The Representation of Space and the Hippocampus in Rats, Robots and Humans*

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Experimental evidence suggests that the hippocampus represents locations within an allocentric representation of space. The environmental inputs that underlie the rat's representation of its own location within an environment (in the firing of place cells) are the distances to walls, and different walls are identified by their allocentric direction from the rat. We propose that the locations of goals in an environment is stored downstream of the place cells, in the subiculum. In addition to firing rate coding, place cells may use phase coding relative to the theta rhythm of the EEG. In some circumstances path integration may be used, in addition to environmental information, as an input to the hippocampal system. A detailed computational model of the hippocampus successfully guides the navigation of a mobile robot. The model's behaviour is compared to electrophysiological and behavioural data in rats, and implications for the role of the hippocampus in primates are explored.

Introduction

Spatial locations may be defined in many different frames of reference. For example, it might be useful to know that your car is parked near to a particular visual landmark (such as a tall building), or that the gear stick is near your right knee when driving. The former piece of information refers to an 'allocentric' frame of reference (i.e. centred on some aspect of the environment independently of the location and orientation of the body), whereas the latter refers to an 'egocentric' frame of reference (i.e. a frame related to a part of the body). These two pieces of information will be useful for different tasks. The allocentric information is useful for returning to your car and the egocentric information is useful for changing gear, but the reverse is not true.

More generally, the immediate perception of object locations will be initially in the frame of reference attached to the sensory receptor concerned (e.g. retina). To act upon such an object with a particular effector will require translation of the representation of its location into a frame of reference related to the effector. Thus short-term storage of object locations for the purposes of acting upon these objects might be best stored in an 'egocentric' frame of reference. By contrast, the long-term storage of the locations of objects that we can move around might best be done in a unitary 'allocentric' frame of reference, with a recall process translating this information into egocentric reference frames relative to the current configuration of the body.

Evidence from single-unit recording in rats and primates, and neuropsychology in humans gives some support to this distinction, and suggests that different brain regions might support the different types of representation. Neurons in monkey parietal cortex appear to be involved in the representation of object locations in egocentric co-ordinates (i.e. position relative to hand or eye or head), see e.g. Hyvarinen and Poranen (1974); Mountcastle *et al.* (1975); Andersen *et al.* (1985); Colby (1990). 'Place cells' and 'head-direction cells' in and around the hippocampus of the rat appear to represent the rat's allocentric location and orientation within an environment, respectively, see e.g. O'Keefe and Nadel (1978), Taube *et al.* (1990), and below. A common symptom of damage to the parietal lobes is optic ataxia, i.e. impaired visually guided reaching, and the parietal damage may induce a wide variety of impairments to sensory and motor processing of egocentric in-

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formation (see e.g. Heilman *et al.* (1982); Vallar (1998); Karnath (1998)). In contrast, damage to the hippocampal region and medial temporal lobes may produce topographical amnesia (e.g. Habib and Sirigu (1987); Maguire *et al.* (1996)), as well as the more common long-term amnesia for events (see Scoville and Milner (1957); Tulving (1983)). These issues are explored further in Burgess *et al.* (1998) and Milner *et al.* (1998).

In this paper we consider the allocentric representation of space in the hippocampus of the rat, what sensory inputs support it, and how it might be used to guide behaviour. Our hypotheses regarding place cell firing as the neural basis of navigation are explored by instantiation as a neural network simulation, and verified by being implemented on a mobile robot. The firing of simulated neurons can be compared to the experimental data from single unit recordings, and the behaviour of the robot can be compared to data from rat navigation. Finally we draw some parallels between the spatial role of the hippocampus in the rat and the possible allocentric and egocentric roles of the right hippocampus and right inferior parietal cortex in humans, following a recent functional neuroimaging study of navigation in humans (Maguire *et al.,* 1998).

The Representation of Space in and around the Hippocampus of the Rat

Spatially tuned neurons (place cells) in the hippocampus of freely-moving rats tend to fire at a high rate only when the rat is in a particular portion of its environment. Interestingly, head-direction cells with the complimentary pattern of spatial firing to place cells have been found near to the hippocampus in the dorsal pre-subiculum. These cells code for the facing direction of the rat's head (Taube at al., 1990). Lesions of the hippocampus impair the rat's ability to return to a (hidden) previously visited reward site, see e.g. Morris *et al.* (1982). Taking these results together, the hippocampal system appears to form part of the neural basis of navigation (O'Keefe and Nadel, 1978). However, it is still not clear how the striking spatial correlates of the firing of these cells arises, nor how they contribute to the generation of the animal's behaviour.

Some of the characteristics of this system may be important in terms of deducing the neural mechanisms underlying navigation. Visual stimuli at or beyond the edge of the rat's reachable environment are sufficient to control the overall orientation of the place and head-direction representations. Rotation of these stimuli can be shown to cause rotation of the receptive fields of place and head-direction cells about the centre of a symmetrical environment. However objects placed within the environment do not show this control.

In simple walled environments it seems likely that the rat uses the allocentric direction of each wall to distinguish it from the next, and that the distance from two or more of the walls determines the firing rate of each place cell (O'Keefe and Burgess, 1996; Burgess *et al.,* 1997). The role of distant visual cues may relate to the rat's internal sense of direction, and thus, indirectly to place cell firing. Local cues, distant visual cues and the rat's internal sense of orientation (possibly vestibular and proprioceptive in origin) all appear to contribute to the rat's internal sense of direction, and can each be systematically manipulated (Jeffery *et al.,* 1997). What mechanisms pass distance information to the hippocampus? Some authors have argued that purely internal signals (i.e. vestibular and proprioceptive), occasionally reset with respect to the real world by tactile (McNaughton *et al.,* 1996a) or visual (McNaughton *et al.,*1996b) information drive place cell firing. However a mixture of visual, olfactory, auditory, tactile and internal information determined by what is available in a particular environment is more likely (e.g. Hill and Best, 1981).

Phase coding: a powerful form of temporal coding

There are also temporal aspects to place cell firing. Whenever a rat is moving its head, the EEG shows a characteristic sinusoidal oscillation of around 7–12 Hz (called the theta rhythm in rats). There is evidence that the time of firing of spikes by a place cell carries information relating to the relative position of the place cell's receptive field ('place field') from the rat (O'Keefe and Recce, 1993). As the rat runs through a place field on a linear track, the phase of the theta rhythm at which the place cell fires systematically shifts from a late phase as the rat enters the field to an early one as it leaves the field. Thus spikes fired at a late phase tend to come from cells with place fields centred ahead of the rat and those fired at an early phase from those with fields centred behind the rat (Burgess *et al.,* 1994).

These neuronal responses amount to a type of 'phase coding', in which the meaning of the time of firing of a spike could in principle be read off against the phase of an oscillator (in this case the extra-cellular theta rhythm, or the firing rate of theta cells) by some downstream process. This ability to de-reference the information contained in cell firing is an important consideration. For example, the problem of binding together the features of different objects in a crowed scene might be solved by those cells responding to features of the same object firing synchronously (see Roelfsema, this volume, for a review), but leaves open the question of how to de-reference this information to find the attributes of a particular object. With phase coding, each object might have its own phase: those cells firing at a particular phase denoting all of the features of a particular object.

A Model of the Hippocampus and Navigation

Over the past few years we have developed a neural network model to examine the contribution of place cells to navigation (see Burgess *et al.* (1997)). Here we describe a test of this model by implementing it on a mobile robot: forcing it to use real-world inputs, and seeing if it can indeed direct the navigation of a robot. Part of our motivation was to investigate the extent to which unsophisticated real-world sensors could provide sufficiently accurate visual, or odometric information for a proposed model to work. This is a reasonable test since the rat's visual and odometric systems also appear to be relatively unsophisticated. Rats have wide angle vision but do not necessarily segment stimuli into objects or extract much sensory information beyond the location or motion of the stimulus. The ability of rodents to maintain an estimate of their location and orientation by keeping a cumulative record of their own movements (referred to as 'path integration') is also limited. For example, in experiments in which hamsters are required to return to their point of departure using only path integration, they err significantly after an L shaped route of only 1 m per side or after 5 active or 2 passive rotations in the dark, see Etienne *et al.* (1996).

Overview

Visual estimates of the distances from the robot to the walls of the environment are used to drive the firing of 'sensory cells', these drive an intermediate layer of cells (corresponding to the entorhinal cortex) and thence place cells (PCs). The walls are identified by their allocentric direction from the robot. The estimate of the allocentric direction (orientation) of the robot is maintained by odometry and sightings of the North wall which is visually distinct from the other walls and serves to polarise the environment. When the robot encounters a goal location a reinforcement signal prompts one-shot Hebbian learning in connections from the place cells to a set of goal cells. The subsequent firing rates of these cells provide a continuous estimate of the direction and proximity of the goal location, enabling navigation (see Burgess *et al.* (1997)).

Physical implementation

A Khepera miniature robot is used with on-board video and a ring of short-range infra-red proximity detectors to provide artificial visual and haptic information. Two independently driven wheels allow movement around a rectangular environment formed by white walls and a dark floor. Visual processing consists solely of filtering for horizontal dark-light edge points formed where a wall meets the floor, and finding the row (y) in the image containing the most dark-light edge points and the column (x) of the centroid of the edge points on that row. The distance to the wall is estimated from y, and the bearing of the wall to the robot is estimated using x. One wall (the North wall) is marked by a dark horizontal stripe along the top: its presence is detected by filtering for horizontal light-dark edge points.

Control of the robot proceeds in steps: the proximity detectors are read, the robot rotates on the spot to face in the estimated orientations N S E W capturing an image at each orientation. After each rotation the acquired image is used to estimate the distance to the wall and to correct the robot's estimated orientation to agree with the estimate of its angle to the wall. If no wall was perceived by the IR proximity detectors the robot moves 3 cm forward in the desired direction. Each step corresponds to 0.1 s (one theta cycle, see below) implying a speed of 30 cm/s for the rat. During exploration, each movement is made in a random direction within 30° of the previous direction (unless a wall is perceived). During navigation, each movement is made in the direction indicated by the output of the neural network model.

The neural network

A rectangular array of cells encodes the visual inputs to the simulated hippocampus. They are organised such that each row of cells codes for the distance to a particular wall, with each cell tuned to respond maximally at a particular distance. The tuning of the visual cells to the distance of particular walls is as follows: cell i in the row coding for distances from the West wall has firing rate:

$$\frac{A \exp\{-(x-d_i)^2/2\sigma^2(d_i)\}}{\sqrt{2\pi\sigma^2(d_i)}}$$

where x is the distance from the wall (estimated visually), d_i is the distance at which the cell responds maximally, the amplitude $A = 500$. The width of the response curve increases with the distance of peak response as $\sigma(x) = \sigma_0(L^2 + x^2)/L^2$. This reflects the decreasing reliability of the estimate of x at large distances.

All connections in the model take value 0 or 1 ('on' or 'off'), and each cell fires at a rate proportional to the amount by which its net input exceeds a threshold. Each cell in the entorhinal layer receives hard-wired connections from 2 sensory cells related to 2 orthogonal walls. The connections from the entorhinal layer to the place cell layer include an element of unsupervised competitive learning (see Burgess *et al.* (1994)).

Depending on which connections to a PC have been turned on, its place field will maintain a fixed distance from two orthogonal walls, or reflect more than two inputs all peaked at fixed distances from walls of the environment. Thus some place fields will change in amplitude and shape when the environment is changed in size or shape consistent with experimental data. By contrast, the entorhinal cells' receptive fields will all remain at a fixed distance from two walls and will not change shape or amplitude during changes in the shape and size of the environment. Again, this is consistent with what is known about these cells.

A simple model of navigation based on place cell firing could work in the following way. When the rat encounters a 'goal' (i.e. a location in its environment that is associated with reward), a goal cell downstream from the place cells is strongly excited by the attributes of the goal. At the goal, a one-shot Hebbian increment is induced in the synaptic connections to the goal cell from the place cells that are active at the goal location. As the rat moves away from the goal location, the net activity of place cells with strong connections to the goal cell will be a monotonically decreasing fraction of the total place cell activity. Consequently the activation of each goal cell will code for the proximity of a goal location, and thus could be used as an evaluation function in a gradient-ascent-type search for the goal, i.e. the rat could return to the goal location simply by moving around so as to increase the firing rate of the appropriate goal cell.

In fact we use a more complicated model of learning of the goal location in which one-shot Hebbian association of the PCs active at the goal location to a set of 'goal cells' sets up a 'population vector' that codes for the direction of the goal during subsequent navigation (see Burgess *et al.* (1994)). This has advantages over the simple model such as enabling rats to take short-cuts towards the goal, and does not require the rat to hunt around to determine the direction in which to move.

The firing of these goal cells drives navigation of the robot, enabling it to return to a previously visited but unmarked goal location. The goal cell population vector is an allocentric direction (e.g. Northwest), and must be translated into an egocentric direction (e.g. left) before being used. This transformation is simple given that the robot knows its own orientation, and might be expected to occur in the basal ganglia, or in the posterior parietal cortex.

Performance and Discussion

Two rectangular environments of size 50×50 cm and 50×75 cm were used to test the robot. The robot successfully returns to an unmarked reward location having visited it once previously. The robot also shows generalisation in returning to the goal from novel starting locations. The robot per-forms well in maintaining estimates of the distance and direction of each wall relative to it. Put another way, relative to its environment the robot shows good self-localisation and maintenance of sense of direction.

The behaviour of the 'hidden layers' of the neural network compares well with electrophysiological recordings from the corresponding areas of the hippocampal system. The system is tested by expanding the environment after the goal location has been learned. This generates behavioural predictions determined by the precise choice of goal cell output mechanism, and can be compared to experiments in gerbils by Collett *et al.* (1986).

The hippocampus and navigation in primates

Whether or not analogues of place cells exist in the hippocampus of monkeys remains a controversial question. One problem is the technical difficulty of performing electrophysiological recordings in freely moving monkeys. However, using a mobile robot to allow navigation around the testing room, Ono *et al.* (1991) have found place specific responses in the hippocampus. More recently Rolls *et al.* (1997) have reported the existence of cells in the primate hippocampus that respond whenever the monkey looks at a particular spatial location. These results indicate that the primate hippocampus may have an analogous role in spatial processing to that of the rat, but also indicate some of the ways in which their roles might differ. For further discussion of these issues see Burgess *et al.* (1998).

We have recently begun to apply our research into the neural mechanisms of rat navigation to humans, by using functional imaging of subjects navigating in a virtual reality town (Maguire *et al.*, 1998). In this task regional cerebral blood flow (rCBF) in the right hippocampus was found to be significantly elevated during navigation compared to following a trail of arrows. Interestingly, rCBF in the right hippocampus and (to a lesser degree) the right inferior parietal cortex was found to correlate significantly with the accuracy of heading towards the goal. We interpret these findings as consistent with our picture of the output of the hippocampal system providing the direction of the goal from the animal's current location, with the parietal cortex calculating the egocentric body-turns required to reach the goal, avoiding obstacles on the way. Interestingly, speed of navigation was found to correlate with rCBF in the right caudate nucleus of the basal ganglia. This finding might indicate a possible source for the firing of 'speed cells', recorded on axons near the hippocampus in rats, whose firing rate is linearly proportional to speed of running, see O'Keefe *et al.* (1998).

The reported similarity between the navigation of rats and young infants (Hermer and Spelke, 1994) and our recent work on human navigation raises the prospect of testing some of the predictions of our model of navigation in behavioural experiments on humans.

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