes of these structures.

The significant correlation between performance of RTL patients in the primed trials and the volume of the left temporopolar cortex is more unexpected but very interesting. Indeed, it can be hypothesized that the ability to take advantage of the presence of the avatar to change the visual perspective taking strategy relies on the temporopolar cortex. The left temporopolar cortex is known to be involved in many aspects of verbal and autobiographical memory (see Dupont, 2002, for review). However, as recently reviewed by Olson *et al.* (2007), many studies in the literature have suggested that the temporopolar cortices are also involved in socio-emotional regulation, face processing and more relevant to the present study, theory of mind. Consistent with such views, the present data suggest that the left temporopolar cortex may play a critical role in visual perspective taking in space. Further studies will be needed to assess the exact nature of such role.

Involvement of the right MTL structures in viewpoint recognition

In the viewpoint recognition task, the aim was to assess the involvement of MTL structures in the capacity to imagine the perspective of another observer on the current visual scene. The results showed that RTL patients were severely impaired in the incorrect priming condition, but answered as accurately as the control subjects in the correct priming condition. In contrast, LTL patients did not differ from control subjects whatever the condition (correct versus incorrect priming). This suggests that the right MTL structures were crucial to perform the task correctly in the incorrect priming condition but not in the correct priming condition, and therefore that the processes at work in each of the two conditions are different. Furthermore, the positive correlation between the performance of the LTL patients and the volume of the right hippocampus suggests that, among the different structures of the right MTL, it is the hippocampus that is crucial.

Using the same viewpoint recognition task as in our study, Amorim (2003) showed that the performance of control subjects varied linearly according to the angular difference between the initial and test viewpoints in the incorrect priming condition but not in the correct priming condition. He explained this result by arguing that, in both correctly and incorrectly primed trials, subjects performed spatial updating before perspective change (i.e. before the time of testing), but that in the incorrectly primed trials, subjects also recalled their initial viewpoint at the time of testing in order to reconstruct the expected viewpoint again and compare it to their current (test) viewpoint. In the present study, we did not find any effect of viewpoint angular difference on accuracy, likely due to methodological limitations (e.g. the size of the patient groups). However, our neuropsychological data suggest that the results reported by Amorim may rather reflect different ways of imagining the perspective of another observer, one of them specifically involving the right MTL.

Recently, Michelon and Zacks (2006) distinguished two kinds of visual perspective taking. In their study, when subjects were asked to report whether an object was to the left or to the right of an avatar, response times increased with increasing angular distance between the participant and the avatar, suggesting that subjects performed spatial updating. In contrast, when subjects were asked to indicate if one object was visible or not from the viewpoint of the avatar, response times were independent of the angle between the subject and the avatar but increased with the distance between the avatar and the object, suggesting that subjects mentally traced the avatar's line of sight to perform the task.

Accordingly, it can be hypothesized that when imagining the perspective of the avatar in our viewpoint recognition task, subjects used a strategy similar to the second kind of perspective taking described by Michelon and Zacks (2006): subjects may have traced the avatar's line of sight and memorized what should be seen on that line when tested from the avatar's perspective. This process would not involve the right MTL. At the time of testing, subjects would just have to compare 'their own line of sight' to the one expected. In the event of incongruence between the two (incorrect priming condition), a process of verification would be engaged consisting of recalling the initial viewpoint and then performing spatial updating to reconstruct the expected viewpoint and compare it to the current (test) viewpoint. This process of verification, on the other hand, would involve the right MTL structures, and in particular the right hippocampus.

Conclusion

In light of the present study, it appears that visual perspective taking may involve different strategies, depending on the task to be performed (object location versus viewpoint recognition) as well as on the context in which the task is performed (correct priming versus incorrect priming). Accordingly, visual perspective taking may involve different brain areas, and in particular different MTL structures, depending on these factors. New paradigms are now needed to assess more precisely this complex question of visual perspective taking. In particular, probe trials may be included in the future versions of perspective taking paradigms in order to be able to distinguish between the different possible strategies used by subjects (Astur *et al.*, 2004; Bohbot *et al.*, 2004). Another way would be to force the subjects to use one or another strategy in different conditions by manipulating the instructions given to them (Amorim and Stucchi, 2007).

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