

Neural Representation of Navigational Relevance Is Rapidly Induced and Long Lasting

Successful navigation is facilitated by the presence of landmarks. Previous functional magnetic resonance imaging (fMRI) evidence indicated that the human parahippocampal gyrus automatically distinguishes between landmarks placed at navigationally relevant (decision points) and irrelevant locations (nondecision points). This storage of navigational relevance can provide a neural mechanism underlying successful navigation. However, an efficient wayfinding mechanism requires that important spatial information is learned quickly and maintained over time. The present study investigates whether the representation of navigational relevance is modulated by time and practice. Participants learned 2 film sequences through virtual mazes containing objects at decision and at nondecision points. One maze was shown one time, and the other maze was shown 3 times. Twenty-four hours after study, event-related fMRI data were acquired during recognition of the objects. The results showed that activity in the parahippocampal gyrus was increased for objects previously placed at decision points as compared with objects placed at nondecision points. The decision point effect was not modulated by the number of exposures to the mazes and independent of explicit memory functions. These findings suggest a persistent representation of navigationally relevant information, which is stable after only one exposure to an environment. These rapidly induced and long-lasting changes in object representation provide a basis for successful wayfinding.

Keywords: fMRI, human navigation, learning and memory, memory formation, parahippocampal gyrus

Introduction

Evidence from animal as well as human studies has consistently shown the involvement of the mediotemporal lobe, including the hippocampal formation and the parahippocampal region, in spatial memory and navigation (e.g., O'Keefe and Nadel 1978; Maguire, Burgess, and others 1998; Burgess and others 1999; Shelton and Gabrieli 2002; Voermans and others 2004). Recent neuroimaging studies emphasize the importance of the parahippocampal gyrus itself rather than the hippocampus for the recognition of familiar as well as novel spatial environments and scenes (Aguirre and others 1996; Maguire, Frith, and others 1998; Epstein and others 1999, 2003; Düzel and others 2003; Rosenbaum and others 2004). The parahippocampal place area (PPA), a functional part of the parahippocampal gyrus, responds more to the visual presentation of scenes than to the presentation of faces or single objects (e.g., Epstein and Kanwisher 1998). Epstein and others (2005) showed that scene representations in the PPA become more and more viewpoint invariant over time. Moreover, these scene representations are more reliable in good navigators than in bad navigators stressing the involvement of the parahippocampal gyrus in spatial representations and navigational skills.

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A recent functional magnetic resonance imaging (fMRI) study by Janzen and van Turenout (2004) has shown that the parahippocampal gyrus responds not only to scenes but also to the recognition of single objects that have previously been seen in a navigationally relevant location (objects at decision points). Increased activity in the parahippocampal gyrus during the recognition of navigationally relevant compared with navigationally irrelevant objects was observed immediately after learning a route through a maze. These rapid changes in the neural representation of objects as a function of navigational relevance could provide a useful mechanism for wayfinding.

To successfully find a way through a maze, information about relevant locations should, however, not only be learned quickly but also be maintained over time. The present event-related fMRI study investigates whether the selective representation of navigationally relevant objects in the parahippocampal gyrus is modulated by time and practice. Twenty volunteers learned film sequences through 2 virtual mazes. To examine whether the selective representation of navigational relevance in the parahippocampal gyrus is modulated by practice, one maze was shown one time and the other maze was shown 3 times. Objects were placed at decision points (intersections) or nondecision points (simple turns). Twenty-four hours after the study phase, event-related fMRI data of the whole brain were acquired during recognition of the objects in isolation. Participants decided whether they had seen the objects in the mazes or not. If the representation of navigational relevance in the parahippocampal gyrus is long lasting, we expect to find increased activity for decision as compared with nondecision point objects even after such a long delay. To control for the possibility that effects of navigational relevance are simply due to paying more attention to objects at decision points, participants were instructed to pay attention to toys during learning. Half of the objects were attended objects (toys), and the other half were nonattended objects from other categories (nontoy), placed at decision and at nondecision points.

Materials and Methods

Participants

Twenty healthy human adults (10 females) gave informed written consent before participating in the experiment. All participants were right handed according to self-report. Mean age was 22.4 years (range 18-34 years). The study was approved by the CMO Committee on Research Involving Human Subjects (Region Arnhem-Nijmegen).

Design and Procedure

The experiment was divided into 2 parts: a study phase outside the scanner and a recognition phase on the next day (24 h later) during which functional images of the whole brain were acquired. Participants were given the following standardized written instruction for the study phase: "You apply for a job in a museum that exhibits belongings of

famous people. You will be guided through 2 sections of the museum. Through one section you will be guided one time and through the other section 3 times. The exhibits are placed on tables along the wall. Importantly, after training, you should be able to guide a children's tour through the museum. Therefore, while you are watching the film sequences pay special attention to toys and other things interesting for children."

The architecture software (3D TraumhausDesigner 4.0, Data Becker GmbH & CO.KG, Düsseldorf, Germany) was used to create the film sequences through a virtual reality museum presented on a 1.60-GHz-M Pentium 4 personal computer with 512 MB of RAM and a 15.0"XGA LCD-Screen. The virtual museum consisted of 2 mazes of the same shape. In each maze, 72 three-dimensional, colored objects were placed on tables. In total, 144 different objects were included in the mazes. In real world dimensions, each maze had a length of 279 feet and was 112 feet wide in relation to a simulated eye level of 5.6 feet. The 2 mazes were shown in separate film sequences, lasting 8.5 min each. The order in which the 2 film sequences were presented and the number of presentations (1 time and 3 times) was counterbalanced over participants.

Objects were placed at decision points (D-objects) or at nondecision points (ND-objects). Decision points were right-angled intersections, and nondecision points were simple right-angled turns. Attended objects (toys) and nonattended objects (nontoy) were equally assigned to decision and nondecision points. In the film sequences, a right or left turn was made both at decision and nondecision points. This way, the effects of motion were not confounded with those of navigational relevance. Participants had no control over the timing in the virtual environment to ensure that the amount of time spent at decision and nondecision points was matched (an object was visible on average 5 s in the visual focus and 11 s total).

One day (24 h) after the study phase, fMRI time series were obtained while participants performed a simple object recognition task. In this recognition phase, participants were instructed to decide as accurately and as quickly as possible whether they had seen the object in the former film sequences by pressing either a yes or a no response key. Responses were given with the index and the middle fingers of the right hand. A trial consisted of a fixation cross centered on the screen, followed by an object for 500 ms shown from a canonical perspective on a white background. Thus, during scanning, no maze-related information was presented. The average interstimulus interval was 4000 ms, jittered between 3000 and 5000 ms in steps of 250 ms, and counterbalanced over conditions. A total number of 252 stimuli were included in the recognition task. All stimuli were presented rapidly in a randomly intermixed order to prevent participants from anticipating and changing strategies for the different event types. The entire stimulus material consisted of 8 sets of 18 objects each, belonging to the following event types: D-object toy shown once, D-object toy shown 3 times, ND-object toy shown once, ND-object toy shown 3 times, D-object nontoy shown once, D-object nontoy shown 3 times, ND-object nontoy shown once, and ND-object nontoy shown 3 times. Three sets of 36 objects each were included as distractor objects: novel toys, novel nontoy, and scrambled objects. The scrambled objects were constructed from experimental objects using mosaic scrambling. Mean word frequency as well as frequency range was equal for all sets of objects.

Scanning Parameters

A 3-T magnetic resonance imaging system (Siemens TRIO, Erlangen, Germany) was used to acquire functional images of the whole brain (455). Using a gradient-echo echo planar scanning sequence, 36 axial slices were obtained for each participant (voxel size $3 \times 3 \times 3$ mm, repetition time = 2290 ms, field of view = 192, echo time = 30 ms, flip angle = 75°). All functional images were acquired in one run that lasted for 17 min. Following the acquisition of functional images, a high-resolution anatomical scan (T_1 -weighted magnetization prepared rapid gradient echo, 176 slices) was acquired.

Data Analysis

The fMRI data were analyzed using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands). Functional images were corrected for motion and slice scan time acquisition. Data were temporally smoothed with a high-pass filter removing low-frequency nonlinear drifts below 3 or fewer cycles per time course. Functional images were coregistered

with the anatomical scan and transformed into Talairach coordinate space using the 9-parameter landmark method of Talairach and Tournoux (1988). Images were spatially smoothed with a full width half maximum Gaussian kernel of 6 mm.

Statistical analyses were performed in the context of the general linear model, including 11 effects of interests and confounds. Event-related hemodynamic responses for each of the different event types were modeled as delta functions convolved with a synthetic hemodynamic response function. Whole brain group analyses treating subjects as a random factor were performed. Specific effects were tested by applying linear contrasts to the parameter estimates for each event as obtained in the random effects group analyses. The statistical threshold at the voxel level was set at $P < 0.001$, uncorrected for multiple comparisons. Region of interest analyses of the parahippocampal region were performed as follows. First, we functionally defined the region by selecting all voxels showing an effect of decision versus nondecision points in the group analysis. Then, we obtained the beta weights (i.e., the regression coefficients) as indexes of effect size for all voxels included in these regions of interest, separately for all individual subjects, for each of the event types. These regionally averaged beta weights were analyzed in repeated measurement analyses of variance (ANOVAs). Specific effects were tested by applying t -contrasts to the regionally averaged beta weights obtained for the different event types.

Results

Behavioral Results

The accuracy data were entered in an ANOVA with the factors number of exposures (seen one time and seen 3 times), decision point (objects at decision and at nondecision points), and attention (toys and nontoy). The data showed an effect of number of exposures during study ($F_{1,19} = 4.9$, $P < 0.05$). Objects presented one time evoked more errors (52.7%) than objects presented 3 times (41%; $t_{19} = 2.21$, $P < 0.05$). No significant differences in error rates (misses) were observed for objects placed at decision (46%) and at nondecision points (47.6%). Error rates showed an effect of the attentional manipulation during study ($F_{1,19} = 40.98$, $P < 0.001$). Error rates were lower for toys (36.6%) than for nontoy (57%; $t_{19} = -6.4$, $P < 0.001$). The data showed an interaction of the factors decision point and attention ($F_{1,19} = 7.14$, $P < 0.05$). An effect of decision point was observed for toys (D-object toys: 33.5%; ND-object toys: 39.6%; $t_{19} = -3.7$, $P < 0.001$) but not for nontoy (D-object nontoy: 58.4%; ND-object nontoy: 55.6%; $t_{19} = 1.0$, $P = 0.33$). No other significant interactions were observed. False positive responses were 12.9% for the novel toys and 10.3% for the novel nontoy. Scrambled objects evoked 0.5% false positives. Overall task performance was above chance level (70% correct).

Response times showed an effect of number of exposures during study ($F_{1,19} = 4.41$, $P < 0.05$). Responses were significantly faster for objects presented 3 times compared with objects presented once (mean response latencies were 943 and 991 ms, respectively, $t_{19} = 2.099$, $P < 0.05$). Response times showed a trend effect of the attentional manipulation during study ($F_{1,19} = 4.049$, $P = 0.059$). Response times were faster for toys than for nontoy (mean response latencies were 952 and 982 ms, respectively, $t_{19} = 2.012$, $P < 0.05$). No significant effect of decision point and no interaction between the factors number of exposures, attention, and decision point were observed.

fMRI Results

All objects included in the 2 mazes compared with a low-level visual baseline (scrambled objects) activated bilateral

occipitotemporal cortices (left middle occipital gyrus: $x = -47$, $y = -68$, $z = -5$; right middle occipital gyrus: $x = 43$, $y = -66$, $z = -6$; left inferior temporal gyrus: $x = -47$, $y = -47$, $z = -13$; right inferior temporal gyrus: $x = 46$, $y = -50$, $z = -13$) known as the ventral visual pathway (Ungerleider and Mishkin 1982). Increased activity ($P < 0.0001$) was additionally found bilaterally in the hippocampus (left: $x = -32$, $y = -24$, $z = -10$; right: $x = 33$, $y = -19$, $z = -12$), the parahippocampal gyrus (left: $x = -29$, $y = -29$, $z = -15$; right: $x = 28$, $y = -26$, $z = -17$), the middle frontal gyrus (left: $x = -31$, $y = 24$, $z = 10$; right: $x = 33$, $y = 26$, $z = 8$), and the left superior parietal lobe ($x = -27$, $y = -68$, $z = 32$).

To investigate effects of navigational relevance of object location, we compared fMRI responses to D-objects with responses to ND-objects. This comparison revealed an increase in activity for D-objects in the parahippocampal gyrus bilaterally (Fig. 1). No other brain regions showed an effect of navigational relevance. To investigate this effect in the parahippocampal gyrus in more detail, a region of interest analysis was performed on all voxels showing a decision point effect (see Materials and Methods). An ANOVA of the averaged beta weights was performed separately for the right and the left parahippocampal gyrus. In the right parahippocampal gyrus, apart from a main effect of decision point (decision vs. nondecision points, $F_{1,19} = 18.94$, $P < 0.001$), a main effect of attention was observed ($F_{1,19} = 5.88$, $P < 0.05$) showing decreased neural activity for objects (toys) previously attended to during study. Importantly, no main effect of number of exposures ($F_{1,19} = 0.59$, $P = 0.45$) and no significant interactions between the factors number of exposures, attention, and decision point were observed ($F_{1,19} = 0.14$, $P = 0.71$). *T*-contrasts showed significant effects for decision points compared with nondecision points for both toys (seen once: $t_{19} = 2.27$, $P < 0.05$) and nontoy (seen once: $t_{19} = 2.09$, $P < 0.05$; seen 3 times: $t_{19} = 2.1$, $P < 0.05$). No significant effect was observed for toys seen 3 times ($t_{19} = 1.01$, $P = 0.33$).

Analysis of regional responses in the left parahippocampal gyrus revealed a main effect of decision point (decision vs. nondecision points, $F_{1,19} = 27.03$, $P < 0.001$), but no other main effects (attention: $F_{1,19} = 1.82$, $P = 0.19$; number of exposures: $F_{1,19} = 1.39$, $P = 0.25$) or significant interactions were observed. *T*-contrasts showed significant effects for decision points compared with nondecision points for both toys (seen once: $t_{19} = 2.02$, $P < 0.05$) and nontoy (seen once: $t_{19} = 2.67$, $P < 0.001$; seen 3 times: $t_{19} = 2.64$, $P < 0.001$). No significant effect was observed for toys seen 3 times ($t_{19} = 1.53$, $P = 0.14$).

To examine whether the effect of navigational relevance is dependent on remembering having seen an object in the maze, we analyzed neural responses in the parahippocampal gyrus separately for remembered and forgotten objects (Fig. 2). Remembered objects were all objects in the maze that were indicated by the participants as “seen”, and forgotten objects were all objects in the maze that were indicated as “not seen” (errors).

An ANOVA including the factors hemisphere (right and left parahippocampal gyri), accuracy (remembered and forgotten objects), and object location (decision and nondecision points) was conducted. A main effect for the factor accuracy was found ($F_{1,19} = 8.24$, $P < 0.01$). Remembered objects showed increased neural activity as compared with forgotten objects. This effect was significantly stronger for the left parahippocampal gyrus as compared with the right parahippocampal gyrus ($F_{1,19} = 22.63$, $P < 0.001$). A main effect for the factor object location was observed ($F_{1,19} = 33.33$, $P < 0.001$). *T*-contrasts for decision as compared with nondecision point objects showed significant decision-point related increases in neural activity for remembered as well as forgotten objects in the right (remembered: $t_{19} = 3.36$, $P < 0.01$; forgotten: $t_{19} = 3.96$, $P < 0.001$) and the left parahippocampal gyri (remembered: $t_{19} = 3.98$, $P < 0.001$; forgotten: $t_{19} = 3.86$, $P < 0.001$). No interactions were observed.

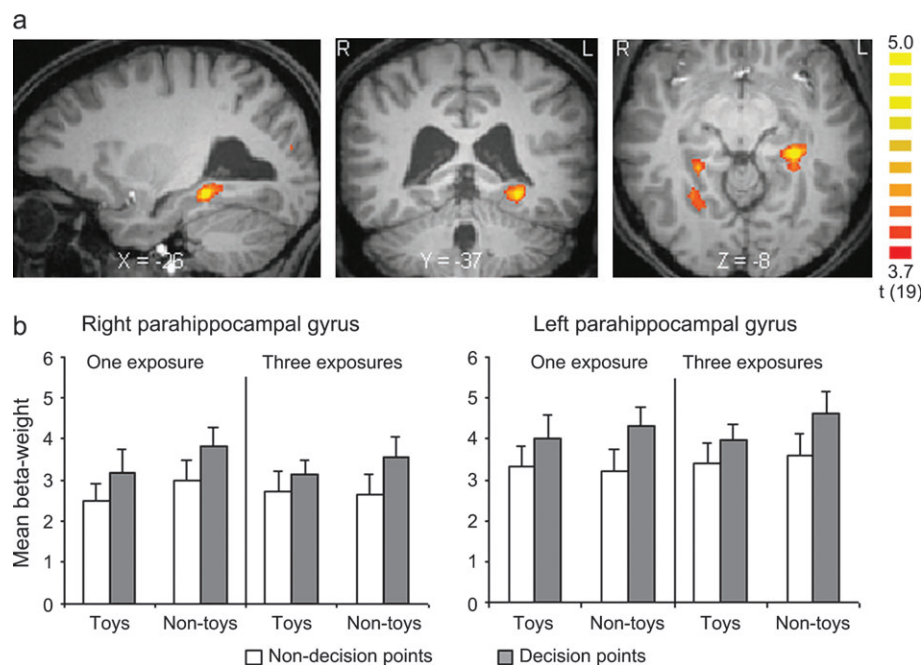


Figure 1. (a) Increased activity in the parahippocampal gyrus for decision point as compared with nondecision point objects. Location of peak activation, expressed in millimeters as Talairach coordinates was $x = -26$, $y = -37$, $z = -8$ for the left and $x = 24$, $y = -41$, $z = -8$ for the right parahippocampal gyrus ($P < 0.001$). (b) Regionally averaged beta weights for the left and the right parahippocampal gyrus showing increased activity for decision as compared with nondecision point objects separately for toys and nontoy after one and 3 exposures to the maze. Bars indicate standard errors across participants.

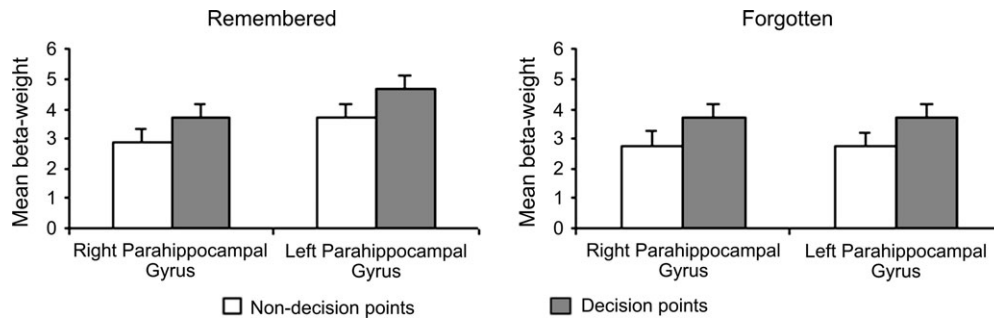


Figure 2. Regionally averaged beta weights for the right and left parahippocampal gyrus showing a decision point effect for remembered as well as forgotten objects. Bars indicate standard errors across participants.

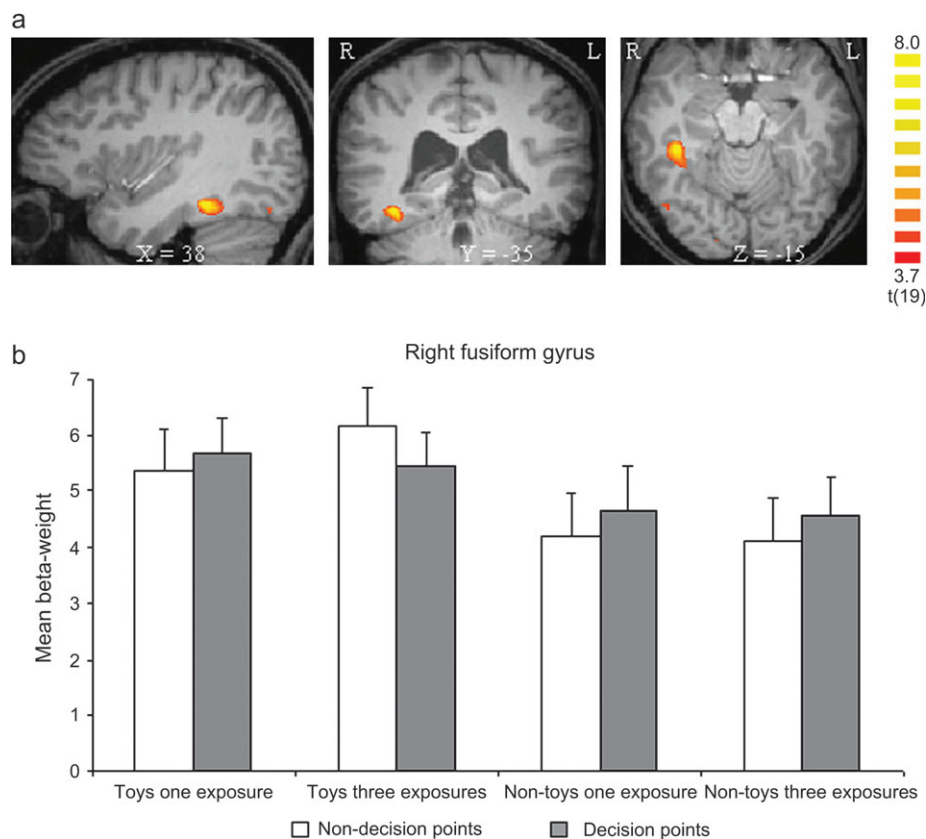


Figure 3. (a) Increased activity for attended objects (toys) compared with nonattended objects (nontoy) in the right fusiform gyrus. Location of peak activation, expressed in millimeters as Talairach coordinates was $x = 38$, $y = -35$, $z = -15$ ($P < 0.0001$). (b) Regionally averaged beta weights for the right fusiform gyrus showing increased activity for toys compared with nontoy objects separately for decision and nondecision points after one and 3 exposures to the maze. Bars indicate standard errors across participants.

Comparing event-related fMRI responses to toys with those to nontoy objects revealed increased activity in the right fusiform gyrus (Fig. 3). An ANOVA of subjects' averaged beta weights obtained for all voxels in this region showed a main effect of attention (toys vs. nontoy, $F_{1,19} = 61.59$, $P < 0.001$). No main effect of the factors number of exposures and decision point was observed, nor did we observe any significant interactions.

Brain regions showing an effect of number of exposures included the bilateral inferior parietal lobe, the right inferior temporal gyrus, and the medial aspect of the frontal lobe (see Table 1). These regions showed increased activity for objects seen 3 times during study as compared with objects seen only once. Importantly, no interaction between number of exposures and navigational relevance was observed (see Fig. 1).

Additionally, we analyzed whether male and female participants showed differential effects of navigational relevance. No significant main effect for male and female participants and no interactions resulted.

Between-Study Comparison

To investigate whether the observed increase in activity in the parahippocampal gyrus is modulated by time, we compared the results of the present study with the results of a previous study (Janzen and van Turenout 2004) in which design, materials, and task were identical to the present study. The only difference with the present study was that in the previous study we used a delay of 20 min between study phase and scanning.

For each subject in each study, beta weights were extracted from the region in the parahippocampal gyrus showing a decision point effect, as described for the region of interest analysis in Materials and Methods. Beta weights were entered in an ANOVA with the factors navigational relevance, attention, and the between-study factor delay. Significant main effects were observed for the factors navigational relevance ($F_{1,38} = 32.98$, $P < 0.001$) and attention ($F_{1,38} = 10.316$, $P < 0.01$). Importantly, no significant interaction between the factors navigational relevance and delay and no other interactions were observed. Although the decision point effects were larger after the 24-h delay, this difference did not reach significance (see Fig. 4). This might be due to the limited power of a between-study comparison.

When comparing the size of the brain regions showing a decision point effect in the 2 studies, we saw an enlargement for the present study. Comparing the number of voxels showed that after a 1-day delay, the enlargement of parahippocampal involvement was 254 voxels in the right hemisphere (reported voxel sizes are $1 \times 1 \times 1$ mm) and 790 voxels in the left hemisphere.

Discussion

In the present event-related fMRI study, we examined whether the selective representation of navigationally relevant objects is

modulated by time and practice of route learning. Consistent with our previous findings (Janzen and van Turennout 2004), the data show that the parahippocampal gyrus differentially responds to objects that have previously been placed at navigationally relevant locations. Importantly, this neural marking of navigationally relevant objects in the parahippocampal gyrus was still observed after a one-day delay between studying a spatial environment and object recognition, clearly indicating that the coding of navigational relevance is long lasting. The differential response to navigationally relevant objects in the parahippocampal gyrus was independent of paying attention to a specific object category during study. Although the behavioral results showed that the attentional manipulation during study was effective, no interaction between the factors navigational relevance and attention was observed in the fMRI data. This result rules out the possibility that coding of navigational information is simply due to paying more attention to objects at decision points compared with objects placed at nondecision points. On the contrary, previously attended objects (toys) showed a decrease in activity compared with nonattended objects (nontoy) in the right parahippocampal gyrus. In the left parahippocampal gyrus, the direction of the effect is the same; however, the difference did not reach significance. Recently, attention has been shown to modulate effects of repetition-related decreases in neural activity showing larger effects for attended as compared with unattended objects (Vuilleumier and others 2005; Yi and Chun 2005). The decrease in activity that we observed for the attended as compared with the unattended objects could possibly reflect such repetition-related effects. The decrease could also be related to a more efficient stimulus encoding during study for toys as compared with nontoy (e.g., Gabrieli and others 1997). The present study does not allow us to distinguish between the possible explanations. However, the opposite direction of the effects together with the absence of an interaction between the effect of navigational relevance and simply paying attention to objects during study provides clear evidence for a dissociation.

When comparing previously attended objects (toys) with nonattended objects (nontoy), the brain imaging data showed strong increased activity in the right fusiform gyrus. This result is in line with studies showing increased neural activity in ventral occipitotemporal regions related to paying attention to objects (Kanwisher and Wojciulik 2000; Vuilleumier and others 2001). Importantly, this increase in the right fusiform gyrus was not affected by navigational relevance and number of exposures (Fig. 3), again emphasizing a dissociation of the effects.

The present results demonstrate quite conclusively that our earlier findings (Janzen and van Turennout 2004) are reliable and maintained over time. They provide clear evidence for a long-lasting representation of navigationally relevant objects in the parahippocampal gyrus. This involvement of the parahippocampal gyrus in the representation of navigational information could therefore point towards an efficient neural mechanism underlying wayfinding. Previous results have shown the involvement of the medial temporal lobe during actual navigation (e.g., Maguire, Burgess, and others 1998). However, important spatial information can only be helpful to guide later wayfinding behavior if it is maintained over time. Our data provide first evidence for a long-lasting representation of navigationally relevant object information in the parahippocampal gyrus.

Table 1

Increased brain activity for objects seen 3 times during study

Anatomical region	Talairach coordinates			Brodmann area	Volume (mm ³)
	x	y	z		
Right					
Middle temporal gyrus	53	-14	-12	21	27
Inferior temporal gyrus	59	-39	-11	21	27
Left					
Medial aspect of frontal lobe	-1	58	15	10	61
Superior frontal gyrus	-14	-1	59	6	4
Inferior parietal lobe	-37	-73	30	40	29
Inferior temporal gyrus	-59	-40	-10	21	13

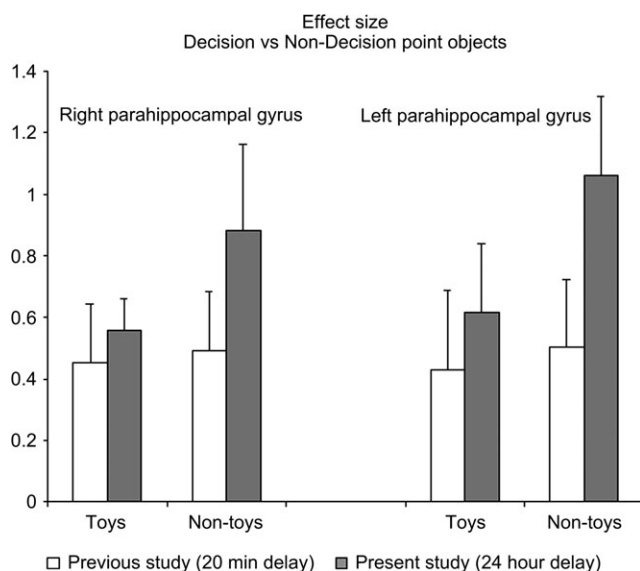


Figure 4. Effect sizes of the decision point effect for the previous and the present study separately for the right and the left parahippocampal gyrus as well as for toys and nontoy.

When comparing all objects included in the mazes with scrambled objects, we observed increased activity in the ventral visual pathway (Ungerleider and Mishkin 1982) including the medial temporal lobe and the hippocampus. The increase in activity in bilateral hippocampus is in line with data showing that the hippocampus plays a critical role in recognition memory (Stark and Squire 2001). On the other hand, the hippocampal activity can be related to the recognition of possible (objects in the mazes) as compared with impossible objects, that is, scrambled objects (Schacter and others 1995).

A between-study comparison of the present and a previous study (Janzen and van Turennout 2004) showed that the decision point effect was maintained over time (Fig. 4). The brain areas showing increased activity for decision point objects as compared with nondecision point objects were larger after a 24-h delay than after a 20-min delay. Although no hard conclusions can be drawn from the between-study comparisons, the results clearly show that the effect does not get smaller overnight. On the contrary, the data suggest that the effect gets bigger.

This result is in line with evidence from memory research that demonstrates consolidation of spatial representations. Animal as well as human studies have shown that memory consolidation is especially dependent on medial temporal lobe structures including the hippocampus and the parahippocampal gyrus (Alvarez and Squire 1994, for an overview, see Maquet and others 2003). Moreover, a recent positron emission tomography study by Peigneux and others (2004) demonstrated consolidation of spatial memories during slow wave sleep in humans. We observed that the time-induced enhancement of the decision point effect was larger for unattended objects than for attended objects, possibly suggesting that spatial memory consolidation efficiently functions without attentional demands. Whether the long-lasting representation of navigational relevance gets stronger with time and reflects spatial memory consolidation in the parahippocampal gyrus needs to be systematically investigated in further studies.

Importantly, the coding of navigational relevance was independent from the number of exposures to the maze (Fig. 1), pointing out the effectiveness of the underlying neural way-finding mechanism. To successfully find a way through a spatial environment, information about relevant locations should not only be maintained over time but also be learned quickly. Our data show a persistent representation of navigationally relevant information. This selective representation is already stable after only one exposure to a maze and remains unchanged with additional maze practice.

Although practice did not affect the effect of decision points, behavioral results from both accuracy data as well as response times strongly indicate that object recognition was improved after multiple exposures to the maze. Response times were significantly shorter for objects presented 3 times compared with objects seen only once. Similarly, the error rates were less for objects seen 3 times as compared with objects seen only once. Brain imaging data showed increased activity especially in the bilateral inferior parietal and medial frontal lobe for objects seen 3 times as compared with objects seen only once. Previous results on practice-related changes in neural activity show a variety of neural patterns in multiple brain regions (Kelly and Garavan 2005). Increases in activity (e.g., Gauthier and others 1999; Olesen and others 2004) as well as decreases (e.g., Van Turennout and others 2003; Landau and others 2004) have been reported, depending on tasks, training methods, stimuli,

and time courses used. In line with our results, Olesen and others (2004) showed increased prefrontal and parietal activity after extensive training on a visuospatial working memory task. Regardless of these practice-related increases, our results clearly show that no interaction occurred between navigational relevance and practice.

We additionally tested whether the effect of navigational relevance is dependent on explicit memory of having seen an object before. The increase in activity in the parahippocampal gyrus for objects at decision points was observed for remembered as well as forgotten objects (Fig. 2). This result shows that explicit memory of having seen an object before is not necessary for the representation of navigational relevance. Declarative memory theories propose conscious awareness as necessary for memory retrieval from the medial temporal lobe (Squire 1992). The automatic reactivation of navigational relevance during object recognition shows that even without remembering having seen an object, information about relevant spatial locations is represented.

Remembered objects showed a stronger increase in activity as compared with forgotten objects in the left parahippocampal gyrus. Greater activity in the left parahippocampal gyrus for correctly remembered objects was reported by Cansino and others (Cansino and others 2002). In this study, a source memory task was used in which participants judged whether an object had been previously presented, and subsequently, if yes, in which of 4 corners of the screen. The recognition task used in the present study did not explicitly test source memory. Nevertheless, because objects were previously seen in a maze, the left lateralized effect of explicit memory in the parahippocampal gyrus could possibly be related to the retrieval of source information. However, because no consistent pattern has been reported in the literature (for a recent review, see Henson 2005), further studies are needed that investigate lateralized effects of recognition memory.

A large amount of literature has focused on the involvement of the parahippocampal gyrus in scene processing (e.g., Epstein and others 2003). The PPA has been established as a functional area showing increased activity to scenes as compared with single objects or faces (e.g., Epstein and Kanwisher 1998). Our results show that the presence of a scene is not crucial to activate this region. Objects in isolation that have been previously encoded in navigationally relevant situations are represented in bilateral parahippocampal gyrus. This finding is consistent with Bar and Aminoff (2003) who show that the parahippocampal cortex responds more to isolated objects that are strongly associated with a specific context compared with objects with a weak contextual association. Bar and Aminoff (2003) suggest that the posterior part of the parahippocampal region is related to spatially specific representations, whereas the anterior part stores more abstract representations. Our present as well as previous results (Janzen and van Turennout 2004) showing increased activity in the posterior region of the parahippocampal gyrus for objects previously seen in navigationally relevant contexts compared with objects seen in places with less relevance support this assumption. Our coordinates of peak activity in the parahippocampal gyrus are similar to those reported in other studies (Epstein and Kanwisher 1998; Bar and Aminoff 2003). The location of the PPA (e.g., Epstein and Kanwisher 1998) in the posterior parahippocampal gyrus suggests a functional division of this region. Future research is necessary to make exact predictions of the specific involvement

of different parts of the parahippocampal region in object representation.

Further research is also needed to examine the precise role of the parahippocampal gyrus in successful wayfinding as well as actual navigation through more complex environments. A recent fMRI study by Hartley and others (2003) found increased activity in the parahippocampal gyrus for wayfinding as compared with route following. This parahippocampal activity during wayfinding was independent of participants' performance in finding accurate shortcuts. This is consistent with our finding that activity in the parahippocampal gyrus is independent of participants' performance in object recognition and provides support for the assumption of a basic and highly automatic wayfinding mechanism that is already stable after single experience in a spatial environment. Future studies are necessary to further investigate the parahippocampal involvement during navigation and possible effects of performance.

In conclusion, our results demonstrate that navigationally relevant information about objects acquired during maze learning is persistently stored in the parahippocampal gyrus. The representation of navigational relevance is already stable after only one exposure to an environment. The information is automatically activated during object recognition and independent of attentional demands. These rapidly induced and long-lasting changes in object representation could efficiently support successful navigation.

Notes

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