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Research Report

From brain synapses to systems for learning and memory: Object recognition, spatial navigation, timed conditioning, and movement control☆

*Stephen Grossberg**

Center for Adaptive Systems, Graduate Program in Cognitive and Neural Systems, Center for Computational Neuroscience and Neural Technology, Department of Mathematics, Boston University, Boston, MA 02215, United States

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ABSTRACT

This article provides an overview of neural models of synaptic learning and memory whose expression in adaptive behavior depends critically on the circuits and systems in which the synapses are embedded. It reviews Adaptive Resonance Theory, or ART, models that use excitatory matching and match-based learning to achieve fast category learning and whose learned memories are dynamically stabilized by top-down expectations, attentional focusing, and memory search. ART clarifies mechanistic relationships between consciousness, learning, expectation, attention, resonance, and synchrony. ART models are embedded in ARTSCAN architectures that unify processes of invariant object category learning, recognition, spatial and object attention, predictive remapping, and eye movement search, and that clarify how conscious object vision and recognition may fail during perceptual crowding and parietal neglect. The generality of learned categories depends upon a vigilance process that is regulated by acetylcholine via the nucleus basalis. Vigilance can get stuck at too high or too low values, thereby causing learning problems in autism and medial temporal amnesia. Similar synaptic learning laws support qualitatively different behaviors: Invariant object category learning in the inferotemporal cortex; learning of grid cells and place cells in the entorhinal and hippocampal cortices during spatial navigation; and learning of time cells in the entorhinal–hippocampal system during adaptively timed conditioning, including trace conditioning. Spatial and temporal processes through the medial and lateral entorhinal–hippocampal system seem to be carried out with homologous circuit designs. Variations of a shared laminar neocortical circuit design have modeled 3D vision, speech perception, and cognitive working memory and learning. A complementary kind of inhibitory matching and mismatch learning controls movement.

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*Correspondence to: Center for Adaptive Systems, Boston University, 677 Beacon Street, Boston, MA 02215, United States. Fax: +1 617 353 7755.
E-mail address: steve@bu.edu
URL: http://cns.bu.edu/~steve

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1. Linking brain mechanisms to behavioral functions: Unity and complementarity

Einstein famously said that "A scientific theory should be as simple as possible, but no simpler". In the case of how brains learn and remember, the very phrase "the search for the engram" (Lashley, 1950, 1960; Thompson, 1976) invokes a simplicity that may be too simple to meet the adaptive demands that are placed on advanced brains by ever-changing and often unpredictable environments. Before the proper level of simplicity can be asserted with conviction, a linkage needs to be made between brain mechanisms of learning and memory and the behavioral functions that they realize.

Lashley (1950, 1960) already realized that the substrates of learning and memory are distributed throughout many parts of the brain. However, being distributed does not necessarily imply being mechanistically similar. The current article reviews the conclusion drawn from neural models of learning and memory that, at least when one links brain mechanisms to behavioral functions, it seems that there is no single engram.

One reason for this is that different behavioral functions sometimes require computationally *complementary* brain mechanisms (Grossberg, 2000). It is argued below, for example, that brain mechanisms in the What cortical stream for learning categories for object recognition and spatial navigation are complementary to motor mechanisms in the Where cortical stream that control the movements needed to reach and manipulate these objects.

Despite the need for complementarity, there seem to nonetheless be some remarkable unities in the brain mechanisms that underlie very different functions. These include the mechanisms that are used to represent objects in the inferotemporal and prefrontal cortices (Cao et al., 2011; Carpenter and Grossberg, 1987, 1993; Chang et al., 2014; Grossberg, 1980; Fazl et al., 2009; Foley et al., 2012) and space and time representations in the entorhinal–hippocampal system (Grossberg and Merrill, 1992, 1996; Grossberg and Schmajuk, 1989; Grossberg and Pilly, 2012; Pilly and Grossberg, 2012; Mhatre et al., 2012). The computational homology between spatial and temporal representations has inspired the term *neural relativity* (Gorchetchnikov and Grossberg, 2007; Grossberg and Pilly, 2012).

2. Learning and memory by complementary cortical streams for recognition and action

Both perceptual/cognitive and spatial/motor processes undergo learning and memory. Neural models of these processes have proposed, and many experiments have supported, the hypothesis that perceptual/cognitive and spatial/motor processes often use different learning and memory laws to carry out their disparate behavioral functions.

2.1. Excitatory match learning vs. inhibitory mismatch learning

As summarized in Fig. 1, perceptual/cognitive processes in the What ventral cortical processing stream often use *excitatory matching* and *match-based learning* to create predictive representations of objects and events in the world. This kind of learning enables humans and other sufficiently advanced animals to rapidly learn new facts without being forced to just as rapidly forget what they already know. Such a competence was invaluable in the dangerous world in which our ancestors evolved. It is also useful in our advanced societies today, since it enables us to confidently go out into the world without fearing that, in learning to recognize new information, such as a face, we will suddenly forget other useful information, such as the faces of our family and friends. This is sometimes called the problem of *catastrophic forgetting*.

Grossberg (1980) has called the problem whereby the brain learns quickly and stably without catastrophically forgetting its past knowledge the *stability–plasticity dilemma*. Solving this problem during perceptual and cognitive development and learning was one of the main motivations behind the discovery of Adaptive Resonance Theory, or ART. The stability–plasticity dilemma must be solved by every brain system that needs to rapidly and adaptively respond to the flood of signals – the "blooming buzzing confusion" of James (1890) – that subserves even the most ordinary experiences. If the brain's design is parsimonious, then similar design principles should operate in all brain systems that can rapidly learn yet stably remember an accumulating knowledge base in response to changing conditions throughout life. The discovery of such principles should clarify how the brain unifies diverse sources of information into coherent moments of conscious experience. ART describes several of these principles and the neural mechanisms that realize them.

Match-based learning solves the stability–plasticity dilemma and is the kind of learning used in ART. Match-based learning coexists with excitatory matching. Examples of excitatory matching occur when a learned top-down expectation is sufficiently well matched against a bottom-up input pattern. Such a match can support a resonant state wherein gain amplification of the matched pattern, synchronization of the activities that are amplified, and attentional focusing occur. ART has predicted,

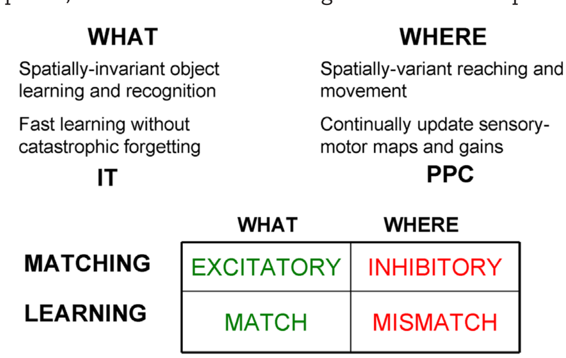

Fig. 1 – Complementary What and Where cortical processing streams for spatially-invariant object recognition and spatially-variant spatial representation and action, respectively. Perceptual and recognition learning use top-down excitatory matching and match-based learning that achieves fast learning without catastrophic forgetting. Spatial and motor learning use inhibitory matching and mismatch-based learning that enable rapid adaptation to changing bodily parameters. IT = inferotemporal cortex, PPC = posterior parietal cortex. See text for details. [Reprinted with permission from Grossberg (2009).]