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Memory for events and their spatial context: models and experiments

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The computational role of the hippocampus in memory has been characterized as: (i) an index to disparate neocortical storage sites; (ii) a time-limited store supporting neocortical long-term memory; and (iii) a content-addressable associative memory. These ideas are reviewed and related to several general aspects of episodic memory, including the differences between episodic, recognition and semantic memory, and whether hippocampal lesions differentially affect recent or remote memories. Some outstanding questions remain, such as: what characterizes episodic retrieval as opposed to other forms of read-out from memory; what triggers the storage of an event memory; and what are the neural mechanisms involved? To address these questions a neural-level model of the medial temporal and parietal roles in retrieval of the spatial context of an event is presented. This model combines the idea that retrieval of the rich context of real-life events is a central characteristic of episodic memory, and the idea that medial temporal allocentric representations are used in long-term storage while parietal egocentric representations are used to imagine, manipulate and re-experience the products of retrieval. The model is consistent with the known neural representation of spatial information in the brain, and provides an explanation for the involvement of Papez's circuit in both the representation of heading direction and in the recollection of episodic information. Two experiments relating to the model are briefly described. A functional neuroimaging study of memory for the spatial context of life-like events in virtual reality provides support for the model's functional localization. A neuropsychological experiment suggests that the hippocampus does store an allocentric representation of spatial locations.

Keywords: memory; space; episodic; model; hippocampus

1. INTRODUCTION

One of the brain's most important and self-defining functions is to provide memory for the personally experienced events in our daily lives. The function of this 'episodic' memory system has been studied for many years. Much of this work, both experimental and theoretical, has focused on: how functionally to dissociate episodic memory from other forms of memory; which behavioural measures most purely reflect its operation; how and if it breaks down into component processes; the time courses over which these processes act; and which brain regions support them. These issues are discussed at length elsewhere in this issue. This article focuses on how these processes happen in the brain, i.e. how the actions of neurons and synapses in different brain regions conspire to produce an episodic memory system. Of course, the success of this enterprise depends crucially on both the interpretation of the above ideas and experiments, and on the ability to make predictions regarding them. It is worth noting at this stage that we will pay particular attention to one of the brain regions involved in episodic memory (the hippocampus), and to one of the

distinguishing characteristics of episodic memory (the ability to retrieve the rich spatial context of an event). These choices reflect biases of the authors: that the hippocampus is the central player in the neural support of episodic memory; that it is important to consider the spatial locations of the protagonists in an event in understanding both its encoding and retrieval; and that computational modelling benefits from knowledge of the neuronal representations involved—for which the spatial domain provides the richest data.

The article is organized as follows. We start with a brief review of what has become a generic framework for modelling the hippocampal and neocortical roles in long-term memory for personal experience, following from the work of David Marr (1971). We consider some of the ways in which this model has been developed over the years in terms of general theoretical issues concerning memory, such as time-courses, capacities, representations and interference. We attempt to relate these issues to questions regarding the nature of episodic memory as compared with other forms of memory. In §3 we discuss a neural-level model of the medial temporal and parietal processes involved in the retrieval of the spatial context of an event (Becker & Burgess 2001). This model relates to the Marr-type models given that the subject's spatial location provides one way for the hippocampus to index events. It

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also relates to the idea that allocentric (i.e. world-centred) representations are used in long-term storage of the spatial locations of the landmarks forming the event's spatial context, while egocentric (i.e. body-centred) representations are used in imagery.

The final section (§ 4) concerns experiments testing some of the model's assumptions and predictions. The first experiment is a functional neuroimaging study of retrieval of the spatial context of lifelike events using virtual reality to provide a rich spatial context (Burgess *et al.* 2001), supporting the model's suggested mapping of functions onto structures in the brain. The second experiment is a neuropsychological study of a single case of hippocampal pathology, Jon (Vargha-Khadem *et al.* 1997), providing evidence that the hippocampus supports an allocentric representation of the locations of objects (King *et al.* 2001).

2. A GENERIC HIPPOCAMPO-NEOCORTICAL MODEL OF LONG-TERM MEMORY

As the inspiration for a host of models of the hippocampal and neocortical roles in memory, Marr's (1971) paper 'Simple memory: a theory for archicortex' is the starting point for this section (see Willshaw & Buckingham 1990 for an excellent synopsis and evaluation). In brief, Marr suggests that the hippocampus provides a mechanism for rapidly storing the day's events for later transfer to the neocortex, whose role (described in his 1971 paper) is to reorganize and classify this information as relevant to the animal. During encoding, the neocortical representation of an event is mapped onto a 'simple representation' in the hippocampus via connections with modifiable synapses (the reverse mapping also being learned in modifiable return connections). He notes that this simple representation 'needs to be formed only of those parts of [the event] . . . through which [it] will later be addressed' (p. 32). Modifiable synapses on the hippocampus's recurrent collaterals also play a role—associating together elements of the simple representation so as to enable subsequent pattern completion (the 'collateral effect'). During retrieval, a subset of the neocortical event representation can cause reactivation of the entire 'simple representation' in the hippocampus and thence reactivation of the entire neocortical representation. The majority of the paper concerns physiological details and capacity considerations, assuming that the hippocampus must be able to store, at minimum, one day's events for transfer during the night's sleep.

The general scheme envisaged by this model, and the many subsequent related models, is illustrated in figure 1. Below, we use this generic model as a framework to illustrate various computational issues concerning episodic memory, and how they have been addressed by the model and the developments to it proposed over the years.

(a) *The hippocampal representation: indexes, content and context*

The nature of the 'simple representations' of events stored in the hippocampus has some implications for the functioning of an episodic memory system. Below, we refer to these representations as 'event codes' or 'codes' for brevity. Such codes might be purely abstract
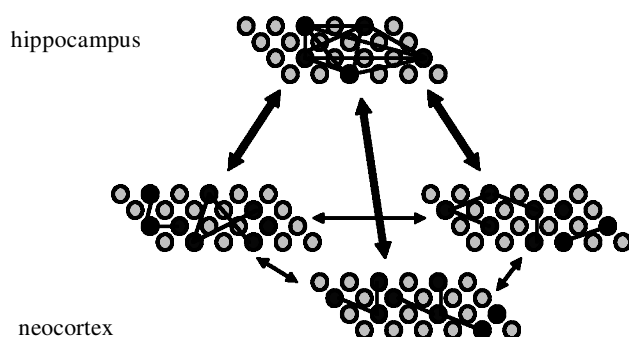

Figure 1. The generic hippocampo-neocortical model of long-term memory. Relatively dense recurrent connections and sparse representations in the hippocampus enable efficient pattern completion. Connections between neocortex and hippocampus allow the hippocampal representation of an event to be associated with its sensory details, including reactivation of the representations in different neocortical areas dealing with different sensory modalities. Abstracted semantic representations may also be learned over time in neocortex. The recurrent connections within each neocortical area allow unimodal recognition.

representations, or might include elements of the context or content of an event, as discussed below. The separation of information relating to an event into 'context' and 'content' is made in several models, often without definition. If an event is defined as a temporally localized change in the state of the world (e.g. 'she dropped her ticket'), then the change in the world that forms the event is the content, while the remaining ongoing state of the world forms the event's external context.

One way to avoid interference during the retrieval of neocortical event representations would be to ensure that the event codes are unique to each event. The process of generating unique codes from potentially similar events is known as 'pattern separation', a role that has been ascribed to the dentate gyrus with its large numbers of cells and very sparse activity (McNaughton & Morris 1987). In the limit of completely unique codes for each event, the hippocampus essentially provides an index (see Teyler & DiScenna 1986), i.e. a set of codes that can be used to reactivate the content of the memory via the return projections to the neocortex. Sparse coding also ameliorates the problem of 'catastrophic interference' that can occur during rapid learning of distributed representations (McClelland *et al.* 1995). This problem can also be avoided in other ways, such as limiting the maximum size of connection weights in an associative network (Hopfield 1982).

The retrieval of stored codes is aided by the collateral effect: incomplete patterns of activation can be completed by a process of 'pattern completion' ascribed to region CA3 with its long-range recurrent collaterals. In this process, region CA3 acts an 'auto-associative memory' in which stored patterns of activity are attractor states such that the system will return to the most similar stored pattern from any initial state (Willshaw *et al.* 1969; Kohonen 1972; Gardner-Medwin 1976; Hopfield 1982). Another advantage of distinct (i.e. orthogonal) event codes is to reduce interference during this process of

pattern completion. For this reason, Marr suggests that the simple representations be formed by populations of cells with very sparse activity.

Note that the operation of pattern completion and pattern separation in the same system can cause conflicting effects (see e.g. McClelland *et al.* 1995). When a pattern of activity in the neocortex gives rise to a pattern of activity in the hippocampus, hippocampal pattern completion will tend to map that activity onto the most similar stored event code. However, this code will not necessarily represent the event with the most similar neocortical representation due to the pattern separation in the mapping from neocortex to hippocampus. These effects can give rise to counter-intuitive results, e.g. enabling models to fit the confusing experimental data that shows hippocampal dependence in some tasks requiring event-unique codes but not in other similar tasks (O'Reilly & Rudy 2000).

The alternative to abstracted event-unique codes is codes that reflect the content or context of the event itself in some way. A simple associative memory in which the elements of the representation of the event are associated equally with all other elements of the representation provides one way to achieve this. However, as implied by Marr's description of simple representations, some aspects of an event seem better able to cue associative retrieval than others, while other aspects of an event can be associatively retrieved more easily than others. The name of someone one met on a single occasion is a good example of both asymmetries (a good cue, but sometimes hard to retrieve), while the location of the meeting is often both a good cue and relatively easy to retrieve. The sequential position of an item in a list of items is another example of a good cue that is relatively hard to retrieve itself (Jones 1976). Considerations such as these demand at least asymmetrical associations, and have fuelled the theoretical distinctions made between the context and content of an event (e.g. Raaijmakers & Shiffrin 1981) and between the stored record and the 'header' by which it is referenced (Morton *et al.* 1985). Other approaches to generating event codes have included using an efficient compression of the event representations (Gluck & Myers 1996) and endogenously generated temporally varying codes (Levy 1996). One idea to which we will return is that the hippocampal role in episodic memory might relate to the provision of the spatio-temporal context of the event (O'Keefe & Nadel 1978).

(b) *Learning rates, cross-modal binding and consolidation*

Marr suggests that the hippocampus provides a mechanism for rapidly capturing the day's events as they happen, so as to allow the relevant information to be appropriately categorized in the neocortex. This process may occur overnight, freeing up the memory capacity of the hippocampus for the next day's events. Many subsequent models have elaborated on this basic idea, proposing different time-scales and mechanisms by which relevant information is abstracted and incorporated into neocortical systems (see e.g. McClelland *et al.* 1995; Murre 1996). The proposed transfer of episodic information from hippocampus to neocortex, such that memory for this information would then be immune to subsequent

hippocampal damage, remains controversial to this day. Such a process acting over days or weeks is clearly at odds with the human neuropsychological data, and it is questionable whether such a process could occur even over several decades (see e.g. Cipolotti *et al.* 2001). One recent development of the model proposes that, over time, events can be rehearsed, creating new event-codes on each rehearsal (Nadel & Moscovitch 1997). This allows for the possibility that, while a complete lesion of the medial temporal lobe impairs retrieval of all memories, the older the memory, the more robust it will be to partial damage.

A related distinction, between fast hippocampal learning and slower neocortical learning, has arisen from consideration of the physical constraints on learning to associate information from different sensory modalities represented in disparate cortical areas. Damasio's (1989) solution was that 'convergence zones' must exist in the brain to enable such long-range associations to be formed via association with representations in such a convergence zone. Many subsequent models have identified the hippocampus (or, less specifically, the medial temporal lobe) as a convergence zone, so that rapid learning of hippocampal simple representations can allow subsequent, slower, learning of long-range associations between the different neocortical areas (Alvarez & Squire 1994; Murre 1996; Moll & Miikkulainen 1997). Again, it is questionable whether or not the slower process of cross-modal association can, in time, render the hippocampal representations completely redundant.

(c) *Implications for encoding versus retrieval and functional subdivisions of memory*

The encoding of episodic memories in this type of model raises some interesting considerations. The presence of the collateral effect in CA3 means that the activation of neurons participating in an event code will depend both on the afferent input from the neocortical representation and on the feedback received from other neurons in CA3. This has the advantage, during retrieval, of encouraging the system to settle on a previously learned event-code. However, when a new event has to be encoded, a new hippocampal event-code needs to be generated in the absence of interference from previously stored information. One solution is that the mossy fibre synapses from the dentate gyrus onto the CA3 pyramidal cells act as 'detonator' synapses (being physically large and near to the cell body) that impose the new pattern of activity during encoding, while recurrent collaterals dominate retrieval (McNaughton & Morris 1987; see also Treves & Rolls 1992). An alternative proposal, and a mechanism, for the switching between encoding and retrieval modes concerns the supply of acetylcholine (ACh) to the hippocampus by the medial septum (Hasselmo *et al.* 1996; see also Murre 1996). On this account, increased delivery of ACh suppresses the feedback excitation in CA3, allowing encoding of new information. This increased delivery of ACh is effectively determined by the novelty of the neocortical inputs to the hippocampus compared with previously stored events. One very positive aspect of this idea is that it captures some of the importance of the fornix (an enormous fibre bundle connecting the hippocampus to the medial

septum and other subcortical structures). In the model, sectioning the fornix will prevent the learning of new memories due to lack of ACh, corresponding to the experimental observation that sections of the fornix produce similar impairments to lesioning the hippocampus (see e.g. Aggleton & Pearce 2001; Gaffan & Hornak 1997; Aggleton & Brown 1999). Interestingly, lesions to the fornix often spare memories encoded prior to the lesion (Spiers *et al*. 2001*b*).

With regard to distinctions between different types of memory, it is interesting to consider the idea that event-unique simple representations are rapidly stored in the hippocampus, while the meaning of an event in relation to the animal's lifetime experience is abstracted into the neocortex over a longer period of time. This would suggest that semantic memories arise from combinations of hippocampal event-unique memories but eventually they can become independent of the hippocampus. This corresponds well with the idea that memory for the unique content and context of a specific event (episodic memory) depends on the hippocampus, while semantic memory depends on other areas of the temporal lobe (see e.g. Graham & Hodges 1997). However, it does not correspond so well with the idea that semantic information can be acquired despite bilateral hippocampal pathology (Vargha-Khadem *et al*. 1997). The possibility of partial sparing of the hippocampus and episodic memory (Squire & Zola 1998), or the use of external rehearsal of information (Baddeley *et al*. 2001), might provide explanations in these cases.

Similarly it is interesting to consider the implications of the idea that the hippocampus mediates associations between disparate cortical areas for the neural bases of different types of memory. Clearly, effects mediated by the familiarity of single stimuli might be supported by the association of elements within each of the neocortical areas alone. Thus recognition of previously presented stimuli would depend on neocortical rather than hippocampal areas, while correct recognition of a pair of cross-modal associates amongst equally familiar distractors would require the hippocampus. Recent evidence indicates that simple recognition memory does not depend on the hippocampus but on nearby neocortical areas (Vargha-Khadem 2001; Zhu *et al*. 1996; Murray & Mishkin 1998; Vargha-Khadem *et al*. 1997; Wan *et al*. 1999; Aggleton & Brown 1999; Holdstock *et al*. 2000; Baxendale *et al*. 1997; Baddeley *et al*. 2001; but see also Manns & Squire 1999; Zola *et al*. 2000), whereas there is some evidence that recognition of cross-modal associations is impaired by bilateral damage restricted to the hippocampus (Holdstock *et al*. 2000; Vargha-Khadem *et al*. 1997). More extensive unilateral damage may also impair the binding of elements within the same modality (Kroll *et al*. 1996). The logical extension of this idea is that episodic memory requires the full recollection of an event and its context in all of its multimodal detail and so will require an intact hippocampus.

3. A MODEL OF RETRIEVAL OF THE SPATIAL CONTEXT OF AN EVENT

The models reviewed in § 2 provide insights into some of the general computational issues behind the construction of a long-term memory system, some of which we have related to the nature of episodic memory in particular. Other issues specifically concerning episodic memory remain to be fully addressed by computational models. One such issue is the nature of episodic encoding, such as how (or if) experience is chopped up into discrete events and what aspects of an event contribute to context or index representations as opposed to content representations. We return to this issue in the final part of § 5.

A second issue concerns the details of the mechanism of episodic retrieval, as opposed to other forms of read-out from memory, e.g. pattern completion might equally well apply to recognition or semantic memory.

A third issue concerns the nature of the neural representations involved in the processes of episodic memory, something not addressed by models of the retrieval of purely abstract binary codes.

In this section we consider the specific problem of remembering the spatial layout of a familiar environment. As well as being an important aspect of memory in its own right, this problem serves as an instructive example of context-dependent memory (retrieval of the spatial context of an event) for which detailed experimental data exists regarding the neural representations and mechanisms involved. Thus we hope to relate the insights of the more general attempts to model memory both to a specifically episodic task and to the vast literature regarding the functional neuroanatomy of spatial information processing in the mammalian brain.

There are three ideas behind the rationale for this model. First, that the ability to retrieve the rich spatio-temporal context of real-life events, as opposed to simply recognizing their content, is a determining characteristic of episodic memory (Gardiner & Java 1993). Second, that allocentric (i.e. world-centred) representations are suited to long-term storage of spatial locations (as the subject's body will have moved between presentation and recall) while egocentric (i.e. body-centred) representations are suited to imagining, manipulating and re-experiencing the products of retrieval (as sensory perception is egocentric and any actions must be specified egocentrically) (Goodale & Milner 1992; Milner *et al*. 1999; Burgess *et al*. 1999). Third, that the allocentric spatial representations of the hippocampus in rats have become co-opted to form part of the episodic memory system in humans by providing spatial context and making use of the additional inputs of a linear sense of time (on the right) and language (on the left) (O'Keefe & Nadel 1978). For further discussion of the model and details of simulations see Becker & Burgess (2001). Recce & Harris (1996) describe an alternative model in which a hippocampal place code indexes spatial maps permanently stored in the parietal cortex. The functional architecture of the model is shown in figure 2. Below we describe the various components of the model and how it works.

(a) *Medial temporal areas*

The ventral visual processing stream encodes the visual features of the subject's environment and terminates in the perirhinal cortex. The parahippocampus encodes the distance and allocentric direction of any landmarks (large objects or barriers) around the subject. Each neuron here is broadly tuned to respond to the presence of any
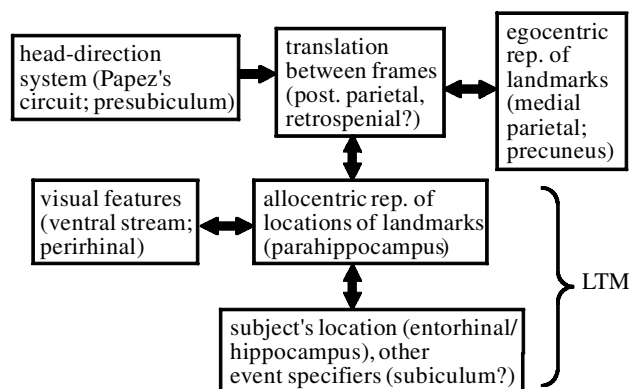
Figure 2. The functional architecture of the model of the encoding and retrieval of the spatial context of an event (see also Becker & Burgess 2001). LTM, long-term memory; post., posterior; rep., representation.

landmark at a specific distance and bearing from the subject in a manner analogous to the likely functional inputs to the rat hippocampus (O'Keefe & Burgess 1996; Hartley *et al.* 2000). The hippocampus provides a representation of the current location of the subject, each neuron responding in a manner analogous to hippocampal place cells in the rat (O'Keefe & Nadel 1978). In primates, this might become a representation of the current location of gaze (Robertson *et al.* 1998) without further change to the model. The hippocampus is simply simulated as a single layer of recurrently connected neurons, i.e. ignoring the functional contributions of areas other than CA3 such as the entorhinal cortex, dentate gyrus and CA1, but taking advantage of the bidirectional connectivity to subiculum and parahippocampus that they provide. Bidirectional associations exist between the perirhinal and parahippocampal areas (associating landmark locations and visual features), and between the parahippocampus and hippocampus, allowing the parahippocampal representation to drive the hippocampus, as in Hartley *et al.* (2000), and *vice versa* (see figure 3). Recurrent connections within the hippocampus are arranged to form a continuous attractor (Samsonovich & McNaughton 1997), to enable pattern completion in the firing of place cells such that the firing rates of all of the place cells are always consistent with the subject being in a single location.

Evidence for this assignment of structure to function includes the following. The perirhinal cortex is the crucial structure for matching or non-matching to the visual features of an object (Murray & Mishkin 1998). As well as being implicated in a specific scheme for encoding the spatial locations of environmental boundaries by deductions from the activation of place cells (O'Keefe & Burgess 1996), this role for the parahippocampus has also been supported by functional neuroimaging of the human parahippocampal response to spatial scenes (Epstein & Kanwisher 1998). Evidence that the human hippocampus provides an allocentric representation of location is presented in § 4. We also note that the 'spatial context' represented in the medial temporal system includes landmarks such as environmental boundaries but does not necessarily include all of the objects found within an environment. This is consistent with experiments showing

which environmental features affect place cell firing (O'Keefe & Burgess 1996; Cressant *et al.* 1997). It is also consistent with behavioural data suggesting that the structural features of a room are represented within a single spatial framework while the room's contents are not (Wang & Spelke 2000).

(b) *Encoding the location of an event*

In previous models of rat navigation (Burgess *et al.* 1994; Burgess & O'Keefe 1996) we postulated the existence of 'goal cells' that could encode the location of a reward site after one instance of encountering the reward (e.g. the submerged platform in a water maze, or a location containing food or water). These cells are associated to the specific non-spatial attributes of different types of reward, causing the appropriate cell to be activated by the reward. They should be located immediately downstream of the place cells, e.g. in the subicular complex or the nucleus accumbens. In the 'simple model' of Burgess & O'Keefe (1996), Hebbian learning in the projections to a goal cell from active place cells at the moment the rat encounters the goal cause the goal cell's firing rate to subsequently indicate the rat's proximity to the goal location. This occurs simply because more place cells with potentiated connections to the goal cell will be active the closer the rat gets to the goal location in its subsequent perambulations (see figure 4).

To encode the location of an event, we postulate a similar mechanism: 'event cells' in the subiculum associated with non-spatial aspects of the event. These cells would be activated by the specific non-spatial attributes of an event so that Hebbian learning causes a bidirectional association with the place cells representing the location of the event. In this way, activating an event cell via some non-spatial characteristic of the event can cause reactivation of the place cell representation of its location. Likewise, activating the place cell representation of a location can cause the activation of cells representing the events that happened there. Note that to produce a more general model of retrieval of non-spatial information would require changes throughout the model, perhaps reflecting a generalization of hippocampal function from spatial memory in the right hemisphere to episodic memory in the left hemisphere (Spiers *et al.* 2001*a*).

(c) *Parietal areas and the head-direction circuit*

Neurons in the medial parietal area (the precuneus) encode the distance and egocentric directions (angle relative to the head) of environmental landmarks so as to form a fully-egocentric imageable representation. Different parts of this image can be inspected via foveation or covert shifts of attention. The mappings between allocentric and body-centred and between body-centred and head-centred representations occur in the posterior parietal area. For simplicity, simulations (as shown in figures 3 and 5) consider only the translation between allocentric and body-centred representations (i.e. the simulated subject cannot rotate its head relative to its body). The two types of representation are translated into each other by making use of the subject's orientation in the world (encoded in a set of 'head-direction cells'). This occurs via an expanded set of cells whose responses are
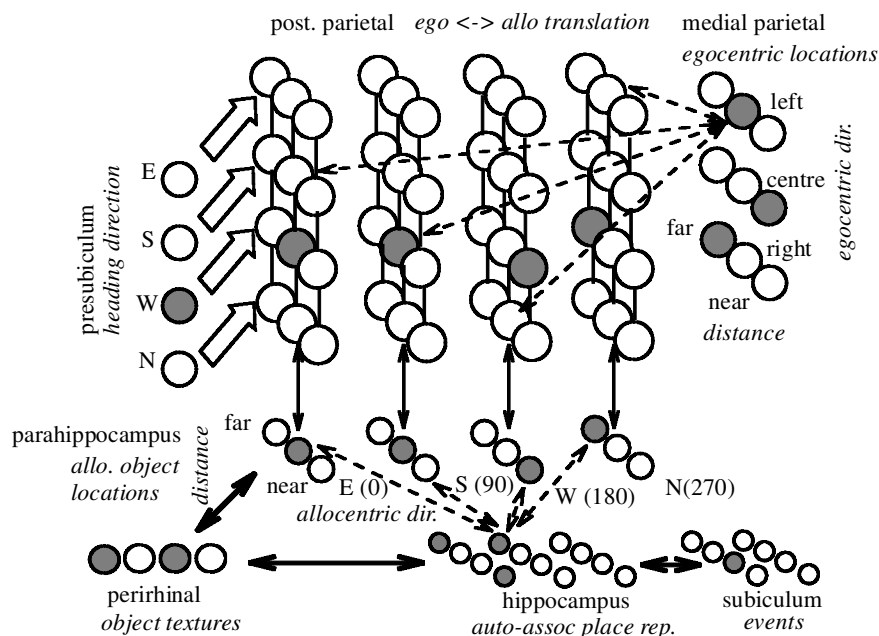
Figure 3. Detail of the model of encoding and retrieval of the spatial context, with an illustration of possible cell activations when facing west, with landmarks nearby to the west, farther away to the east and south and far away to the north (see also Becker & Burgess 2001). allo., allocentric; auto-assoc., auto-associative; dir., direction; ego, egocentric; post., posterior; rep., representation.
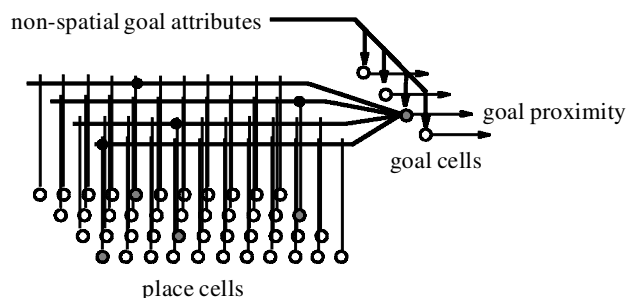

Figure 4. A simple model for encoding and retrieving a spatial location, adapted from Burgess & O'Keefe (1996). When a goal is encountered, synapses between active place cells and a 'goal cell' associated with the particular attributes of the goal are potentiated (active cells are shown as grey circles, potentiated synapses as black circles). The subsequent firing of the goal cell indicates the similarity of the current place cell representation to the representation of the goal location and thus indicates the proximity of the rat to the goal. A similar mechanism can be used to store the spatial location of an event.

modulated by both the position of the stimulus relative to the body and the orientation of the body in the world—see Pouget & Sejnowski (1997) for successful use of this type of model of parietal coordinate transforms. The posterior parietal area consists of layers of neurons repeating the parahippocampal representation (the neurons in each layer have a bidirectional connection to the corresponding neurons in the parahippocampus). The activity of the neurons in each layer is modulated by the activity of a particular head-direction cell. Given the correct representation of head direction, this allows

parietal egocentric representations of the set of environmental landmarks to activate the allocentric parahippocampal representation and *vice versa*.

Evidence for this assignment of structure to function includes the following. Neurons in parietal area 7a have been shown to have the correct 'gain field' modulation of response to the egocentric (retinal) location of a stimulus by the position of the animal's eyes (Andersen *et al.* 1985), head (Duhamel *et al.* 1992) or body (Snyder *et al.* 1998) to effect the appropriate coordinate transformations. The precuneus has been found to be activated by imagery of the products of retrieval from memory (see e.g. Fletcher *et al.* 1996). Neurons encoding the current head direction have been recorded in rats in the mammillary bodies, anterior thalamus and presubiculum (see e.g. Taube 1998). It is interesting to note that the circuit of regions known to be involved in encoding the current head direction in the rat corresponds closely with the circuit (known as Papez's circuit since the 1930s) that has been closely associated with human episodic memory (see e.g. Aggleton & Pearce 2001; Aggleton & Brown 1999; Gaffan & Hornak 1997; Delay & Brion 1969).

(d) *Functional overview*

During exploration of an environment, egocentric sensory input is translated into the allocentric parahippocampal representation of landmark locations via the posterior parietal cortex. As each landmark is foveated, the association between the perirhinal representation of the visual features of a landmark and its parahippocampal representation is learned. The association between the patterns of parahippocampal and hippocampal activations at given positions within the environment could also be learned during exploration (Burgess

(*a*)
schematized Milan square

(*b*)
HC act given texture = 1

(*c*)
PH act + head direction

(*d*)
PC act + query direction

(*e*)
PR activations – control

(*f*)
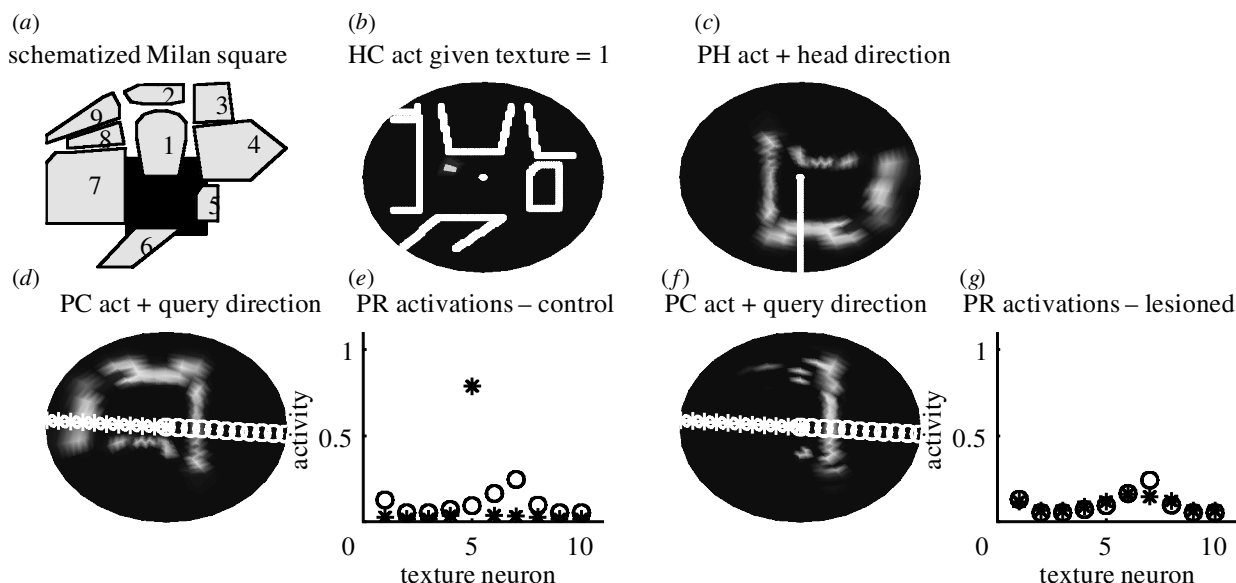PC act + query direction

(*g*)
PR activations – lesioned

Figure 5. Simulation of retrieval of spatial information in the Milan square experiment of Bisiach & Luzzatti (1978) (adapted from Becker & Burgess 2001). (*a*) Training consists of simulated exploration of the square (shaded area, north is up). The system is cued to imagine being near to the cathedral (i.e. the perirhinal cell for the texture of building 1 and parahippocampal cell for a building at a short distance north are activated) and the hippocampal-parahippocampal-perirhinal system settles. (*b*) The hippocampus settles to a location in the north-west corner of the square (hippocampal cell activity shown as the brightness of the pixel corresponding to the location of each cell's place field). (*c*) The parahippocampus correctly retrieves the locations of the other buildings (parahippocampal cell activity shown as the brightness of the pixel for the location encoded by each cell, relative to the subject at the centre). A line indicates that the imagined head-direction is south. (*d*) Medial parietal cell activity: the parahippocampal map has been correctly rotated given head-direction south (straight ahead is up), stars indicate a direction of inspection to the left, circles to the right. (e) Perirhinal cell activations correctly showing building 5 to the left and building 7 to the right. (*f*) Effect of a right parietal lesion on the medial parietal representation (note lack of activation on the left) and (g) PR activations (note decrease in activation of building 5 when inspection is to the left). HC, hippocampal; act, activation; PH, parahippocampal; PC, parietal cortex; PR, perirhinal.

et al. 1994), or might simply be already hard-wired (Hartley *et al.* 2000). Similarly, the recurrent connections between place cells, such that cells representing similar locations support each other, might also be learned, or be already hard-wired (Samsonovich & McNaughton 1997). In the cases of hard-wired connection existing before exposure to the environment, these connections effectively determine that the appropriate place cells are active at the appropriate locations.

During retrieval of a spatial scene from a particular point of view, partial input is supplied to the medial temporal system, such as the presence of a particular visual feature in a particular direction. Retrieval of the spatial context of a specific event occurs as described above (see 'encoding the location of an event'). In either case, pattern completion occurs, involving the bidirectional associations between all three areas and within the hippocampus, such that the system settles on a place, landmark and visual feature representation consistent with the specifying inputs. An imageable egocentric representation is then produced in the precuneus via translation in the posterior parietal cortex, making use of the current head direction. Finally, inspecting (i.e. attending to) one part of the imageable representation is modelled by boosting the activation of neurons in that part of the image. This extra activation flows back through the posterior parietal and parahippocampal parts of the model to activate the perirhinal representation of the visual features at that part of the image.

(e) *Simulation of the effect of parietal lesions*

In their famous experiment on representational neglect, Bisiach and Luzzatti (1978) asked patients with hemispatial neglect following right parietal damage to imagine standing in the familiar Piazza del Duomo from their home town of Milan. Interestingly, when asked to imagine facing towards the cathedral they neglected to describe the buildings to the left of that viewpoint, while, when asked to imagine facing away from the cathedral they neglected the buildings to the left of that viewpoint. Their ability to describe the buildings on both sides of the Piazza over the two trials is consistent with having an intact viewpoint-independent representation of the Piazza, but an impaired mechanism for extracting a viewpoint-dependent representation for imagery (see also Baddeley & Lieberman 1980). This experiment can be simulated by our model, by making a selective lesion to the neurons on the left side of the egocentric representation, the posterior parietal neurons that project to them, or by biasing the inspection of this representation so that its left side is neglected (see figure 5 and Becker & Burgess 2001). We note that caloric irrigation, or other means of manipulating the head-direction signal, causes a mistranslation between egocentric and allocentric representations. In some circumstances this can rotate part of the left of the scene that would otherwise be neglected further to the right, ameliorating the neglect of this part of the scene—consistent with some experimental data (Guariglia *et al.* 1998).
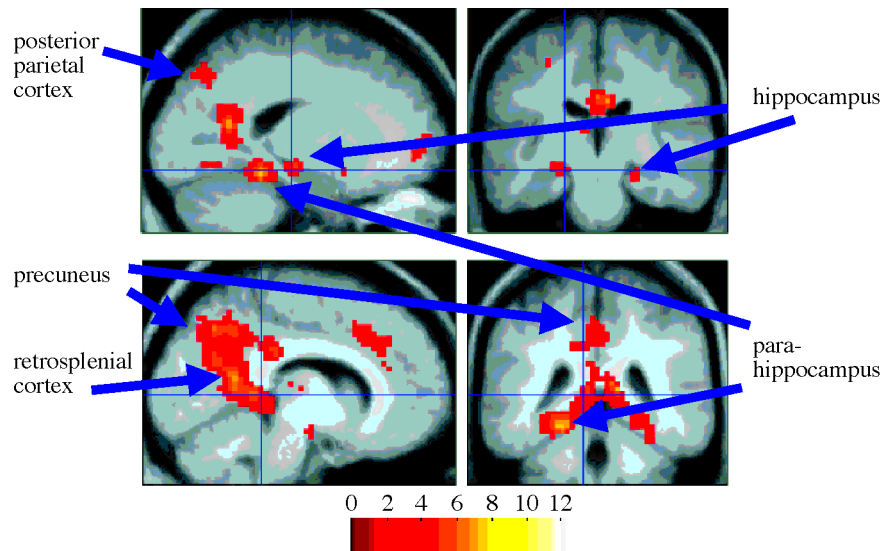
Figure 6. Regions of activation in memory for the spatial context of an event compared with a non-memory control condition (adapted from Burgess *et al.* 2001). In the memory condition subjects had to choose which of two objects was received in the current location in a virtual reality town. In the non-memory condition they had to choose the widest. The figure shows the results of an event-related random-effects functional magnetic resonance imaging (fMRI) analysis of 13 subjects with threshold $P < 0.01$ uncorrected. The colour bar shows Z-score equivalents. See text for details.

4. EXPERIMENTAL SUPPORT FOR THE SPATIAL MODEL

(a) *Localization of retrieval functions*

In a recent functional neuroimaging study (Burgess *et al.* 2001) we examined the neural systems involved in the retrieval of the spatial context of an event. In brief, subjects followed a route through a town (presented using virtual reality), meeting one of two characters in one of two places along the route. During each of 16 encounters a different object was passed from the character to the subject. Scanning occurred during retrieval which was tested by returning the subject to the scene of an event, in the presence of one of the characters, and giving them a forced choice of two objects. Two conditions are of interest here: 'place', in which the object that had been received in the current location had to be chosen; and 'width', in which the widest object had to be chosen. The areas activated in the place condition relative to the width condition are shown in figure 6. They show good correspondence with the areas predicted by the model, with the additional feature of a continuous strip of activation running from medial temporal to medial parietal areas, through the retro-splenial cortex and up the parieto-occipital sulcus. We suppose that this activation reflects the buffering of the locations of scene elements in the successively translated frames of reference (allocentric, body-centred, head-centred) between the parahippo-campus and the precuneus.

Additionally, we saw activation of all of the prefrontal areas usually activated in previous experiments on memory for laboratory stimuli such as lists of words, etc. (bilateral anterior, dorso- and ventro-lateral prefrontal cortex, anterior cingulate). We ascribed these activations to sorting out the interference caused by the highly similar context of the events used in our study (16 events occurring in two places) and in previous experiments on

lists of items presented in the scanner but not in studies of the richly diverse events in autobiography (Maguire *et al.* 2000). This would be broadly consistent with neuro-psychological studies of the medial temporal and prefrontal roles in memory (see e.g. Incisa-della & Milner 1993; Smith *et al.* 1995).

(b) *Allocentric representation of space in the human hippocampus*

To test whether or not the hippocampus is specifically involved in storing allocentric (or viewpoint-independent) representations we designed a test for this (King *et al.* 2001) and administered it to a patient with bilateral hippocampal pathology, Jon (Vargha-Khadem *et al.* 1997). In brief, the subject was given a viewpoint from the rooftops surrounding a small town square, using a virtual reality presentation. During presentation, *n* objects appeared sequentially in different locations around the square. During testing, *m* copies of each object were presented in different locations, with the subject asked to indicate which was in the same location as at presentation. Between presentation and testing, the subject's viewpoint might be changed to another location overlooking the square.

Compared with previous tests (e.g. Abrahams *et al.* 1997; Holdstock *et al.* 2000; Roskos *et al.* 1998), this test included several features to favour the use of an allo-centric representation and checks to rule out the use of alternative egocentric strategies. The most notable features were that: (i) a single representation of all object locations would have to be constructed cumulatively due to their sequential presentation; (ii) instantaneous transfer between viewing locations prevents gradual updating of an initial egocentric representation using 'path integration'; and (iii) reaction times were recorded and two different angular changes of position used so that any signs of mental rotation could be monitored (none were found). Thus, although both allocentric and

egocentric representations could be used to solve the same viewpoint condition, solution of the changed viewpoint condition solely on the basis of storing egocentric snapshots at presentation would be difficult.

Patient Jon's performance as a function of list length (tested using two foils) indicated a massive deficit in performance in the changed viewpoint condition. His span was over 13 items in the same viewpoint condition, but he was at chance at all list lengths greater than one in the changed viewpoint condition. As expected, healthy controls performed slightly better than Jon in the same viewpoint condition and vastly better in the changed viewpoint condition. By increasing the number of foils to five, so that controls performed as well as or worse than Jon in the same viewpoint condition but still significantly better in the different viewpoint condition, we formally demonstrated Jon's additional impairment for allocentric representation.

5. DISCUSSION

The model of hippocampo-neocortical interaction proposed by Marr (1971), and its subsequent development by many authors, has provided a computational framework within which to consider the processes involved in long-term memory. A strict interpretation of its principal motivation, that the hippocampus acts as a temporary store from which useful information is transferred into neocortical long-term memory, remains unsupported by convincing experimental data to this day. Nonetheless, it has provided computational insights into several aspects of the functioning of the episodic memory system and its relationship to other memory systems. It supports the utility of rapidly storing a high-level representation that can be used to recall the detailed multimodal information comprising an event. It suggests an explanation for the presence of long-range recurrent collaterals in area CA3 of the hippocampus—to provide pattern completion of the hippocampal representations during retrieval. Most interestingly for the concerns of this paper, it provides computational explanations for the separation of processes supporting episodic, semantic and recognition memory, and suggests some neurophysiological mechanisms relating to the encoding of new memories.

This type of model can be applied to the specifically episodic task of retrieving the spatial context of an event. This provides an additional set of constraints for modelling, given the detailed current state of knowledge regarding the neural representation of spatial information in the mammalian brain. In the model we have presented, the location of the subject during the event forms the hippocampal representation used to retrieve other information and in which pattern completion occurs (see also Recce & Harris 1996). Both this hippocampal representation and the parahippocampal representation of landmark locations are 'allocentric', in being independent of the orientation of the subject. The use of allocentric representations, in long-term storage makes sense, in that the orientation and position of body parts will change between presentation and recall (see also Goodale & Milner 1992; Burgess *et al.* 1999) and links the spatial role of the hippocampus in rats to its role in episodic memory in humans (see also O'Keefe & Nadel 1978). However,

sensory perception produces egocentric representation, and the ability to perform visual imagery on the products of retrieval also requires an egocentric representation. The model proposes that egocentric imagery occurs in medial parietal areas, while translation of information between egocentric and allocentric representations is supported by the posterior parietal cortex. Interestingly, this translation requires knowledge of the subject's heading direction, linking the role of mammillary body–anterior thalamic–presubicular circuit in encoding head-direction in the rat (see e.g. Taube 1998) to the apparent role of this circuit in episodic memory in humans (see e.g. Aggleton & Brown 1999; Gaffan & Hornak 1997). The model provides a computational framework for understanding the operation of several brain areas within the retrieval of episodic information and predicts the effects of parietal lesions, hippocampal lesions and manipulations of the subject's perceived head-direction on the retrieval of the spatial context of episodic memories.

The assumptions of the spatial model can be tested experimentally. In §4 we described two experiments regarding these assumptions. The proposed localization of the processes involved in the retrieval of episodic memory were examined in a functional neuroimaging study of memory for the spatial context of an event (Burgess *et al.* 2001). For this study, a virtual reality presentation was used to provide both a rich spatial context for the events and a controllable way to simulate lifelike events in which the subject can actively participate. The areas activated in this experiment were surprisingly consistent with the model's proposed functional localization, with the addition of a continuous stream of activation from parahippocampus to medial parietal areas, running through the retrosplenial cortex. We hypothesize that this activation corresponds to buffering of the intermediate representations between the allocentric parahippocampal representation and the head-centred medial parietal one.

The proposed role for the hippocampus, particularly the proposal that it stores an allocentric representation of location, was tested in a patient with focal bilateral hippocampal pathology, Jon (Vargha-Khadem *et al.* 1997). For this we used virtual reality to present objects located in three-dimensional space and tested recognition memory for their locations. By changing the subject's viewpoint between presentation and recall, and controlling for alternative, egocentric, strategies we attempted to test directly for the storage of viewpoint-independent information. Jon's enormous impairment when the viewpoint was changed but only mild impairment from the same viewpoint strongly indicates a role for the hippocampus in storing allocentric representations of object locations. It is possible that this rare deficit in recognition memory (at which he generally performs well) is related to Jon's wider problems in episodic memory, possibly via a role for hippocampal storage of allocentric information as outlined in the spatial model.

If at least part of the index to episodic memory (be it hippocampal or otherwise) relates to the spatial context of an event, it should be possible to test experimentally. Indirect evidence can be found in considering the effect of completing a task involving moving from one location to another on the storage of that event in memory (Barreau 1997). Young children (around four years old) showed a

more robust memory for such events when tested after their completion than when tested in transit. Interestingly, the pattern of errors made by these children depended on the order in which different events were questioned. These data can largely be captured by a surprisingly simple model of the interaction of short- and long-term storage systems in supporting episodic memory (Morton & Barreau 2001).

In conclusion, we have discussed how attempts to model the hippocampal and neocortical roles in long-term memory have provided insights into some of the features of episodic memory. To further investigate the neural mechanisms specifically relevant to episodic memory, we have proposed a detailed model of an example of contextually cued recall—the retrieval of the spatial context of an event. This has enabled us to tie together findings from neurophysiology, functional neuroanatomy and neuropsychology relating to episodic memory. The model also makes experimental predictions regarding the interaction of space and memory in all of these fields. To illustrate the types of experiment addressed by the model, we described a functional neuro-imaging study of the retrieval of spatial context and a neuropsychological study of the representation of location stored by the human hippocampus.

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