

The rhythmic theta state of the hippocampal formation  
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The hippocampus receives digested sensory information via entorhinal cortex. From there the encoded information is sent out to dentate gyrus and hippocampus proper (CA1-3). Interconnections lead to subiculum and ultimately back to entorhinal cortex. Together this limbic ring is the hippocampal formation.

The hippocampal formation generates a persistent pattern of synaptic strengths that causes pyramidal cells to fire in specific locations in the environment, becoming "place cells". Collectively these represent a learned context that can be compared to the incoming sensory information. When there is lack of correspondence, exploration is triggered to reduce the conflict: homeostasis, negative feedback control.

Exploration is associated with rhythmic activity (4-10 Hz theta rhythm), paced by the septum, generated in all components of the hippocampal formation. Theta activity enhances place cell signals and suppresses noise. The rhythm also helps to synchronize firing, optimizing the formation of stable representations. Theta state associated tonic delivery of septal ACh to hippocampal muscarinic receptors is sufficient for contrast enhancement, but theta oscillation is required for use of place cell signals in behavior.

Recent work by Ben Tessler in my lab has focused on attempting to enhance theta activity by applying transcranial electrical stimulation, an inexpensive, non-invasive way to stimulate brain. He has found that stimulation with theta-frequency interference patterns reaches deep enough to augment hippocampal theta activity, whereas stimulation with theta frequency sine waves does not. This method has potential applications in enhancement of learning and even reduction of seizures, since generalized inhibition is increased during theta.