Head direction cells

Many mammals possess neurons called head direction (HD) cells, which are active only when the animal's head points in a specific direction within an environment. These neurons fire at a steady rate (i.e. they do not show adaptation), but show a decrease in firing rate down to a low baseline rate as the animal's head turns away from the preferred direction (usually returning to baseline when facing about 45° away from this direction).

These cells are found in many brain areas, including the post-subiculum, retrosplenial cortex, the thalamus (the anterior and the lateral dorsal thalamic nuclei), lateral mammillary nucleus, dorsal tegmental nucleus, striatum and entorhinal cortex (Sargolini et al, Science, 2006).

The system is related to the place cell system, which is mostly orientation-invariant and location-specific, while HD cells are mostly orientation-specific and location-invariant. However, HD cells do not require a functional hippocampus, where strong place cells are found, to show their head direction specificity. Head direction cells are not sensitive to geomagnetic fields (i.e. they are not "magnetic compass" cells), and are neither purely driven by nor are independent of sensory input. They strongly depend on the vestibular system, and the firing is independent of the position of the animal's body relative to its head.

Some HD cells exhibit anticipatory behaviour: the best match between HD activity and the animal's actual head direction has been found to be up to 95 ms in future. That is, activity of head direction cells predicts, 95 ms in advance, what the animal's head direction will be.

Vestibular influences

The HD compass is inertial: it continues to operate even in the absence of light. Experiments have shown that the inertial properties are dependent on the vestibular system, especially the semicircular canals of the inner ear, which respond to rotations of the head. The HD system integrates the vestibular output to maintain a signal of cumulative rotation. The integration is less than perfect, though, especially for slow head rotations. If an animal is placed on an isolated platform and slowly rotated in the dark, the alignment of the HD system usually shifts a little bit for each rotation. If an animal explores, in the dark, an environment with no directional cues, the HD alignment tends to drift slowly and randomly over time.

Visual influences

One of the most interesting aspects of head direction cells is that their firing is not fully determined by sensory features of the environment. When an animal comes into a novel environment for the first time, the alignment of the head direction system is arbitrary. Over the first few minutes of exploration, the animal learns to associate the landmarks in the environment with directions. When the animal comes back into the same environment at a later time, if the head direction system is misaligned, the learned associations serve to realign it.

It is possible to temporarily disrupt the alignment of the HD system, for example by turning out the lights for a few minutes. Even in the dark, the HD system continues to operate, but its alignment to the environment may gradually drift. When the lights are turned back on and the animal can once more see landmarks, the HD system usually comes rapidly back into the normal alignment. Occasionally the realignment is delayed: the HD cells may maintain an abnormal alignment for as long as a few minutes, but then abruptly snap back. If these sorts of misalignment experiments are done too often, the system may break down. If an animal is repeatedly disoriented, and then placed into an environment for a few minutes each time, the landmarks gradually lose their ability to control the HD system, and eventually, the system goes into a state where it shows a different, and random, alignment on each trial.
There is evidence that the visual control of HD cells is mediated by the postsubiculum. Lesions of the postsubiculum do not eliminate thalamic HD cells, but they often cause the directionality to drift over time, even when there are plenty of visual cues. Thus, HD cells in postsub-lesioned animals behave like HD cells in intact animals in the absence of light. Also, only a minority of cells recorded in the postsubiculum are HD cells, and many of the others show visual responses. In familiar environments, HD cells show consistent preferred directions across time as long as there is a polarizing cue of some sort that allows directions to be identified (in a cylinder with unmarked walls and no cues in the distance, preferred directions may drift over time).

History

Head direction cells were first noticed by James B. Ranck, Jr., in the rat postsubiculum, a structure that lies near the hippocampus on the dorsocaudal brain surface. Ranck reported his discovery in a brief abstract in 1984. A postdoctoral fellow working in his laboratory, Jeffrey S. Taube, made these cells the subject of his research, and summarized his findings in a pair of papers in the Journal of Neuroscience in 1990.[1] [2] These seminal papers served as the foundation for all of the work that has been done subsequently. Taube, after taking a position at Dartmouth College, has devoted his career to the study of head direction cells, and has been responsible for a number of the most important discoveries, as well as writing several key review papers.

The postsubiculum has numerous anatomical connections. Tracing these connections led to the discovery of head direction cells in other parts of the brain. In 1993, Mizumori and Williams reported finding HD cells in a small region of the rat thalamus called the lateral dorsal nucleus.[3] Two years later, Taube found HD cells in the nearby anterior thalamic nuclei.[4] Chen et al. found limited numbers of HD cells in posterior parts of the neocortex.[5] The observation in 1998 of HD cells in the lateral mammillary area of the hypothalamus completed an interesting pattern: the parahippocampus, mammillary nuclei, anterior thalamus, and retrosplenial cortex are all elements in a neural loop called the Papez circuit, proposed by Walter Papez in 1939 as the neural substrate of emotion. Limited numbers of robust HD cells have also been observed in the hippocampus and dorsal striatum. Recently, substantial numbers of HD cells have been found in the medial entorhinal cortex, intermingled with spatially-tuned grid cells.

The remarkable properties of HD cells, most particularly their conceptual simplicity and their ability to maintain firing when visual cues were removed or perturbed, led to considerable interest from theoretical neuroscientists. Several mathematical models were developed, which differed on details but had in common a dependence on mutually excitatory feedback to sustain activity patterns: a type of working memory, as it were.[6]

For a review on the HD system and place field system, see Muller (1996): "A quarter of a Century of Place Cells", Sharp et al. (2001): "The anatomical and computational basis of rat HD signal".

Notes
[1] Taube et al., 1990a
[2] Taube et al., 1990b
[5] Chen et al., 1994

References
Head direction cells

doi:10.1007/BF00243212. PMID 7843305.


Article Sources and Contributors

Contributors: Bnjjkl, Cadillac, Digfarnough, EncycloPetey, IceCreamAntisocial, Katharineamy, Lootie496, Melaen, M6t01633, M6t8lv, PigFlu Onik, Rich Farnbrough, Rjulinsm, Tabletop, 9 anonymous edits

License

Creative Commons Attribution-Share Alike 3.0 Unported
http://creativecommons.org/licenses/by-sa/3.0/
Grid cell

A grid cell is a type of neuron that has been found in the brains of rats and mice; and it is likely to exist in other animals including humans. In a typical experimental study, an electrode capable of recording the activity of an individual neuron is implanted in the cerebral cortex of a rat, in a part called the dorsomedial entorhinal cortex, and recordings are made as the rat moves around freely in an open arena. For a grid cell, if a dot is placed at the location of the rat's head every time the neuron emits an action potential, then as illustrated in the adjoining figure, these dots build up over time to form a set of small clusters, and the clusters form the vertices of a grid of equilateral triangles. This regular triangle-pattern is what distinguishes grid cells from other types of cells that show spatial firing correlates. By contrast, if a place cell from the rat hippocampus is examined in the same way (i.e., by placing a dot at the location of the rat's head whenever the cell emits an action potential), then the dots build up to form small clusters, but frequently there is only one cluster (one "place field") in a given environment, and even when multiple clusters are seen, there is no perceptible regularity in their arrangement.

Grid cells were discovered in 2005 by Edvard Moser, May-Britt Moser and their students Torkel Hafting, Marianne Fyhn and Sturla Molden at the then Centre for the Biology of Memory (CBM) in Norway. The arrangement of spatial firing fields all at equal distances from their neighbors led to a hypothesis that these cells encode a cognitive representation of Euclidean space. The discovery also suggested a mechanism for dynamic computation of self-position based on continuously updated information about position and direction.

What makes grid cells especially interesting is that the regularity in grid spacing does not derive from any regularity in the environment or in the sensory input available to an animal. In other words, grid cells appear to encode a type of abstract spatial structure that is constructed inside the brain and imposed on the environment by the brain with no regard for the sensory features of the environment. Thus, the discovery of grid cells may provide a verification of Immanuel Kant's theory that Euclidean space constitutes a synthetic a priori—a structure that is not purely logical but is constructed by the mind without requiring information from the environment. (In more modern terminology, a "synthetic a priori" is a structure that comes from nature rather than nurture; i.e., a structure that is innate rather than learned).

Background

In 1971, John O'Keefe and Jonathon Dostrovsky reported the discovery of place cells in the rat hippocampus—cells that fire action potentials when an animal passes through a specific small region of space, which is called the place field of the cell. This discovery, although controversial at first, led to a series of investigations that culminated in the 1978 publication of a book by O'Keefe and his colleague Lynn Nadel called The Hippocampus as a Cognitive Map—the book argued that the hippocampal neural network instantiates cognitive maps as hypothesized by the psychologist Edward C. Tolman. This theory aroused a great deal of interest, and motivated hundreds of
Grid cells are neurons that fire when a freely moving animal traverses a set of small regions (firing fields) which are roughly equal in size and arranged in a periodic triangular array that covers the entire available environment. Cells with this firing pattern have been found in all layers of the dorsocaudal medial entorhinal cortex (dMEC), but cells in different layers tend to differ in other respects. Layer II contains the largest density of pure grid cells, in the sense that they fire equally regardless of the direction in which an animal traverses a grid location. Grid cells from deeper layers are intermingled with cells with conjunctive grid and head direction properties (i.e., in layers III, V and VI there are cells with a grid-like pattern that fire only when the animal is facing a particular direction).

Grid cells that lie next to one another (i.e., cells recorded from the same electrode) usually show the same grid spacing and orientation, but their grid vertices are displaced from one another by apparently random offsets. Cells recorded from separate electrodes at a distance from one another, however, frequently show different grid spacings. Cells that are located more ventrally (that is, farther from the border between the entorhinal cortex and postrhinal cortex) generally have larger firing fields at each grid vertex, and correspondingly greater spacing between the grid vertices. The total range of grid spacings is not well established: the initial report described a roughly twofold range of grid spacings (from 39 cm to 73 cm) across the dorsalmost part (upper 25%) of the MEC, but there are indications of considerably larger grid scales in more ventral zones. Brun et al. (2008) recorded grid cells from multiple levels in rats running along an 18 meter track, and found that the grid spacing expanded from about 25 cm in their dorsalmost sites to about 3 m at the ventralmost sites. These recordings only extended 3/4 of the way to the ventral tip, so it is possible that even larger grids exist.

Grid cell activity does not require visual input, since grid patterns remain unchanged when all the lights in an environment are turned off. When visual cues are present, however, they exert strong control over the alignment of
the grids: rotating a cue card on the wall of a cylinder causes grid patterns to rotate by the same amount. Grid patterns appear on the first entrance of an animal into a novel environment, and usually remain stable thereafter. When an animal is moved into a completely different environment, grid cells maintain their grid spacing, and the grids of neighboring cells maintain their relative grid vertex offsets.

Interactions with hippocampal place cells

When a rat is moved to a different environment, the spatial activity patterns of hippocampal place cells usually show "complete remapping"—that is, the pattern of place fields reorganizes in a way that bears no detectable resemblance to the pattern in the original environment. If the features of an environment are altered less radically, however, the place field pattern may show a lesser degree of change, referred to as "rate remapping", in which many cells alter their firing rates but the majority of cells retain place fields in the same locations as before. Fyhn et al. (2007) examined this phenomenon using simultaneous recordings of hippocampal and entorhinal cells, and found that in situations where the hippocampus shows rate remapping, grid cells show unaltered firing patterns, whereas when the hippocampus shows complete remapping, grid cell firing patterns show unpredictable shifts and rotations.

Theta rhythmicity

Neural activity in nearly every part of the hippocampal system is modulated by the limbic theta rhythm, which has a frequency range of about 6–9 Hz in rats. The entorhinal cortex is no exception: like the hippocampus, it receives cholinergic and GABAergic input from the medial septal area, the central controller of theta. Grid cells, like hippocampal place cells, show strong theta modulation. Grid cells from layer II of the MEC also resemble hippocampal place cells in that they show phase precession—that is, their spike activity advances from late to early phases of the theta cycle as an animal passes through a grid vertex. Most grid cells from layer III do not precess, but their spike activity is largely confined to half of the theta cycle. The grid cell phase precession is not derived from the hippocampus, because it continues to appear in animals whose hippocampus has been inactivated by a local anesthetic.

Possible functions

Many species of mammals can keep track of spatial location even in the absence of visual, auditory, olfactory, or tactile cues, by integrating their movements—the ability to do this is referred to in the literature as path integration. A number of theoretical models have explored mechanisms by which path integration could be performed by neural networks. In most models, such as those of Samsonovich and McNaughton (1997) or Burak and Fiete (2009), the principal ingredients are (1) an internal representation of position, (2) internal representations of the speed and direction of movement, and (3) a mechanism for shifting the encoded position by the right amount when the animal moves. Because cells in the MEC encode information about position (grid cells) and movement (head direction cells and conjunctive position-by-direction cells), this area is currently viewed as the most promising candidate for the place in the brain where path integration occurs. However, the question remains unresolved, as in humans the entorhinal cortex does not appear to be required for path integration. Burak and Fiete (2009) showed that a computational simulation of the grid cell system was capable of performing path integration to a high level of accuracy.

Hafting et al. (2005) suggested that a place code is computed in the entorhinal cortex and fed into the hippocampus, which may make the associations between place and events that are needed for the formation of memories. In contrast to a hippocampal place cell, a grid cell has multiple firing fields, with regular spacing, which tessellate the environment in a hexagonal pattern. The unique properties of grid cells are as follows:

1. Grid cells have firing fields dispersed over the entire environment (in contrast to place fields which are restricted to certain specific regions of the environment)
2. The firing fields are organized into a hexagonal grid
3. Firing fields are generally equally spaced apart, such that the distance from one firing field to all six adjacent firing fields is approximately the same (though when an environment is resized, the field spacing may shrink or expand different in different directions; Barry et al. 2007)

4. Firing fields are equally positioned, such that the six neighboring fields are located at approximately 60 degree increments

The grid cells are anchored to external landmarks, but persist in darkness, suggesting that grid cells may be part of a self-motion based map of the spatial environment.

See also

• Border cells, discovered in 2008.

References


External links

• Centre for the Biology of Memory (CBM) (http://www.cbm.ntnu.no/english)
Article Sources and Contributors


Image Sources, Licenses and Contributors


License

Creative Commons Attribution-Share Alike 3.0 Unported
http://creativecommons.org/licenses/by-sa/3.0/
Place cell

Place cells are neurons in the hippocampus that exhibit a high rate of firing whenever an animal is in a specific location in an environment corresponding to the cell's "place field". These neurons are distinct from other neurons with spatial firing properties, such as grid cells, border cells, head direction cells, and spatial view cells. In the CA1 and CA3 hippocampal subfields, place cells are believed to be pyramidal cells, while those in the dentate gyrus are believed to be granule cells.\[2\]

Place cells were first described in rats by O'Keefe and Dostrovsky.\[3\] Based on this discovery, O'Keefe and Nadel hypothesized that the primary function of the rat hippocampus is to form a cognitive map of the rat's environment.\[4\] Ekstrom and colleagues have found cells with similar properties in the human hippocampus, using extracellular recordings from epilepsy patients undergoing invasive monitoring of their brain activity.\[5\]

Place fields

Place cells show increased frequency of firing when an animal is in a specific area referred to as the cell's place field. The firing rate increase can be quite dramatic, from virtually zero outside the field to as much as 100 Hz (for brief periods) in the middle of the place field. When a rat forages randomly in an environment, place fields are only weakly modulated by the direction the rat faces, or not at all. However, when an animal engages in stereotyped behaviour (e.g. shuttling between goal locations), place cells tend to be active in the place field on passes in one direction only.\[6\]

On initial exposure to a new environment, place fields become established within minutes. The place fields of cells tend to be stable over repeated exposures to the same environment. In a different environment, however, a cell may have a completely different place field or no place field at all. This phenomenon is referred to as "remapping". In any particular environment, roughly 40-50% of the hippocampal place cells will be active.\[7\][8]

In an environment with few or no directional cues (for instance, a circular environment surrounded by black curtains), place fields will tend to have a fixed radial position, but the entire set of place fields may rotate around the maze as predicted by a theory that rats are slowly losing their orientation.\[9\] If a polarizing cue is introduced (commonly a large white rectangle of paper), place fields will tend to have fixed positions relative to the cue. If the cue is moved while the animal can see it, place fields will tend to remain unaffected; however, if the animal is briefly removed from the environment then the cue is moved and the animal returned, the place fields will rotate so as to maintain their position relative to the cue card. Although visual cues seem to be the primary determinant of place cell
firing, it is worth noting that firing persists in the dark, suggesting that proprioception or other senses contribute as well.

In an environment in which a rat is constrained to walk along a linear track, place fields will often have a directional component in addition to a place component. A place cell that fires at a particular location while the rat walks in one direction along the track will not necessarily fire as the rat visits that location from the other direction. If the rat frequently turns around at the same point, however, place fields there will often be independent of direction.

The size of place fields and their signal to noise ratio varies depending on the region of brain in consideration. In the hippocampus, place fields are smallest and sharpest at the dorsal pole, becoming larger toward the ventral pole.\textsuperscript{[10]}

This may reflect the topography of projections to the hippocampus. For example, the ventral hippocampus receives much more input from the amygdala, while dorsal hippocampus is more preferentially innervated by entorhinal cortex.

Spatial modulated cells are also found in the entorhinal cortex, which feed input from neocortex into the hippocampus. Neurons in the lateral entorhinal cortex exhibit little spatial selectivity,\textsuperscript{[11]} while neurons of the medial entorhinal (MEA) cortex exhibit multiple "place fields" that are arranged in an hexagonal pattern, and are therefore called "grid cells". These fields and spacing between fields increase from the dorso-lateral MEA to the ventro-medial MEA\textsuperscript{[12],[13]}


Phase precession

The hippocampus is one of many brain structures that can show a characteristic 4-12 Hz oscillation, theta rhythm, in an EEG recording. The oscillation has been observed in all mammalian species tested. In both rats and humans, it is associated with real or virtual movement through space.

When a neuron discharges, it can be said to fire in relation to the current phase of a theta cycle (0-360 degrees). When a rat enters a cell's place field, the cell will initially discharge when perisomatic inhibition is weakest. For theta recorded in the CA1 pyramidal cell layer, this approximately corresponds with the peak of the oscillation. On each following cycle as the rat progresses through the field, the cell will discharge at earlier and earlier phases, typically stopping just before the trough of the cycle (as recorded in CA1 stratum pyramidale). In other words, the place cell produces a rhythmic discharge of a slightly higher frequency than the ongoing theta oscillation.

Because place fields of different cells overlap, at any particular time the rat will be at different distances in different fields, so each place cell will fire at a different phase of theta, allowing the rat's position to be determined with good precision. This potentially provides an alternative temporal code for location. Phase precession also results in the compression of temporal sequences of place cell firing - a phenomenon believed to facilitate synaptic plasticity. There is evidence that phase precession is related to depolarisation of the neuron, such that the firing rate and firing phase of the cell are tightly coupled. However, phase precession can also be robustly independent of firing rate in freely moving animals. This caveat of phase precession, which alludes to the potential neural mechanisms underlying it, requires further investigation before arriving at a definitive answer.

References

[1] Skaggs et al., 1996


**External links**

- Neural Basis of Spatial Memory (http://www.bris.ac.uk/synaptic/research/projects/memory/spatialmem.htm), from Bristol University
- Place Cells in the Hippocampus (http://homepages.nyu.edu/~eh597/place.htm)
Article Sources and Contributors


Image Sources, Licenses and Contributors


License

Creative Commons Attribution-Share Alike 3.0 Unported
http://creativecommons.org/licenses/by-sa/3.0/