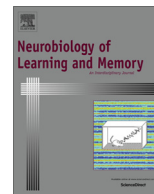


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Editorial

Pattern separation and pattern completion in the hippocampal system. Introduction to the Special Issue



For a memory system such as the hippocampus in which associatively modifiable recurrent collateral connections between a population of neurons such as the CA3 pyramidal cells are believed to store memories (Kesner & Rolls, 2015; McNaughton & Morris, 1987; Rolls, 1987; Treves & Rolls, 1991, 1994), it is important that the memory representations to be stored are as orthogonal or uncorrelated as possible, to maximize the storage capacity. Only if the sets of neuronal firing, each representing a different memory, are relatively uncorrelated with each other will the number of memories that can be stored approach the theoretical limit for an autoassociation or attractor network (Rolls, 2012a; Treves & Rolls, 1991). In this situation, there is great interest in how the hippocampal system may perform pattern separation of the patterns to be stored in CA3 to make them relatively uncorrelated (Kesner & Rolls, 2015; Treves & Rolls, 1992).

At the same time, an important property of a memory system is that it can complete a whole memory when just a partial cue for retrieval is provided. An example is the retrieval of a whole episodic memory from one part of it, for example who was present at a particular place and time (Rolls, 2010). Pattern completion is an inherent property of an autoassociation or attractor network such as the CA3 recurrent collateral system is believed to be (Rolls, 2008, 2016a), and there is also therefore great interest in the mechanisms for pattern completion in the hippocampal system.

The concepts of pattern separation and pattern completion also apply to other systems with recurrent collateral associatively modifiable connections, such as the local recurrent collateral networks that are a major architectural feature of the neocortex and olfactory cortex. There is therefore great interest in how pattern separation, pattern completion, and the concept of attractor networks may apply to these other cortical systems (Rolls, 2016a).

In this context, the papers in this Special Issue consider the roles of pattern separation and pattern completion in many neural systems, including the hippocampal system illustrated in Fig. 1 with the forward projections from the cortex to the hippocampus (blue), and the backprojections from the hippocampus to the neocortex (green).

Edmund Rolls provides some of the foundations, theoretical and empirical, for understanding pattern separation and pattern completion in the hippocampus and neocortex (Rolls, 2016b).

Raymond Kesner shows how some of these concepts have been tested in the rat, with evidence from the effects of selective damage to different parts of the hippocampal system, and with inge-

nious behavioral tests of different types of memory processing (Kesner, Kirk, Yu, Polansky, & Musso, 2016).

James Knierim and Joshua Neuneubel describe studies in a local–global cue mismatch (double-rotation) experiment in which recordings were made from cells in the anterior thalamus, entorhinal cortex, dentate gyrus (DG), CA3, and CA1 regions. Compared to the standard cue environment, the change in the DG representation of the cue-mismatch environment was greater than the changes in its entorhinal inputs, providing support for the theory of pattern separation in the DG. In contrast, the change in the CA3 representation of the cue-mismatch environment was less than the changes in its entorhinal and DG inputs, providing support for a pattern completion/error correction function of CA3. They suggest that whereas DG may perform an automatic pattern separation function, the attractor dynamics of CA3 allow it to perform a pattern separation or pattern completion function, depending on the nature of its inputs and the relative strength of the internal attractor dynamics (Knierim & Neuneubel, 2016).

Eduard Keleman and Andre Fenton describe evidence that the separate subsets of place-related neuronal activity in the rat hippocampus at any one time may reflect ongoing cognitive demands (Keleman & Fenton, 2016).

Stephen Johnstone, Fred Gage, and colleagues review evidence that adult neurogenesis of dentate granule cells may help to support pattern separation, the process by which similar patterns of neuronal inputs are transformed into distinct neuronal representations, permitting the discrimination of highly similar stimuli in hippocampus-dependent tasks. They consider the mechanisms by which the new dentate granule cells may implement this contribution to pattern separation (Johnstone, Shtrahman, Parylak, Goncalves, & Gage, 2016).

Helen Scharfman and Catherine Myers raise a new idea related to the complex circuitry of the dentate gyrus and CA3 where CA3 pyramidal cell projections to the dentate may play a potentially important role in the sparse firing of dentate granule cells, considered important in pattern separation (Scharfman & Myers, 2016).

Christopher Shay, Michael Hasselmo, and colleagues describe findings in entorhinal cortex slices that suggest that the ability of medial entorhinal cortex stellate cells to fire rebound spikes in response to a specific range of phases of inhibition could support complex attractor dynamics that provide completion and separation to maintain the spiking activity of specific grid cell populations (Shay, Ferrante, Chapman, & Hasselmo, 2016).

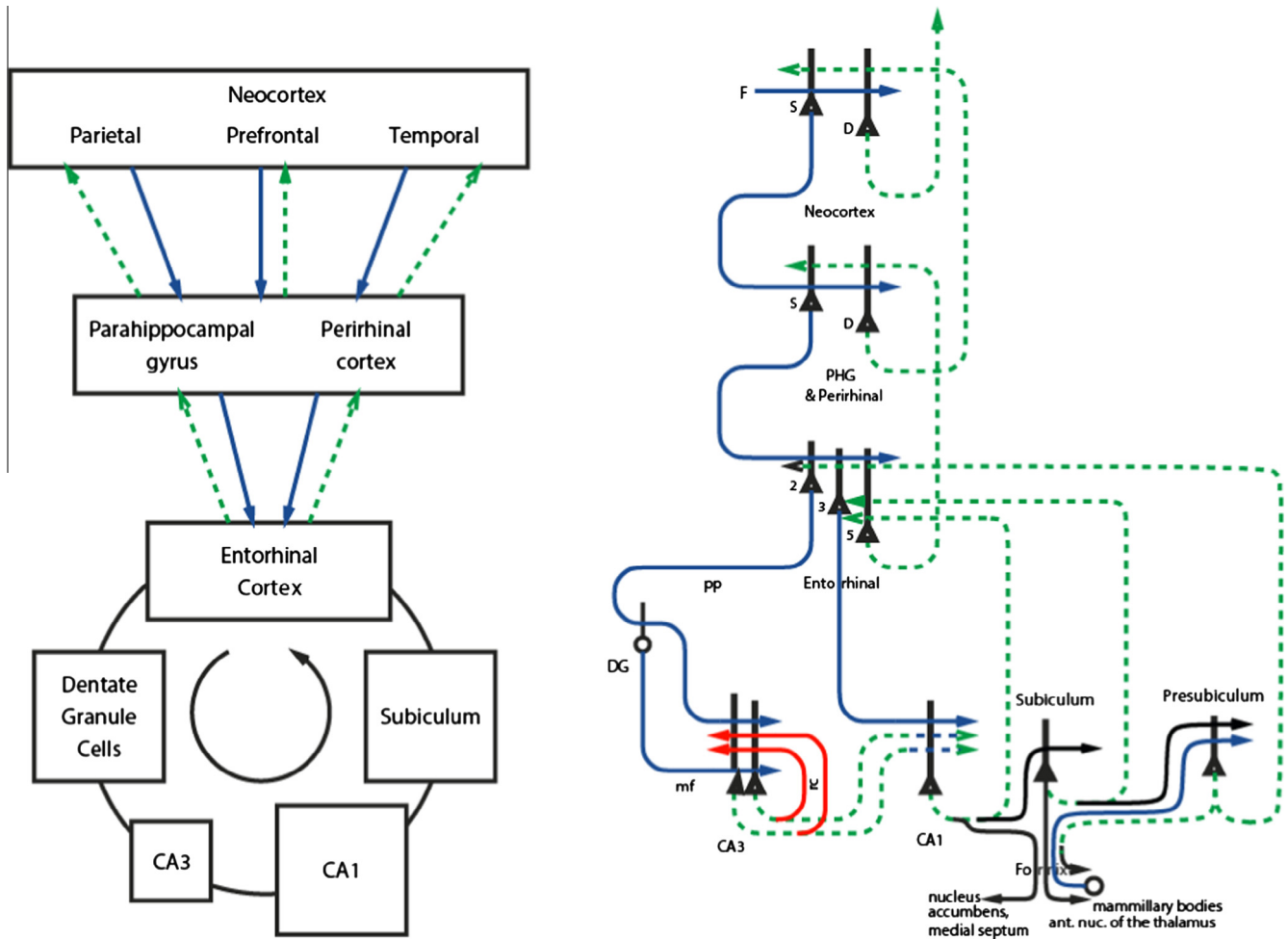


Fig. 1. Forward connections (blue solid lines) from areas of cerebral association neocortex via the parahippocampal gyrus and perirhinal cortex, and entorhinal cortex, to the hippocampus; and backprojections (green dashed lines) via the hippocampal CA1 pyramidal cells, subiculum, and parahippocampal gyrus back to the neocortex. There is great convergence in the forward connections down to the single network implemented in the CA3 pyramidal cells; and great divergence again in the backprojections. Left: block diagram. Right: more detailed representation of some of the principal excitatory neurons in the pathways. Abbreviations – D: Deep pyramidal cells. DG: Dentate Granule cells. F: Forward inputs to areas of the association cortex from preceding cortical areas in the hierarchy. mf: mossy fibres. PHG: parahippocampal gyrus and perirhinal cortex. pp: perforant path. rc: recurrent collaterals of the CA3 hippocampal pyramidal cells shown in red. S: Superficial pyramidal cells. 2: pyramidal cells in layer 2 of the entorhinal cortex. 3: pyramidal cells in layer 3 of the entorhinal cortex. The thick lines above the cell bodies shown as triangles represent the dendrites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Briant Kent, Martha Hvoslef-Eide, Lisa Saksida and Timothy Bussey (Kent, Hvoslef-Eide, Saksida, & Bussey, 2016) describe evidence that the formation of conjunctive representations in the hierarchically organized ventral visual stream through the perirhinal and entorhinal cortex make an important contribution to pattern separation, which is important for object representations (Rolls, 2012b, 2016a), as well as memory representations.

Ilana Bennett and Craig Stark provide evidence that in humans integrity of the perforant path, which provides input to the dentate gyrus from entorhinal cortex, was associated with mnemonic discrimination, a behavioral outcome designed to load on pattern separation (Bennett & Stark, 2016).

David Sheppard, Paul Gilbert, and colleagues provide evidence that suggests that spatial pattern separation may be less efficient in a subset of healthy older adults with subtle memory decline who are carriers of the apolipoprotein E-e4 (APOE-e4) allele (Sheppard et al., 2016).

The advances described in this Special Issue attest to the advantages of combining theoretical and empirical approaches to the study of the neurobiology of learning and memory. The advances also attest to the utility of attractor networks with their pattern

completion capability for information storage in the brain as well as short-term memory and decision-making; to the importance of competitive and related networks in pattern separation; and to the importance of pattern association networks in memory retrieval (Rolls, 2016a).

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