BRAIN RESEARCH 1621 (2015) 270–293

Available online at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

Brain Research

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

ARTICLE INFO

Article history:
Accepted 6 November 2014
Available online 20 November 2014

Keywords:
Learning
Memory
Adaptive resonance theory
Attention
Category learning
Predictive remapping
Eye movement
Spatial navigation
Grid cell
Place cell
Time cell
Adaptively controlled conditioning
Autism
Medial temporal amnesia
mGluR
Laminar cortical circuits
3D vision
Speech perception
Cognitive working memory

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.

This article is part of a Special Issue entitled SI: Brain and Memory.

© 2014 Elsevier B.V. All rights reserved.

☆Invited review article for a special issue on: **Brain and Memory: Old Arguments and New Perspectives** Michel Baudry and Gary Lynch, Eds. Brain Research.

*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

http://dx.doi.org/10.1016/j.brainres.2014.11.018
0006-8993/© 2014 Elsevier B.V. All rights reserved.

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,

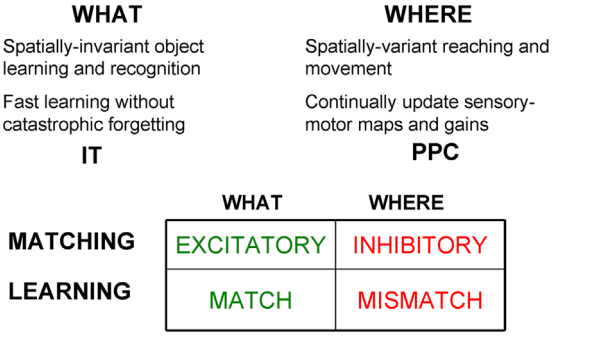

Fig. 1 – Complementary What and Where cortical processing streams for spatially-invariant object recognition and spatially-variant spatial representation and action, respectively. Perceptual and recognition learning use top-down excitatory matching and match-based learning that achieves fast learning 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).]

moreover, that fast learning can occur only during such a resonant state – hence the term *adaptive* resonance – and that "all conscious states are resonant states". ART hereby predicted a link between processes of Consciousness, Learning, Expectation, Attention, Resonance, and Synchrony, the so-called CLEARS processes. All current experimental evidence seems to be compatible with this family of predictions. See Grossberg (2007, 2012) for reviews.

Although it is predicted that "all conscious states are resonant states", it is not predicted that "all resonant states are conscious states". Indeed, some resonant states, such as the storage of a sequence of events in working memory before rehearsal occurs (see Grossberg and Pearson, 2008 for a review), or the entorhinal–hippocampal resonances that may dynamically stabilize the learning of entorhinal grid cells and hippocampal place cells (see Section 8), are not accessible to consciousness.

2.2. *Learning to be an expert in a changing body*

Match learning, and by extension ART, does not describe the only kind of learning that the brain needs to accomplish autonomous adaptation to a changing world. If only for this reason, ART is not a theory about "everything". There are just as essential, but complementary, spatial/motor processes in the Where dorsal cortical processing stream that often use *inhibitory matching* and *mismatch-based learning* (Fig. 1) to continually update spatial maps and sensory-motor gains as our bodily parameters change through time (Bullock and Grossberg, 1988; Bullock et al., 1998; Gaudiano and Grossberg, 1991; Georgopoulos et al., 1982, 1986). Indeed, we do not want the learned spatial representations and motor gains that controlled our infant bodies to be remembered and used to control our adult bodies. In this sense, catastrophic forgetting is a good property during spatial and motor learning.

Inhibitory matching is illustrated by how we make an arm movement. To make such a movement, a representation of where the arm is now (its *present position vector*) is subtracted from a representation of where we want the arm to move (its *target position vector*), thereby computing a *difference vector* that represents the direction and distance of movement needed to attain the target. After moving to the target, the target and present positions agree, so the difference vector is zero. This sort of matching is thus inhibitory (Bullock and Grossberg, 1988).

Neither type of matching and learning is sufficient to design an adaptive autonomous agent, but each is necessary. By combining these two types of processes together, our brains can incrementally learn and stably remember perceptual and cognitive representations of a changing world, leading to a self-stabilizing front end that solves the stability–plasticity dilemma and enables us to become increasingly expert in understanding the world and predicting outcomes in the world. At the same time, our brains can adaptively update their representations of where objects are and how to act upon them using bodies whose parameters change continuously through time due to development, exercise, illness, and aging.

2.3. *Why procedural memories are not conscious*

Brain systems that use inhibitory matching and mismatch learning cannot generate excitatory resonances. Hence, if "all conscious states are resonant states", then spatial and motor representations are not conscious. This way of thinking provides a mechanistic reason why declarative memories (or "learning that"), which are the sort of memories learned by ART, may be conscious, whereas procedural memories (or "learning how"), which are the sort of memories that control spatial orienting and action, are not conscious (Cohen and Squire 1980).

2.4. *Spatially-invariant recognition vs. spatially localized action*

There is another basic reason why these complementary What and Where processes need to work together. The What stream attempts to learn spatially-invariant object categories, so that a combinatorial explosion does not occur wherein every view of every object at every position and distance needs to be represented by a different category.

Indeed, learning in the What cortical stream leads to recognition categories that tend to be increasingly independent of object size and position at higher cortical levels. The anterior inferotemporal cortex exhibits such invariance (Bar et al., 2001; Sigala and Logothetis, 2002; Tanaka et al., 1991). Although how this occurs needs careful discussion (e.g., Zoccolan et al., 2007), such object invariance prevents a combinatorial explosion in memory of object representations that otherwise would need to be learned at every perceived size and position. Cao et al. (2011) and Grossberg et al. (2011) have used ART to simulate recent neurophysiological data about properties of invariant category learning and recognition in inferotemporal cortex.

In becoming spatially invariant, recognition categories lose information about how to direct action towards the locations in space where desired objects may be found. In contrast, the Where stream learns spatial maps that do enable us to locate such desired objects, as well as the movement gains that enable us to accurately act with respect to them. On the other hand, Where stream spatial processing gives up information about which objects are in those spatial locations. Interactions between the What and Where stream ("What–Where fusion") overcome these complementary deficiencies to enable learned spatially-invariant object representations to control actions towards desired goals in space (e.g., Brown et al., 2004; Fazl et al., 2009; Grossberg, 2009), including actions that are learned by observing a teacher who experiences the world from a different perspective, by sharing joint attention during social cognition (Grossberg and Vladusich, 2010).

In summary, because of their different types of matching and learning, perceptual and cognitive learning provide a self-stabilizing front end to control the more labile spatial and motor learning that enables changing bodies to effectively act upon recognized objects in the world.

2.5. *Synaptic learning laws that support complementary computing*

Object, spatial, and temporal representations all use a family of learning laws whose variations are called gated steepest descent, normalized gated steepest descent, instar, outstar, fuzzy ART, and adaptive threshold learning laws. These variations of ART learning laws all support match-based

learning and excitatory matching. Indeed, when these synaptic learning laws are embedded into ART networks, their learning turns on when resonance occurs, and turns off when a big enough mismatch occurs between the predicted state (e.g., a learned top-down expectation) and the actual data (e.g., a bottom-up input pattern).

The motor representations use variations of vector associative map, or VAM, learning laws that support mismatch-based learning and inhibitory matching (Gaudiano and Grossberg, 1991, 1992). In VAM learning laws, the difference vectors that control actions also serve as error signals that drive the learning process. Just as ART learning laws are triggered by a context-sensitive state, namely a resonance, VAM learning laws are modulated by whether or not the system is in a postural or movement state. Learning during a fixed posture can adaptively change movement gains to help achieve desired target positions. Shutting off learning during movement prevents learning from undermining correctly calibrated gains. All these movement systems have GO and STOP, or burster and pauser, signals that can be used to control the modulatory signals that gate learning off and on.

3. Equations for short-term memory, medium-term memory, and long-term memory

Despite the need for specialization to accommodate requirements such as complementary computing, all of the neural learning laws that the author has introduced to model a wide range of behavioral functions, and that are used by many other modellers, can be characterized using a small set of equations for short-term memory, or STM; medium-term memory, or MTM; and long-term memory, or LTM). These laws are embedded within a somewhat larger number of modules or microcircuits (e.g., shunting on-center off-surround networks, gated dipole opponent processing networks, associative learning networks, spectral spacing and timing networks, difference vector networks, and the like) which, in turn, are specialized and assembled into *modal* architectures, where the term "modal" stands for modality (e.g., architectures for vision, audition, cognition, cognitive-emotional interactions, sensory-motor control, and the like).

Modal architectures are less general than a Turing or von Neumann architecture for general computing, but far more general than a traditional AI algorithm. They are designed to be capable of general-purpose self-organizing processing of a particular modality of biological intelligence. Their particular specializations of the basic equations and modules have been selected over the millennia by evolutionary pressures. ART networks form part of such modal architectures.

Modal architectures, in turn, embody new paradigms for brain computing, including Complementary Computing (Grossberg, 2000) and Laminar Computing (Grossberg, 1999). As noted above, Complementary Computing describes how the global brain is organized into complementary parallel processing streams whose interactions generate biologically intelligent behaviors. Laminar Computing describes how and why the cerebral cortex is organized into layered circuits whose specializations can support all forms of higher-order biological intelligence. ART networks are embodied in laminar cortical circuitry for vision and visual object recognition; audition, speech, and language; cognitive information processing; and cognitive-emotional dynamics.

Grossberg (1968c, 1969a, 1969b) introduced laws of STM, MTM, and LTM that are used, with suitable variations and specializations, in many contemporary neural models, including ART architectures. One variant of them is:

3.1. STM: Short-term memory dynamics of fast cellular activation and inhibition

$$\frac{dx_i}{dt} = -Ax_i + (B - Cx_i) \times \left[I_i + \sum_{k=1}^{n} f_k(x_k) y_k D_{ki} z_{ki}\right] - (E + Fx_i)\left[J_i + \sum_{k=1}^{n} g_k(x_k) Y_k G_{ki} Z_{ki}\right]. \quad (1)$$

This equation describes the activity, or potential, x_i, of the ith cell (population) in a network of n interacting neurons. It includes both the Additive and Shunting models that were introduced in Grossberg (1968c, 1969a). In the shunting model, the parameters $C \neq 0$ and $F \neq 0$. The parameter $E = 0$ when there is "silent" shunting inhibition, whereas $E \neq 0$ describes the case of hyperpolarizing shunting inhibition. In the Additive model, parameters $C = F = 0$. The excitatory interaction term $\left[I_i + \sum_{k=1}^{n} f_k(x_k) y_k D_{ki} z_{ki}\right]$ describes an external input I_i plus the total excitatory feedback signal $\left[\sum_{k=1}^{n} f_k(x_k) y_k D_{ki} z_{ki}\right]$ that is a sum of signals from other populations via their output signals $f_k(x_k)$. These output signals are often interpreted in terms of the spiking frequencies that are generated by potential x_k. The term D_{ki} is a constant connection strength between cell populations k and i, whereas terms y_k and z_{ki} describe MTM and LTM variables, respectively. The inhibitory interaction term $\left[J_i + \sum_{k=1}^{n} g_k(x_k) Y_k D_{ki} Z_{ki}\right]$ has a similar interpretation.

Eq. (1) assumes "fast inhibition"; that is, inhibitory interneurons respond instantaneously to their inputs. Slower finite-rate inhibition, with activities X_i that are computed by inhibitory interneurons, uses an equation like (1) to describe the temporal evolution of the inhibitory activities. The output signals from these inhibitory interneurons provide the inhibitory feedback signals to the excitatory activities. With slow inhibition, the inhibitory feedback signals would be $g_k(X_k)$ instead of $g_k(x_k)$.

3.2. MTM: Habituative transmitter gates and depressing synapses

$$\frac{dy_i}{dt} = H(K - y_i) - L f_k(x_k) y_k. \quad (2)$$

Eq. (2) describes how the strength y_i of the *habituative transmitter gate*, or *depressing synapse* (Abbott et al., 1997), or *dynamic synapse* (Tsodyks, Pawelzik, and Markram, 1998), in the excitatory feedback term of (2) accumulates at a fixed rate H to its maximum value K via term $h(K - y_i)$ and is inactivated, habituated, or depressed via a mass action interaction between the feedback signal $f_k(x_k)$ and the gate concentration y_k. The mass action term may be more complex than this in some situations; e.g., Gaudiano and Grossberg (1991, 1992). The habituative transmitter gate Y_k in the inhibitory feedback

term of (1) obeys a similar equation. It should be noted that not all signals are habituative.

3.3. LTM: Gated steepest descent learning combines Hebbian and anti-Hebbian properties

$$\frac{dz_{ij}}{dt} = Mf_i(x_i)\left[h_j(x_j) - z_{ij}\right] \tag{3}$$

and

$$\frac{dz_{ij}}{dt} = Mf_j(x_j)\left[h_i(x_i) - z_{ij}\right]. \tag{4}$$

Eq. (3) describes the *outstar learning* equation, by which an ith source cell can sample and learn a distributed spatial pattern of activation across a network of sampled cells. When the gating signal $f_i(x_i)$ is positive, the adaptive weights z_{ij} can learn about the activity-dependent signals $h_j(x_j)$ across the sampled network of cells. Then each z_{ij} converges via term $\left[h_j(x_j) - z_{ij}\right]$ to a time-average of the signals $h_i(x_i)$ at a rate determined by $f_i(x_i)$. As a result, z_{ij} can either increase or decrease through time while tracking $h_i(x_i)$. This tracking operation is called *steepest descent*; hence the general name of such a learning law: *gated steepest descent*. When the gating, or sampling, signal $f_i(x_i)$ equals zero, then neither learning nor forgetting can occur.

Eq. (4) describes another variant of learning by gated steepest descent; namely, the *instar learning* equation, by which the adaptive weights z_{ij} that abut the jth target cell can, when $f_j(x_j)$ is positive, sample and learn the distributed pattern of signals $h_i(x_i)$ that are passing through their synapse. The adaptive tuning of these weights converts term $\sum_{k=1}^{n} f_k(x_k)y_k D_{ki} z_{ki}$ in (1) into an adaptive filter whereby an input pattern can more effectively activate the cells that were able to sample it during prior learning. This is the learning equation that was used in the competitive learning and self-organizing map models in Grossberg (1976a, 1978), and later applied by Kohonen (1984). The catastrophically unstable memories of competitive learning and self-organizing maps in response to dense non-stationary series of input patterns led to the introduction of ART as a way to dynamically stabilize learned memories using matching and attentional focusing by top-down expectations upon bottom-up input patterns.

There are many variations of these gated steepest descent equations that are been used in networks that support different behavioral functions; e.g., normalized gated steepest descent, doubly-gated learning, spike-timing dependent learning, etc. It should also be noted that not all connections are adaptive. Variations of the following *normalized instar learning* law have been used to learn maps of orientation and ocular dominance in cortical area V1 (Grossberg and Seitz, 2003; Grossberg and Williamson, 2001), grid cells and place cells in the entorhinal cortex and hippocampal cortex, respectively (Grossberg and Pilly, 2012, 2014; Mhatre et al., 2012), and recognition categories in the inferotemporal cortex (Carpenter and Grossberg, 1987, 1993):

$$\frac{dz_{ij}}{dt} = Mf_j(x_j)\left[h_i(x_i)(A - z_{ij}) - z_{ij}\sum_{k\neq i} h(x_k)\right]. \tag{5}$$

In (5), the term $-z_{ij}\sum_{k\neq i} h(x_k)$ describes a competition for synaptic activity by other signals converging on the jth cell. Rewrite (5) as

$$\frac{dz_{ij}}{dt} = Mf_j(x_j)\left[Ah_i(x_i) - z_{ij}\sum_{k} h(x_k)\right], \tag{6}$$

and then as

$$\frac{dz_{ij}}{dt} = Mf_j(x_j)\sum_{k} h(x_k)\left[\frac{Ah_i(x_i)}{\sum_{k} h(x_k)} - z_{ij}\right]. \tag{7}$$

The sum $z_i = \sum_j z_{ij}$ over all the weights z_{ij} in (7) that converge onto the j^{th} cell obeys:

$$\frac{dz_i}{dt} = Mf_j(x_j)\sum_{k} h(x_k)[A - z_i]. \tag{8}$$

Eq. (8) shows that the total synaptic weight z_i converges to A, and thus is normalized with a value that is independent of the total number of connections that abut the jth cell. This property is often called *conservation* of total synaptic weight.

This sort of learning law is experimentally supported by data about the competition among developing axons that abut a target neuron for limited target-derived neurotrophic factor in order to survive (Cabelli et al., 1995, 1997; Purves, 1988), and about the conservation of total synaptic weight by balanced synaptic depression and potentiation (Royer and Pare, 2003).

4. When learning is not Hebbian: Combining LTP and LTD

4.1. Gated steepest descent learning

As noted above, gated steepest descent learning weights can increase (long-term potentiation, or LTP) or decrease (long-term depression, or LTD) during the learning process. One reason for this assumption is that these weights learn about *distributed patterns* of inputs across a network, as was first mathematically proved in Grossberg (1968a, 1968b), not just about a single input through a single connection between pairs of cells, as postulated by Hebb (1949).

If the initial value of a weight that learns by gated steepest descent is smaller than the activity in a pattern that it is learning, then the weight will increase during learning (LTP). However, if the initial weight value is larger than the activity in a pattern that it is learning, then the weight will decrease during learning (LTD). Likewise, if two or more patterns are sampled sequentially in time during learning, one with larger activities and another with smaller activities at a given cell, then the corresponding adaptive weight may first increase and then decrease to track the average of the activities that it samples through time.

Reflecting this difference in the assumed functional units of learning, Hebb (1949) asserted that adaptive weights can only increase during learning whenever there is temporally contiguous pre- and post-synaptic pairing of inputs. Due to this property, weights could saturate at their maximum values as learning trials continue, assuming that all biological computations, including the computation of adaptive weights, have finite maximum values. They could then become useless for dealing with changes in environmental contingencies such as those that

might require a later reduction of weight. Such a reduction in weight can occur, for example, during reinforcement learning when a previously reinforced cognitive-emotional association, such as a conditioned reinforcer or incentive motivational adaptive weight, is later extinguished in favor of different reinforcing contingencies (Dranias et al., 2008; Grossberg, 1972, 1975; Kamin, 1969; Pavlov, 1927).

Despite this basic problem of Hebbian learning, it has become commonplace for many experimental neuroscientists to reflexively label results about associative learning as being examples of Hebbian learning. This attribution does not sufficiently take into account what Hebb actually wrote.

Outstars and instars were the first mathematically defined neural learning laws to combine both Hebbian (weight increase, LTP) and anti-Hebbian (weight decrease, LTD) properties, so that they can they track the patterns with which they are associated in time. These tracking properties were mathematically proved in a series of articles in the 1960s and early 1970s for increasingly complicated learning situations; e.g., for spatial pattern learning in outstars and recurrent networks (Grossberg, 1968b, 1969a), serial list learning (Grossberg, 1969c; Grossberg and Pepe, 1971), learning of arbitrarily complicated space-time patterns (Grossberg, 1969d) as in the case of birdsong (Hahnloser et al., 2002), and category learning in competitive learning and self-organizing map models (Grossberg, 1976a).

Instars and outstars were joined at recurrent competitive networks in Grossberg (1976a) to show how to learn arbitrary maps from m-dimensional to n-dimensional vectors. In this *universal recoding* model, instars use their adaptive filters to enable the m-dimensional input vectors to selectively activate category cells as part of a competitive learning or self-organizing map model, after which the category cells read out the n-dimensional output vectors that they learn using outstar learning. This type of instar–outstar map learning scheme was called *counter propagation* by Hecht-Nielsen (1987). ART shows, in addition, how to learn maps whose adaptive weights are dynamically self-stabilizing, by using learned top-down expectations from the category cells that are matched against the m-dimensional input patterns. The top-down expectations also often use outstar learning; e.g., Carpenter and Grossberg (1987).

4.2. *Monotonic weights during match-modulated category learning*

As noted above, if adaptive weights could only get larger or smaller through time whenever temporally contiguous pre- and post-synaptic inputs were paired, then they could become "stuck" at maximum or minimum values that may not adapt to changes in environmental contingencies. However, some category learning models do posit adaptive weights that can only change monotonically through time, such as fuzzy ART and fuzzy ARTMAP (Carpenter et al., 1991, 1992). Because of the monotonic change through time of these weights, they are guaranteed to converge to a limit. The problem is to ensure that the limiting values enable useful category recognition behaviors. Unlike the Hebb rule, this is ensured by control processes that prevent learning except when there is a good enough match between a currently active learned top-down expectation and bottom-up input pattern. Temporally contiguous pre- and post-synaptic pairing of inputs is not sufficient. See Section 6 for a discussion of how such matching happens.

5. Neurophysiological data about LTP and LTD

Bliss and Lomo (1973) using the anesthetized rabbit preparation, and Bliss and Gardner-Medwin (1973) using the unanesthetized rabbit, provided the first demonstration of a long-term potentiation (LTP) of synaptic efficacy following tetanic stimulation of afferent fibers in the perforant path to dentate gyrus synapse in the hippocampus. Long-tem depression (LTD) has also been reported in the hippocampus, including at area CA1 pyramidal cells, in pathways that can also induce LTP at higher rates of stimulation (e.g., Dudek and Bear, 1992; Levy et al., 1983; Levy and Desmond, 1985, Levy and Steward, 1983; Mulkey and Kalenka, 1992). Such LTP and LTD effects have also been reported in the cerebral cortex, including in the visual cortex of cats and rats (e.g., Artola and Singer, 1987, 1993; Fregnac et al., 1994; Kirkwood et al., 1995; Komatsu et al., 1981; Singer, 1983), among other structures in a literature that is, by now, vast.

These results do not disclose, however, how shared synaptic properties may control different behavioral functions in different parts of the brain, or how and why particular combinations of functions are controlled by specific brain regions. For example, how do similar learning laws contribute to the learning of categories for visual object recognition by inferoretmporal and prefrontal cortex, as well as to spatial navigation via the entorhinal–hippocampal system? Why are both spatial navigation (space!) and adaptively timed conditioning (time!) represented in the medial and lateral streams, respectively, of the entorhinal–hippocampal system? This article reviews some of the network- and system-level interactions that are proposed to give rise to such behavioral properties.

6. Adaptive resonance theory: Fast category learning without catastrophic forgetting

6.1. *Solving the stability–plasticity dilemma*

One emerging family of neural models controls how the visual cortex learns, recognizes, and remembers invariant visual object recognition categories and how this process is linked to object and spatial attention, predictive remapping, consciousness, and object search in the visual cortex. All these models build upon the category learning and memory capabilities of Adaptive Resonance Theory, or ART, models (Carpenter, 1997, 2003; Carpenter and Grossberg, 1987, 1993; Carpenter et al., 1991, 1992; Grossberg, 1976a, 1976b, 1978, 1980).

All of the main ART predictions have received increasing support from psychological and neurobiological data since ART was introduced in Grossberg (1976a, 1976b), and ART is currently the cognitive and neural theory of recognition learning and memory with the broadest explanatory and predictive range. Successive developments of ART have explained and predicted increasingly large behavioral and neurobiological data bases, ranging from normal and abnormal aspects of human and animal perception and cognition, to the spiking and

oscillatory dynamics of hierarchically-organized laminar thalamocortical networks in multiple modalities. Indeed, some ART models explain and predict behavioral, anatomical, neurophysiological, biophysical, and even biochemical data. In this sense, they provide a growing set of examples capable of partially solving the classical mind/body problem. See Grossberg (2012) for a review of these developments.

6.2. Top-down matching, resonance, attention, and fast learning

ART solves the stability–plasticity dilemma by proposing how top-down expectations focus object attention on salient combinations of visual features, and characterizes how attention may operate via a form of self-normalizing "biased competition" (Desimone, 1998). There is a convergence across models of how to mathematically instantiate the ART attentional circuit that have grown out of the results about the properties of shunting on-center off-surround networks that were originally proved in Grossberg (1973). For example, the "normalization model of attention" (Reynolds and Heeger, 2009) simulates several types of experiments on attention using the same equation for self-normalizing attention as the distributed ARTEXture (dARTEX) model (Bhatt et al., 2007, equation (A5)) used to simulate human psychophysical data about Orientation-Based Texture Segmentation (OBTS, Ben-Shahar and Zucker, 2004).

When a good enough match occurs between a top-down learned expectation, that is read out by a currently active recognition category, and a bottom-up input pattern, a synchronous resonant state emerges that embodies an attentional focus. This resonance is capable of driving fast learning of bottom-up recognition categories and top-down expectations within the attentional focus that can refine previous knowledge; hence the name *adaptive* resonance. It has been mathematically proved that match learning within an ART model leads to stable memories of arbitrary events presented in any order (e.g., Carpenter and Grossberg, 1987, 1991). Simple learning laws, such as variants of instar and outstar learning, can solve the stability–plasticity dilemma when they are modulated by the results of such an attentional match. In particular, the adaptive weights in bottom-up pathways that help to learn recognition categories are often normalized instar or fuzzy ART laws (Eq. (5)), whereas the weights in top-down pathways that help to learn expectations are often outstar laws (Eq. (3)).

6.3. Matching and synchronous oscillations

The resonance process is predicted to take place in the What cortical stream, notably in the sensory, temporal, and prefrontal cortices, where top-down expectations are matched against bottom-up inputs. When a top-down expectation achieves a good enough match with bottom-up data, the emerging attentional focus is often realized by oscillatory dynamics that synchronize the firing properties of the resonating neurons.

These match-sustained oscillations were predicted to occur in Grossberg (1976b), where they were called *order-preserving limit cycles* to specify that the oscillating activities do not reverse their relative sizes through time, in keeping with the idea that resonating features preserve their relative importance during the resonant event. Such oscillations are currently called *synchronous oscillations* (e.g., Eckhorn et al., 1988; Engel et al., 2001; Gray and Singer, 1989). Several subsequent modeling studies have simulated how these oscillations can explain data about such varied properties as fast synchronization by cooperative feature linking during perceptual grouping and attentional matching (Grossberg and Somers, 1991), perceptual framing, temporal order judgments, and stochastic resonance (Grossberg and Grunewald, 1997), and analog sensitivity of fast synchronization of perceptual grouping by the laminar circuits of visual cortex (Yazdanbakhsh and Grossberg, 2004). Of particular interest are simulations within realistic spiking laminar cortical circuits of faster gamma oscillations during a top-down attentional match and slower beta oscillations during a big enough mismatch, with the mismatch initiated within the deeper layers of the cortex (Grossberg and Versace, 2008). This gamma/beta prediction has received neurophysiological support from several labs in different parts of the brain (e.g., Berke et al., 2008; Buffalo et al., 2011; Buschman and Miller, 2009). The prediction is consistent with the possibility that other neural mechanisms can also cause such oscillatory frequencies.

6.4. The cycle of resonance and reset

Match learning has a serious potential weakness: If a brain can only learn when there is a good enough match between bottom-up data and learned top-down expectations, then how can it ever learn anything that is really novel? When learning first begins, and no learned recognition categories exist, then a novel input pattern can activate a potential future category that has the best match with it via the small, random initial weights in the bottom-up pathways. Then contrast enhancement via the rules of competitive learning and self-organizing maps (Grossberg, 1976a; Kohonen, 1984; von der Malsburg, 1973) can strengthen these bottom-up weights to ensure a better match with the input pattern in the future. However, this can occur only if, on the first learning trial, the activated category can read out top-down signals that provide a good enough match with the novel input pattern to allow learning to proceed. In order for a top-down expectation to match the features that activate *any* new recognition category, all of its top-down adaptive weights initially have large values, which are pruned by the learning of a particular expectation to match the feature patterns that activate the category. After this first category is learned, its large learned weights can compete with the small random weights in the bottom-up filter to interfere with learning about new objects and events. How is this problem overcome in a situation where the learning is unsupervised, and no external teacher is available to force the selection of a correct answer?

ART proposes that this problem is solved by an interaction between complementary processes of *resonance* and *reset* that are predicted to control properties of attention and memory search, respectively. These processes help our brains to balance between the complementary demands of processing the familiar and the unfamiliar, the expected and the unexpected. A big enough mismatch, which is computed within the attentional system, is proposed to activate a

complementary *orienting system*, which is activated by unexpected and unfamiliar events (Fig. 2b and c), and which includes the nonspecific thalamus and the hippocampal system. See Carpenter and Grossberg (1993) and Grossberg and Versace (2008) for consistent data. Output signals from the orienting system rapidly reset the recognition category that has been reading out the poorly matching top-down expectation. The cause of the mismatch is hereby removed, thereby freeing the system to activate a different recognition category (Fig. 2d). In this way, a reset event triggers memory search, or hypothesis testing, which automatically leads to the selection of a recognition category that can better match the input.

6.5. *Memory consolidation and direct access to globally best match*

As sequences of inputs are practiced over learning trials, the search process eventually converges upon stable categories. It has been mathematically proved (e.g., Carpenter and Grossberg, 1987) that familiar inputs directly access the category whose prototype provides the globally best match, without undergoing any search, while unfamiliar inputs continue to activate the orienting subsystem to trigger memory searches for new or better-fitting categories until they become familiar. In other words, ART provides a solution of the local minimum problem and clarifies how familiar objects can be rapidly recognized even as the total number of learned memories increases dramatically. The processes of search and category learning continue until the memory capacity, which can be chosen arbitrarily large, is fully utilized.

6.6. *Vigilance, acetylcholine, and nucleus basalis*

A *vigilance* parameter controls how big a mismatch is needed to drive a memory search. Low vigilance permits the learning of general and abstract categories because it tolerates large mismatches between the currently active top-down expectation and the bottom-up input exemplar with which it is being matched. High vigilance forces learning of more specific and concrete categories, with individual input exemplars learning to activate their own categories in the limit of very high vigilance.

Vigilance is computed within the orienting system of an ART model (Fig. 2b–d), where the total bottom-up excitation from all the active features in an input pattern I is reduced by the total inhibition from all the feature detectors that it activates (see F_1 in Fig. 2). If the ratio of the total activity across the active features in F_1 (that is, the "matched" features) to the total activity due to all the features in I is less than a *vigilance* parameter ρ (Fig. 2b), then a nonspecific reset, or arousal, wave is activated (Fig. 2c), which can drive the search for another category with which to classify the exemplar. This can be accomplished by letting ρ multiply the bottom-up inputs I to the orienting system; that is, ρ is the gain of the bottom-up inputs to the orienting system. The orienting system is activated when the total excitatory input ρI is greater than the total inhibition from the features X^* across F_1 that survive top-down matching; that is, when $\rho|I| - |X^*| > 0$, where $|.|$ denotes the number of positive inputs or matched features. Rewriting this inequality as $\rho > |X^*||I|^{-1}$ shows that the orienting system is activated whenever ρ is chosen higher than the ratio of active X^* matched features in F_1 to total features in I. In other words, the vigilance parameter controls how bad a match can be before search for a new category is initiated. If the vigilance parameter is low, then many exemplars can all influence the learning of a

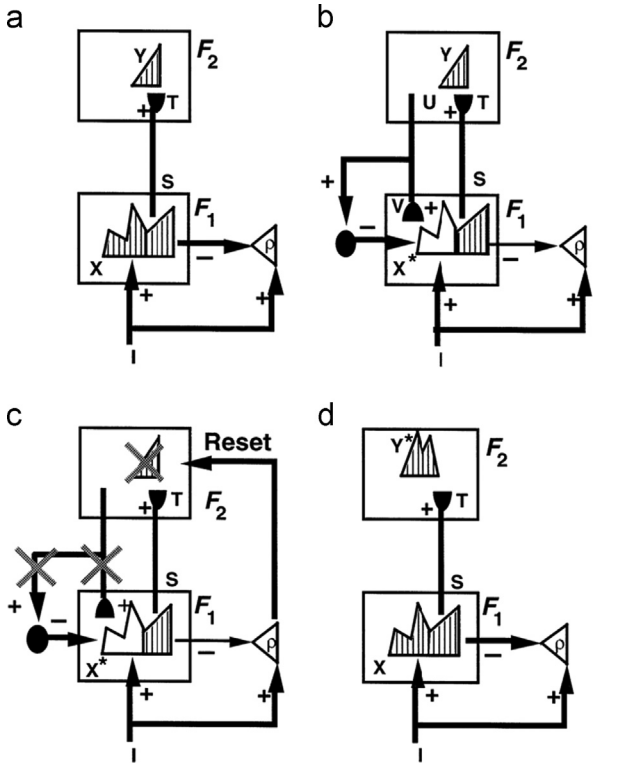

Fig. 2 – Search for a recognition code within an ART learning circuit: (a) Input pattern I is instated across feature detectors at level F_1 as an activity pattern X, while it nonspecifically activates the orienting system A with gain ρ, which is called the *vigilance* parameter. Output signals from activity pattern X inhibits A and generates output pattern S. S is multiplied by learned adaptive weights to form the input pattern T. T activates category cells Y at level F_2. (b) Y generates the top-down signals U which are multiplied by adaptive weights and added at F_1 cells to form a *prototype* V that encodes the learned expectation of active F_2 categories. If V mismatches I at F_1, then a new STM activity pattern X^* (the hatched pattern) is selected at F_1. X^* is active at I features that are confirmed by V. Mismatched features (white area) are inhibited. When X changes to X^*, total inhibition decreases from F_1 to A. (c) If inhibition decreases sufficiently so that the total inhibition due to X^* is less than the total excitation due to I multiplied by the vigilance parameter ρ, then A is activated and releases a nonspecific arousal burst to F_2; that is, "novel events are arousing". Arousal resets F_2 by inhibiting Y. (d) After Y is inhibited, X is reinstated and Y stays inhibited as X activates a different activity pattern Y^*. Search for better F_2 category continues until a better matching or novel category is selected. When search ends, an attentive resonance triggers learning of the attended data. [Adapted with permission from Carpenter and Grossberg (1993).]

shared prototype, which eliminates all the features that are not shared with all the exemplars, thereby leading to learning of an abstract category. If the vigilance parameter is high, then even a small difference between a new exemplar and a known prototype (e.g., *F* vs. *E*) can drive the search for a new category with which to represent *F*, thereby leading to learning of a more exemplar-like category.

Vigilance can vary across learning trials. For example, during supervised learning, it may be controlled by a process of *match tracking* (Carpenter et al., 1991, 1992) whereby a predictive error (e.g., *E* is predicted in response to *F*) causes the vigilance parameter ρ to increase just enough to trigger reset and search for a better-matching category. Match tracking gives up the minimum amount of generalization in the learned categories to search for a better-matching category. It hereby "tracks" the degree of match between input exemplar and matched prototype, and thus increases vigilance by the minimum amount needed to trigger a reset and search for a new category. Match tracking hereby realizes a Minimax Learning Rule that conjointly *maximizes* category generality while it *minimizes* predictive error. Otherwise expressed, match tracking uses the least memory resources that can correct errors in classification.

ART predicts how vigilance may be controlled by acetycholine via the nucleus basalis of Meynert (Grossberg and Versace, 2008; Palma et al., 2012; Palma et al., 2012), thereby proposing a more precise interpretation of various data about the role of acetylcholine in cortical dynamics (e.g., Kraus et al., 1994; van Der Werf et al., 2002).

6.7. *Vigilance diseases: Autism and amnesia*

Various mental disorders seem to include problems with vigilance control, leading to the hypothesis that it may be useful to classify the symptoms due to vigilance malfunctions as illustrations of "vigilance diseases". Autism and medial temporal amnesia seem to be examples of such diseases. It should be clear, however, that a problem with vigilance is not the only problem that individuals with these mental disorders may have.

Persistent high vigilance has been predicted to cause symptoms of hyperspecific category learning and attentional deficits in some autistic individuals (Grossberg and Seidman, 2006). This prediction has been tested through psychophysical experiments done with high-functioning autistic individuals (Church et al., 2010; Vladusich et al., 2010). It is also consistent with reports of abnormal cholinergic activity in the parietal and frontal cortices of autistic individuals that is correlated with abnormalities in the nucleus basalis (Perry et al., 2001; Rubenstein and Merzenich, 2003).

Persistent low vigilance has been predicted to cause some symptoms of medial temporal amnesia (Carpenter and Grossberg, 1993). A lesion of the hippocampus removes the orienting system from cortico-hippocampal interactions (Fig. 2). Memory search is hereby prevented, and the ability to learn new categories is impaired. A hippocampal lesion has the effect of causing vigilance to equal zero. Learning that occurs without mismatch-mediated reset and memory search can only form general categories.

Relevant data from amnesic individuals have been reported by Knowlton and Squire (1993), who showed that amnesic subjects and normal subjects perform equally well on easy categorization tasks, but amnesic subjects perform far worse on more demanding tasks. To explain these data, Knowlton and Squire (1993) posited two separate memory systems. However, Zaki et al. (2003) quantitatively fit these data with a single exemplar-based model whose sensitivity parameter was chosen lower for amnesic than for normal subjects. This exemplar model is usually expressed in terms of formal algebraic equations. When the formal exemplar model is interpreted as a real-time dynamic process undergoing only locally defined interactions, its operations include a top-down attentional matching process akin to that in ART. A low sensitivity parameter *c* in this exemplar model (see their Eq. (4)) then plays a role similar to that played by a low vigilance parameter ρ in an ART model (Amis et al., 2014).

7. Invariant object category learning, attention, predictive remapping, and search

In order to achieve autonomous learning and memory in a mobile organism, ART models are embedded within larger architectures that can solve several fundamental problems that arise when searching a scene. The first architecture of this type is called the ARTSCAN model (Fazl et al., 2009; Grossberg, 2009). ARTSCAN predicts how an observer can learn to recognize objects when seen from multiple perspectives, and thereby to learn view-invariant object categories while scanning a 2D scene with eye movements. As the eyes scan a scene, two successive eye movements may focus on different parts of the same object or on different objects. How does the brain avoid erroneously classifying views of different objects together under unsupervised learning conditions, even before the brain knows what the object is? ARTSCAN proposes how the brain controls eye movements that enable it to learn multiple view-specific categories of a given object and to associatively link them with view-invariant category representations of that object, and only that object. See Fig. 3 for a macrocircuit of the more comprehensive ARTSCAN Search model.

7.1. *Attentional shrouds and Where-to-What modulation of invariant category learning*

To accomplish view-invariant object category learning during free scanning of a 2D scene, the ARTSCAN model predicts a critical role for spatial attentional signals from the Where cortical stream in modulating invariant category learning in the What cortical stream. Several studies have reported that the distribution of spatial attention can configure itself to fit an object's form. Form-fitting spatial attention is sometimes called an *attentional shroud* (Tyler and Kontsevich, 1995). ARTSCAN explains how an object's pre-attentively formed surface representation in prestriate cortical area V4 may induce such a form-fitting attentional shroud in parietal cortex. In particular, feedback between the surface representation and the shroud are predicted to form a *surface-shroud resonance* that locks spatial attention on the object's surface. I have predicted that such a

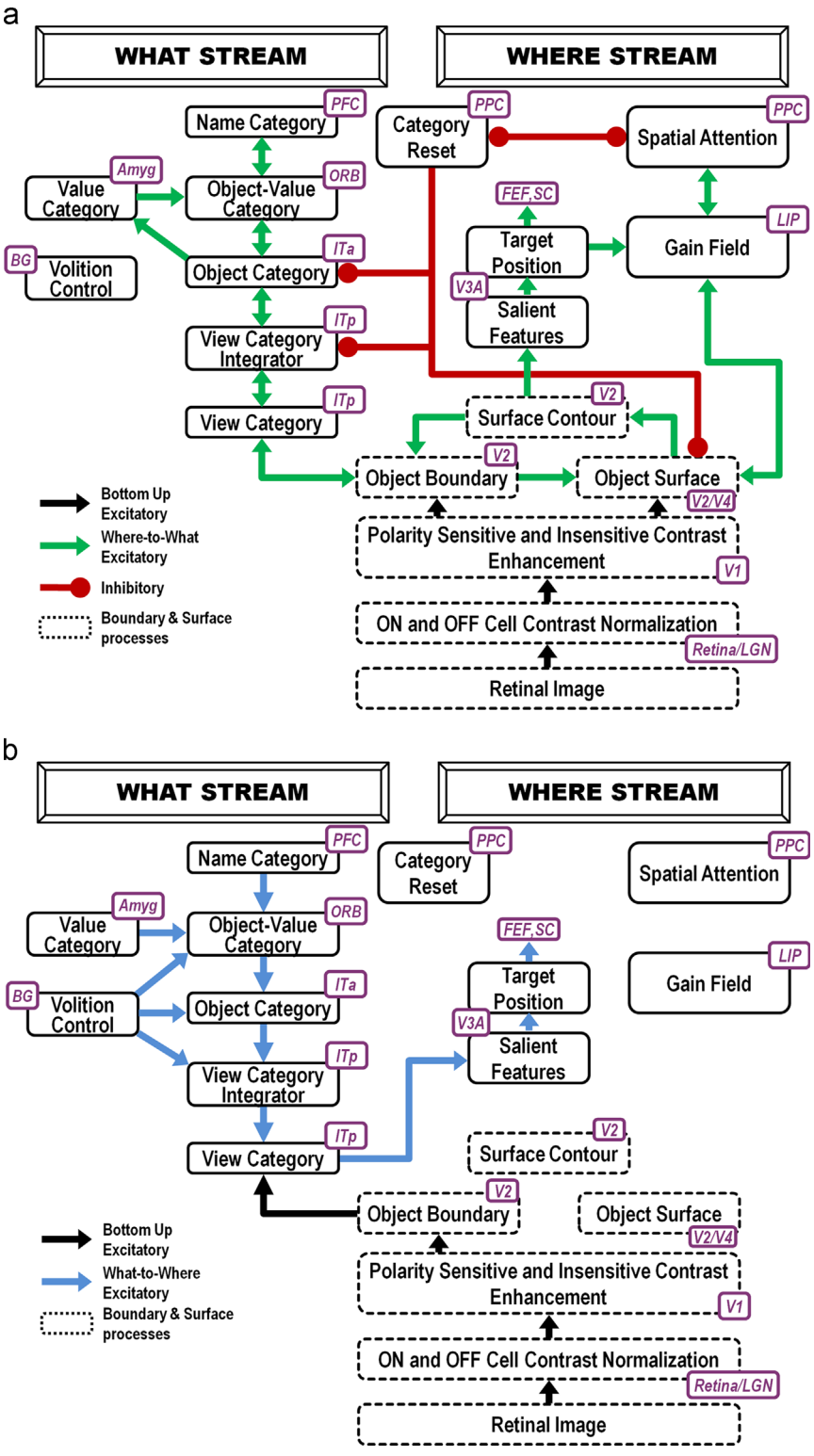

Fig. 3 – ARTSCAN Search diagram. The dashed boxes indicate the boundary and surface process. (a) Category learning. The arrows represent the excitatory cortical processes from the Where cortical stream to the What cortical stream whereby invariant category learning and recognition, and reinforcement learning, occur. The connections ending in circular disks indicate inhibitory connections. (b) One pathway for controlling top-down primed search for a valued object from the What to the Where cortical stream. The green arrows represent bottom-up image-driven processes and the blue arrows represent top-down processes from the What cortical stream to the Where cortical stream. ITa: anterior part of inferotemporal cortex, ITp: posterior part of inferotemporal cortex, PPC: posterior parietal cortex, LIP: lateral intraparietal cortex, LGN: lateral geniculate nucleus, ORB: orbitofrontal cortex, Amyg: amygdala, BG: basal ganglia, PFC: prefrontal cortex, SC: superior colliculus, V1 and V2: primary and secondary visual areas, V3 and V4: visual areas 3 and 4. [Reprinted with permission from Chang et al. (2014).]

surface-shroud resonance supports conscious perception of the object's visible surface qualia. After such a resonance locks attention upon a surface, it can also propagate top-down to lower cortical areas, such as V1 and V2, and bottom-up to higher cortical areas, such as prefrontal cortex, to synchronize them all to support the conscious percept, as discussed more completely in the next section.

While this surface-shroud resonance remains active, it also has other important functions: First, it ensures that eye movements tend to end at locations on the object's surface, thereby enabling different views of the same object to be sequentially explored, as confirmed by Theeuwes et al. (2010). Second, it keeps the emerging view-invariant object category active while different views of the object are learned by view-specific categories and associated with it.

This latter function works as follows: As each view-specific category is learned by the What stream, say in posterior inferotemporal cortex (ITp), it focuses object attention via a learned top-down expectation on the critical features in the visual cortex (e.g., in prestriate cortical area V4) that will be used to recognize that view and its variations in the future. Such a view-specific category and its learned top-down expectation are modeled by ART. When the first such view-specific category is learned, it also activates a cell population at a higher cortical level, say anterior inferotemporal cortex (ITa), that will become the view-invariant object category (Fig. 3a).

Suppose that the eyes or the object move sufficiently to expose a new view whose critical features are significantly different from the critical features that are used to recognize the first view. Then the first view category is reset, or inhibited. This happens due to the mismatch of its learned top-down expectation, or prototype of attended critical features, with the newly incoming view information. This top-down prototype focuses object attention on the incoming visual information. Object attention hereby helps to control which view-specific categories are learned by determining when the currently active view-specific category should be reset, and a new view-specific category should be activated. Such a reset is controlled by the usual balance between resonance and reset in any ART model (Section 6.4).

However, the view-*invariant* object category should *not* be reset every time a view-*specific* category is reset, or else it can never become view-invariant. This is what the attentional shroud accomplishes: It inhibits a tonically-active reset signal that would otherwise shut off the view-invariant category when each view-specific category is reset (Fig. 3a). As this process is iterated, and the eyes foveate a sequence of views on a single object's surface through time, they trigger learning of a sequence of view-specific categories, and each of them is associatively linked through learning with the still-active view-invariant category.

When the eyes move off an object, its attentional shroud collapses in the Where stream, thereby transiently disinhibiting the parietal reset mechanism that shuts off the view-invariant category in the What stream. This shroud-mediated reset mechanism between the Where and What cortical streams is different from the top-down mismatch-mediated reset within the What stream that resets the individual view-specific categories.

When the eyes look at a different object, its shroud can form in the Where stream and a new view-specific category can be learned that can, in turn, activate the cells that will become a new view-invariant category in the What stream.

Are there data that support these model predictions and that can be used to further test and develop the model? Chiu and Yantis (2009) have described rapid event-related fMRI experiments in humans showing that a spatial attention shift causes a domain-independent transient parietal burst that correlates with a change of categorization rules. This transient parietal signal is a marker against which further experimental tests of model mechanisms can be based. It supports the predicted sequence of V4-parietal surface-shroud collapse (shift of spatial attention), transient parietal burst (reset signal), and collapse of the currently active invariant object category in cortical area ITa (shift of categorization rules). The transient parietal burst is domain-independent because any object's surface-shroud resonance can inhibit it, and the burst itself can inhibit any view-invariant object category. These and related results (e.g., Cabeza et al., 2008; Corbetta et al., 2000; Yantis et al., 2002) are consistent with the model prediction of how different regions of the parietal cortex maintain sustained attention to a currently attended object (e.g., the shroud) and control transient attention switching (e.g., the reset burst) to a different object.

7.2. *Conscious awareness of visual qualia: Crowding and parietal neglect*

The ARTSCAN model enables an answer to be proposed to the following fundamental question: What brain event subserves conscious awareness of visual qualia? The background leading to this proposal unifies two streams of neural modeling. ART predicts that "all conscious states are resonant states" and the FACADE theory of 3D vision and figure-ground perception (e.g., Grossberg, 1994) predicts that "all consciously visible percepts are surface percepts". Combining these two predictions raises the question: What sort of resonance supports conscious visible surface percepts?

I have predicted that a surface-shroud resonance supports conscious percepts of an object's visible surface qualia. After such a resonance locks attention upon a surface, it can also propagate top-down to lower visual areas where finer visual features are represented, such as V1 and V2, and bottom-up to regions as high as prefrontal cortex, and can synchronize them all to support the conscious percept. A wide range of data are naturally explained by this prediction, such as data about crowding (Green and Bavelier, 2007; He et al., 1996; Intriligator and Cavanagh, 2001; Levi, 2008) and data about parietal neglect (Driver and Mattingley, 1998; Mesulam, 1999).

Crowding probes the relationship between seeing and recognition (and thus learning and memory) by showing how seeing and recognition of individual objects can fail during certain conditions. ARTSCAN provides a deceptively simple explanation of crowding (Foley et al., 2012). It predicts that we consciously see an object only when its surface features are included within a surface-shroud resonance. When crowding occurs, however, such a resonance may not isolate an individual object. This can happen, for example, if the cortical magnification factor, among other factors, causes multiple, peripherally-viewed, object surfaces to all share a

single surface-shroud resonance. Since surface-shroud resonances create a link between conscious perception and the categories that we used to recognize objects, objects that share a single surface-shroud resonance cannot be individually recognized.

Parietal neglect describes how a parietal lesion can cause a patient to consciously ignore the corresponding region of space. ART proposes that neglect may happen because, despite the fact that the lesion may leave the visual cortex intact, the corresponding surface-shroud resonance cannot form to support a conscious percept of the corresponding object surface.

7.3. *Seeing and knowing via two kinds of attention and resonance*

Models like ARTSCAN illustrate how two different types of resonances may occur that support the difference between seeing and knowing. A *surface-shroud resonance* coordinates What and Where stream representations of surfaces and spatial attention, respectively. It supports conscious seeing of an object's surface qualia. The attention that occurs during such a resonance is spatial attention. A *feature-category resonance* coordinates What stream representations of object features and their recognition categories, as modeled by ART. It supports knowing what the object is. The attention that occurs during such a resonance is object attention. During conscious awareness of an object, both kinds of resonances may be active, and even synchronous, to support seeing the object and knowing what it is.

7.4. *Invariant object learning, recognition, predictive remapping, and search*

The pARTSCAN (positional ARTSCAN) model (Cao et al., 2011) builds upon ARTSCAN to propose how an observer can learn view-, size-, and positionally-invariant object categories in a 2D scene. pARTSCAN suggests a role for persistently firing cells in the inferotemporal cortex (Brunel, 2003; Fuster and Jervey, 1981; Miyashita and Chang, 1988; Tomita et al., 1999) in this process. Such persistence represents a specific kind of short-term memory that is reset when spatial attention shifts from one object to another.

The 3D ARTSCAN model (Grossberg et al., in press) extends ARTSCAN to propose how the brain maintains the stability of binocularly fused representations of a 3D scene as the eyes fixate different objects in the scene. Each eye movement requires a new binocular match of an object's features, yet perceptual stability is maintained. This competence requires that *predictive remapping* occurs (Duhamel et al., 1992; Gottlieb et al., 2005; Mathot and Theeuwes, 2010; Melcher, 2007; Melcher, 2008–2009; Saygin and Sereno, 2008; Sommer and Wurtz, 2006; Tolias et al., 2001; Umeno and Goldberg, 1997) via gain fields (Andersen et al., 1985; Andersen and Mountcastle, 1983; Deneve and Pouget, 2003; Gancarz and Grossberg, 1999; Grossberg and Kuperstein, 1986; Pouget et al., 2003) to ensure that predictive eye position information enables the attentional shrouds and binocularly matches to be computed in head-centered coordinates that are stable as the eyes move.

The dARTSCAN (distributed ARTSCAN) model (Foley et al., 2012) clarifies why visual backgrounds do not become dark when spatial attention, via a surface-shroud resonance, is focused on a particular object, how Where stream motion-activated transient attentional components and What stream sustained attentional components interact (Corbetta et al., 2008; Corbetta and Shulman, 2002; Dosenbach et al., 2007, 2008; Egeth and Yantis, 1997), and how prefrontal priming interacts with parietal attention mechanisms to influence search efficiency.

The ARTSCAN Search model (Fig. 3; Chang et al., 2014) builds upon pARTSCAN view-, size-, and positionally-invariant object category learning and recognition via Where-to-What stream interactions. It can also learn to focus motivated attention upon such an object using a combination of conditioned reinforcer learning and incentive motivational learning during cognitive-emotional interactions (Grossberg, 1975; Grossberg and Seidman, 2006). Finally, it can search a 2D scene for a valued goal object using What-to-Where stream top-down ART expectations and basal ganglia volition (Fig. 3b), hereby proposing a neurobiologically-grounded solution of the Where's Waldo problem.

Combining all of these developments within a 3D ARTSCAN Search model enables learning of view-, size-, and positionally-invariant object categories of objects in a 3D scene, and search of such a scene to detect, attend, recognize, and look at a valued target object in it, without disrupting perceptual stability during the search.

8. Laminar cortical dynamics of vision, speech, and cognition

How similar learning mechanisms may govern different functions is exemplified at multiple organizational levels. For example, although all neocortex seems to share many basic anatomical features, notably its characteristic organization into six horizontal layers and sublaminae, their specializations in different cortical regions may support vision, or speech, or cognition. Figs. 4–6 summarize three examples of the LAMINART family of laminar cortical architectures: the 3D LAMINART model (Cao and Grossberg, 2005, 2012; Grossberg and Yazdanbakhsh, 2005) of 3D vision and figure-ground separation, the cARTWORD model of speech learning and perception (Grossberg and Kazerounian, 2011), and the LIST PARSE model of cognitive working memory and learned list unitization or chunking (Grossberg and Pearson, 2008). These models illustrate how functional diversity may arise even when the synaptic learning laws *and* the overall anatomical architecture share many features.

8.1. *Laminar computing: A revolutionary new paradigm for intelligent computation*

These LAMINART models illustrate the computational paradigm of Laminar Computing (Grossberg, 2007, 2012) whose goal is to clarify how specializations of the characteristic bottom-up, top-down, and horizontal interactions in the cerebral cortex embody different types of biological intelligence. Laminar Computing proposes how this can happen, while explaining

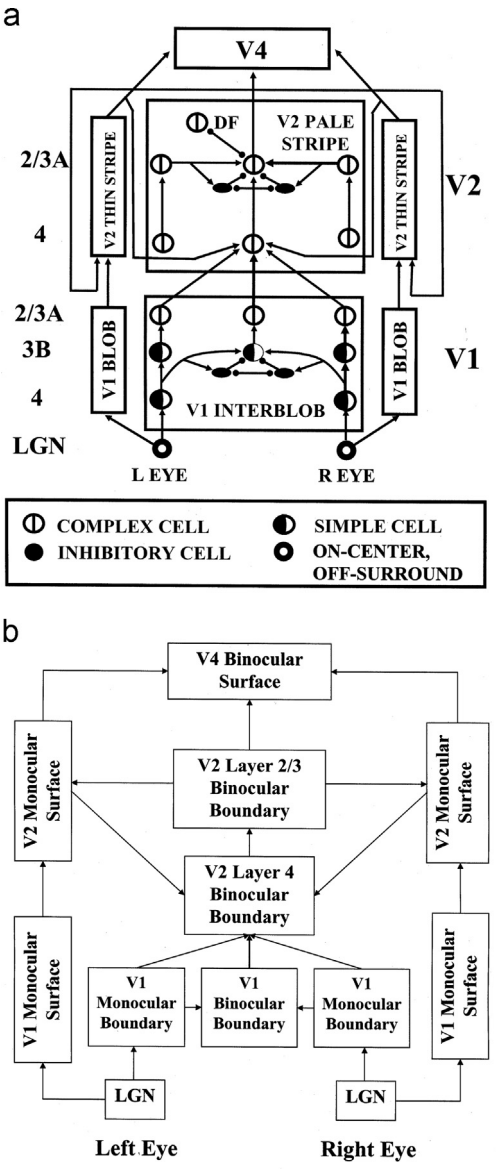

Fig. 4 – (a) The 3D LAMINART model circuit diagram. The model consists of a (V1 Interblob)–(V2 Pale Stripe)-V4 boundary stream which computes 3D perceptual groupings, and a (V1 Blob)–(V2 Thin Stripe)-V4 surface stream which computes 3D surface representations of lightness, color, and depth. The two processing streams interact to overcome their complementary computational deficiencies (Grossberg, 1994) and create consistent 3D boundary and surface percepts. (b) A block diagram of the 3D LAMINART model. [Reproduced with permission from Cao and Grossberg (2005).]

how the laminar design of neocortex enables it to support (1) self-stabilizing development, learning, and memory that solve the stability–plasticity dilemma, (2) probabilistic decisions that reconcile the demands of automatic data-driven bottom-up processing and task-selective attentive top-down processing, and (3) *analog coherence*, or the ability to unify the sensitivity of analog computing and the stability of digital computing. LAMINART hereby embodies the best properties of feedforward and feedback processing, digital and analog processing, and bottom-up data-driven processing and top-down attentive hypothesis-driven processing.

8.2. *Fast feedforward vs. slower feedback processing of unambiguous vs. ambiguous data*

When unambiguous information is processed, such as a familiar and well-rendered scene, a LAMINART architecture (Fig. 7) can quickly group the scene in a fast feedforward sweep of activation that passes directly through layer 4 to 2/3 and then on to layers 4 to 2/3 in subsequent cortical areas (Fig. 7c and e). This property clarifies how recognition can be so fast in response to unambiguous scenes; e.g., Thorpe et al. (1996).

On the other hand, if there are multiple possible groupings in a scene, say in response to a complex textured scene, then competition among these possibilities due to inhibitory interactions in layers 4 and 2/3 (black cells and synapses in Fig. 7) can cause all cell activities to become smaller, because activities in the model's competitive circuits are *self-normalizing*, or tend to conserve the total activity of the circuit. This property emerges from the architecture's shunting on-center off-surround networks, which also enable input contrasts to be processed over a large dynamic range without saturation (Douglas et al., 1995; Grossberg, 1973, 1980; Heeger, 1992).

8.3. *Trading certainty against speed: Real-time probabilities that run as fast as they can*

Said in another way, these self-normalizing circuits carry out a type of real-time probability theory in which the amplitude of cell activity covaries with the certainty of the network's selection, or decision, about a grouping. Amplitude covaries with processing speed and, due to the feedback interactions within these circuits, the coherence and synchronization of cell activations. Low activity slows down feedforward processing in the circuit because it takes longer for cell activities to exceed output thresholds and to activate subsequent cells above threshold. Network uncertainty is resolved through feedback (Fig. 7c and e): Active layer 2/3 grouping cells feed back signals to layers 6-then-4-then-2/3 to close a cortical feed back loop that contrast-enhances and amplifies the winning grouping to a degree and at a rate that reflect the amount of statistical evidence for that grouping. As the winning grouping emerges, and weaker groupings are suppressed, the activities of the winning cells become more active and synchronous, and thus can resume transmitting this cortical decision to subsequent processing stages.

In summary, a LAMINART circuit "runs as fast as it can" in response to the available evidence, trading certainty against speed: It operates in a fast feedforward mode when there is little uncertainty, and automatically engages a slower feedback mode when there is uncertainty. Feedback selects a winning decision that enables the circuit to speed up again, since activation amplitude, synchronization, and processing speed both increase with certainty. Such decision-making properties go beyond the Bayesian statistical approaches to biological intelligence that are so popular today.

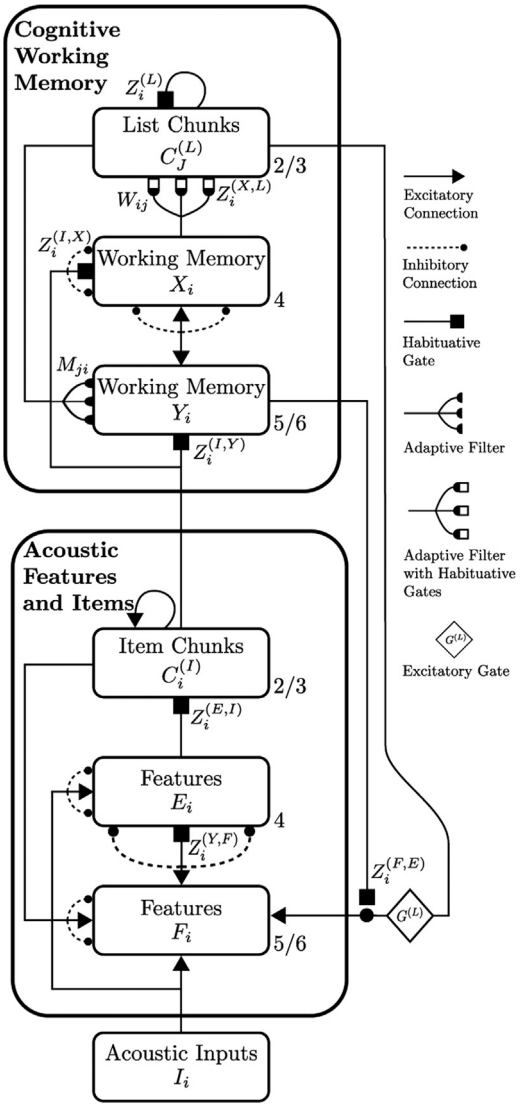

Fig. 5 – The cARTWORD model describes a hierarchy of levels responsible for the processes involved in speech and language perception. Each level is organized into laminar cortical circuits, wherein deep layers (6 and 4) are responsible for processing and storing inputs, and superficial layers (2/3) are proposed to group distributed patterns across these deeper layers into learned unitized representations. The lowest level is responsible for processing acoustic features (cell activities F_i and E_i) and items (cell activities $C_i^{(I)}$), whereas the higher level is responsible for storing of sequences of acoustic items in working memory (activities Y_i and X_i), and representing these stored sequences of these items as unitized, context-sensitive representations by list chunks (activities $C_J^{(L)}$) in a network, called a *masking field*, that is capable of selectively representing lists of variable length. [Reprinted with permission from Grossberg and Kazerounian (2011).]

8.4. *Combining the stability of digital with the sensitivity of analog computing*

The LAMINART model also embodies a novel kind of hybrid computing that simultaneously realizes the stability of digital computing and the sensitivity of analog computing. This is true because the feedback loop between layers 2/3-6-4-2/3 that selects or confirms a winning grouping (Fig. 7c and e) has the property of *analog coherence* (Grossberg, 1999; Grossberg et al., 1997; Grossberg and Raizada, 2000; Yazdanbakhsh and Grossberg, 2004); namely, this feedback loop can synchronously choose and store a winning grouping, while suppressing losing groupings, without losing analog sensitivity to amplitude differences in the input pattern. Such synchronous storage in the feedback loop provides the stability of digital computing – for example, the feedback loop exhibits hysteresis that can preserve the stored pattern against external perturbations – while preserving the sensitivity of analog computation—so that it can weigh the evidence for a grouping and translate evidence into the graded activities of the winning grouping.

9. Spatial navigation: Entorhinal grid cell and hippocampal place cell learning

9.1. *Place cells and spatial navigation*

Section 7 noted how an ART category learning circuit could be embedded in larger architectures that can autonomously carry out invariant object category learning as the eyes search a scene. Are similar laws of learning and memory used to accomplish behavioral competences that may seem to a casual observer to be totally unrelated? One affirmative example concerns how spatial navigation is controlled. This example is particularly relevant to classical data about LTP and LTD because these data were recorded in the hippocampus, and the hippocampus and medial entorhinal cortex (MEC) play an important role in the control of spatial learning, memory, and navigation (Davis et al., 1992; Morris et al., 1982; Parron and Save, 2004).

Place cells in the hippocampus fire whenever a rat is in a specific localized region, or "place", in an environment (O'Keefe and Dostrovsky, 1971). They can also exhibit multiple firing fields when an animal navigates in large spaces (Fenton et al., 2008; Henriksen et al., 2010; Park et al., 2011). The ensemble of all place cells enables an animal to localize itself in an environment. Research on place cells has clarified that they receive two kinds of inputs: one conveying information about the sensory, notably visual, context experienced from a given place, and the other from a navigational, or path integration, system that tracks relative position in the world by integrating angular and linear velocity self-movement estimates for instantaneous rotation and translation, respectively. An important open problem is to explain how sensory context and path integration information are combined to control navigation; e.g., Chen et al. (2013).

9.2. *Grid cells and path integration*

What is the source of path integration inputs to place cells? More generally, how do place cells get learned? *Grid cells* in the superficial layers of medial entorhinal cortex (MEC) provide inputs to hippocampal place cells, and the primary determinants of their firing are path integration inputs (McNaughton et al., 2006). Grid cells are so called because each of them, unlike a place cell, fires at multiple spatial

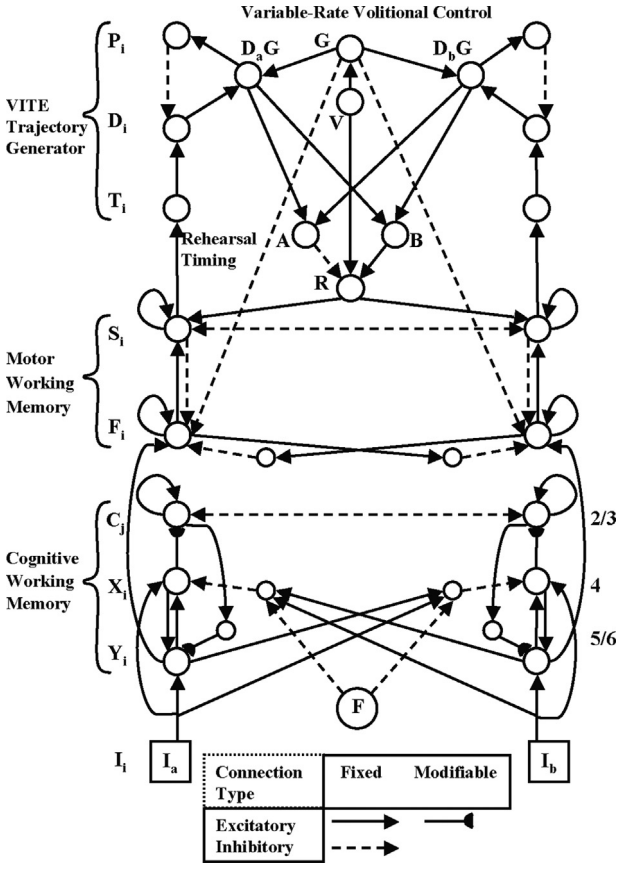

Fig. 6 – Circuit diagram of the LIST PARSE model. An Item and Order working memory is realized by a recurrent shunting on-center off-surround network in layers 4 and 6 of the Cognitive Working Memory, which is assumed to occur in ventrolateral prefrontal cortex. The list chunks are learned in layer 2/3. Outputs from the Cognitive Working Memory to the Motor Working Memory interact with a Vector Integration To Endpoint (VITE) trajectory generator (Bullock and Grossberg, 1988; see Section 9), modulated by the basal ganglia, to perform sequences of variable length at variable speeds. Solid arrows indicate fixed excitatory connections. Solid lines with hemi-disks indicate learned connections. Dashed arrows indicate fixed inhibitory connections. Only 1-item chunks (*C*) and their feedback connections within a single Cognitive Working Memory channel are shown, whereas the model uses chunks of various sizes in layer 2/3 and feedback from layer 2/3 to layer 5/6 of the Cognitive Working Memory is broadly distributed. Also, only the excitatory projections from Cognitive Working Memory to the Motor Plan Field ($Y \rightarrow F$) are shown. [Reprinted with permission from Grossberg and Pearson (2008).]

positions that form a regular hexagonal grid during navigation in an open field (Hafting et al., 2005). Grid cells also exhibit a gradient of spatial scales along the dorsoventral axis of the MEC, with larger receptive fields towards the ventral end, and anatomically neighboring cells sharing similar grid spacings and orientations but having different spatial phases that are not topographically organized.

9.3. *Both grid and place cells are learned from self-organizing maps that obey the same laws*

Despite their dramatically different appearance, the receptive fields of grid cells and place cells can be learned within successive processing stages in a hierarchy of self-organizing maps, wherein each processing stage obeys the same laws, including the normalized instar law of Eq. (5). This GridPlaceMap model has been developed with both rate-based and spiking neurons (Pilly and Grossberg, 2012, 2013); see Fig. 8. The difference in appearance of the cell receptive fields emerges from the different statistical properties of their input patterns (Fig. 9). The receptive fields that are learned by the GridPlaceMap model fit neurophysiological data about grid and place cells and their development in juvenile rats (Langston et al., 2010; Wills et al., 2010).

Due to the inputs that they receive from multiple scales of developing grid cells, the learned hippocampal place fields can represent much larger spaces than the grid cells, indeed spaces whose spatial scale may be the least common multiple of grid cell scales (Gorchetchnikov and Grossberg, 2007). These least common multiple scales are large enough to let place cells support navigational behaviors. In addition to both grid cell and place cell properties emerging from the same self-organizing map equations, albeit at different processing levels, at both of these processing levels, the self-organizing maps amplify and learn to categorize the most energetic and frequent co-activations of their inputs.

9.4. *Top-down attention stabilizes grid and place cell memory*

In the GridPlaceMap model, place cells are spatial category cells that are activated by multiple scales of entrohinal grid cells in a self-organizing map. However, when Grossberg (1976a, 1978) introduced the modern laws for competitive learning and self-organizing maps, he proved that they can learn well in response to sparse input environments, indeed with Bayesian properties, but that they exhibit catastrophic forgetting in response to dense non-stationary environments. Grossberg (1976b) introduced ART as an enhanced model capable of dynamically stabilizing its category learning in response to arbitrary environments.

If, in fact, grid and place cell learning occur in self-organizing maps, then, as in all self-organizing map models, one expects that grid cell and place cell learning are dynamically stabilized by ART top-down attentive matching mechanisms (Section 6). Anatomical and neurophysiological data from several labs support this hypothesis.

The anatomy of the hippocampal system supports the possibility that such attentive feedback exists, since feedback pathways exist from the hippocampal CA1 region to the entorhinal cortex. Neurophysiological data also support the predicted role of attention in hippocampal learning. For example, Kentros et al. (2004) showed that "conditions that maximize place field stability greatly increase orientation to novel cues. This suggests that storage and retrieval of place cells is modulated by a top-down cognitive process resembling attention and that place cells are neural correlates of spatial memory" (p. 283). It has similarly been proposed that

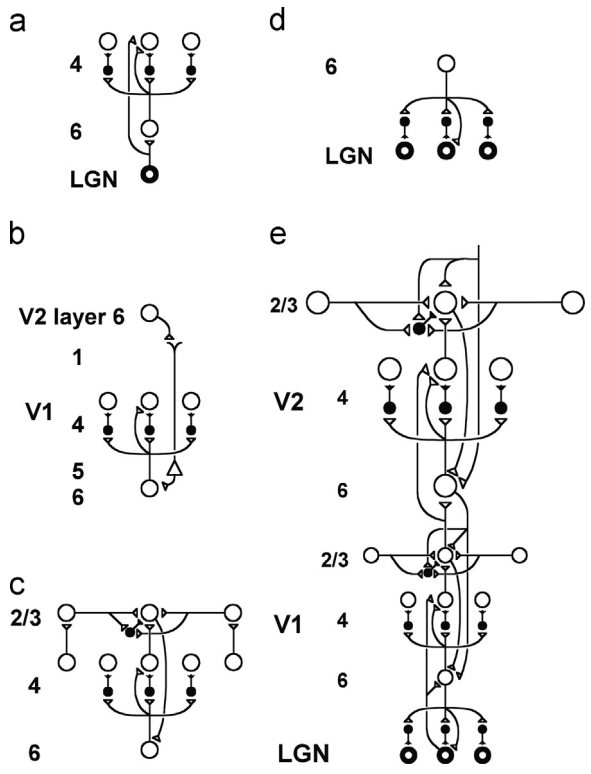

Fig. 7 – The LAMINART model clarifies how bottom-up, horizontal, and top-down interactions within and across cortical layers in V1 and V2 interblob and pale stripe regions, respectively, carry out bottom-up adaptive filtering, horizontal grouping, and top-down attention. Similar interactions seem to occur in all six-layered cortices. See text for details. [Reprinted with permission from Raizada and Grossberg (2001).]

learning of place cell receptive fields reflects an "automatic recording of attended experience" (Morris and Frey, 1997, p. 1489). These experiments clarify that cognitive processes like attention play a role in hippocampal learning and memory stability, just as they do in learning object categories, and interact with NMDA receptors to mediate long-lasting hippocampal place field memory in novel environments (Kentros et al., 1998). Thus, the learning of grid cells and place cells in the medial entorhinal cortex and hippocampus may be viewed as part of a specialized ART system for learning spatial representations as an animal or human navigates its environment, just as the learning of invariant object categories in the inferotemporal cortex may be viewed as part of a specialized ART system for learning object representations as an animal or human scans its environment.

9.5. *Unifying angular and linear acceleration, grid and place, and space and time*

In addition to showing how both grid cells and place cells can be learned using the same equations, including learning laws, at different levels of a model hierarchy, the GridPlaceMap model also illustrates two other parsimonious and elegant sets of properties that are predicted to arise from specializations of homologous circuits.

The first homology concerns the fact that path integration inputs to the model are sensitive to both angular velocity and linear velocity during movement. Angular velocity is processed by a well-known type of cell, a head-direction cell (Ranck, 1984; Taube et al., 1990). The GridPlaceMap model and its precursor (Mhatre et al., 2012) predicted the existence of a cell that is sensitive to linear velocity as well. It is called a *stripe cell*. Both head direction cells and stripe cells are predicted to exist within similar types of ring attractor circuits (e.g., Song and Wang, 2005), where they receive angular and linear velocity signals and process them into a form that inputs to model stripe cells. See Fig. 9 for a simulation of stripe cell responses. Recent experiments have reported cell properties that are consistent with those predicted by stripe cells (Krupic et al., 2012; Sargolini et al., 2006).

9.6. *Neural relativity: Spectral timing and spectral spacing in the hippocampus*

The second homology concerns the fact that the entorhinal–hippocampal system processes information about both space and time: In addition to supporting spatial navigation with grid and place cells, it can also support adaptively timed conditioning (Smith, 1968; Thompson et al., 1987). Why, from a mechanistic viewpoint, are both spatial and temporal representations processed in the same part of the brain? The fact of this convergence is consistent with data and hypotheses about a possible role of hippocampus in episodic learning and memory, since episodic memories typically combine both spatial and temporal information about particular autobiographical events; e.g., Eichenbaum and Lipton (2008).

As noted in Section 9.3, multiple scales of entorhinal grid cells can cooperate in a self-organizing map to form place cell receptive fields. These multiple grid cell scales form along a dorsoventral spatial gradient in the entorhinal cortex such that grid cells have increasingly large spatial scales (that is, larger spatial intervals between activations in a hexagonal grid) in the ventral direction. Grid cells with several different spatial scales along the dorsoventral gradient can cooperate to learn place cells that can represent spaces much larger than those represented by individual grid cells (Grossberg and Pilly, 2012). In fact, place cells that are learned from these grid cells are capable of representing the lowest common multiple of the grid cell scales that activate them (Gorchetchnikov and Grossberg, 2007; Pilly and Grossberg, 2012). These place cell spatial scales are large enough to be useful in spatial navigation. In this way, a "spectrum" of small grid cell spatial scales can be combined in place cells to represent much larger and behaviorally relevant spaces. This homology has led to the name Spectral Spacing for the mechanism whereby grid cells give rise to place cells.

With this background, we can begin to see a similarity in how the entorhinal–hippocampal system deals with both space and time. In the case of spatial representation, the issue is how to generate spatial representations on behaviorally relevant scales. The cooperation of multiple, but smaller, scales of entorhinal grid cells to learn hippocampal place cells accomplishes this. In the case of temporal representation, a

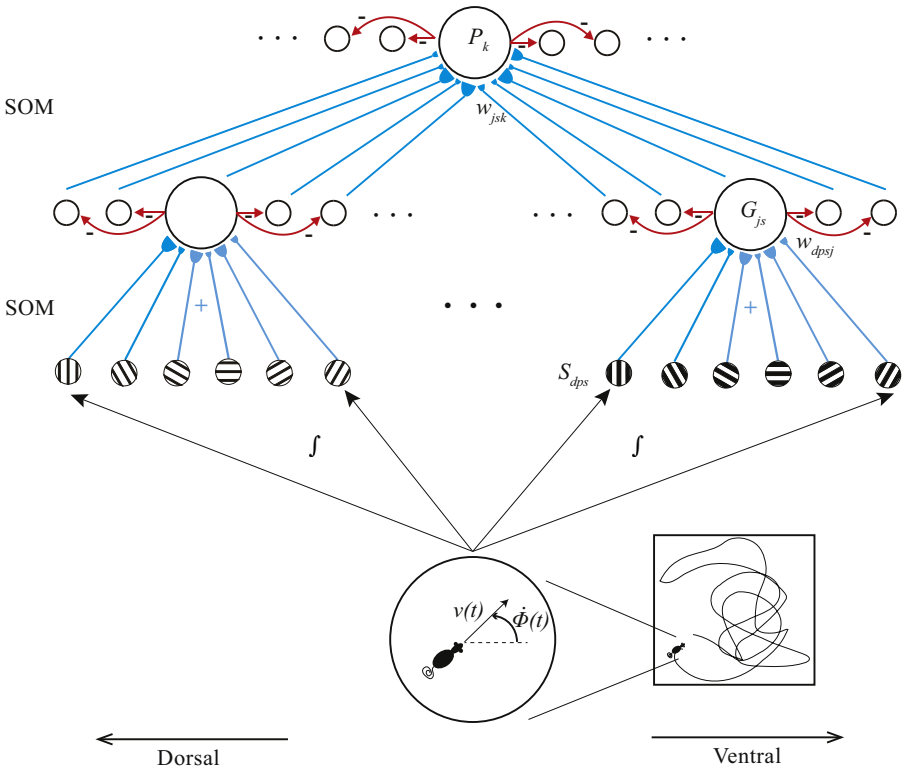

Fig. 8 – The GridPlaceMap self-organizing map hierarchy of grid and place cell activation and learning: Stripe cells in either the parasubiculum (PaS) or the deeper layers of medial entorhinal cortex (MEC), self-organizing grid cells in layer II of MEC, and self-organizing place cells in hippocampal area CA3 learn to represent position in increasingly large spaces based on internally generated signals corresponding to translational and rotational movements during navigation. [Reprinted with permission from Pilly and Grossberg (2012).]

spectrum of small time scales can be combined to represent longer and behaviorally relevant durations of cell activation, as occur, for example, during trace conditioning (Moyer et al., 1990; Solomon et al., 1986). A model that accomplishes this is called the Spectral Timing model (Grossberg and Merrill, 1992, 1996; Grossberg and Schmajuk, 1989).

The Spectral Timing model shows how large temporal intervals can be bridged by a spectrum of cells, or cell sites, with different reaction rates can learn to match the statistical distribution of expected delays in reinforcement. Although each of these cells, or cell sites, reacts relatively briefly at different times, their population response as a whole can bridge a much longer time interval, ranging from hundreds of milliseconds to seconds, that can be tuned by learning to match temporal experimental contingencies.

Spectrally-timed learning has Weber law properties such that larger inter-stimulus intervals between unconditioned and conditioned stimuli lead to learned response curves with broader variances, a property that is also called "scalar timing" (Gibbon, 1991; Roberts, 1981; Roberts et al., 1989; Smith, 1968). Hippocampal "time cells" with all the properties required to achieve spectral timing, including the Weber law, have been reported (MacDonald et al., 2011); in particular, "… the mean peak firing rate for each time cell occurred at sequential moments, and the overlap among firing periods from even these small ensembles of time cells bridges the entire delay. Notably, the spread of the firing period for each neuron increased with the peak firing time …."

It remains to be shown whether the spectrum of time cells arises from a gradient in a single rate parameter, as is predicted by the Spectral Timing model. How Spectral Timing can bridge long temporal intervals using such a gradient has been modeled in terms of calcium dynamics in the metabotropic glutamate receptor (mGluR) system within the cerebellum (Fiala et al., 1996). The most parsimonious prediction is that a similar mechanism holds in all cases of spectral timing throughout the brain, including cerebellum, hippocampus, and basal ganglia (Brown et al., 1999; Fiala et al., 1996; Grossberg and Merrill, 1992, 1996; Grossberg and Schmajuk, 1989).

9.7. *Lateral stream for time and medial stream for space*

The Spectral Timing model reflects the part of entorhinal–hippocampal dynamics that is devoted to representing objects and events, notably adaptively timed durations of these events, and includes lateral entorhinal cortex. The Spectral Spacing model reflects a complementary part of entorhinal–hippocampal dynamics that is devoted to representing spatial representations, and includes medial entrorhinal cortex. Both of these processing streams are joined in the hippocampus to support spatial navigation as well as episodic learning and memory (Eichenbaum and Lipton, 2008).

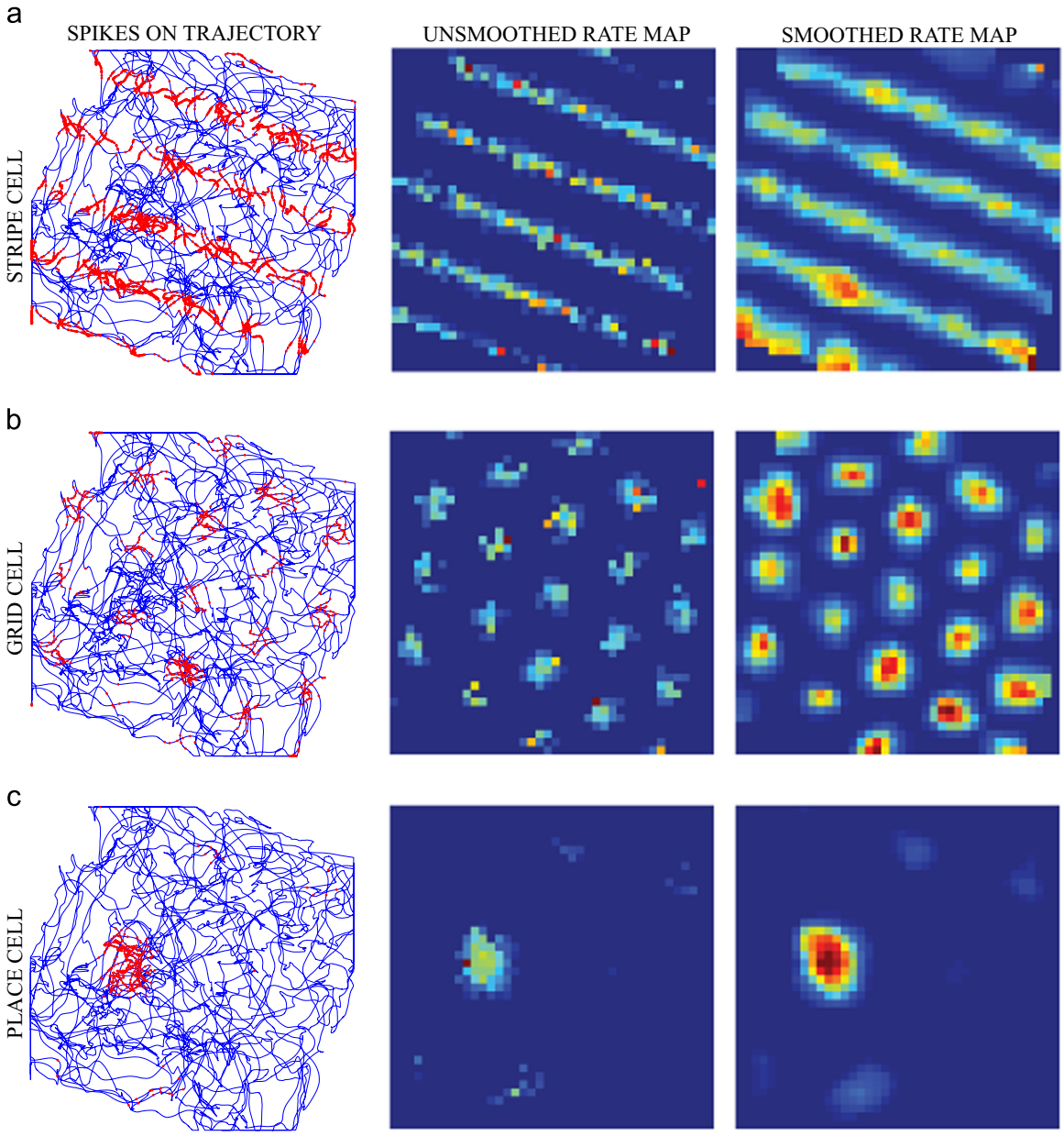

Fig. 9 – Spatial responses of representative (a) stripe cells, (b) grid cells, and (c) place cells. The first column shows the spike locations (red dots) of the cells superimposed on the trajectory of the navigating model animal, or animat, during a trial. The second and third columns show the unsmoothed and smoothed spatial rate maps, respectively, of the cells. See Pilly and Grossberg (2013) for how spike recordings are converted into rate maps. [Reprinted with permission from Pilly and Grossberg (2013).]

This heuristic homology between spatial and temporal representations in these parallel streams is supported by rigorous mathematical modeling and data simulations. Grossberg and Pilly (2012) developed the Spectral Spacing model to show that neural mechanisms that enable a dorsoventral gradient of grid cell spatial scales to be learned are formally the same as mechanisms which enable a gradient of temporal scales to form in the Spectral Timing model. This claim was supported by quantitative simulations of challenging data about parametric neurophysiological properties of grid cells along the dorsoventral gradient that could not be explained without this assumption. Thus, it may be that space and time are both in the hippocampus because they exploit shared computational mechanisms. The phrase "neural relativity" has been introduced to summarize this predicted property of the entorhinal–hippocampal system.

Given the prediction and simulations of mGluR involvement in Spectral Timing, it is natural to ask if mGLuR plays a central role in controlling the dorsoventral gradient in Spectral Spacing as well.

10. Movement control: Inhibitory matching and mismatch learning

10.1. *Complementary computing for object recognition and movement control*

ART-based learning of object representations in the What stream uses excitatory matching and match-based learning. Where stream learning for the control of movement, in contrast, often uses computationally complementary processes of inhibitory matching and mismatch-based learning (Fig. 1). Correspondingly, the What stream learns object representations that strive to become positionally-invariant, whereas the Where stream represents the positions and actions that enable recognized objects to be manipulated.

Excitatory matching and match-based learning can solve the stability–plasticity dilemma. In contrast, inhibitory matching and mismatch-based learning can continually update the spatial maps and sensory-motor gains that are used to move as our bodily parameters change through time (Bullock and Grossberg, 1988; Bullock et al., 1998; Gaudiano and Grossberg, 1991; Georgopoulos et al., 1982, 1986). Indeed, we would be ill-served by spatial and motor learning processes that solve the stability–plasticity dilemma, since we do not want the spatial representations and motor gains that were suitable for controlling our infant bodies to be remembered as we grow up and used to control our adult bodies. In this sense, catastrophic forgetting is a good property during spatial and motor learning.

10.2. *Target position, present position, and difference vector*

As an example of inhibitory matching, consider how we make an arm movement. To make such a movement, a representation of where the arm is now (its *present position vector*) is subtracted from a representation of where we want the arm to move (its *target position vector*), thereby computing a *difference vector* that represents the direction and distance of movement needed to attain the target. After moving to the target, the target and present positions agree, so the difference vector is zero. In other words, this sort of matching is inhibitory (Bullock and Grossberg, 1988). The difference vector is volitionally gated, or multiplied, by a basal ganglia GO signal that determines when and how fast the movement will occur (Bullock and Grossberg, 1988; Bullock et al., 1998).

Such a volitionally-gated difference vector computation is, for example, used in the Vector Integration To Endpoint, or VITE, model, and its variants, for computing arm movement trajectories (Bullock et al., 1998, 1993; Bullock and Grossberg, 1988). Let T denote the target position vector, P the present position vector, D the difference vector, and G the volitional GO signal (Fig. 10). Then:

$$\frac{dD}{dt} = a(-D + T - P) \tag{9}$$

and

$$\frac{dP}{dt} = G[D]^{+}, \tag{10}$$

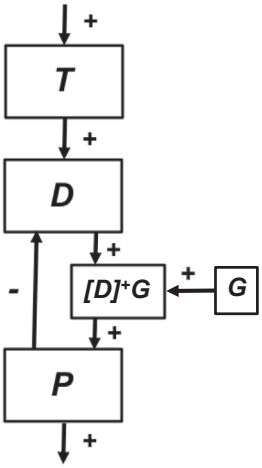

Fig. 10 – Vector Integration To Endpoint circuit (Bullock and Grossberg, 1988) for control of movement trajectories. *T* is the target position vector, *P* the outflow present position vector, *D* the difference vector, and *G* the volitional GO signal that multiplies, or gates, *D*. See text for details.

where $[D]^{+} = max(D, 0)$. Eq. (9) says that D computes a time-average of the difference $(T–P)$ between the target and present position vectors, and (10) says that the present position vector P integrates the difference vector D at a rate proportional to the GO signal G until P equals T, whence the movement stops.

10.3. *Difference vectors as error signals for learning*

During motor learning, a difference vector can also generate error signals when the same target position and present position are encoded but not properly calibrated. These error signals activate a form of mismatch learning that eliminates the mismatch through time by recalibrating system maps and gains to be consistent. The following pair of equations illustrate how this can happen by replacing Eq. (9) by

$$\frac{dD}{dt} = a(-D + TZ - P) \tag{11}$$

and

$$\frac{dZ}{dt} = bf(T)(-cZ - dD). \tag{12}$$

In this learning process, the adaptive weight Z in Eq. (12) changes in response to a non-zero difference vector D at times when the target position T and present position P represent the same position, but are not properly calibrated. The weight Z increases if D is negative, and decreases if D is positive. Learning continues until the adaptive weight Z in Eq. (12), by acting as an adaptive gain that multiplies the target position T in Eq. (11), causes D to approach zero at the appropriate times.

Neural models explain and predict data about how mismatch learning may tune spatial representations and adaptive motor gains in basal ganglia, cerebellum, motor cortex, parietal cortex, and prefrontal cortex (Brown et al., 1999, 2004; Fiala et al., 1996; Grossberg and Paine, 2000; Guenther, 1995; Guenther et al., 1994). Models that carry out computation and learning by difference vectors are often called Adaptive

Vector Integration To Endpoint (aVITE) or Vector Associative Map (VAM) models (Gaudiano and Grossberg, 1991, 1992).

10.4. *Joining ART and VAM: Self-stabilizing expertise in evolving bodies*

In summary, perceptual/cognitive processes often use ART-like excitatory matching and match-based learning to create self-stabilizing representations of objects and events that enable us to gain increasing expertise as we learn about the world. Complementary spatial/motor processes often use VAM-like inhibitory matching and mismatch-based learning to continually update spatial maps and sensory-motor gains to compensate for bodily changes throughout life. Together (Fig. 1) these complementary predictive and learning mechanisms create a self-stabilizing perceptual/cognitive front end for intelligently manipulating the more labile spatial/motor processes which enable our changing bodies to act effectively upon a dynamic world.

REFERENCES

Abbott, L.F., Varela, K., Sen, K., Nelson, S.B., 1997. Synaptic depression and cortical gain control. Science 275, 220–223.

Amis, G., Carpenter, G.A., Ersoy, B., Grossberg, S., 2014. Cortical Learning of Recognition Categories: Towards Resolving the Exemplar vs. Prototype Debate. Submitted for publication.

Andersen, R.A., Essick, G.K., Siegel, R.M., 1985. Encoding of spatial location by posterior parietal neurons. Science 230, 456–458.

Andersen, R.A., Mountcastle, V.B., 1983. The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex. J. Neurosci. 3, 532–548.

Artola, A., Singer, W., 1987. Long-term potentiation and NMDA receptors in rat visual cortex. Nature 330, 649–652.

Artola, A., Singer, W., 1993. Long-term depression of excitatory synaptic transmission and its relationship to long-term potentiation. Trends Neurosci. 16, 480–487.

Bar, M., Tootell, R.B.H., Schacter, D.L., Greve, D.N., Fischl, B., Mendola, J.D., Rosen, B.R., Dale, A.M., 2001. Cortical mechanisms specific to explicit object recognition. Neuron 29, 529–535.

Ben-Shahar, O., Zucker, S., 2004. Sensitivity to curvatures in orientation-based texture segmentation. Vis. Res. 44, 257–277.

Berke, J.D., Hetrick, V., Breck, J., Green, R.W., 2008. Transient 23- to 30-Hz oscillations in mouse hippocampus during exploration of novel environments. Hippocampus 18, 519–529.

Bhatt, R., Carpenter, G., Grossberg, S., 2007. Texture segregation by visual cortex: perceptual grouping, attention, and learning. Vis. Res. 47, 3173–3211.

Bliss, T.V.P., Lomo, T., 1973. Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. J. Physiol. (London) 232, 331–356.

Bliss, T.V.P., Gardner-Medwin, A.R., 1973. Long-lasting potentiation of synaptic transmission in the dentate area of the unanaesthetized rabbit following stimulation of the perforant path. J. Physiol. (London) 232, 357–374.

Brown, J., Bullock, D., Grossberg, S., 1999. How the basal ganglia use parallel excitatory and inhibitory learning pathways to selectively respond to unexpected rewarding cues. J. Neurosci. 19, 10502–10511.

Brown, J.W., Bullock, D., Grossberg, S., 2004. How laminar frontal cortex and basal ganglia circuits interact to control planned and reactive saccades. Neural Networks 17, 471–510.

Brunel, N., 2003. Dynamics and plasticity of stimulus selective persistent activity in cortical network models. Cerebral Cortex 13, 1151–1161.

Buffalo, E.A., Fries, P., Landman, R., Buschman, T.J., Desimone, R., 2011. Laminar differences in gamma and alpha coherence in the ventral stream. Proc. Natl. Acad. Sci. U.S.A. 108, 11262–11267.

Bullock, D., Cisek, P., Grossberg, S., 1998. Cortical networks for control of voluntary arm movements under variable force conditions. Cerebral Cortex 8, 48–62.

Bullock, D., Grossberg, S., 1988. Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. Psychol. Rev. 95, 49–90.

Bullock, D., Grossberg, S., Guenther, F.H., 1993. A self-organizing neural model of motor equivalent reaching and tool use by a multijoint arm. J. Cogn. Neurosci. 5, 408–435.

Buschman, T.J., Miller, E.K., 2009. Serial, covert shifts of attention during visual search are reflected by the frontal eye fields and correlated with population oscillations. Neuron 63, 386–396.

Cabelli, R.J., Hohn, A., Shatz, C.J., 1995. Inhibition of ocular dominance column formation by infusion of NT-4/5 or BDNF. Science 267, 1662–1666.

Cabelli, R.J., Shelton, D.L., Segal, R.A., Shatz, C.J., 1997. Blockade of endogenous ligands of trkB inhibits formation of ocular dominance columns. Neuron 19, 63–76.

Cabeza, R., Ciaramelli, E., Olson, I.R., Moscovitch, M., 2008. The parietal cortex and episodic memory: an attentional account. Nat. Rev. Neurosci. 9, 613–625.

Cao, Y., Grossberg, S., 2005. A laminar cortical model of stereopsis and 3D surface perception: closure and da Vinci stereopsis. Spat. Vis. 18, 515–578.

Cao, Y., Grossberg, S., 2012. Stereopsis and 3D surface perception by spiking neurons in laminar cortical circuits: a method of converting neural rate models into spiking models. Neural Networks 26, 75–98.

Cao, Y., Grossberg, S., Markowitz, J., 2011. How does the brain rapidly learn and reorganize view- and positionally-invariant object representations in inferior temporal cortex?. Neural Networks 24, 1050–1061.

Carpenter, G.A., 1997. Distributed learning, recognition, and prediction by ART and ARTMAP neural networks. Neural Networks 10, 1473–1494.

Carpenter, G.A., 2003. Default ARTMAP. In: Proceedings of the International Joint Conference on Neural Networks (IJCNN'03), pp. 1396–1401.

Carpenter, G.A., Grossberg, S., 1987. A massively parallel architecture for a self-organizing neural pattern recognition machine. Comput. Vis. Graphics Image Process. 37, 54–115.

Carpenter, G.A., Grossberg, S., 1991. Pattern Recognition by Self-Organizing Neural Networks. MIT Press, Cambridge, MA.

Carpenter, G.A., Grossberg, S., 1993. Normal and amnesic learning, recognition, and memory by a neural model of cortico-hippocampal interactions. Trends Neurosci. 16, 131–137.

Carpenter, G.A., Grossberg, S., Markuzon, N., Reynolds, J.H., Rosen, D.B., 1992. Fuzzy ARTMAP: a neural network architecture for incremental supervised learning of analog multidimensional maps. IEEE Trans. Neural Networks 3, 698–713.

Carpenter, G.A., Grossberg, S., Reynolds, J.H., 1991. ARTMAP: supervised real-time learning and classification of nonstationary data by a self-organizing neural network. Neural Networks 4, 565–588.

Carpenter, G.A., Grossberg, S., Rosen, D.B., 1991. Fuzzy ART: fast stable learning and categorization of analog patterns by an adaptive resonance system. Neural Networks 4, 759–771.

Chang, H.-C., Grossberg, S., Cao, Y., 2014. Where's Waldo? How perceptual cognitive, and emotional brain processes

cooperate during learning to categorize and find desired objects in a cluttered scene. Front. Integr. Neurosci. http://dx.doi.org/10.3389/fnint.2014.0043 (http://journal.frontiersin.org/Journal/10.3389/fnint.2014.00043/full).
Chen, C., King, J.A., Burgess, N., O'Keefe, J., 2013. How vision and movement combine in the hippocampal place code. Proc. Natl. Acad. Sci. U.S.A. 110, 378–383.
Chiu, Y.C., Yantis, S., 2009. A domain-independent source of cognitive control for task sets: shifting spatial attention and switching categorization rules. J. Neurosci. 29, 3930–3938.
Church, B.A., Krauss, M.S., Lopata, C., Toomey, J.A., Thomeer, M.L., Coutinho, M.V., Volker, M.A., Mercado, E. (2010). Atypical categorization in children with high-functioning autism spectrum disorder. Psychon. Bull. Rev., 17, 862–868.
Cohen, N.J., Squire, L.R., 1980. Preserved learning and retention of a pattern-analyzing skill in amnesia: dissociation of knowing how and knowing that. Science 210, 207–210.
Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., Shulman, G.L., 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nat. Neurosci. 3, 292–297.
Corbetta, M., Patel, G., Shulman, G.G., 2008. The reorienting system of the human brain: from environment to theory of mind. Neuron 58, 306–324.
Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201–215.
Davis, S., Butcher, S.P., Morris, R.G., 1992. The NMDA receptor antagonist D-2-amino-5-phosphonopentanoate (D-AP5) impairs spatial learning and LTP in vivo at intracerebral concentrations comparable to those that block LTP in vivo. J. Neurosci. 12, 21–34.
Deneve, S., Pouget, A., 2003. Basis functions for object-centered representations. Neuron 37, 347–359.
Desimone, R., 1998. Visual attention mediated by biased competition in extrastriate visual cortex. Philos. Trans. Roy. Soc. London, Ser. B 353, 1245–1255.
Dosenbach, N.U., Fair, D.A., Cohen, A.L., Schlaggar, B.L., Petersen, S.E., 2008. A dual-networks architecture of top-down control. Trends Cogn. Sci. 12, 99–105.
Dosenbach, N.U.F., Fair, D.A., Miezin, F.M., Cohen, A.L., Wenger, K.K., Dosenbach, R.A.T., Fox, M.D., Snyder, A.Z., Vincent, J.L., Raichle, M.E., Schlagger, B.L., Petersen, S.E., 2007. Distinct brain networks for adaptive and stable task control in humans. Proc. Natl. Acad. Sci. U.S.A. 104, 11073–11078.
Douglas, R.J., Koch, C., Mahowald, M., Martin, K.A.C., Suarez, H.H., 1995. Recurrent excitation in neocortical circuits. Science 269, 981–985.
Dranias, M., Grossberg, S., Bullock, D., 2008. Dopaminergic and non-dopaminergic value systems in conditioning and outcome-specific revaluation. Brain Res. 1238, 239–287.
Driver, J., Mattingley, J.B., 1998. Parietal neglect and visual awareness. Nat. Neurosci. 1, 17–22.
Dudek, S.M., Bear, M.F., 1992. Homosynaptic long-term depression in area VA1 of hippocampus and effects of N-methyl-D-aspartate receptor blockade. Proc. Natl. Acad. Sci. U.S.A. 89, 4363–4367.
Duhamel, J.R., Colby, C.L., Goldberg, M.E., 1992. The updating of the representation of visual space in parietal cortex by intended eye movements. Science 255, 90–92.
Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., Reitbock, H.J., 1988. Coherent oscillations: a mechanism of feature linking in the visual cortex? Biol. Cybern. 60, 121–130.
Eichenbaum, H., Lipton, P.A., 2008. Towards a functional organization of the medial temporal lobe memory system: role of the parahippocampal and medial entorhinal cortical areas. Hippocampus 18, 1314–1324.
Egeth, H.E., Yantis, S., 1997. Visual attention: control, representation, and time course. Annu. Rev. Psychol. 48, 269–297.
Engel, A.K., Fries, P., Singer, W., 2001. Dynamics predictions: oscillations and synchrony in top-down processing. Nat. Rev. Neurosci. 2, 704–716.
Fazl, A., Grossberg, S., Mingolla, E., 2009. View-invariant object category learning, recognition, and search: how spatial and object attention are coordinated using surface-based attentional shrouds. Cogn. Psychol. 58, 1–48.
Fenton, A.A., Kao, H.-Y., Neymotin, S.A., Olypher, A., Vayntrub, Y., Lyton, W.W., Ludvig, N., 2008. Unmasking the CA1 ensemble place code by exposures to small and large environments: more place cells and multiple, irregularly arranged, and expanded place fields in the larger space. J. Neurosci. 28, 11250–11262.
Fiala, J.C., Grossberg, S., Bullock, D., 1996. Metabotropic glutamate receptor activation in cerebellar Purkinje cells as substrate for adaptive timing of the classically conditioned eye blink response. J. Neurosci. 16, 3760–3774.
Foley, N.C., Grossberg, S., Mingolla, E., 2012. Neural dynamics of object-based multifocal visual spatial attention and priming: object cueing, useful-field-of-view, and crowding. Cogn. Psychol. 65, 77–117.
Fregnac, Y., Burke, J.P., Smith, D., Friedlander, M.J., 1994. Temporal covariance of pre- and postsynaptic activity regulates functional connectivity in the visual cortex. J. Neurophysiol. 71, 1403–1421.
Fuster, J.M., Jervey, J.P., 1981. Inferotemporal neurons distinguish and retain behaviorally relevant features of visual stimuli. Science 212, 952–955.
Gancarz, G., Grossberg, S., 1999. A neural model of saccadic eye movement control explains task-specific adaptation. Vis. Res. 39, 3123–3143.
Gaudiano, P., Grossberg, S., 1991. Vector associative maps: unsupervised real-time error-based learning and control of movement trajectories. Neural Networks 4, 147–183.
Gaudiano, P., Grossberg, S., 1992. Adaptive vector integration to endpoint: self-organizing neural circuits for control of planned movement trajectories. Hum. Mov. Sci. 11, 141–155.
Georgopoulos, A.P., Kalaska, J.F., Caminiti, R., Massey, J.T., 1982. On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. J. Neurosci. 2, 1527–1537.
Georgopoulos, A.P., Schwartz, A.B., Kettner, R.E., 1986. Neuronal population coding of movement direction. Science 233, 1416–1419.
Gibbon, J., 1991. The origins of scalar timing. Learn. Motiv. 22, 3–38.
Gorchetchnikov, A., Grossberg, S., 2007. Space, time and learning in the hippocampus: how fine spatial and temporal scales are expanded into population codes for behavioral control. Neural Networks 20, 182–193.
Gottlieb, J., Kusunoki, M., Goldberg, M.E., 2005. Simultaneous representation of saccade targets and visual onsets in monkey lateral intraparietal area. Cerebral Cortex 15, 1198–1206.
Gray, C.M., Singer, W., 1989. Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. Proc. Natl. Acad. Sci. U.S.A. 86, 1698–1702.
Green, C.S., Bavelier, D., 2007. Action-video-game experience alters the spatial resolution of vision. Psychol. Sci. 18, 88–94.
Grossberg, S., 1968a. Global ratio limit theorems for some nonlinear functional differential equations, II. Bull. Am. Math. Soc. 74, 101–105.
Grossberg, S., 1968b. Some nonlinear networks capable of learning a spatial pattern of arbitrary complexity. Proc. Natl. Acad. Sci. U.S.A. 59, 368–372.

Grossberg, S., 1968c. Some physiological and biochemical consequences of psychological postulates. Proc. Natl. Acad. Sci. U.S.A. 60, 758–765.
Grossberg, S., 1969a. On learning and energy-entropy dependence in recurrent and nonrecurrent signed networks. J. Stat. Phys. 1, 319–350.
Grossberg, S., 1969b. On the production and release of chemical transmitters and related topics in cellular control. J. Theor. Biol. 22, 325–364.
Grossberg, S., 1969c. On the serial learning of lists. Math. Biosci. 4, 201–253.
Grossberg, S., 1969d. Some networks that can learn, remember, and reproduce any number of complicated space-time patterns, I. J. Math. Mech. 19, 53–91.
Grossberg, S., 1972. A neural theory of punishment and avoidance, II: Quantitative theory. Math. Biosci. 15, 253–285.
Grossberg, S., 1973. Contour enhancement, short-term memory, and constancies in reverberating neural networks. Stud. Appl. Math. 52, 213–257.
Grossberg, S., 1975. A neural model of attention, reinforcement, and discrimination learning. Int. Rev. Neurobiol. 18, 263–327.
Grossberg, S., 1976a. Adaptive pattern classification and universal recoding, I: Parallel development and coding of neural feature detectors. Biol. Cybern. 23, 121–134.
Grossberg, S., 1976b. Adaptive pattern classification and universal recoding, II: Feedback, expectation, olfaction, and illusions. Biol. Cybern. 23, 187–202.
Grossberg, S., 1978. A theory of human memory: self-organization and performance of sensory-motor codes, maps, and plans. In: Rosen, R., Snell, F. (Eds.), Progress in Theoretical Biology, vol. 5. Academic Press, New York, NY, pp. 233–374.
Grossberg, S., 1980. How does a brain build a cognitive code?. Psychol. Rev. 87, 1–51.
Grossberg, S., 1994. 3D vision and figure-ground separation by visual cortex. Percept. Psychophys. 55, 48–120.
Grossberg, S., 1999. How does the cerebral cortex work? Learning, attention and grouping by the laminar circuits of visual cortex. Spat. Vis. 12, 163–186.
Grossberg, S., 2000. The complementary brain: unifying brain dynamics and modularity. Trends Cogn. Sci. 4, 233–246.
Grossberg, S., 2007. Consciousness CLEARS the mind. Neural Networks 20, 1040–1053.
Grossberg, S., 2009. Cortical and subcortical predictive dynamics and learning during perception, cognition, emotion and action. Philos. Trans. R. Soc. London, Ser. B 364, 1223–1234.
Grossberg, S., 2012. Adaptive Resonance Theory: how a brain learns to consciously attend, learn, and recognize a changing world. Neural Networks 37, 1–47.
Grossberg, S., Grunewald, A., 1997. Cortical synchronization and perceptual framing. J. Cogn. Neurosci. 9, 117–132.
Grossberg, S., Kazerounian, S., 2011. Laminar cortical dynamics of conscious speech perception: a neural model of phonemic restoration using subsequent context in noise. J. Acoust. Soc. Am. 130, 440–460.
Grossberg, S., Kuperstein, M., 1986. Neural Dynamics of Adaptive Sensory-motor Control: Ballistic Eye Movements. Amsterdam, New York North-Holland.
Grossberg, S., Markowitz, J., Cao, Y., 2011. On the road to invariant recognition: explaining tradeoff and morph properties of cells in inferotemporal cortex using multiple-scale task-sensitive attentive learning. Neural Networks 24, 1036–1049.
Grossberg, S., Merrill, J.W.L., 1992. A neural network model of adaptively timed reinforcement learning and hippocampal dynamics. Cogn. Brain Res. 1, 3–38.
Grossberg, S., Merrill, J.W.L., 1996. The hippocampus and cerebellum in adaptively timed learning, recognition, and movement. J. Cogn. Neurosci. 8, 257–277.
Grossberg, S., Mingolla, E., Ross, W.D., 1997. Visual brain and visual perception: how does the cortex do perceptual grouping? Trends Neurosci 20, 106–111.
Grossberg, S., Paine, R.W., 2000. A neural model of corticocerebellar interactions during attentive imitation and predictive learning of sequential handwriting movements. Neural Networks 13, 999–1046.
Grossberg, S., Pearson, L., 2008. Laminar cortical dynamics of cognitive and motor working memory, sequence learning and performance: toward a unified theory of how the cerebral cortex works. Psychol. Rev. 115, 677–732.
Grossberg, S., Pepe, J., 1971. Spiking threshold and overarousal effects in serial learning. J. Stat. Phys. 3, 95–125.
Grossberg, S., Pilly, P.K., 2012. How entorhinal grid cells may learn multiple spatial scales from a dorsoventral gradient of cell response rates in a self-organizing map. PLoS Comput. Biol. 8 (10), 31002648, http://dx.doi.org/10.1371/journal.pcbi.1002648.
Grossberg, S., Pilly, P.K., 2014. Coordinated learning of grid cell and place cell spatial and temporal properties: multiple scales, attention, and oscillations. Philos. Trans. R. Soc. London, Ser. B 369, 20120524.
Grossberg, S., Raizada, R., 2000. Contrast-sensitive perceptual grouping and object-based attention in the laminar circuits of primary visual cortex. Vis. Res. 40, 1413–1432.
Grossberg, S., Schmajuk, N.A., 1989. Neural dynamics of adaptive timing and temporal discrimination during associative learning. Neural Networks 2, 79–102.
Grossberg, S., Seidman, D., 2006. Neural dynamics of autistic behaviors: cognitive, emotional, and timing substrates. Psychol. Rev. 113, 483–525.
Grossberg, S., Seitz, A., 2003. Laminar development of receptive fields, maps, and columns in visual cortex: the coordinating role of the subplate. Cerebral Cortex 13, 852–863.
Grossberg, S., Somers, D., 1991. Synchronized oscillations during cooperative feature linking in a cortical model of visual perception. Neural Networks 4, 453–466.
Grossberg, S., Versace, M., 2008. Spikes, synchrony, and attentive learning by laminar thalamocortical circuits. Brain Res. 1218, 278–312.
Grossberg, S., Vladusich, T., 2010. How do children learn to follow gaze, share joint attention, imitate their teachers, and use tools during social interactions? Neural Networks 23, 940–965
Grossberg, S., Williamson, J.R., 2001. A neural model of how horizontal and interlaminar connections of visual cortex develop into adult circuits that carry out perceptual groupings and learning. Cerebral Cortex 11, 37–58.
Grossberg, S., Yazdanbakhsh, A., 2005. Laminar cortical dynamics of 3D surface perception: stratification, transparency, and neon color spreading. Vis. Res. 45, 1725–1743.
Grossberg, S., Srinivasan, K., Yazdanbakhsh, A. Binocular fusion and invariant category learning due to predictive remapping during scanning of a depthful scene with eye movements. Frontiers in Psychology: Percept. Sci., in press.
Guenther, F.H., 1995. Speech sound acquisition, coarticulation, and rate effects in a neural network model of speech production. Psychol. Rev. 102, 594–621.
Guenther, F.H., Bullock, D., Greve, D., Grossberg, S., 1994. Neural representations for sensory-motor control, III: Learning a body-centered representation of 3-D target position. J. Cogn. Neurosci. 6, 341–358.
Hafting, T., Fyhn, M., Molden, S., Moser, M.B., Moser, E.I., 2005. Microstructure of a spatial map in the entorhinal cortex. Nature 436, 801–806.
Hahnloser, R.H.R., Kozhevnikov, A.A., Fee, M.S., 2002. An ultra-sparse code underlies the generation of neural sequences in a songbird. Nature 419, 65–70.
He, S., Cavanagh, P., Intriligator, J., 1996. Attentional resolution and the locus of visual awareness. Nature 383, 334–337.

Hebb, D.O., 1949. The Organization of Behavior. Wiley, New York, NY.
Hecht-Nielsen, R., 1987. Counterpropagation networks. Appl. Opt. 26, 4979–4983.
Heeger, D.J., 1992. Normalization of cell responses in cat striate cortex. Visual Neurosci. 9, 181–197.
Henriksen, E.J., Colgin, L.L., Barnes, C.A., Witter, M.P., Moser, M.B., Moser, E.L., 2010. Spatial representation along the proximodistal axis of CA1. Neuron 68, 127–137.
Intriligator, J., Cavanagh, P., 2001. The spatial resolution of visual attention. Cogn. Psychol. 43, 171–216.
James, W., 1890. The Principles of Psychology. Harvard University Press, Cambridge, MA.
Kamin, L.J., 1969. Predictability, surprise, attention and conditioning. In: Campbell, B.A., Church, R.M. (Eds.), Punishment and Aversive Behavior. Appleton-Century-Crofts, New York, NY.
Kentros, C.G., Agniotri, N.T., Streater, S., Hawkins, R.D., Kandel, E. R., 2004. Increased attention to spatial context increases both place field stability and spatial memory. Neuron 42, 283–295.
Kentros, C., Hargreaves, E., Hawkins, R.D., Kandel, E.R., Shapiro, M., Muller, R.V., 1998. Abolition of long-term stability of new hippocampal place cell maps by NMDA receptor blockade. Science 280, 2121–2126.
Kirkwood, A., Lee, H.-K., Bear, M.F., 1995. Co-regulation of long-term potentiation and experience-dependent synaptic plasticity in visual cortex by age and experience. Nature 375, 328–331.
Knowlton, B.J., Squire, L.R., 1993. The learning of categories: parallel brain systems for item memory and category knowledge. Science 262, 1747–1749.
Kohonen, T., 1984. Self-organization and Associative Memory. Springer-Verlag, New York, NY.
Komatsu, Y., Toyama, K., Maeda, J., Sakaguchi, H., 1981. Long-term potentiation investigated in a slice preparation of striate cortex of young kittens. Neurosci. Lett. 26, 269–274.
Kraus, N., McGee, T., Littman, T., Nicol, T., King, C., 1994. Nonprimary auditory thalamic representation of acoustic change. J. Neurophysiol. 72, 1270–1277.
Krupic, J., Burgess, N., O'Keefe, J., 2012. Neural representations of location composed of spatially periodic bands. Science 337, 853–857.
Langston, R.F., Ainge, J.A., Couey, J.J., Canto, C.B., Bjerknes, T.L., Witter, M.P., Moser, E.I., Moser, M.B., 2010. Development of the spatial representation system in the rat. Science 328, 1576–1580.
Lashley, K.S., 1950. In search of the engram. In: Society for Experimental Biology, Symposium 4. Physiological Mechanisms in Animal Behavior. Cambridge University Press, Cambridge, England2–31.
Lashley, K.S., 1960. In search of the engram. In: F.A., Beach, Hebb, D.O. (Eds.), The Neuropsychology of Lashley. McGraw-Hill, New York, NY, pp. 345–360.
Levi, D.M., 2008. Crowding—an essential bottleneck for object recognition: a mini-review. Vis. Res. 48, 635–654.
Levy, W.B., Brassel, S.E., Moore, S.D., 1983. Partial quantification of the associative synaptic learning rule of the dentate gyrus. Neuroscience 8, 799–808.
Levy, W.B., Desmond, N.L., 1985. The rules of elemental synaptic plasticity. In: Levy, W.B., Anderson, J., Lehmkuhle, S. (Eds.), Synaptic Modification, Neuron Selectivity and Nervous System Organization. Erlbaum, Hillsdale, NJ, pp. 105–121In: Levy, W.B., Anderson, J., Lehmkuhle, S. (Eds.), Synaptic Modification, Neuron Selectivity and Nervous System Organization. Erlbaum, Hillsdale, NJ, pp. 105–121.
Levy, W.B., Steward, O., 1983. Temporal contiguity requirements for long-term associative potentiation/depression in the hippocampus. Neuroscience 8, 791–797.
MacDonald, C.J., Lepage, K.Q., Eden, U.T., Eichenbaum, H., 2011. Hippocampal "time cells" bridge the gap in memory for discontiguous events. Neuron 71, 737–749.
Mathot, S., Theeuwes, J., 2010. Evidence for the predictive remapping of visual attention. Exp. Brain Res. 200, 117–122.
McNaughton, B.L., Battaglia, F.P., Jensen, O., Moser, E.I., Moser, M.B., 2006. Path integration and the neural basis of the 'cognitive map'. Nat. Rev. Neurosci. 7, 663–678.
Melcher, D., 2007. Predictive remapping of visual features precedes saccadic eye movements. Nat. Neurosci. 10, 903–907.
Melcher, D., 2008. Dynamic, object-based remapping of visual features in trans-saccadic perception. J. Vis. 8, 1–17.
Melcher, D., 2009. Selective attention and the active remapping of object features in trans- saccadic perception. Vis. Res. 49, 1249–1255.
Mesulam, M.-M., 1999. Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. Philos. Trans. R. Soc. London, Ser. B 354, 1325–1346.
Mhatre, H., Gorchetchnikov, A., Grossberg, S., 2012. Grid cell hexagonal patterns formed by fast self-organized learning within entorhinal cortex. Hippocampus 22, 320–334.
Miyashita, Y., Chang, H.S., 1988. Neuronal correlate of pictorial short-term memory in the primate temporal cortex. Nature 331, 68–70.
Morris, R.G.M., Frey, U., 1997. Hippocampal synaptic plasticity: role in spatial learning or the automatic recording of attended experience? Philos Trans. R. Soc. London, Ser. B 1360, 1469–1503.
Morris, R.G.M., Garrud, P., Rawlins, J.N.P., O'Keefe, J., 1982. Place navigation impaired in rats with hippocampal lesions. Nature 297, 681–683.
Moyer, J.R., Deyo, R.A., Disterhoft, J.F., 1990. Hippocampectomy disrupts trace eye-blink conditioning in rabbits. Behav. Neurosci. 104, 243–252.
Mulkey, R.M., Malenda, R.C., 1992. Mechanisms underlying induction of homosynaptic long-term depression in area CA1 of the hippocampus. Neuron 9, 967–975.
O'Keefe, J., Dostrovsky, J., 1971. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. Brain Res. 34, 171–175.
Palma, J., Grossberg, S., Versace, M., 2012. Persistence and storage of activity patterns in spiking recurrent cortical networks: modulation of sigmoid signals by after-hyperpolarization currents and acetylcholine. Front. Comput. Neurosci. 6, 42 (Doi: 10.3389.fncom.2012.00042).
Palma, J., Versace, M., Grossberg, S., 2012. After-hyperpolarization currents and acetylcholine control sigmoid transfer functions in a spiking cortical model. J. Comput. Neurosci. 32, 253–280.
Park, E.H., Dvorak, D., Fenton, A.A., 2011. Ensemble place codes in hippocampus: CA1, CA3, and dentate gyrus place cells have multiple place fields in large environments. PLoS One 6, e22349.
Parron, C., Save, E., 2004. Evidence for entorhinal and parietal cortices involvement in path integration in the rat. Exp. Brain Res. 159, 349–359.
Pavlov, I.P., 1927. Conditioned Reflexes. Oxford University Press.
Perry, E.K., Lee, M.L.W., Martin-Ruiz, C.M., Court, J.A., Volsen, S.G., Merrit, J., Folly, E., Iversen, P.E., Bauman, M.L., Perry, R.H., Wenk, G.L., 2001. Cholinergic activity in autism: abnormalities in the cerebral cortex and basal forebrain. Am. J. Psychiatry 158, 1058–1066.
Pilly, P.K., Grossberg, S., 2012. How do spatial learning and memory occur in the brain? Coordinated learning of entorhinal grid cells and hippocampal place cells. J. Cogn. Neurosci. 24, 1031–1054.

Pilly, P.K., Grossberg, S., 2013. Spiking neurons in a hierarchical self-organizing map model can learn to develop spatial and temporal properties of entorhinal grid cells and hippocampal place cells. PLoS One, http://dxdoi.org/10.1371/journal.pone.0060599.
Pouget, A., Dayan, P., Zemel, R.S., 2003. Inference and computation with population codes. Annu. Rev. Neurosci. 26, 381–410.
Purves, D., 1988. Body and Brain: A Trophic Theory of Neural Connections. Harvard University Press, Cambridge, MA.
Raizada, R., Grossberg, S., 2001. Context-sensitive bindings by the laminar circuits of V1 and V2: a unified model of perceptual grouping, attention, and orientation contrast. Visual Cognit. 8, 431–466.
Ranck Jr, J.B., 1984. Head-direction cells in the deep cell layers of dorsal presubiculum in freely moving rats. In: Proceedings of the Annual Conference of the Society for Neuroscience. Anaheim, CA. vol. 10, p. 599.
Reynolds, J.H., Heeger, D.J., 2009. The normalization model of attention. Neuron 61, 168–185.
Roberts, S., 1981. Isolation of an internal clock. J. Exp. Psychol. Anim. Behav. Processes 7, 242–268.
Roberts, W.A., Cheng, K., Cohen, J.S., 1989. Timing light and tone signals in pigeons. J. Exp. Psychol. Anim. Behav. Processes 15, 23–25.
Royer, S., Pare, D., 2003. Conservation of total synaptic weight through balanced synaptic depression and potentiation. Nature 422, 518–522.
Rubenstein, J.L.R., Merzenich, M.M., 2003. Model of autism: increased ratio of excitation/inhibition in key neural systems. Genes Brain Behav. 2, 255–267.
Sargolini, F., Fyhn, M., Hafting, T., McNaughton, B.L., Witter, M.P., Moser, M.-B., Moser, E.L., 2006. Conjunctive representation of position, direction, and velocity in entorhinal cortex. Science 312, 758–762.
Saygin, A.P., Sereno, M.I., 2008. Retinotopy and attention in human occipital, temporal, parietal, and frontal cortex. Cerebral Cortex 18, 2158–2168.
Sigala, N., Logothetis, N.K., 2002. Visual categorization shapes feature selectivity in the primate temporal cortex. Nature 415, 318–320.
Singer, W., 1983. Neuronal activity as a shaping factor in the self-organization of neuron assemblies. In: Basar, E., Flohr, H., Haken, H., Mandell, A.J. (Eds.), Synergetics of the Brain. Springer-Verlag, New York, NY, pp. 89–101 (1983).
Smith, M.C., 1968. CS–US interval and US intensity in classical conditioning of the rabbit's nictitating membrane response. J. Comp. Physiol. Psychol. 3, 679–687.
Solomon, P.R., Vander Schaaf, E.R., Thompson, R.F., 1986. Hippocampus and trace conditioning of the rabbit's classically conditioned nictitating membrane response. Behav. Neurosci. 100, 729–744.
Sommer, M.A., Wurtz, R.H., 2006. Influence of the thalamus on spatial vision processing in frontal cortex. Nature 444, 374–377.
Song, P., Wang, X.J., 2005. Angular path integration by moving "hill of activity": a spiking neuron model without recurrent excitation of the head-direction system. J. Neurosci. 25, 1002–1014.
Tanaka, K., Saito, H., Fukada, Y., Moriya, M., 1991. Coding visual images of objects in the inferotemporal cortex of the macaque monkey. J. Neurophysiol. 66, 170–189.
Taube, J.S., Muller, R.U., Ranck Jr, J.B., 1990. Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. J. Neurosci. 10, 420–435.
Theeuwes, J., Mathot, S., Kingstone, A., 2010. Object-based eye movements: the eyes prefer to stay within the same object. Atten. Percept. Psychophys. 72, 597–601.
Thompson, R.F., 1976. The search for the engram. Am. Psychol. 31, 209–227.
Thompson, R.F., Clark, G.A., Donegan, N.H., Lavond, G.A., Lincoln, D.G., Maddon, J., Mamounas, L.A., Mauk, M.D., McCormick, D.A., 1987. Neuronal substrates of discrete, defensive conditioned reflexes, conditioned fear states, and their interactions in the rabbit. In: Gormenzano, I., Prokasy, W.F., Thompson, R.F. (Eds.), Classical Conditioning third ed Erlbaum Associates, Hillsdale, NJ, pp. 371–399.
Thorpe, S., Fize, D., Marlot, C., 1996. Speed of processing in the human visual system. Nature 381, 520–522.
Tolias, A.S., Moore, T., Smirnakis, S.M., Tehovnik, E.J., Siapas, A.G., Schiller, P.H., 2001. Eye movements modulate visual receptive fields of V4 neurons. Neuron 29, 757–767.
Tomita, H., Ohbayashi, M., Nakahara, K., Hasegawa, I., Miyashita, Y., 1999. Top-down signal from prefrontal cortex in executive control of memory retrieval. Nature 401, 699–703.
Tsodyks, M., Pawelzik, K., Markram, H., 1998. Neural networks with dynamic synapses. Neural Comput. 10, 821–835.
Tyler, C.W., Kontsevich, L.L., 1995. Mechanisms of stereoscopic processing: stereoattention and surface perception in depth reconstruction. Perception 24, 127–153.
Umeno, M.M., Goldberg, M.E., 1997. Spatial processing in the monkey frontal eye fields, I: Predictive visual responses. J. Neurophysiol. 78, 1373–1383.
van Der Werf, Y.D., Witter, M.P., Groenewegen, H.J., 2002. The intralaminar and midline nuclei of the thalamus. Anatomical and functional evidence for participation in processes of arousal and awareness. Brain Res. 39, 107–140.
Vladusich, T., Lafe, F., Kim, D.-S., Tager-Flusberg, H., Grossberg, S., 2010. Prototypical category learning in high-functioning autism. Autism Res. 3, 226–236.
Von der Malsburg, C., 1973. Self-organization of orientation sensitive cells in the striate cortex. Biol Cybern. 14, 85–100.
Wills, T.J., Cacucci, F., Burgess, N., O'Keefe, J., 2010. Development of the hippocampal cognitive map in preweanling rats. Science 328, 1573–1576.
Yantis, S., Schwarzbach, J., Serences, J.T., Carlson, R.L., Steinmetz, M.A., Pekar, J.J., Courtney, S.M., 2002. Transient neural activity in human parietal cortex during spatial attention shifts. Nat. Neurosci. 5, 995–1002.
Yazdanbakhsh, A., Grossberg, S., 2004. Fast synchronization of perceptual grouping in laminar visual cortical circuits. Neural Networks 17, 707–718.
Zaki, S.R., Nosofsky, R.M., Jessup, N.M., Unversagt, F.W., 2003. Categorization and recognition performance of a memory impaired group: evidence for single-system models. J. Int. Neuropsychol. Soc. 9, 394–406.
Zoccolan, D., Kouh, M., Poggio, T., DiCarlo, J.J., 2007. Trade-off between object selectivity and tolerance in monkey inferotemporal cortex. J. Neurosci. 27, 12292–12307.