

# Considerations Arising From a Complementary Learning Systems Perspective on Hippocampus and Neocortex

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**ABSTRACT:** We discuss a framework for the organization of learning systems in the mammalian brain, in which the hippocampus and related areas form a memory system complementary to learning mechanisms in neocortex and other areas. The hippocampal system stores new episodes and "replays" them to the neocortical system, interleaved with ongoing experience, allowing generalization as cortical memories form. The data to account for include: 1) neurophysiological findings concerning representations in hippocampal areas, 2) behavioral evidence demonstrating a spatial role for hippocampus, 3) and effects of surgical and pharmacological manipulations on neuronal firing in hippocampal regions in behaving animals. We hypothesize that the hippocampal memory system consists of three major modules: 1) an invertible encoder subsystem supported by the pathways between neocortex and entorhinal cortex, which provides a stable, compressed, invertible encoding in entorhinal cortex (EC) of cortical activity patterns, 2) a memory separation, storage, and retrieval subsystem, supported by pathways between EC, dentate gyrus and area CA3, including the CA3 recurrent collaterals, which facilitates encoding and storage in CA3 of individual EC patterns, and retrieval of those CA3 encodings, in a manner that minimizes interference, and 3) a memory decoding subsystem, supported by the Shaffer collaterals from area CA1 to area CA3 and the bi-directional pathways between EC and CA3, which provides the means by which a retrieved CA3 coding of an EC pattern can reinstate that pattern on EC. This model has shown that 1) there is a trade-off between the need for information-preserving, structure-extracting encoding of cortical traces and the need for effective storage and recall of arbitrary traces, 2) long-term depression of synaptic strength in the pathways subject to long-term potentiation is crucial in preserving information, 3) area CA1 must be able to exploit correlations in EC patterns in the direct perforant path synapses. © 1997 Wiley-Liss, Inc.

**KEY WORDS:** consolidation, amnesia, memory, interleaved learning

## INTRODUCTION

Lesions of the hippocampal system produce a profound deficit in some forms of new learning and a temporally graded, retrograde amnesia for material experienced in a period of time preceding the lesion (Winocur, 1990; Squire, 1992; Kim and Fanselow, 1992; Zola-Morgan and Squire, 1990). These findings, and a computational analysis of neural learning systems, have led us to propose that the brain makes use of complementary

learning systems (McClelland et al., 1995). One of these, called the *neocortical learning system*, is specialized for the gradual extraction of structure from ensembles of events and experiences, leading to the acquisition of connection weights among neurons that support generalization. Chomsky (1957) and Marr (1971) have stressed that experiences hardly ever repeat exactly. However, they do share with other experiences common structure, which we believe the neocortical learning system exploits so that appropriate responses to novel inputs can be made.

In McClelland et al. (1995) we argue that for the cortical system to extract structure, it must employ a strategy we call *interleaved learning*, in which exposure to and learning about the contents of one episode of experience is interleaved with ongoing exposure to and learning about other experiences. We stress that, as discussed in McClelland et al. (1995), the extraction of shared structure depends on interleaved learning in all known connectionist learning algorithms, biologically plausible or otherwise, including, for example, simple Hebbian learning, reinforcement learning, and back-propagation. According to this theory, temporally graded retrograde amnesia represents the gradual acquisition of memories by the neocortical system through this interleaved learning process. The function of the second system, the *hippocampal memory system*, is to store new memories and retrieve them while they remain in storage so that they can be "played back" to the neocortical system for interleaved learning with other memories and ongoing experience. We should note that all memories are subject to gradual decay from both the hippocampal system and from the neocortical system, although those that are the most strongly encoded and remain of behavioral relevance throughout the life span may be refreshed so that they persist, and perhaps can remain in storage in both systems throughout life. However, it appears that in older adults at least, most memories from late childhood and adolescence are no longer hippocampus dependent, since older hippocampal amnesics (ages 47–65) appear approximately equivalent to normal subjects on material from the first two decades of life (MacKinnon and Squire, 1989). On the other hand, the

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