PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1997 **352**, 1475-1480
doi: 10.1098/rstb.1997.0134

Hippocampal involvement in human topographical memory: evidence from functional imaging

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SUMMARY

Functional brain imaging in humans is beginning to reveal a network of brain regions that subserve topographical learning: the medial parietal lobe, the posterior cingulate gyrus, occipitotemporal areas, the parahippocampal gyrus and the right hippocampus. These findings illuminate the patient lesion literature where all of these brain regions have been implicated at one time or another in cases of topographical disorientation. Once topographical information is acquired, the neuroanatomy that supports its use from either episodic or semantic memory is similar to that activated during encoding. The specific contributions of extrahippocampal regions within the topographical memory system are being revealed, such as the role of the right parahippocampal gyrus in object-in-place encoding. The right hippocampus is clearly involved in processing spatial layouts over long as well as short time-courses, and participates in both the encoding and the retrieval of topographical memory. The ventromedial orbitofrontal cortex is recruited when information in the topographical memory system is not sufficient to produce direct navigation to a goal place.

1. INTRODUCTION

The ability of humans to orient and navigate successfully in the large-scale spatially extended environments that constitute the real world is commonly referred to as topographical orientation. Wayfinding is complex and not a unitary process; there are many aspects to it including attentional, perceptual and mnestic components. Topographical disorientation, therefore, can occur because of disturbance to one or more component processes. Cases of topographical disorientation are occasionally reported and are typically described in terms of perceptual or mnestic difficulties, such as perceptual disturbance where there is an agnosia for landmarks and buildings even in well-known surroundings, often found in association with prosopagnosia (Landis *et al.* 1986; Patterson & Zangwill 1944); or a topographical memory disturbance, where buildings and landmarks can be recognized and recalled, but the memory for their place in space and spatial relationships is dysfunctional (Bottini *et al.* 1990; DeRenzi *et al.* 1977; Maguire *et al.* 1996*b*; Habib & Sirigu 1987).

Some general conclusions about the neural basis of topographical orientation systems can be drawn from the patient literature. Damage to several brain regions can produce topographic deficits or one sort or another. These include the posterior parietal lobe, the occipital lobe, hippocampal formation and parahippocampal gyrus. However, the dearth of relatively pure cases of topographical disorientation and the mixed picture of deficits typically present in many of the reported cases leave many questions about the neural instantiation of topographical orientation remaining to be answered. More distinct conclusions about memory for the spatial layouts of environments are possible from work with animals, particularly rodents, where the hippocampus has been found to have a significant role in processing spatial information which is independent of the location or orientation of a navigating animal, i.e. processing spatial information in an allocentric frame of reference. The hippocampus has been proposed to maintain a cognitive map of the spatial layout of learned environments (O'Keefe & Nadel 1978), and complex spike cells within the rat hippocampus have been found to exhibit spatially localized firing (O'Keefe & Dostrovsky 1971).

Functional brain imaging provides the opportunity to explore cognitive processes *in vivo* in neurologically normal humans. This paper describes how positron emission tomography (PET) in particular has extended our understanding of the anatomy of topographical memory. Several questions will be addressed. For example, what brain regions are involved in the learning of a spatially extended environment? What distinct functions might the various regions perform in the context of topographic learning? Similar questions are asked about the retrieval of previously learned environmental information. In addition, are the brain regions subserving topographical memory processes common also to those serving non-topographical memory? Currently there have been a limited number of functional imaging studies examining topographical memory. This is not surprising given the restrictive environment of brain scanners and the complexity of

Phil. Trans. R. Soc. Lond. B (1997) **352**, 1475–1480
Printed in Great Britain

the cognitive processing engendered by environmental cognition. Examining topographical memory or wayfinding in this context necessitates the use of novel stimuli to simulate exploration and navigation.

2. TOPOGRAPHICAL LEARNING

(*a*) *Findings*

The four functional imaging studies of topographical learning reported at this time and their findings will be briefly reviewed, with subsequent discussion of the broader issues surrounding these results.

Maguire *et al.* (1996*a*) used PET to measure regional cerebral blood flow (rCBF) while subjects watched and memorized film footage. In one case the film depicted navigation in an urban area (topographical memory), whereas in another the film footage to be remembered was of a similar urban area but the camera was stationary while people, cars, etc. moved past (episodic memory). On the basis of viewing the second film, therefore, it was not possible to construct an internal spatial map of the environment, but the tasks were comparable in terms of demands on memory. When changes in rCBF associated with episodic memory encoding were subtracted from the changes in rCBF associated with topographical memory, focal and significantly increased activation of the medial parietal region, the parahippocampal cortex and hippocampus on the right and the parahippocampal cortex on the left resulted (see figure 1). However, a comparison of control tasks with the activity during the episodic memory condition without a navigation component revealed patterns of activation that, notably, did not include the medial temporal region. Such comparisons revealed activation of the middle occipital gyrus (area 19) and the cuneus, and bilateral activation of the middle frontal gyri. Aguirre *et al.* (1996) used functional magnetic resonance imaging (fMRI) and a computer simulation of a maze-like environment with objects located in it to examine topographical learning. They too report activation of the parahippocampus and medial parietal region associated with encoding of the maze.

Using PET, Maguire *et al.* (1997) also measured changes in rCBF while normal subjects explored and learned virtual reality environments. One experiment involved an environment containing salient objects and textures that could be used to discriminate between different rooms. A second experiment involved a plain empty environment in which rooms were distinguishable only by their shape. The purpose of using this environment was to extend the investigation of the topographical memory-acquisition process beyond previous studies by examining its neural substrates where environmental inputs were more specifically identifiable (i.e. the presence or absence of landmarks). Learning in both cases activated a network of bilateral occipital, medial parietal and occipitotemporal regions and the posterior cingulate cortex. The presence of salient objects and textures in an environment additionally resulted in increased activity in the right parahippocampal gyrus. This region was not activated during exploration of the empty environment.

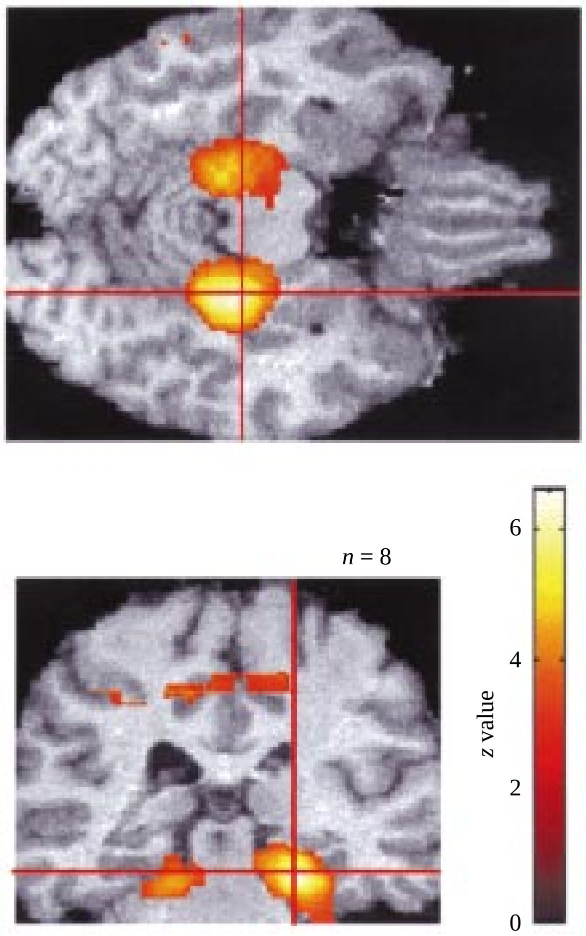

Figure 1. Statistical parametric map (SPM) showing the location of increases in cerebral blood flow in transverse and coronal sections while subjects watched film footage of navigation through a town (topographical memory) compared with a non-navigation memory (episodic memory) condition. The map is superimposed onto a template magnetic resonance image (MRI) to facilitate anatomical localization. Areas activated are the parahippocampal cortex and hippocampus on the right, with activation of the parahippocampal gyrus on the left, and the medial parietal lobe ($p < 0.001$). Data from Maguire *et al.* (1996*a*).

(*b*) *Implications*

Based on the findings of these four experiments, a quite consistent pattern of brain activations is observed in association with topographical learning. Not surprisingly, compared with low-level baseline tasks, striate and extrastriate regions are involved, the other elements of the network being medial parietal and occipitotemporal areas, the posterior cingulate cortex, the parahippocampal gyrus, and in the study of Maguire *et al.* (1996*a*) the right hippocampus. This is compatible with patient findings, where lesions in all of these brain areas have been implicated at one time or another in topographical disorientation.

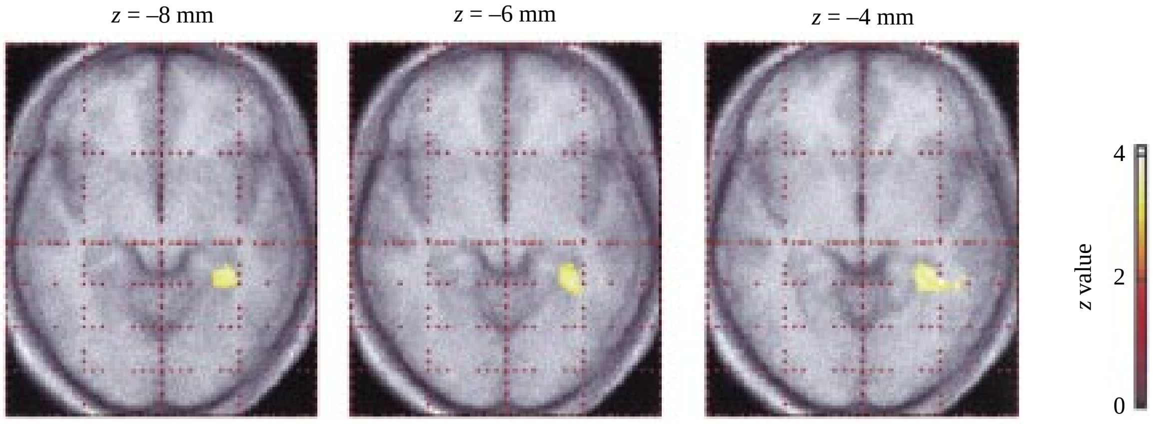

Figure 2. Activation in the right hippocampus during the recall of routes around London by taxi drivers compared with a famous landmark recall task. Activation is located here on relevant transverse sections of the averaged MRI scan of the 11 taxi drivers. Data from Maguire *et al*. (1997*b*).

It would seem that the processing of environmental space in humans, as in rats, relies on hippocampal formation involvement. This is congruent with the patient findings alluded to previously (Habib & Sirigu 1987; Maguire *et al*. 1996*b*). The hippocampal formation is not consistently activated in functional imaging studies of episodic memory, although damage to this area is known to give rise to amnesia (Scoville & Milner 1957; Mayes 1988). It has been suggested that perhaps the lack of hippocampal activation in such studies is because the task-associated activity of the hippocampus is of a magnitude beyond the sensitivity of the PET camera. However, this is clearly not the case given its activation in the first study described here and its activation in other functional imaging studies (see, for example, Vandenberghe *et al*. 1996). A more likely explanation is that the hippocampus maintains a level of continuous activity throughout tasks, experimental and control, so that in effect its activity is cancelled out during many cognitive subtractions. However, tasks such as the film viewing of naturalistic navigation, with the processing demand to represent complex large-scale space, may activate the hippocampus beyond its normal level. Two of the studies involving simulated or virtual-reality environments (Aguirre *et al*. 1996; Maguire *et al*. 1997*b*, experiment 1), although associated with increased activity in the parahippocampal cortex, did not demonstrate changes in activity in the hippocampus proper. It may be that the normal level of hippocampal activity was enough to support the demands of these tasks, which, although they attempted to simulate real environments, did not embrace the true complexities and richness of the real world, designed as they were in a maze-like way.

Cognitive models of environmental learning commonly describe predictable stages in the development of allocentric representations of large-scale space (Siegal & White 1975). Typically, a significant role is ascribed to distinctive features or landmarks as the initial anchor points of topographical memory formation, and there is empirical support for the importance of landmarks in facilitating spatial and route-learning tasks (Allen *et al*. 1978; Garling *et al*. 1982; Presson 1987; Tlauka & Wilson 1994). In the studies by Maguire *et al*. (1997*b*), the purpose of comparing the encoding of the virtual environment with objects or landmarks present with that of an environment with no objects was to pinpoint what areas might be specifically interested in object-in-place encoding in large-scale space. The finding that the parahippocampal gyrus is significantly involved in the encoding of an environment within which salient objects are located accords with the distinct role of this area in cognitive models of environmental learning. It further provides evidence that the parahippocampal gyrus provides the neural substrate for landmark or object-in-place encoding within the larger system for topographical learning in humans.

Increased activity in the medial parietal lobe, the precuneus, is commonly reported in functional imaging memory studies (Grasby *et al*. 1993; Fletcher *et al*. 1995*a*; Buckner *et al*. 1996). This has been interpreted as being associated with the retrieval of visual imagery in episodic memory. Fletcher *et al*. (1995*b*) confirmed this in a study in which the recall of imageable word pairs, but not of non-imageable word pairs, was associated with significant activation of the precuneus. All functional imaging studies of topographical memory encoding report the precuneus as active. Activity in this region may relate to the construction of an internal representation of large-scale environments, and seems compatible with the role of the precuneus in imagery. The posterior cingulate cortex is also an active region during topographical learning. Cammalleri *et al*. (1996) report a case of topographical disorientation in a patient after a lesion to the right caudal cingulate cortex. Sutherland *et al*. (1988) found that rats with aspiration of the posterior cingulate cortex were impaired in their ability to swim to a place in space by using distal cues. Vogt *et al*. (1992) suggest that the posterior cingulate cortex may contribute to spatial orientation because of its anatomical interposition between parietal regions and the parahippocampal gyrus. They propose that the posterior cingulate cortex may participate in the transformation from a parietal (egocentric) frame of reference to a parahippocampal system based on an allocentric frame of reference. The activation of the precuneus, posterior cingulate cortex and parahippocampal gyrus during exploration of the environment may be evidence of this spatial orientation pathway.

The encoding of verbal episodic memory in functional imaging studies is typically associated with activation of the left dorsolateral prefrontal cortex and the medial parietal region but not the medial temporal region (Fletcher *et al.* 1995*a*; Shallice *et al.* 1994). This pattern of activation was indeed observed with the non-topographic memory encoding in the study by Maguire *et al.* (1996*a*). Notably, the activations in all cases associated with topographical learning are in the posterior brain, and even relative to very low-level baseline tasks, such as watching a screen change colour, no increased activation of the prefrontal cortices is observed. Interestingly, case reports of patients in whom topographical disorientation is the primary deficit are most consistently reported after posterior brain lesions.

The ability to navigate in large-scale space is one humans share with a multitude of other species. Many species with a smaller relative area of prefrontal cortex than humans (e.g. birds) are able to navigate successfully; this observation suggests that perhaps other more posterior brain areas are most involved in such abilities. Other work has found that it is the size of the hippocampus relative to the size of the telencephalon that varies according to whether spatial skills are critical to survival. For example, in food-storing birds the hippocampus is reported as larger than in species that cache food to a lesser extent (Sherry *et al.* 1992; Hampton *et al.* 1995). It is, of course, possible that frontal regions become recruited into topographical memory encoding under circumstances that have not yet been examined in functional imaging studies, or perhaps become more active during topographical memory retrieval.

3. TOPOGRAPHICAL MEMORY RETRIEVAL

(*a*) *Findings*

The retrieval or use of topographic information is of two types. The first are those recently formed memories that may still retain a specific spatiotemporal reference and therefore be classified as episodic in nature (Tulving 1983). The retrieval of such memories may conceivably still involve a degree of active encoding if knowledge of the spatial layout of the environment is still being verified or consolidated. Aguirre *et al.* (1996) scanned subjects while they navigated to specific objects within the environment after they had learned it (and been scanned). They report the activation of the same network of regions during retrieval as encoding, including the parahippocampal gyrus and precuneus. Ghaem *et al.* (1996) asked subjects to learn a short route and then scanned them as they imagined walking along the route. They reported activation of the posterior cingulate, precuneus and bilateral hippocampal/parahippocampal region.

Most human behaviour, however, takes place in environments with which we are very familiar; knowledge of their spatial layout has entered the domain of general facts about the world often referred to as semantic memory. The neural substrates of topographical memories of long standing (i.e. over several years) have been examined in a recent study by Maguire *et al.* (1997*b*). The aim of this study was primarily to test subjects on their knowledge of complex routes where all subjects could be tested on the same stimuli and with a high level of retrieval success, where there was no encoding of new environmental information during the performance of the tasks. This study also assessed the retrieval of landmark knowledge where such knowledge was not confounded by location information about position within a large-scale spatial layout. This was achieved by using a task where famous landmarks were known, but their large-scale spatial context was not. This study also examined topographical memory (landmarks or spatial layouts) and non-topographic semantic memory retrieval to ascertain whether common brain regions subserve semantic memory irrespective of memory type. To examine well-established topographical memory, subjects were all licensed London taxi drivers of many years' experience. Official London taxi drivers must train for approximately three years, passing stringent examinations of spatial knowledge before receiving a licence. Subjects overtly recalled the relevant memories during PET scanning.

Comparison of the activity during the routes-recall task with that during the landmark recall task revealed activation of the medial parietal lobe, the posterior cingulate cortex, and also the right hippocampus (figure 2). There was no significant activation of frontal regions associated with this comparison. The landmarks task, compared with the baseline, also resulted in activation of the posterior cingulate cortex, the medial parietal lobe, and occipitotemporal regions including the parahippocampal gyrus. In this case, however, there was no activation of the hippocampus but there was significant activation of left inferior and middle frontal gyri. In comparison with a baseline task, the recall of non-topographical memory, in this case plots from very familiar famous films, activated left frontal regions, the left middle temporal gyrus and the left angular gyrus.

(*b*) *Implications*

It appears that both topographical learning and recall (from episodic or semantic memory) have broadly the same network of brain regions as their neural substrate. Thus, for topographical memory at least, the distinction between episodic and semantic memory appears to have no anatomical basis. The right hippocampus is clearly involved in processing spatial layouts over long as well as short time-courses, and participates in both the encoding and the retrieval of topographical memory.

Both landmarks and routes activated occipitotemporal regions, the posterior cingulate gyrus, the medial parietal area and the parahippocampal gyrus.

The involvement of many of the same brain regions, both dorsal and ventral, in routes and landmark memory indicates that the topographical memory system may be primed to receive relevant topographical information even when the landmarks have no context within large-scale space. It was noted previously that topographical learning was associated with brain regions different from those involved in non-topographical episodic memory encoding. The use of familiar film plots as stimuli in the Maguire *et al.* (1997*a*) study engaged subjects in memory recall at a similar level and with characteristics broadly similar to those of the routes task, such as the recall of information in a specific temporal sequence (i.e. progression along a route or progression of a storyline). Except for cerebellar activity, the recall of film plots was associated with brain regions different from those activated during the routes task. Most activity was left-sided and there was no activation of occipitotemporal or medial temporal regions compared with the baseline. However, as with the landmarks tasks, the recall of film plots resulted in activation of the left inferior frontal gyrus. In this case, topographical memory for large-scale space was clearly not recalled via this mechanism and, as with topographical learning, caused increased neuronal activity in the posterior brain alone. It might be argued that the taxi drivers, who were very knowledgeable about the spatial layout of London, were so practised that their responses were automatic. However, the task required them to plan the shortest routes between start and destination points and analysis of verbal output clearly demonstrated that subjects reflected on their responses in a considered manner.

The taxi-driver study and that of Maguire *et al.* (1996*a*), where activation of the hippocampus proper during topographical learning was also recorded, contrast with the other two topographical memory studies (Aguirre *et al.* 1996; Maguire *et al.* 1997*b*), in which hippocampal activation was not found. These latter two studies employed computer-simulated environments, whereas the taxi study and that of Maguire *et al.* (1996*a*) involved memory for real-world environments. Real environments are more complex than the simulations used to date and involve the potential for using many routes to navigate to a goal, as reflected in the task put before the taxi drivers to find the shortest route to a destination. The recruitment of the hippocampus when real-world environments are involved may reflect its role in higher-level spatial manipulation and decision-making.

Recent evidence to support this idea has come from work by E. A. Maguire, N. Burgess, J. G. Donnett, C. D. Frith & J. O'Keefe (in preparation). Subjects were scanned by using PET while they performed retrieval tasks in a complex computer-simulated town, which they had spent some time learning before scanning. Subjects either found their way to specified destinations in the town as learned, or had to find their way when access points were changed (for example, when some doors were closed that were previously open), forcing them to take detours. Subjects' performances were recorded and analysed for strategy during scanning. There was increased activation of the right hippocampus when reaching a destination by the shortest route compared with the activity during a control task. Being lost in comparison with baseline tasks resulted in activation of the ventromedial orbitofrontal region.

The findings from this study would seem to indicate that the right hippocampus is concerned with finding a short route to a destination; this result is compatible with its suggested role in supporting an allocentric spatial map. Activation of the same ventromedial orbitofrontal region has been found by Elliott *et al.* (1997) looking at the effect of feedback on planning and guessing: the ventromedial orbitofrontal cortex was activated more strongly during guessing than during planning. This result may suggest that subjects are more reliant on external feedback during guessing to provide an assessment of performance. This may have been the case when subjects were lost in the town. Lesions in the ventromedial orbitofrontal region are known to produce deficits when decision-making strategies must yield a choice (Bechara *et al.* 1996). The activation here may reflect such decision-making elicited by being lost.

It is notable that many of the medial temporal activations observed in functional-imaging topographical memory studies in this paper are bilateral. This is compatible with the previous finding of deficits in topographical memory formation as a result of unilateral lesions of the left or right medial temporal lobe in humans (Maguire *et al.* 1996*b*). The most recent work using virtual environments may throw light on the differential contributions the left and right hippocampus may be making to topographical memory in humans.

4. COMMENT

Functional imaging studies have revealed a network of brain regions in humans that support topographical learning. This illuminates the patient lesion findings in which cases of topographical disorientation result from insults to various and disparate brain regions. The parallels with animal work, in terms of the involvement of the hippocampus in the mapping of space, are also clear. Once topographical information is acquired, the neuroanatomy that supports its use and retrieval is very similar to that used in its acquisition. Functional imaging is also starting to reveal the particular functions of various elements of the topographical learning system, illuminating the specific contributions of extra-hippocampal areas. Regions of the frontal cortex are implicated when topographical knowledge is not complete. The right hippocampus is involved at both encoding and retrieval.

Most human spatial behaviour takes place in large-scale, spatially extended environments. This requires the ability to recall points in space that cannot be perceived simultaneously in one field of view. This ability, common to most animals, is subserved in humans by a network of brain regions involving the hippocampus. The brain regions developed for this phylogenetically old ability, particularly the hippocampus, have undoubtedly now also been recruited for other non-topographical functions with similar processing requirements. The exact kind of processing mechanisms extant in this domain remain to be specified.

Support from The Wellcome Trust is gratefully acknowledged. Thanks to my collaborator on all studies, Chris Frith; and to collaborators on the virtual reality work, John O'Keefe, Neil Burgess and Jim Donnett.

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