Doughnuts in the Brain: A Toroidal Attractor Theory of the Cognitive Map

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The hippocampal formation of the mammalian brain is crucial to the storage and consolidation of 'episodic' memories: memories for experiences that unfold in space and time. The hippocampus accomplishes its role in memory by generating a unique code reflecting the spatio-temporal context of experiences. This code provides a tag or 'index' that links together sub-components of a given experience stored in a distributed form throughout the neocortex. The generation of the hippocampal code is founded on internal (a priori) mechanisms for keeping track of spatial location, and for appending information about external and internal events onto an internal spatial coordinate system or 'cognitive map'. Neurons in thalamus and midbrain ('head-direction cells') generate a 1-D periodic signal of relative head orientation in the horizontal plane as animals rotate their heads; cells in medial entorhinal cortex ('grid cells') fire in a strikingly regular, 2-D periodic, spatial pattern (‘grid field’) when an animal moves about its world. Head-direction and grid cells can be explained by a theory in which the corresponding underlying synaptic matrices determine ring (1-D) or toroidal (2-D ‘doughnut-like’) manifolds of allowed states (‘attractors’) of network activity. The speed by which the neuronal state is updated relative to the animal’s physical motion in space sets the scale of the 2-D grid field, and there are multiple such grid cell modules, each with a different movement gain, and thus each expressing a different spatial scale. Next, sets of neurons in hippocampus ('place cells'), which receive spatially periodic grid field information at multiple spatial scales, appear to provide unique (‘essentially’ non-periodic) codes for spatial location, by a Fourier synthesis-like summation on their inputs. Finally, external input to this network modulates the firing rate (but not relative location) of place cell firing, thus generating a conjunctive code for ‘what’ happened ‘where’. Although they exhibit a high degree of experience-dependent neural plasticity, these networks appear to be wired up by a self-organizing process in early post-natal development in a manner that is independent of experience (a priori). Thus, in a sense, Immanuel Kant was correct.