

## **Theta Rhythm and the Origin of Variable Spatial Scaling Along the Septo-Temporal Axis of the Hippocampus**

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The spatial scaling of place specific activity in the rodent hippocampus varies systematically from high spatial resolution at the septal pole to low spatial resolution at the temporal pole (Jung et al., 1994; Kjelstrup et al., 2003). In principle, this variable scaling permits the read-out of spatial proximity relationships from spatial population vector correlations over much larger spaces than would be possible from a fixed-scale encoding scheme, while still maintaining high resolution. What is the physiological basis of this variable resolution?

Decoupling movement in space from ambulatory motion, by having the animal activate and ride on a mobile platform, results in marked attenuation of the amplitude of the local theta rhythm and of the depth of modulation of pyramidal activity at the theta frequency. There is a corresponding enlargement of the spatial scale factor of 'place cells' in the dorsal hippocampus (Terrazas et al., 2003).

During REM sleep, theta is present in the hippocampal EEG and the hippocampal population vector changes at a rate similar to that during actual movement in space. A less well known, but prevalent condition during sleep (about 20% of total sleep) is the Small Irregular Activity (SIA) state. During SIA, hippocampal EEG becomes flat (i.e., no theta or sharp waves), and a small number of otherwise typical CA1 pyramidal cells becomes tonically active for periods of about 8 sec on average (Jarosiewicz et al., 2002). In other words, the population vector is not updated at all, but appears 'frozen' in one state.

Such observations support the hypothesis (originally proposed by O'Keefe and Nadel, 1978) that the self-motion signal that updates the hippocampal population vector (and hence sets the scale of the spatial representation) is embodied in the theta rhythm. Given the shift in spatial scale factor along the septo-temporal axis, a corollary prediction is that the theta power at a given speed of motion may vary systematically along the septo-temporal axis of the hippocampus. Because the amplitude of the theta rhythm in the EEG varies as a function of electrode location and other factors, such as cell alignment and packing density, and because the parameter of interest is, in any case, the effect of the theta rhythm on cell discharge characteristics, the most appropriate means of testing this hypothesis is to assess depth of modulation of cell discharge with respect to a fixed EEG reference near the hippocampal fissure of the dorsal hippocampus. Using tetrode arrays, multiple single neurons were recorded simultaneously from the dorsal,

intermediate, and deep ventral regions of the hippocampus of rats running on a simple linear track. Depth of modulation in firing rate, referred to the theta rhythm recorded near the hippocampal fissure in the dorsal (septal) region, indeed declined systematically and substantially along the dorso-ventral axis of the hippocampus.

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