

Classification of hippocampal interneurons in freely moving rats

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To supplement functional classifications of hippocampal interneurons based initially on intracellular and juxtacellular staining, we made extracellular recordings of 111 interneurons from the hippocampuses of 18 freely moving rats. The recordings were done as the animals retrieved food pellets scattered into a 76cm diam cylinder. This simple task ensures that the rats spend most of their time running and therefore that the hippocampal EEG dwells most of the time in the theta state. Waveforms were recorded with tetrodes in alveus/oriens, stratum pyramidale and superficial stratum radiatum of CA1 but at the time of writing no depth classification of cells had been made.

In the taxonomy we used, the first separation is into 81 theta-modulated cells whose autocorrelations showed clear oscillations at the average frequency of 8.26 Hz and 30 theta independent cells whose autocorrelations were unmodulated by the theta rhythm. The distribution of an "oscillation score" is strongly bimodal and moreover separates the cells of the two types in other ways. For example, the average duration of the negative phase of the extracellular action potential 164 ± 4.6 μ sec for theta-modulated cells and 132 ± 7.5 μ sec for theta-independent cells. The average firing rate is statistically the same for the two cell classes but the firing rate increases much more for the theta-modulated cells as the running speed goes from 0 to 12cm per sec.

We have not yet detected any subtypes for theta-independent cells, but for theta-modulated cells the phase for peak firing rate in theta-phase histograms fall into relatively well-defined groups. Moreover, the peak phases for these groups correspond quite well to fully-identified cell types in anaesthetized rats. A preliminary analysis of the firing of 45 theta-modulated cells in association with sharp wave envelopes during slow wave sleep suggests that several patterns may be seen for cells that have the same peak firing phase during theta.

We conclude that the organization of the hippocampal theta rhythm is very similar during free movement and during urethane-ketamine anaesthesia, despite the considerable difference in characteristic frequency which is around 8 Hz in intact animals and 4Hz in urethane-ketamine anaesthetized animals. One implication is that the oscillation frequency is set in both cases by a unitary source as opposed to a dependence on the intrinsic properties of the interneurons since in the latter case we would expect timing and not phase relations to be preserved.