Introduction to What are the parietal and hippocampal contributions to spatial cognition?, the proceedings of a Discussion held at The Royal Society

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INTRODUCTION

Localizing and acting upon objects in space and finding our way around large-scale environments are fundamental mammalian cognitive capacities. What are the neural substrates and mechanisms underlying these remarkable abilities? Several areas of the cortex have been implicated in spatial perception, cognition and action, including the prefrontal cortex (in particular the sulcus principalis), the parietal cortex and the hippocampus. The parietal cortex has long been identified as the neural substrate of spatial behaviour in primates; a spatial role for the hippocampus has been postulated more recently, most particularly in rats. The respective contributions of these two brain regions to spatial cognition was addressed by the Royal Society discussion meeting of 19 and 20 March 1997, which provides the basis for the collection of papers presented here. The spatial and other functions of the prefrontal cortex have recently been discussed elsewhere (see Roberts *et al*. 1996) and will not be considered further here. Instead we concentrate on the roles of the parietal and hippocampal cortices and their relationships to each other. First we consider the evidence that each is involved in spatial cognition, and then we consider their relative roles. We do not directly address the problem of whether either or both of these areas of the brain are solely devoted to spatial cognition or whether this is merely one of many different functions, or the most obvious manifestation of some more general function, performed by the area in question.

(*a*) ***Parietal cortex***

Evidence for the role of the parietal cortex in spatial perception and cognition has come principally from the human lesion data and from single-unit recording in monkeys. Damage to the parietal cortex in humans, in particular to the right parietal cortex, results in a neglect of the contralateral half of space. This neglect syndrome affects all modalities and is therefore considered to be a spatial deficit rather than a sensory one. The fact that the neglected region of space travels with the movements of the observer has suggested to many that the spatial framework is an egocentric one with its origin on a receptor or body axis. Attempts to identify the framework with particular receptor or body parts, such as the head or trunk, have met with mixed success. For example, when head and trunk axes were dissociated by requiring the patient to turn the head to the right (see, for example, Bisiach *et al*. 1985; Karnath *et al*. 1993) neglect for stimuli occurred on the left side in both frameworks.

A neural correlate of the interaction between eye- and head-centred frameworks has been reported by Andersen and colleagues (Andersen *et al*. 1985). They showed that, whereas neurons in the posterior parietal cortex had visual receptive fields coded in retinal coordinates, the gain of the firing rate was modulated by the orientation of the eyes relative to the head. The neural response to stimulation of the same retinal field increased or decreased as the eyes were moved to point at different locations in head-space. The paper by Pouget & Sejnowski (this volume) presents a computational model of the parietal cortex, which shows how this might be accomplished by means of units that have inputs from both retina and head position, and why this might be functionally advantageous. Andersen (this volume) extends this view by suggesting that the response of parietal neurons may also be affected by the animal's intention to respond to a stimulus.

If parietal neglect reflects distortion of a spatial axis or axes, it might be described better as a geometric transform of a perceptual or motoric framework than as a spatial scotoma. Both Vallar and Karnath (this volume) present evidence in support of this view, although they disagree as to the exact nature of the transform. Vallar considers neglect in terms of a translation of frameworks, whereas Karnath considers it in terms of a rotation.

Perhaps the most intriguing finding in the parietal-neglect literature is that neglect can be ameliorated by sensory stimulation contralateral to the lesion. Caloric stimulation via cold water in the contralateral ear, vibratory stimulation of the neck or optokinetic stimuli all markedly improve the ability of the patient to detect stimuli and to act in the contralesional field. One interpretation of this finding is that the stimulation increases the level of activation of the undamaged cortical tissue. An alternative is that the spatial framework is not itself located in the parietal cortex but instead that this part of the brain contributes information to other brain areas, which use it to maintain the axes of the egocentric coordinate systems in alignment with the eye, head and trunk. Loss of this information can be compensated by increasing inputs from non-damaged sensory inputs.

(*b*) ***Hippocampus***

(i) *Spatial memory*

Evidence for a spatial role for the hippocampal formation comes mainly from single-unit recording in freely moving rats, and from lesion studies, which show an impairment of the performance of hippocampally damaged rats on spatial tasks such as the Morris water maze. Place cells in the hippocampus and head-direction cells in the neighbouring postsubiculum together form a map-like representation (a cognitive map), which could be used to guide animals to a goal in a familiar environment (see Burgess *et al*., this volume). The internal and environmentally derived sensory inputs that support place cell firing are further investigated in the papers by Bures and colleagues and Rotenberg & Muller. In addition to locating the animal in a familiar environment, the map may contain information about such things as the location of rewards and landmarks (see O'Keefe 1976). This is consistent with recent evidence that the location of the animal alone does not account for all of the variance of a place cell's firing rate (Rotenberg & Muller, this volume).

(ii) *Episodic memory*

One suggestion made in the original cognitive-map theory (O'Keefe & Nadel 1978) was that, in addition to locations, the hippocampus might store the time of visits to those locations. Although this was deemed an unnecessary postulate to explain the physiology of the rat hippocampus, it was felt necessary to account for the full range of episodic (or 'event') memory disorders seen following damage to the human medial temporal lobe. Both Morris & Frey (this volume) and Gaffan & Hornak (this volume) suggest that animals may have something akin to episodic memory and that the hippocampus is necessary to store these memories. Morris has found that the NMDA receptor, previously implicated in spatial memory formation, is not necessary for the learning of a new spatial task if the animal has previously learned a spatial task elsewhere. This has led him to suggest that these receptors might be used to incorporate a temporal tag into the spatial maps even in the rat. Gaffan has shown that lesions that damage the fornix, one of the major hippocampal fibre bundles, has a major effect on the abilities of monkeys to remember which stimuli occurred against which backgrounds. He favours O'Keefe & Nadel's suggestion that the spatiotemporal context in which an event occurs might act as a powerful retrieval cue even when the material to be recalled is not, itself, primarily spatial.

Mishkin *et al.* (this volume) report recent evidence that casts doubts on the validity of visual-recognition memory as a good task for assessing hippocampal function in the monkey. They have found that neurotoxic lesions of the amygdala and hippocampus that spare the nearby parahippocampal cortex do not produce a measurable deficit in this task even with delays as long as 40 min. Preliminary evidence also suggests that there is no deficit if the information to be remembered is the location of the object rather than the visual identity of the objects. They also reported on studies of the memory capacity of three young patients who had suffered bilateral damage to the hippocampus at an early age. Although severely amnesic for events, these patients showed a remarkable semantic vocabulary; this observation suggested that their semantic memory systems were compromised to a much smaller extent than were their episodic memory systems. Taken together, these pieces of evidence speak against the declarative memory theory of hippocampal function (Squire 1992), which includes both episodic and semantic components in the hippocampus. They also appear to be inconsistent with the view that the hippocampus serves as a fast-learning device that is necessary for the long-term storage of abstracted semantic information elsewhere in cortex (McClelland *et al.* 1995).

(iii) *Imaging studies*

Mishkin's primate results mesh nicely with PET imaging work reported by Milner and colleagues (this volume). They find that memory tasks that required the subject to remember the location of an item on a panel activated the parahippocampal gyrus but not the hippocampus itself. What does activate the hippocampus? The papers from Berthoz and Maguire provide some answers. Both authors imaged subjects as they navigated in large-scale environments. Berthoz asked subjects to imagine that they were retracing a path they had previously walked along; Maguire asked London taxi drivers to construct a route between several locations in London from their long-term knowledge of its geography. Both groups found activation of the hippocampus during this imagined navigation through a familiar environment. The encoding of large-scale environments also activates the hippocampus, as Maguire found when she scanned subjects while they tried to learn about an environment by watching film clips taken by a camera moving through a small town. More recent PET studies, using virtual-reality environments, show that activation of the hippocampus depends on how accurately the subjects find their way within a familiar environment, as opposed to getting lost.

(*c*) ***What is the relationship between the parietal cortex and the hippocampus?***

There are two classes of hypothesis about how parietal and hippocampal spatial representations might interact. First, the two structures might form complementary parts of a memory system acting in series on incoming sensory information to form representations suitable for different time scales or levels of abstraction. Second, they might act in parallel to provide two different kinds of spatial representation of the information, to be used for different purposes. These alternative possibilities are discussed below.

The first hypothesis about the interaction of hippocampus and parietal cortex is that both brain areas store the same type of spatial information but that they have different time constants, which result in different memory properties. According to this hypothesis, the hippocampus stores all information fed into it but does so over a relatively short timescale, whereas the neocortex abstracts information from the input over several presentations but stores this abstracted information for a long period of time. The most efficient interaction between the two systems might involve the hippocampal system capturing spatiotemporal events online and then slowly feeding them to the parietal cortex over time to allow it to abstract, consolidate, and store the information for the long term (see Marr 1971; McClelland *et al.* 1995). In search of support for this hypothesis, McNaughton and colleagues (Qin *et al.*, this volume) have simultaneously recorded large numbers of neurons, in both the hippocampus and the parietal cortex, as the rat travels along a path, and found evidence that during subsequent sleep episodes there is a rehearsal of the same sequence of spatial-cell activations in each area, but less evidence for an increased interaction between the two areas.

The second hypothesis derives from the view advanced by Ungerleider & Mishkin (1982) that visual information is processed along parallel ventral and dorsal streams concerned, respectively, with 'what' objects are present and 'where' they are. In this view the parietal cortex, as part of the dorsal stream, codes for the spatial location of objects in an egocentric framework, which is appropriate for directing the eyes or hands to look at or grasp them. In contrast, the hippocampal formation, at the meeting point of both streams, is concerned with the representation of objects within a spatial framework. Such a representation could then be used to allow the person or animal to move from one location to another by the most efficient route. Thus parietal and hippocampal areas would cooperate in the solution of spatial tasks, each addressing the relevant egocentric and allocentric components of it. Such a functional relation is consistent with the activations seen in imaging studies of tasks requiring real or imagined movement in large-scale space (see Maguire and Berthoz, this volume) and with the systems-level computational framework laid out by Arbib (this volume).

Conclusion

The papers presented here represent part of the considerable recent progress in several complementary areas of research towards elucidating the neural substrates of spatial cognition. An increasingly detailed understanding is emerging of the neuronal representation of the location of stimuli and actions relative to the eye, head and trunk found in the parietal cortex, and of the representation of location within an environment found in the hippocampus. Data from lesion, neuropsychological and functional imaging studies are also beginning to enable a systems-level understanding of the functions of subregions within the parietal and hippocampal cortices. The resurgence of computational modelling of brain function provides a framework in which to examine and integrate these new data in terms of the mechanisms underlying behaviour at the neuronal and system levels.

One restriction on progress has been that, until recently, behaviour in large-scale space has been less well studied than that in smaller-scale (table-top) tasks, for technical and methodological reasons. However, this imbalance is beginning to be addressed by various approaches, one of the most promising of which is the use of virtual reality in conjunction with functional imaging. Taken together these advances begin to paint a coherent picture of the neural processes underlying the extraordinary capacity for spatial cognition demonstrated in our everyday lives.

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