Hippocampus and Cognitive Maps

(Muller, R.U., Kubie, J.L., Bostock, E.M., Taube, J.S., and Quirk, G.J., "Spatial firing correlates of neurons in the hippocamplal formation of freely moving rats", in *Brain and Space*, J. Paillard, ed., Oxford University Press, 1991, pp 296-333)

The existence of a map-like component of the navigational system in rats is inferred from their ability to solve spatial problems too complex to be solved with a taxon method.

In the *cognitive mapping theory* the ability of rats to swim directly to a hidden goal is interpreted as the an example of the ability to find *geodesics* between arbitrary pairs of points.

O'Keefe and Nadel proposed that the *hippocampus* is the region of the brain in which the mapping capacity of the navigational system is localized.

The Hippocampus

The hippocampus is part of the *limbic lobe* which is the oldest (evolutionary) part of the cortex. The limbic cortex lies at the bottom of the cortex and forms a ring around the brain stem (the Latin for "border" is limbus).

The hippocampus is near the bottom of the limbic lobe, near the temporal lobe of the cortex.

It has been theorized that the limbic system is concerned with emotions, and perception of internal body state, and acts as an interface between the higher cortical areas and the lower level brainstem areas.

In humans, the hippocampus, along with associated structures in the temporal lobes, seems to be involved in the transfer of items from short-term memory to long-term memory, as well as in learning.

The proposition that the hippocampus was the locus of the cognitive map in rats was based on three lines of evidence:

- Lesions of the hippocampus primarily cause deficits in spatial mapping abilities.
- The hippocampal EEG has been shown to be correlated with changes in the locomotor state of the rat (e.g. whether the rat is moving or still).
- Individual hippocampal neurons have firing rates correlated with the activity of the rat.

Place Cells and Maps

Place cells are neurons found in the hippocampus whose firing rate varies strongly with head position of a freely moving rat. A place cell is intensely active only when the head is within a bounded region of space. Outside of this firing field, the cell exhibits very little activity.

Criticisms of the Place Cell Theory

The idea that cells in the hippocampus are *place cells* has been criticized by some. One of the criticisms is based on the observation that these cell's firing rates are not only correlated with spatial location, but also with specific aspects of the animal's behaviour.

It has also been suggested that the hippocampus solves spatial problems with taxons rather than locale methods. In this view, each place cell signals the rat's arrival at a critical locus in a route. In turn, the place cell discharge activates the motion required to go to the next place in the route.

This "taxon" model would predict that place cells would exhibit head orientation specificity as well as head location specificity, since the effective cue configuration (local view) depends on head orientation.

Basic Properties of Place Cells

The study by Muller *et al* looked at measuring the neural activity of hippocampus cells in rats, as a function of spatial head position and head orientation, as rats wandered about in a cylindrical enclosure.

The spatial firing patterns of complex spike cells ("place-like" cells) exhibited distinct firing fields.

Fields vary according to angular location, size and peak firing rate, but each firing field is either elliptic or crescent shaped.

Elliptic fields are usually found away from the cylinder wall, while the peak of the crescent shaped fields are found near the wall.

In rectangular enclosures, linear firing fields, located near the walls, are also found.

The existence of linear and crescent shaped fields is unexpected from a Euclidean mapping model, in which the distance between points is represented by the distance between firing field centres.

Another problem with the Euclidean mapping approach is that, in this approach, the rat's position is represented by the discharge of all cells whose field contains the rat's real-world position. The computed position would then be some sort of weighted average of the positions of the field centres of the active cells, weighted by the discharge rate of each cell.

As the rat approaches a wall, this computed position would be displaced away from the wall, because there are no cells with firing field centres outside the wall.

Directional Properties of Place Cells

Muller *et al* did further experiments, aimed at determining whether place-cell discharge depends on head position.

Their study found almost complete independence of place cell firing rates with head position.

(there is an apparent head direction dependence in the firing rates due to the fact that rats can't direct their head towards the centre of the cylinder when their heads are near to the cylinder wall)

The constancy of firing rate with head orientation occurs even when different head orientations must be associated with different views of salient objects.

Head direction specificity was observed in rats that were trained to run in multi-armed mazes. It is hypothesized that place-cell activity refelcts kinematic properties of the rat's envrionment.