NEURAL CODING

Double code in place cells

Place cells are hippocampal neurons that fire when an animal is in a particular location (the neuron's 'place field'). Although their existence in rodents is well established, it has been difficult to prove that neurons in the human hippocampus respond in the same way. Ekstrom *et al*. took advantage of the opportunity to record from individual neurons in the hippocampi of patients undergoing intracranial recording before potential surgery for epilepsy. They found that hippocampal neurons responded preferentially to specific spatial locations, whereas neurons in the parahippocampal region were more likely to respond to specific views or visual landmarks.

Another recent study, this time in rats, provided more insight into how place cells might code specific types of information. Within a place field, a neuron's firing can vary in both rate and phase relative to the hippocampal theta rhythm. Huxter and colleagues propose that these two measures vary independently of each other, and that each carries different information.

The authors recorded the hippocampal electroencephalogram (EEG) and the firing of individual neurons in the hippocampus in rats as they ran along a linear track. Each place cell fired when the rat was in a particular region of the track, but as the rat moved through this place field the phase of the cell's firing changed — each spike was slightly earlier, with respect to the theta rhythm, than the previous one.

This 'phase precession' means that the relative phase of firing at a given time correlates closely with the position of the animal within the place field of the neuron. The phase also correlates with the firing rate at any given moment, but less strongly.

By comparing the recordings from different trials, Huxter *et al*. showed that phase precession and firing rate can be dissociated, both within and between runs. For example, runs with a high average firing rate and those with a low firing rate showed similar phase precession. This means that the neurons can encode two variables independently.

The relative phase of firing seems to encode the position of the animal within the place field. So what is encoded by the firing rate? Huxter *et al*. find that firing rate correlates with the velocity of the animal, although this correlation varies between cells. They propose that firing rate might code for velocity, but that it might also be influenced by other factors, such as the presence of objects or reinforcers.

As the authors point out, this dual code could be relevant to the involvement of the hippocampus in both spatial and episodic memory. The hippocampus is not the only brain area to show theta EEG activity — other cortical areas do too, raising the possibility that other cortical neurons might also use temporal and rate codes for different functions.

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References and links

ORIGINAL RESEARCH PAPERS Ekstrom, A. D. *et al.* Cellular networks underlying human spatial navigation. *Nature* **425**, 184-187 (2003) | Huxter, J. *et al*. Independent rate and temporal coding in hippocampal pyramidal cells. *Nature* **425**, 828-832 (2003)