Stimulus Dependence of Place Cells in Rats

In the experiments described by Muller *et al*, hungry rats move about in a cylindrical chamber, 76 cm in diameter, looking for food pellets.

The sides of the cylinder is uniformly grey except for a single white sheet of cardboard covering 100 degrees of arc on the wall. This white patch presumably acts as a visual spatial reference cue.

When the cue card was moved to a different angular location on the cylinder wall, the firing field patterns of the place field also rotated.

The rotation of the firing field demonstrates the salience of the cue card.

It was found that, if there was a set of salient stimuli, *removal* of one of the stimuli did not affect the firing field pattern of a place cell.

Thus each place cell appears to be partially controlled by all elements of a stimulus set.

Individual cells are not selectively responsive to particular subsets of the available stimuli.

Location specific firing can be supported by auditory, tactile and olfactory stimuli as well as visual.

Removing all of the stimuli caused the location-specific firing to break down - cells either ceased firing, or fired in a spatially homogeneous fashion.

The results of these cue-deletion experiments provide strong evidence against the theory that place cells are high-order multi-sensory units (like cells in the visual cortex), as that theory would predict that the firing field would depend on the configuration of sensory stimuli.

A possible modification to the sensory place-cell theory, is that some form of *pattern completion* is being performed, where the deleted stimuli are "filled-in".

Representations of Multiple Environments

Some place cells that are silent everywhere in one environment may respond in another environment (an environment here refers to a space with a particular layout of salient sensory stimuli).

About 15% of place cells respond in any particular environment.

This “active subset” of place cells is characteristic for a given environment. The same cells are active each time the rat is returned to the same surroundings.

If a cell is recorded in two sufficiently different environments it may respond in both, only one, or neither environment.

If a cell responds in two different environments, it's firing field patterns in these two environments are usually unrelated.

Major changes in firing pattern occur even if the environments are simple topological variants (e.g. cylindrical vs. rectangular enclosures).

Each environment that is experienced by the rat appears to get “mapped” onto the population of place cells in the hippocampus.

Some changes to the environment result in a complete remapping, such as in moving from a cylindrical to a rectangular enclosure.

Some changes result in no remapping, such as in the case of rotation of the cue stimuli.

Other changes result in a partial remapping, such as in the case of scaling the height and diameter of a cylindrical enclosure. Partial remappings are observed when an opaque or transparent barrier is placed onto the floor of the cylinder. Cells near the barrier have their firing suppresed while cells away from the cylinder walls are unchanged.

The nature of changes in the place cell population associated with remappings argues strongly against the hypothesis of place cells as sensory cells.

The positional firing patterns of individual cells do not stretch to match the distortions expected in going from a cylindrical space to a rectangular space, as would be expected if each cell is triggered only by the local stimulus configuration or view.

Alterations in firing pattern caused by the presence of a barrier seem to be organized in terms of regions and not in terms of changes in stimulus configuration caused by the barrier.

Remappings appear to take the structure of the environment into account and the firing field patterns change in cohesive ways and not independently for individual place cells.

Place-like Cells in MEC

Cells in cortical areas adjacent to the hippocampus (the hippocampal formation) exhibit three types of spatial responses:

- Location specific (hippocampus place cells, MEC, subiculum, dentate gyrus)
- Head direction specific (subiculum and post-subiculum)
- Head position and direction specific (subiculum)

The MEC (medial entorhinal cortex) is the major source of cortical input to the hippocampus. It is the target of "highly processed" sensory information from the polymodal sensory cortical regions.

MEC cells, show place-cell-like behaviour, but unlike those in hippocampus, the MEC cells appear to be active in multiple environments, and the positional firing fields of MEC cells in different envrionments appear to be related.

Thus, MEC cells appear to be more "sensory" than hippocampus cells, and the hippocampus cells may be doing some sort of topological transformation on the output of the MEC.

However, there is cyclical feedback from the hippocampus to the MEC, suggesting that the actual functioning is more complicated.

Head-Direction Specific Cells

Post-Subiculum Cells

Cells that have head direction selectivity are found in the post-subiculum region of the hippocampal formation.

These cells fire only when the rat's head points in a range of angles in the horizontal plane.

The preferred directions for individual cells occur with equal frequency in all directions, so that there is no overall preferred direction for the population of cells.

Directional firing is independent of behaviour; it persists even if the rat is carried about.

Rotations of cue stimuli results in equal rotation of the head-direction firing fields, just as do place cells. This suggests that place cells and head-direction cells use a common angular reference.

Head-direction cell firing fields did not change in different environments, suggesting that there is no analog to the "remapping" observed in place cells. The angular distance between the preferred direction of arbitrary cell pairs is thus the same in all envrionments.

Subiculum Cells

Head-direction specific cells are also found in the subiculum. This area receives input from the post-subiculum as well as the hippocampus.

In addition to head-direction specific cells, the subiculum contains cells which exhibit place-like firing fields, as well as cells which exhibit both position and direction specificity.