Models of Spatial Cognition

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CONTENTS

Neurophysiological research has led to detailed mechanistic theories about how spatial locations and headings are represented in the brain and used in memory and navigation.

INTRODUCTION

0369.001 The term 'spatial cognition' covers processes controlling behaviour that must be directed at particular locations, or responses that depend on the location or spatial arrangement of stimuli. There are many circumstances in which such processes are required for adaptive behaviour, and they are exhibited in creatures as diverse as bees, birds, rats and primates. At the most basic level, an organism must be able to flee from a dangerous location to a safer place. It may also need to return to a location where food is abundant or has been stored; to act upon a stimulus at one location, while temporarily ignoring other stimuli; or to navigate from one place to another by an efficient route, avoiding obstacles. All of these behaviours seem to demand some sort of spatial representation; a neural code that distinguishes one place or spatial arrangement of stimuli from another. Models of spatial cognition describe these representations and the nature of the processes that operate on them to give rise to spatial behaviour.

NEURAL REPRESENTATIONS OF SPACE

0369.002 Models of spatial cognition are constrained by experimental evidence from cognitive psychology, neuropsychology, neuroimaging and neurophysiology. The picture emerging from this evidence is that spatial cognition can be divided into two modes, which are to some extent separated in the mammalian brain.

Broadly speaking, processes involved in action, attention and perceptual constancy involve the parietal neocortex. The importance of parietal processes in spatial attention and action is illustrated by the well-known neuropsychological phenomenon of hemispatial neglect, in which patients with lesions of the right parietal cortex show an attentional bias towards the right. The presence of stimuli on the patient's right side tends to extinguish any response to a stimulus on the left, so that for instance, a patient may shave only the right side of his face, or copy only the right side of a picture. 0369.003

Processes involved in long-term spatial memory, orientation and navigation take place in the hippocampus and adjacent cortical and subcortical structures. Patients with damage to these regions, especially in the right hemisphere, are impaired in a range of topographical memory tasks such as drawing maps or judging the distance between locations. Neuroimaging studies have shown that the right hippocampus is activated during the verbal recall of routes and during navigation in a virtual-reality town, and that its activation correlates with success in the navigation task. 0369.004

This division of labour is something of an oversimplification. Many tasks do not fall comfortably into either memory or action categories, but involve elements of both. Additionally, other brain areas are involved in some spatial tasks, for example prefrontal cortex is implicated in tasks demanding planning, while reflexes and stereotyped or overlearned spatial behaviour will involve subcortical regions such as the basal ganglia and superior colliculus and cerebellum. Additionally, the hippocampus and parietal cortex have important functions that go beyond those outlined above: for example, in humans the hippocampus plays a more general role in memory for personally experienced events. However, the generalization outlined 0369.005

above is useful, because it makes clear some of the important constraints on spatial processing that may pertain to different brain regions.

0369.006 First, the processing modes differ in the spatial and temporal scales over which they operate. Hippocampal processes are concerned with large distances and long timescales, whereas parietal processes are more concerned with short timescales and the space immediately surrounding the body.

0369.007 Second, the processing modes differ in the forms of spatial representation they demand. Parietal processes controlling action in the immediate environment use egocentric representations of space (i.e. locations are represented in terms of their relation to the subject). So, for instance, the firing rates of neurons in the medial interparietal area of monkey parietal cortex, which fire when the animal is about to reach for an object, vary depending on the position of the object relative to the monkey's hand. This is an example of a neural representation in an egocentric (in this case hand-centred) reference frame. Such representations are clearly useful for guiding action over the short term, or where the stimuli whose locations are to be encoded are immediately available to the perceptual system.

0369.008 Egocentric representations have the disadvantage that in order to remain valid over the long term, they must be actively updated to reflect changes in the subject's location and heading. Unless corrected by new sensory information, any errors in this updating process will be cumulative, so that egocentric representations of location are unreliable for long-term storage.

0369.009 In contrast, processes demanding long-term memory of a location should make use of representations that relate locations to each other and to landmarks in the environment, rather than to the subject. Such representations are called world-centred or 'allocentric'. They are map-like in the sense that in there is no privileged location to which all others are related. Instead, they provide a basis from which one's current location and orientation can be computed from one's relationship to sensory cues in the environment. A set of locations represented in an allocentric framework can be thought of as a 'cognitive map'.

0369.010 A cognitive map has several advantages in the context of long-term memory. Over a period of days, months or years, a given place may be approached from different directions on different occasions; the viewpoint-independence of an allocentric representation will thus be useful in navigating towards or recognizing locations over such timescales. Furthermore, locations represented in an allocentric reference frame do not need to be continuously updated in the way that locations in an egocentric reference frame must be. An allocentric form of representation is thus not prone to the cumulative error inherent in such an updating process, making it particularly suitable in tasks where behaviour has to be directed towards a location that is not immediately available to perception. This might occur either because it is far away (as in the case of navigation in large-scale space; for example, returning to a familiar nesting site after a protracted foraging expedition) or because it is hidden (e.g. returning to the location of a hidden food store).

For long-term memory, an allocentric representation of space could provide a solution to some of the shortcomings of egocentric representations. However, it also raises some new questions, not least of which is how a map-like representation can be abstracted from the egocentric information available to sensory systems. What form does the allocentric 'cognitive map' take, and how could it support navigation? In order to understand how allocentric representations are formed, it is useful first to consider the ways in which transformations between different reference frames might be achieved in the parietal cortex. Such transformations are certainly involved in immediate action-orientated processes, but may also occur in the encoding or retrieval of long-term spatial memories. 0369.011

TRANSFORMATION BETWEEN REFERENCE FRAMES

Sensory cortices encode stimulus location egocentrically. For action, it is generally necessary to transform information about the location of a stimulus into a reference frame appropriate to the effector system involved in the response. For instance, visual information about the location of an object is encoded retinotopically in visual cortex (reflecting location in an eye-centred reference frame) and must be transformed into a hand-(or arm-) centred coordinate system in order that it can be used to direct a reaching response. 0369.012

In fact, most actions are likely to require multiple reference frames, as they demand the coordinated action of many effectors moving in concert. There is neurophysiological evidence of the existence of such multiple egocentric reference frames in the parietal cortex of monkeys. As well as cells representing object locations relative to the monkey's hand (mentioned previously), other populations of cells have been discovered where firing rates 0369.013

are determined by the relationship of objects to the monkey's trunk, arm, head and so forth.

0369.014 How does the parietal cortex transform locations represented in one reference frame to another? A three-layer feed-forward neural network can be trained to perform such transformations (e.g. between eye-centred and head-centred coordinates). A layer of input neurons represents locations on the retina and the gaze direction (i.e. the angle of the eye in the head), and a layer of output neurons represents locations relative to the head. Between the input and output layers is a 'hidden' layer of processing neurons. During training, the strengths of connections to and from the hidden layer are gradually changed, so that the output layer produces increasingly accurate transformations of the input. Ultimately, each output neuron has a firing rate determined by stimulus location relative to the head – the connections to and from the hidden layer of neurons translate the eye-centred representation of the stimulus location into a head-centred reference frame, taking into account the gaze direction.

0369.015 What is interesting about this model is the way in which the transformation is achieved. After training, neurons in the middle processing layer between the input and output layers show responses that are modulated by both the location of a stimulus relative to the head, and by its retinal location. This type of encoding is referred to as a 'gain field'. It is a useful form of representation because the combined influences of stimulus location in two different reference frames on the neural response would allow the location of the stimulus to be represented in either reference frame in subsequent processing layers. Gain field responses have been found in neurons in the interparietal sulcus of the monkey posterior parietal cortex. It is plausible that the multiple egocentric representations of location in the posterior parietal cortex are linked by intermediate gain field representations that mediate the translation of location information from one reference frame to another.

NEURAL BASIS OF SPATIAL MEMORY AND ORIENTATION

Place Cells

0369.016 Experiments with rats provided some of the first evidence that the hippocampus was involved in spatial memory and the allocentric representation of space. A popular laboratory task demanding spatial memory is the Morris water maze, in which rats learn to escape from a pool of cloudy water by navigating to a platform hidden beneath its surface. Rats with lesions to the hippocampus are unable to learn the location of the platform in the water maze. The anatomy of the hippocampus is substantially similar in rats and primates, including humans, so there are grounds for believing that the mechanisms of spatial memory and navigation in these diverse species may also be similar. But how does the hippocampus represent locations, such as the location of the hidden platform?

0369.017 Place cells, in areas CA1 and CA3 of the hippocampus, encode the rat's location independently of its heading. They are cells whose firing rates vary depending on where the animal is. In a typical experiment the firing of hippocampal pyramidal cells is recorded as the animal freely explores its environment (typically a low-walled box or a raised platform). A place cell might fire, for instance, whenever the rat is in the northeast corner of the environment, but not elsewhere. Each place cell responds in a different part of the environment, referred to as the cell's place field. Together these firing fields cover the entire area of the box. Each place in the box produces a different pattern of firing in the place cells. By looking at the firing rate of several place cells at once (say 30), one could know to within a few centimetres where in the box the rat is at any time.

0369.018 Place cells could clearly be of importance in representing behaviourally important locations, and their discovery prompted O'Keefe and Nadel to propose that the hippocampus functions as a cognitive map. The mechanisms underlying the neural representation of place are likely to be important in understanding cognitive processes such as navigation and long-term spatial memory, and we will return to the question of how place fields are formed later.

Head Direction Cells

0369.019 Whereas place cells encode the rat's location independently of where it is heading, a complementary system of 'head direction cells' represent the animal's heading independent of its location. Each has a preferred direction (e.g. north) and fires whenever the rat is facing in that direction. Head direction cells are found in the mamillary bodies, anterior thalamus and presubiculum, parts which together with the hippocampus are connected to form an anatomical circuit. Over short periods populations of head direction cells function as a neural compass, tracking changes in heading with a remarkable accuracy. Recorded over longer periods, they do not maintain fixed compass directions: the direction to which a particular cell is tuned depends on sensory (especially visual) cues present in the environment. Rotating all such cues causes a matching change in the head direction cell's response, and if visual cues are absent, the tuning of a cell may gradually drift. Interestingly, the responses of simultaneously recorded head direction cells remain locked together (always maintaining the same angle between preferred directions).

0369.020 A neural compass could clearly be of great use in navigation, but it may also fulfil another, related role in spatial memory. As noted above, an important part of the process of forming a long-term representation of a location may involve transforming egocentric representations of the environment into an allocentric form. One of the essential properties of such a representation is that it is orientation-neutral (i.e. independent of the heading direction at the time of encoding). This means rotating sensory information about the location to be encoded, so that directions are represented in a reference frame that is fixed with respect to the world (i.e. as compass directions) rather than one that is fixed with respect to the direction one is currently facing. The transformation between orientation-specific perceptual and orientation-neutral mnemonic representations could, in principle, be achieved through a 'gain field' mechanism (see above), and would require a representation of heading (analogous to the gaze angle information in the transformation between eye- and head-centred reference frames). Thus the head direction system could be involved in the encoding of long-term memories. This may explain why the anatomical circuit involved in head direction is also implicated in amnesia.

MODELS OF ALLOCENTRIC SPATIAL REPRESENTATIONS

0369.021 We now turn to the question of how allocentric representations of the kind described above might be abstracted from egocentrically encoded sensory information: what makes a place cell fire where it does?

0369.022 A place field's location does not depend on the rat's position relative to any single cue. This can be demonstrated by changing various aspects of the environment while the rat is absent. For instance, the walls making up the perimeter of the box can be swapped around, or the floor of the box replaced, but a place cell will still fire in the same location. Therefore the cell does not fire in response to the distinctive smell of the wall or floor near its firing field. Similarly, removing subsets of visual cues need not affect place cell firing.

0369.023 One way of explaining the independence of place fields to any single external cue is that internal information (e.g. self motion, vestibular and motor efference information) is used to track changes in location over time, with external sensory information simply serving to calibrate this system. This mechanism is often referred to as 'path integration'. Another possibility is that external cues are used, but that a conjunction of several features is required to drive a place cell to fire at a given location. As the hippocampus receives inputs from many areas of sensory cortex, both external cues and path integration information could play a part in controlling place cell activation. Experimental evidence indicates that visual cues are the most important determinants of place cell firing under normal circumstances. However, visual information is not essential; congenitally blind rats have apparently normal place fields.

0369.024 The geometry of the environment is particularly important in determining place field locations. This can be demonstrated by varying the size and shape of the experimental environment. The locations of place fields remain fixed with respect to some of the walls of the environment (usually the nearer walls; Figure 1) even when the box is moved within the laboratory (and thus with respect to many distant visual cues visible over the low walls of the box). Place field locations are not affected when smaller objects placed within the enclosure are moved around, but if the same objects are placed close together so that they form a more substantial barrier to movement, they do affect place field location.

0369.025 These results suggest that the distances and directions of boundaries are represented in the cortical inputs to the hippocampus. These distances and directions are probably determined by external sensory systems, as they would be difficult to compute on the basis of path integration alone. Because place cell firing rates in open environments tend to be independent of the rat's heading, it would appear that the directions of these critical features are represented in an orientation-neutral reference frame (north, south, east, etc.) rather than one specific to the current heading (left, right, ahead, etc.). This suggests that initially egocentric representations of the distance and direction of geometric features of the environment are transformed into an allocentric directional framework, by taking into account the rat's heading, as discussed previously.

Consistent with this idea, manipulations that affect the orientation of the head direction system also affect place field locations. For instance, if distant visual cues are rotated about the centre of the rat's environment, place fields are rotated through a corresponding angle.

A Simple Feedforward Model of Place Field Formation

0369.026 The simplest models of place field formation are feedforward models. Many of these assume that the inputs to the hippocampus are sensitive to landmarks at particular distances and/or directions, but as we have seen some features of the environment (such as distant visual cues or walls) are more important than others.

0369.027 As an example of a feedforward model, let us assume that the inputs to the hippocampus include some that are dependent on the geometry of the environment and in particular its boundaries (Figure 2). These hypothetical cells have the property that they fire strongly when a wall is at a given distance and allocentric direction to the rat. A place cell could receive inputs from many such cells, with the place field reflecting the overlap between the firing fields of its inputs. For instance, a place cell with a firing field in the northeast corner of a box might have one input which responds whenever there is a wall a few centimetres north of the rat, and another that fires when there is a wall a few centimetres to its east. Either stimulus on its own might be insufficient to drive the place cell to fire (so that it does not fire in the northwest corner, for instance), but the combined inputs of cells responding to the north and east walls drive the place cell to fire in the northeast corner. If we change the geometry of the box (for instance doubling its size), the cell will still fire in the northeast corner. Note that in this model the only requirement for path integration or similar processes, is in the tracking of heading.

0369.028 The above model explains data concerning place field locations in boxes of different shapes and sizes, and predicts that there are cells upstream of the hippocampus, each of which fires in response to a boundary at a particular distance and bearing. It also predicts (in line with experimental observations) that even radical alterations of the shape of the environment should result in fields fixed with respect to the nearby walls of the environment. The model makes no mention of learning, and only requires that each place cell is connected to a random selection of inputs in order to account for the observed patterns of place field location in differently shaped environments. Indeed, one can use place fields obtained from the same cell recorded in differently shaped environments to infer which geometric inputs are driving the cell, and thus to predict the behaviour of the cell in a novel environment.

One potential problem with this simple model is that it makes no mention of the abundant lateral connections that are known to exist between cells in area CA3, and is at odds with data showing that markedly different place fields can sometimes be established in different boxes. This phenomenon, known as 'remapping', has been taken as evidence that the place cell system functions as an 'attractor' network. 0369.029

Attractor Networks of Place and Orientation Representations

Attractor networks are neural networks with recurrent connections (i.e. connections between neurons in a single processing 'layer'). These make it possible for any neuron in the interconnected layer to affect the activation of any of the others to which it is directly or indirectly connected, a property that makes their dynamics potentially rather complex. However, with some constraints, such as symmetry in the strength of connections between neurons (connections from A to B are of equal strength to those from B to A), an attractor network is guaranteed to settle into one of a number of possible stable states (attractor states). 0369.030

Place Representations

In an attractor model of place cell firing, spatial inputs from sensory neocortex activate some of the hippocampal pyramidal cells. Activation then flows between cells along the recurrent connections. This gradually changes the pattern of firing in the pyramidal cells (indirectly activating some cells that are not driven directly by the neocortical input and inhibiting some of those that are) until it settles at an attractor state. 0369.031

In 'continuous attractor' networks, the connection strengths are constrained so that rather than having a number of distinct attractor states, the network will move smoothly between attractor states as the input is changed. One way this could be achieved in place cells is for cells with nearby place fields to have strong connections, and for place fields with well-separated fields to have weak (or inhibitory) connections. 0369.032

0369.033 If the inputs to the hippocampus are spatially modulated, and the hippocampal pyramidal cells are connected together to form a continuous attractor network, then one would expect to find a population of place cells that shows the same pattern of activation whenever the animal visits a particular location, with some cells firing strongly, others only weakly. At another location one would see a quite different pattern of activation. As the pattern of active cells changes smoothly as the rat moves from one place to another, the firing rates of individual cells will also vary smoothly between locations, i.e. each cell will have a smooth firing field with some spatial extent – a place field. With appropriate lateral connections, any spatially modulated input could be sufficient to produce place fields, so path integration could play a more significant role in this type of model. However, it would still be difficult to account for the geometric constraints on place field location in terms of a model whose spatial inputs were exclusively internal.

0369.034 A continuous attractor model requires a particular pattern of connection strengths between place cells. These connection strengths might be learned on exposure to a new environment. However, place fields appear to be present on the first exposure to a new environment (within a few minutes) and are stable for at least several days. This suggests that either learning is extremely rapid or that preexisting lateral connections are sufficient to produce the observed fields.

Orientation Representations

0369.035 The head direction system can also be modelled as a continuous attractor network with inputs corresponding to visual cues to orientation and vestibular responses to left-right rotation. In this model, connections between head direction cells are such that for any input, the network will settle into a stable state with a few cells (representing the current heading) firing, and the rest silent: cells representing opposite directions inhibit one another, while there are weak excitatory connections between cells representing neighbouring directions. One can imagine the head direction cells as arranged in a circle, with excitatory connections between neighbouring cells, and inhibitory connections between more distant cells. At any time a cluster of active cells will indicate the direction of the neural compass. By virtue of the hard-wired connections each head direction cell receives from the vestibular system, the activation peak can be driven clockwise or counterclockwise. The visual inputs function to calibrate the system and tie it to the external world.

MODELS OF NAVIGATION

Together, the two types of allocentric representation described above – place and heading – provide the basic tools for spatial memory and navigation. However, it is important to note that they do not in themselves constitute a cognitive map. A map also has to identify important locations and store them for later use: without some representation of an intended destination, information about current location and heading will be of little use in navigation. Furthermore, a cognitive map must also include information about the way in which different places are connected to one another (topology), so that it is possible to plan a route between places that avoids obstacles. Here we must be more speculative about the neural mechanisms, because to date no neurophysiological study has identified neurons that encode either destinations or topology. 0369.036

The recurrent collaterals in region CA3 also figure prominently in models of navigation. Hebb's ideas on the modification of functional connections between cells, and the apparently related process of long-term potentiation of synapses, indicate that strong connections should develop between cells that fire simultaneously. For place cells, this would produce strong connections between cells with nearby fields (as required to form a continuous attractor, see above). However, it would also lead to the topology of space being encoded in the strength of the recurrent connections; in other words, the strength of a connection between place cells could indicate, on average, how long it took the rat to travel between the corresponding place fields. Thus the places along the shortest path between two locations could be found in principle, although how this would work in practice is less clear. 0369.037

Some experiments have shown a temporal asymmetry in long-term potentiation: connections from one cell to another are strengthened most when the first cell fires before the second. This asymmetry would allow the learning of the path taken by an animal as it moved from one place to another. Place cells with firing fields near the beginning of the route will develop strong connections to place cells with fields further along the route. These directional connections could, in principle, be used to store the route but, again, it is less clear how they would be used to guide behaviour in practice. 0369.038

As with models of spatial representation, simple feedforward models may suffice for modelling navigation. Perhaps the simplest model of spatial 0369.039

memory posits that receiving a reward at a particular location causes a 'goal cell' immediately downstream of the hippocampus to fire. This in turn strengthens synaptic connections to it from the place cells active at that location. The subsequent firing of the goal cell would indicate the proximity of the goal. As the animal moves nearer the goal location, more of the place cells with strong connections to the goal cell will fire, increasing the net current input to the goal cell. Thus the animal will be able to return to the goal simply by moving so as to increase the firing rate of the goal cell. More generally, this type of model predicts that the likelihood of searching for a remembered location in a particular place increases with the similarity of the place cell representations of the goal and the place (Figure 3).

0369.040 Other models have looked at the generation of movements in navigation in more detail, enabling the animal to head directly to the goal, rather than hunting around to ascertain the right direction. These models confront the problem of translating allocentric hippocampal information (such as 'the goal is to the north') into egocentric movements (such as 'turn left'). This translation is assumed to occur in the parietal cortex or basal ganglia, again making use of the head direction system to translate between orientation-neutral and orientation-specific reference frames.

CONCLUSION

0369.041 Thanks to neurophysiological data gathered over more than three decades we now have fairly detailed mechanistic theories of the processes involved in forming spatial representations, in translating between representations in different reference frames and in storing them and using them to guide behaviour. These models have now progressed to the point that we can make links between physiology and complex behaviours such as navigation, and thus develop an ever more detailed understanding of spatial cognition.

Further Reading

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Glossary

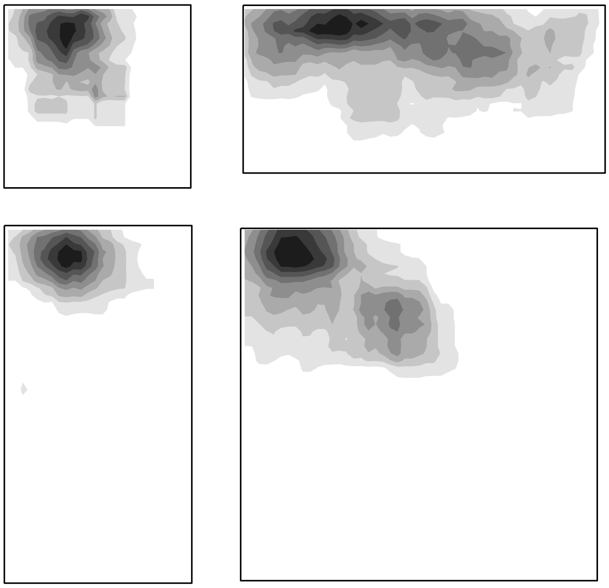
Feedforward neural network Network with a layered architecture where neurons within a layer are connected to neurons in other layers, but not to other cells in the same layer. Activation flows forward through the connections from the input layer, via any intermediate layers (also known as hidden layers) to the output layer; there are no connections in the opposite direction

Recurrent connections Connections between neurons in the same processing layer of a neural network. Activation propagated along these connections may eventually arrive back at its source

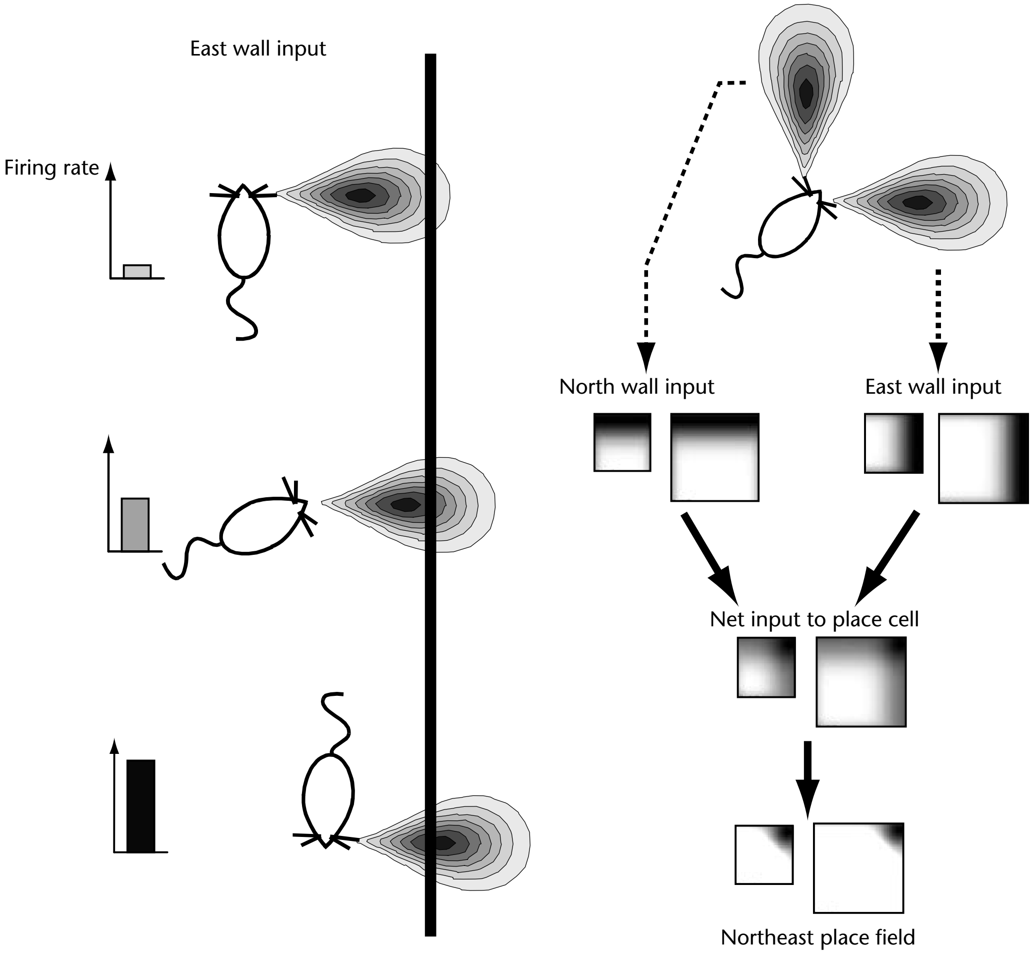
Recurrent collaterals Anatomical connections between cells in CA3 of the hippocampus

Keywords:

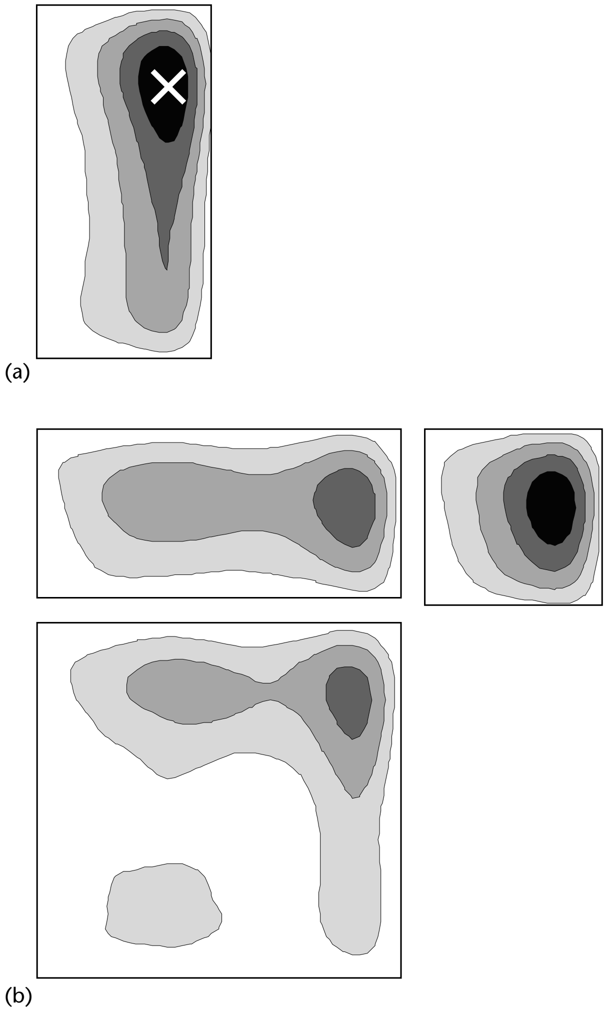
hippocampus; parietal; navigation; orientation; memory



0369f001 **Figure 1.** Place cells in area CA3 of the rat hippocampus have firing rates that vary systematically according to the rat's location. The region where the cell fires is called a place field. The shading indicates the place fields of one cell, recorded as the rat explored four different rectangular boxes. In each case, the cell fires most strongly in the northwest corner of the box (i.e. the location of the field remains fixed relative to the north and west walls). Adapted from O'Keefe J and Burgess N (1996) Geometric determinants of the place fields of hippocampal neurons. *Nature* **381**: 425–428.



0369f002 **Figure 2.** A simple feedforward model of place field formation. In this model place cells have inputs that respond to walls or other boundaries at particular distances and directions from the rat. The left panel shows the receptive field of one such cell (sensitive to a boundary a short distance to the east), and illustrates how the cell's firing rate varies as the rat moves nearer to the wall. Note that the direction that the input cell is tuned to does not depend on the rat's heading. Place fields could be formed by combining several such inputs. The right panel shows how a place field in the northeast corner of two different-sized square boxes can be modelled by combining inputs responsive to north and east walls. The two input cells fire close to the north and east walls respectively (in both boxes). The net input to the place cell is greatest when the rat is in the northeast corner of either box. The place cell's firing rate is a thresholded function of its net inputs: the cell fires only in the northeast corner of the box. Adapted from Hartley T, Burgess N, Lever C, Caccuci F and O'Keefe J (2000) Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus* **10**: 369–379.



0369f003 **Figure 3.** (a) A simple goal cell model of navigation to a stored goal location. When reward is received at location X, a goal cell is activated. Connections from active place cells to the goal cell are strengthened. The goal cell's firing rate will now vary depending on the rat's proximity to X. To return to the stored location the animal must move so as to maximize the firing rate of the goal cell. The firing rate map was made by simulating a large number of place cells each having a random selection of geometric inputs and thus producing a varied selection of place fields which overlapped and covered the entire space of the box. The goal cell firing rate is calculated as the similarity of the place cell firing rates at each location to the stored pattern (firing rates at X). (b) Where will the rat search if the shape of the box is changed? Because we can simulate the firing of the same place cells in different boxes, we can also predict the search locus in environments of different shape. Such predictions will allow us to test the model in behavioural experiments. Adapted from Hartley T, Burgess N, Lever C, Caccuci F and O'Keefe J (2000) Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus* **10**: 369–379.

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Article 369 [Hartley &Burgess]

Bibliography

Burgess et al 2001 - ‘in press’ - please update.

Figures 1-3

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