Circuitry controlling Theta and Non-Theta states of the Hippocampal EEG

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In a series of studies, we have shown that states of the hippocampal EEG (theta and non-theta) are controlled by a system of connections from the brainstem to the diencephalon to the septum/hippocampus. Specifically, two brainstem-originating systems exert pronounced (and opposing) actions on the electrical activity of the hippocampus; that is, hippocampal synchronizing (theta rhythm) and desynchronizing (non-theta) systems, arising from the nucleus pontis oralis (RPO) and median raphe nucleus (MR), respectively. During theta, tonically firing cells of the RPO activate neurons of the supramammillary nucleus which, in turn, convert this steady barrage into a rhythmical pattern of discharge which is relayed to pacemaking cells of the medial septum/vertical limb of the diagonal band nucleus (MS/DBv) to generate theta. During states of hippocampal desynchronization, a subset of 5-HT, septal-projecting MR cells discharge at enhanced rates, activate local GABAergic cells of the MS/DBv which, in turn, inhibit GABAergic/cholinergic pacemaking cells of the MS/DBv in the desynchronization of the hippocampal EEG. In recent reports, we have shown that a 'theta rhythmic signal' exits the hippocampus and 'reverberates' throughout structures of Papez's circuit. Cells that fire rhythmically with theta have been identified in several structures of Papez's circuit (or extended circuit) including the mammillary bodies, the ventral tegmental nucleus (of Gudden), the anteroventral nucleus of the thalamus, and the retrosplenial cortex. Separate reports have identified head direction (HD) cells in the same structures of Papez's circuit. Interestingly, however, theta and HD cells are present in separate subnuclei of structures containing them. HD cells have been shown to be important for a rat's sense of direction and spatial navigation. We have suggested that directional information is critical for a rat (and other species) when engaged in locomotor/exploratory behaviors (theta states) and less so during non-locomotor activities such as grooming or consumatory acts (non-theta states). Accordingly, theta may serve as an important signal involved in the differential processing of HD activity under the two conditions (e.g., locomotion and grooming); that is, only when HD activity is coupled with theta-rhythmic discharge is head direction activity processed and used to guide spatial behaviors. In sum, we have described critical ascending systems involved in controlling theta and non theta states of the hippocampal EEG, and recently identified theta rhythmically firing neurons in structures of Papez's circuit that we suggest may be important for spatial navigation/learning in rats.