

Cortical and subcortical predictive dynamics and learning during perception, cognition, emotion and action

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An intimate link exists between the predictive and learning processes in the brain. Perceptual/cognitive and spatial/motor processes use complementary predictive mechanisms to learn, recognize, attend and plan about objects in the world, determine their current value, and act upon them. Recent neural models clarify these mechanisms and how they interact in cortical and subcortical brain regions. The present paper reviews and synthesizes data and models of these processes, and outlines a unified theory of predictive brain processing.

Keywords: complementary cortical streams; invariant recognition learning; cognitive–emotional dynamics; adaptive timing; working memory; laminar cortical circuits

1. INTRODUCTION: LEARNING AND PREDICTION BY COMPLEMENTARY CORTICAL PROCESSING STREAMS

Advanced brains have an extraordinary capacity to autonomously learn in real time from changing environmental conditions. Accumulating theoretical and empirical evidence suggests that this is accomplished using *complementary* cortical processing streams that embody different predictive and learning mechanisms (Grossberg 2000*b*). As summarized in figure 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. Match-based learning can occur quickly without causing catastrophic forgetting, much as we quickly learn new faces without forcing rapid forgetting of familiar faces. Complementary spatial/motor processes in the ‘where’ dorsal cortical processing stream often use *inhibitory matching* and *mismatch-based learning* to continually update spatial maps and sensory-motor gains as our bodily parameters change through time. As noted in more detail below, these ‘what’ and ‘where’ processes need to work together: the ‘what’ stream learns spatially invariant object categories while the ‘where’ stream learns spatial maps and movement gains. ‘What’–‘where’ interstream interactions enable spatially invariant object representations to control actions towards desired goals in space. No less important, perceptual and cognitive learning provide a self-stabilizing front end to control the more labile spatial/motor learning that enables changing bodies to effectively act upon recognized objects in the world.

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The present paper reviews and synthesizes data and models of these processes, and outlines a unified theory of predictive brain processing.

2. LEARNING OF INVARIANT RECOGNITION CATEGORIES IN THE ‘WHAT’ CORTICAL STREAM

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 (ITa) exhibits such invariance (Tanaka *et al.* 1991; Bar *et al.* 2001; Sigala & Logothetis 2002; Zoccolan *et al.* 2007), which helps to prevent a combinatorial explosion in the memory of object representations at every size and position. Such categorization processes have been predicted to achieve fast learning without experiencing catastrophic forgetting (figure 1). How is this accomplished? Adaptive Resonance Theory, or ART, predicted how ‘what’ stream categorization processes integrate properties of consciousness, learning, expectation, attention, resonance and synchrony (CLEARS, Grossberg 1980). Subsequent experiments have supported this prediction (see Grossberg (2003) and Grossberg & Versace (2008) for reviews).

Predictive ART matching uses a top-down learned expectation that causes an excitatory resonance when it *matches* consistent bottom-up input patterns (figures 1 and 2). The match focuses attention on a *critical feature pattern* of matched object features that resonates synchronously with the recognition category that reads out the top-down expectation. The resonance drives fast learning that incorporates the critical features into the category prototype. Predictive ART learning hereby joins excitatory matching, resonance, synchrony, attention, and match-based learning.

what	where
spatially invariant object learning and recognition	spatially variant reaching and movement
fast learning without catastrophic forgetting	continually update sensory motor maps and gains

IT

PPC

	what	where
matching	excitatory	inhibitory
learning	match	mismatch

Figure 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.

These processes together solve the *stability–plasticity dilemma* (Grossberg 1980); namely, they enable the brain to learn quickly without experiencing catastrophic forgetting. They also clarify why many animals are intentional beings who pay attention to salient objects, why *all conscious states are resonant states*, and how brains can learn both *many-to-one maps* (representations whereby many object views, positions and sizes all activate the same invariant object category; see §13) and *one-to-many maps* (representations that enable us to expertly know many things about individual objects and events; see Carpenter & Grossberg (1992)).

ART predicted that *all* brain representations which solve the stability–plasticity dilemma use variations of CLEARs mechanisms (Grossberg 1978a, 1980). Synchronous resonances are therefore expected to occur between multiple cortical and subcortical areas. Recent data have supported this prediction (e.g. Engel *et al.* 2001).

3. EXPECTATIONS AND BIASED COMPETITION: MODULATORY ON-CENTRE, OFF-SURROUND NETWORK

How are ‘what’ stream top-down expectations computed? Carpenter & Grossberg (1987) mathematically proved that the simplest network which solves the stability–plasticity dilemma is a *top-down, modulatory on-centre, off-surround network*, which provides excitatory priming of features in the on-centre, and driving inhibition in the off-surround. The modulatory on-centre emerges from a balance between the top-down excitation and inhibition. Subsequent modelling studies provide additional evidence for such a circuit (e.g. Gove *et al.* 1995; Grossberg & Myers 2000; Grossberg *et al.* 2004; Dranias *et al.* 2008), and laminar cortical models predict identified cell types (Grossberg 1999; Raizada & Grossberg 2003; Grossberg & Pearson 2008; Grossberg & Versace 2008). Many anatomical and neurophysiological experiments support this prediction

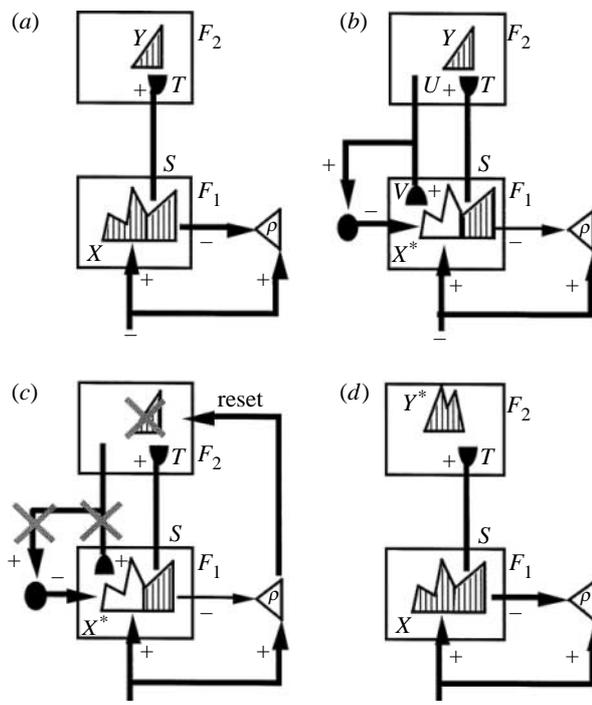


Figure 2. Search for a recognition code within an ART learning circuit. (a) Input pattern I is instated across feature detectors at level F_1 as an activity pattern X , while it non-specifically activates the orienting system A with gain ρ . X inhibits A and generates output pattern S . S is multiplied 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 short term memory (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, A releases a non-specific arousal burst to F_2 , i.e. ‘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 from Carpenter & Grossberg (1993)).

(e.g. Downing 1988; Sillito *et al.* 1994; Steinman *et al.* 1995; Bullier *et al.* 1996; Hupé *et al.* 1997; Caputo & Guerra 1998; Reynolds *et al.* 1999; Somers *et al.* 1999; Mounts 2000; Smith *et al.* 2000; Vanduffell *et al.* 2000), which is more qualitatively called ‘biased competition’ (Desimone 1998; Kastner & Ungerleider 2001).

4. IMAGINING AND PLANNING AHEAD: PREDICTION WITHOUT ACTION

A top-down expectation is not always modulatory. The excitatory/inhibitory balance in the modulatory on-centre of a top-down expectation can be modified by volitional control from the basal ganglia. If, for example, volitional signals inhibit inhibitory interneurons in the on-centre, then read-out of a top-down expectation from a recognition category can fire

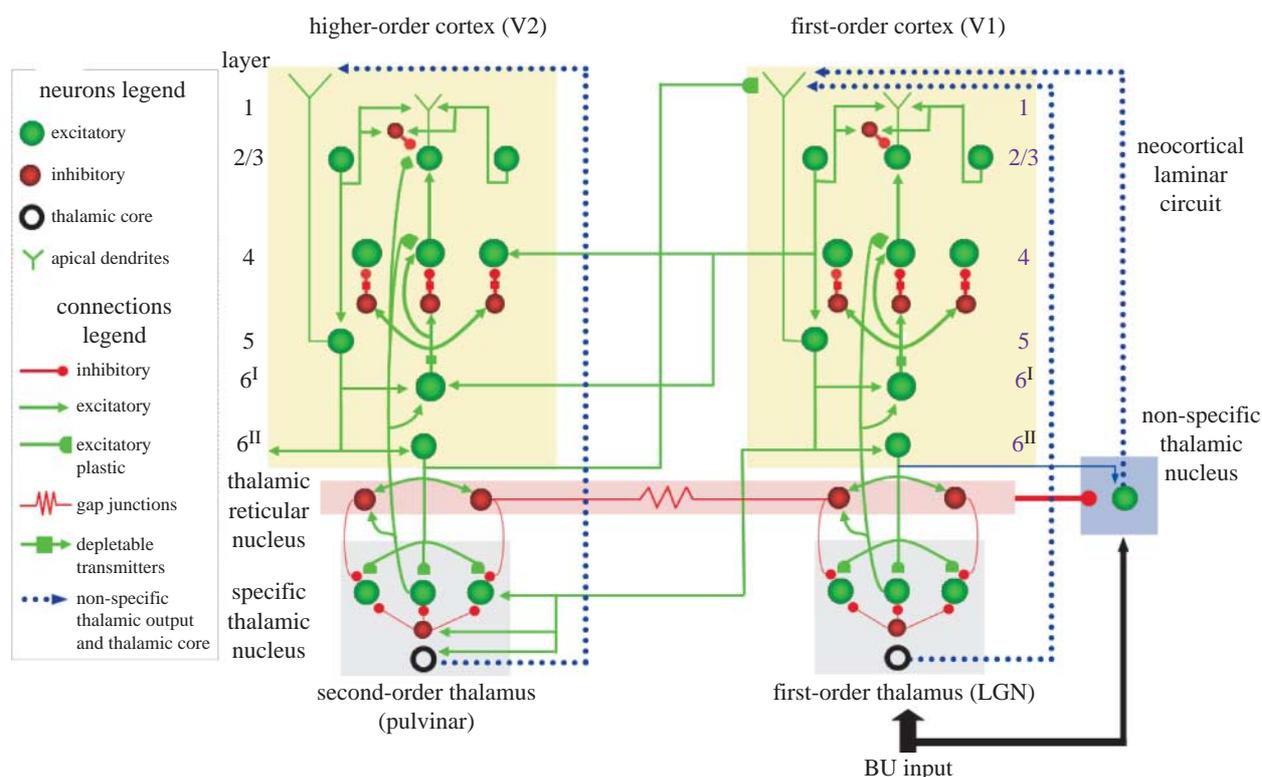


Figure 3. The SMART model clarifies how laminar neocortical circuits in multiple cortical areas interact with specific and non-specific thalamic nuclei to regulate learning on multiple organizational levels, ranging from spikes to cognitive dynamics. ART top-down modulatory on-centre, off-surround networks occur in both corticocortical and corticothalamic circuits. For example, layer 6^{II} of the cortical area V2 sends top-down outputs to the cortical area V1 via layer 1, where they activate apical dendrites of layer 5 cells. Layer 5, in turn, activates layer 6^I, which sends modulatory on-centre, off-surround signals to layer 4. In addition, layer 5 cells activate layer 6^{II}, which sends top-down modulatory on-centre off-surround signals to lateral geniculate nucleus (LGN). These pathways help to regulate stable learning in laminar thalamocortical circuits (adapted from Grossberg & Versace (2008)).

cells in the on-centre prototype and thereby enable mental imagery, thinking, and planning ahead to occur. If these volitional signals become tonically hyperactive, then top-down expectations can fire without overt intention, leading to properties such as schizophrenic hallucinations (Grossberg 2000a). The ability to imagine and plan ahead thus risks having hallucinations, and all these properties follow from using top-down expectations to stabilize predictive learned memories.

5. COMPLEMENTARY ATTENTIONAL AND ORIENTING SYSTEMS: EXPECTED VERSUS UNEXPECTED EVENTS

How does a brain learn about unexpected and unfamiliar events, such as novel objects to recognize, without causing catastrophic forgetting? Within ART, this is achieved by a memory search, or hypothesis testing process that discovers the recognition category that best matches an event or object. Figure 2 illustrates how this is predicted to happen. A bottom-up input pattern I activates an activity pattern X across feature detectors of processing stage F_1 . For example, features of a visual scene may be boundary and surface representations. Vector I represents the relative importance of different features (figure 2a). This feature pattern sends signals S through an adaptive filter to the level F_2 where a recognition category Y is activated by the distributed input T . T is computed by multiplying S by bottom-up adaptive weights that are altered by learning. Active category cells Y send top-down signals U to F_1

(figure 2b). U is converted into the top-down expectation V by being multiplied by top-down adaptive weights. At F_1 , matching between I and V selects that subset X^* of features that are 'expected' by Y . These features define the emerging 'attentional focus'.

If the match is good enough, then the pattern X^* of attended features reactivates category Y which, in turn, reactivates X^* and locks the network into a resonant state that dynamically links, or binds, attended features across X^* with their category Y , and enables fast learning to occur. If the match is not good enough, search for a novel or better matching category continues (figure 2c,d).

Such *match-based learning* stabilizes learned memories in both the bottom-up and top-down adaptive filters (figure 1), and thereby solves the stability-plasticity dilemma. Top-down expectations can also predictively prime events whose future occurrence is sought.

6. SPIKES, SYNCHRONY AND ATTENTIVE LEARNING BY LAMINAR THALAMOCORTICAL CIRCUITS

The synchronous matching ART (SMART) model (figure 3) predicts how finer details about the CLEARS processes may be realized by multiple levels of brain organization. SMART provides a unified functional explanation of single-cell properties, such as spiking dynamics, spike-timing-dependent plasticity and acetylcholine modulation; detailed laminar thalamic

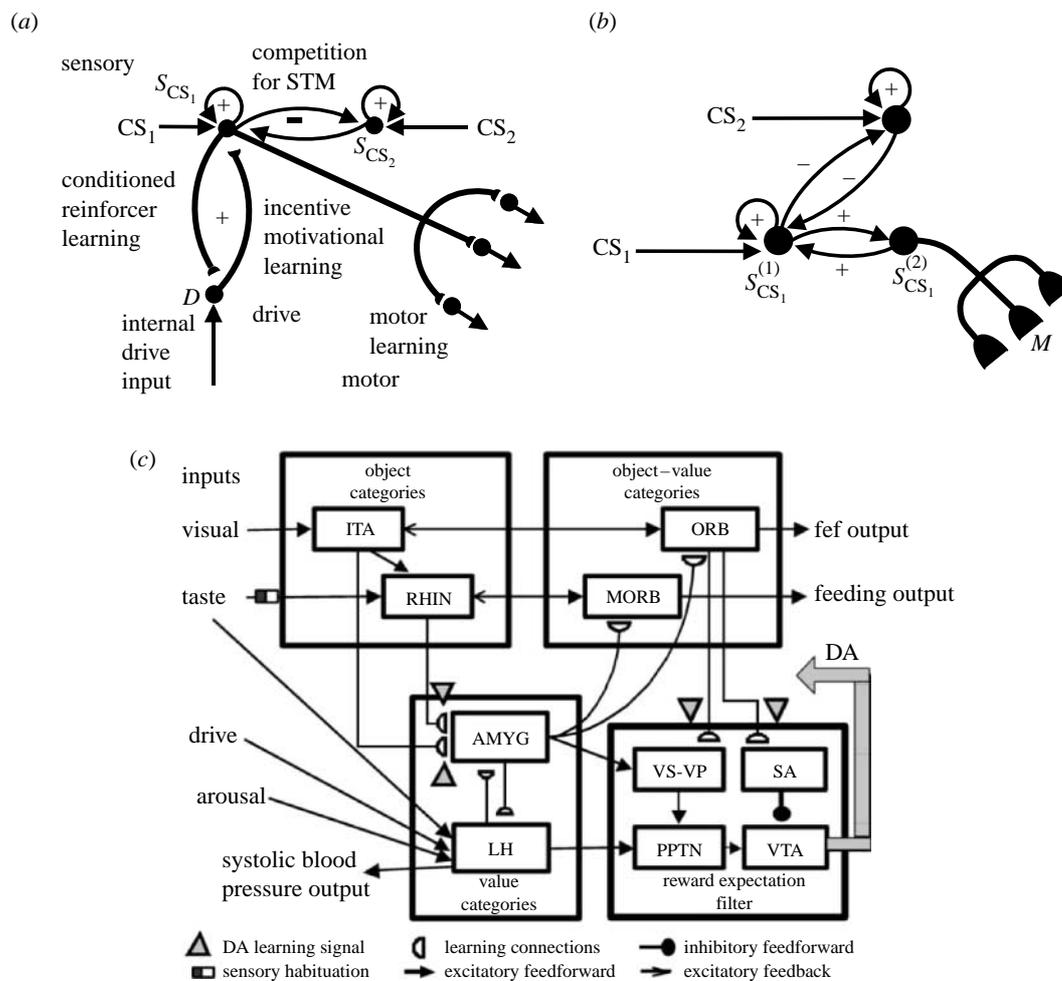


Figure 4. (a) CogEM model: three types of interacting representations (sensory, drive and motor) control three types of learning (conditioned reinforcer, incentive motivational and motor) during reinforcement learning: sensory representations S temporarily store internal representations of sensory events in working memory. Drive representations D are the sites where reinforcing and homeostatic, or drive, cues converge to activate emotional responses. Motor representations M control read-out of actions. Conditioned reinforcer learning enables sensory events to activate emotional reactions at drive representations. Incentive motivational learning enables emotions to generate a motivational set that biases the system to process information consistent with that emotion. Motor learning allows sensory and cognitive representations to generate actions. (b) In order to work well, a sensory representation S must have (at least) two successive stages, $S^{(1)}$ and $S^{(2)}$, so that sensory events cannot release actions that are motivationally inappropriate (adapted from Grossberg & Seidman (2006)). (c) MOTIVATOR model: brain areas in the MOTIVATOR circuit can be divided into four regions that process information about conditioned stimuli (CSs) and unconditioned stimuli (USs): object categories represent visual or gustatory inputs in anterior inferotemporal (ITA) and rhinal (RHIN) cortices. Value categories represent the value of anticipated outcomes on the basis of hunger and satiety inputs in amygdala (AMYG) and lateral hypothalamus (LH). Object-value categories resolve the value of competing perceptual stimuli in medial (MORB) and lateral (ORB) orbitofrontal cortex. The reward expectation filter involves basal ganglia circuitry that responds to unexpected rewards (adapted from Dranias *et al.* (2008)).

and cortical circuit designs and their interactions; aggregate cell recordings, such as current source densities and local field potentials; and single cell and large-scale inter-areal oscillations in the gamma and beta frequency domains. Figure 3 summarizes how these circuits embody the ART matching rule and thereby allow laminar circuits of multiple cortical and thalamic areas to carry out attentive visual learning and information processing.

One of the new SMART predictions concerns how brain oscillations contribute to predictive learning. SMART predicts that *matches* cause gamma oscillations that support attention, resonance, learning and consciousness, whereas *mismatches* inhibit learning by causing slower beta oscillations during reset and hypothesis testing operations (figure 2) that are

initiated in the deeper cortical layers. Three kinds of recent data support this prediction:

- (i) Buffalo *et al.* (2004) have reported beta oscillations in deeper cortical layers,
- (ii) Buschman & Miller (2007) have reported beta oscillations during partial attention shifts; and
- (iii) Berke *et al.* (2008) have reported beta oscillations during hippocampal place cell learning in novel environments.

Place cells can develop within seconds to minutes, and can remain stable for months (Thompson & Best 1990; Wilson & McNaughton 1993; Muller 1996; Frank *et al.* 2004). Place cell learning thus seems to have solved the stability-plasticity dilemma.

Are place cells learned using ART dynamics? The Berke *et al.* (2008) data are consistent with this hypothesis: paradoxically, beta power was very low as a mouse traversed a lap for the first time, grew to full strength on the second and third laps, became low again after 2 min of exploration, and remained low on subsequent days. Beta oscillation power also correlated with the rate at which place cells became spatially selective.

These data can be explained as follows (Grossberg submitted). Gorchetnikov & Grossberg (2007) modelled how place cell receptive fields may be learned in an ART system wherein hippocampal place cells categorize multiple scales of entorhinal grid cells (Hafting *et al.* 2005). In any ART system, top-down adaptive weights are large before learning occurs, so that they can match whatever input pattern first initiates the learning of a new category (Carpenter & Grossberg 1987). Weights are pruned on subsequent learning trials to match the emerging critical feature pattern during mismatch-based reset events. The low beta power on the first lap of exploration can be explained by the initial top-down match. Beta power on subsequent laps can be explained by mismatch events that correlate with the rate at which place cells become spatially selective.

7. COGNITIVE-EMOTIONAL INTERACTIONS ENDOW PREDICTIONS WITH VALUE CONSTRAINTS

Invariant recognition categories can be activated when objects are experienced, but do not reflect the emotional value of these objects. An *invariant* object category can, however, be readily associated through reinforcement learning with one or more drive representations, which are brain sites that represent internal drive states and emotions. Activation of a drive representation by an invariant object category can trigger emotional reactions and motivational decisions that can motivationally modulate the object representations. Recognized objects can hereby trigger the choice and release of actions that realize valued goals in a context-sensitive way.

In figure 4a,b, visually perceived objects are called conditioned stimuli (CS_i). The invariant object categories that they activate are called sensory representations (S_{CS_i}), which, in turn, activate drive representations (D). Figure 4a summarizes how predictive behaviour can be constrained by such external sensory options and internal emotional and motivational requirements.

The amygdala is a drive representation (e.g. Aggleton 1993; LeDoux 1993). Reinforcement learning (figure 4a,b) can convert the event or object (say CS_1) that activates an invariant object category ($S_{CS_1}^{(1)}$) into a *conditioned reinforcer* by strengthening the associative links from the category to the drive representation (D), e.g. learning in inferotemporal-to-amygdala pathways. The invariant object category can also send excitatory projections to the regions of prefrontal cortex ($S_{CS_1}^{(2)}$), such as orbitofrontal cortex. The amygdala (D) also sends projections to orbitofrontal cortex (Grossberg 1975, 1982; Barbas 1995). Reinforcement learning can hereby strengthen amygdala-to-orbitofrontal

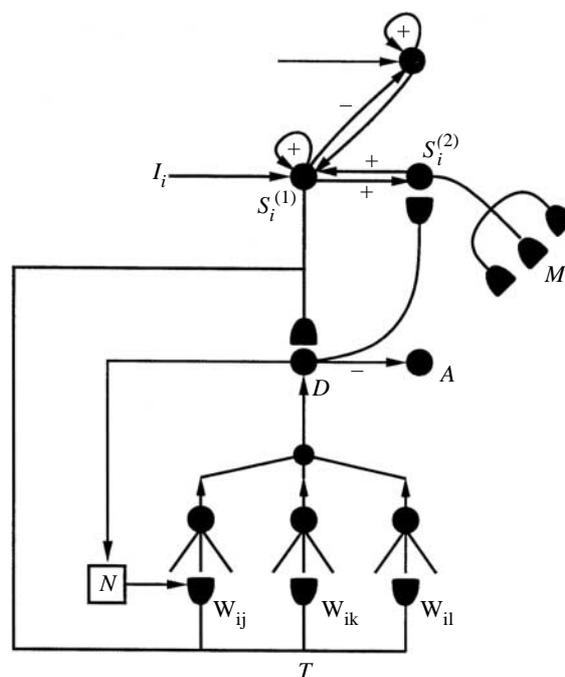


Figure 5. The START model: adaptively timed learning maintains motivated attention (pathway $D \rightarrow S_i^{(2)} \rightarrow S_i^{(1)} \rightarrow D$) while it inhibits activation of the orienting system (pathway $D \rightarrow A$). See text for details (adapted from Grossberg & Merrill (1992)).

pathways, which provide *incentive motivation* to the orbitofrontal representations. Orbitofrontal representations fire most vigorously when they receive convergent inputs from inferotemporal categories and amygdala incentive motivation (Baxter *et al.* 2000; Schoenbaum *et al.* 2003).

Orbitofrontal cells ($S_{CS_1}^{(2)}$) send top-down feedback to sensory cortex ($S_{CS_1}^{(1)}$) to enhance sensory representations that are motivationally salient (figure 4b). Competition among inferotemporal categories chooses those with the best combination of sensory and motivational support. An inferotemporal-amygdala-orbitofrontal feedback loop triggers a cognitive-emotional resonance that supports the basic consciousness of goals and feelings (Grossberg 1975, 2000b; Damasio 1999), and releases learned action commands from prefrontal cortex ($S_{CS_2}^{(1)} \rightarrow M$) to achieve valued goals.

The CogEM, or cognitive-emotional-motor, model that is schematized in figure 4a,b predicted and functionally explained these processes with increasing precision and predictive range since its introduction in Grossberg (1972a,b, 1975, 1982). CogEM top-down prefrontal-to-sensory cortex feedback is another example of ART matching, one that clarifies data about attentional blocking and unblocking (Pavlov 1927; Kamin 1969; Grossberg 1975; Grossberg & Levine 1987). When this CogEM circuit functions improperly, symptoms of various mental disorders result. For example, amygdala or orbitofrontal hypoactivity can lead to symptoms of autism and schizophrenia (Grossberg 2000c; Grossberg & Seidman 2006).

The MOTIVATOR model (Dranijs *et al.* 2008; Grossberg *et al.* 2008) further develops the CogEM model, just as SMART further develops ART (figure 4c). In addition, MOTIVATOR unifies the

CogEM and TELOS models (Brown *et al.* 1999, 2004). TELOS proposes how the basal ganglia trigger reinforcement learning in response to unexpected rewards (Schultz 1998), and gates selection and release of actions that are learned through reinforcement learning. *In vivo*, the basal ganglia and amygdala work together to provide motivational support, focus attention, and release contextually appropriate actions to achieve valued goals. MOTIVATOR clarifies how this interaction happens. The model simulates properties such as food-specific satiety, Pavlovian conditioning, reinforcer devaluation, simultaneous visual discrimination, saccadic reaction times, CS-dependent changes in systolic blood pressure, and discharge dynamics of known cell types.

8. ADAPTIVELY TIMED PREDICTIONS: DISTINGUISHING EXPECTED VERSUS UNEXPECTED DISCONFIRMATIONS

Reinforcement learning must be adaptively timed, since rewards are often delayed in time relative to actions aimed at acquiring them. On the one hand, if an animal or human could not inhibit its exploratory behaviour, then it could starve to death by restlessly moving from place to place, unable to remain in one place long enough to obtain delayed rewards there, such as food. On the other hand, if an animal inhibited its exploratory behaviour for too long while waiting for an expected reward, such as food, then it could starve to death if food was not forthcoming. Being able to predict *when* desired consequences occur is often as important as predicting *that* they will occur. Indeed, to control predictive action, the brain needs to coordinate the ‘what’, ‘why’, ‘when’, ‘where’ and ‘how’ of desired consequences by combining recognition learning, reinforcement learning, adaptively timed learning, spatial learning and sensory-motor learning, respectively.

Adaptive timing requires balancing between *exploratory* behaviour, which may discover novel sources of reward, and *consummatory* behaviour, which may acquire expected sources of reward. A human or animal needs to suppress exploratory behaviour and focus attention upon an expected source of reward when the reward is expected. The spectral timing model (Grossberg & Schmajuk 1989; Fiala *et al.* 1996; Grossberg & Merrill 1992, 1996; Brown *et al.* 1999) accomplishes this by predicting how the brain distinguishes *expected non-occurrences*, or *disconfirmations*, of rewards, which should not interfere with acquiring the delayed goal, from *unexpected non-occurrences*, or *disconfirmations*, of rewards, which can trigger consequences of predictive failure, including the reset of working memory, attention shifts, emotional rebounds and exploratory behaviours. The name ‘spectral timing’ signifies that a population ‘spectrum’ of cell sites with different reaction rates can learn to match the statistical distribution of expected delays in reinforcement over time.

9. SPECTRAL TIMING IN CEREBELLUM AND HIPPOCAMPUS: TIMED ACTION, ATTENTION, AND AUTISM

Adaptive timing occurs during several types of reinforcement learning. For example, classical conditioning is

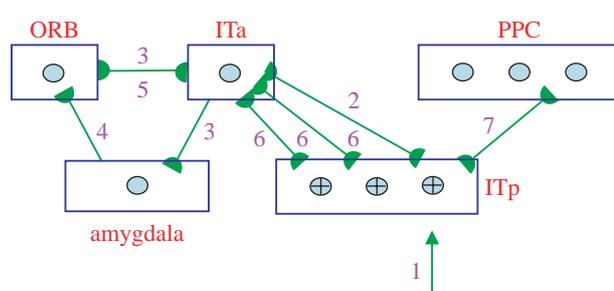


Figure 6. Linking ‘what’ stream recognition to ‘where’ stream action: interactions between the cortical areas ITp, ITa, amygdala, orbitofrontal cortex (ORB) and PPC can bridge the gap between the invariant ITa categories and the parietal target locations. The numbers indicate the order of pathway activations. If there are two numbers, the larger one represents the stage when feedback activates that pathway. See text for details.

optimal at a range of positive interstimulus intervals (ISIs) between the conditioned stimulus (CS) and the unconditioned stimulus (US) that are characteristic of the animal and the task, and is greatly attenuated at zero and long ISIs. Within this range, learned responses are timed to match the statistics of the learning environment (Smith 1968). Although the amygdala is a primary site for emotion and stimulus–reward association, the hippocampus and cerebellum have also been implicated in adaptively timed processing of cognitive–emotional interactions. For example, Thompson *et al.* (1987) distinguished two types of learning that go on during conditioning of the rabbit’s nictitating membrane response: adaptively timed ‘conditioned fear’ learning that is linked to the hippocampus, and adaptively timed ‘learning of the discrete adaptive response’ that is linked to the cerebellum.

A unified explanation of why both hippocampus and cerebellum use adaptively timed learning is given by the START (Spectrally Timed ART) model (figure 5), which unifies the ART and CogEM models (Grossberg & Schmajuk 1987; Grossberg & Merrill 1992, 1996; Fiala *et al.* 1996). CogEM predicts how salient conditioned cues can rapidly focus attention upon their sensory categories (*S*) via a cognitive–emotional resonance with their associated drive (*D*) representations (figure 4). However, what then prevents the actions (*M*) that they control from being prematurely released?

The cerebellum is predicted to adaptively time actions in a task-appropriate way by using a spectrum of learning sites, each sensitive to a different range of delays between the CS and the US. Learning selects those sites whose reaction rates match the ISIs between the CS and the US. Adaptively timed long-term depression (LTD) learning at parallel fibre/Purkinje cell synapses depresses the tonically active output from cerebellar Purkinje cells to cerebellar nuclei. LTD hereby disinhibits target cerebellar nucleus sites that read out adaptively timed learned movement gains at around the time when the US is expected.

Fiala *et al.* (1996) modelled how the metabotropic glutamate receptor (mGluR) system may create the spectrum of delays during cerebellar adaptively timed learning. Subsequent experiments confirmed a role for

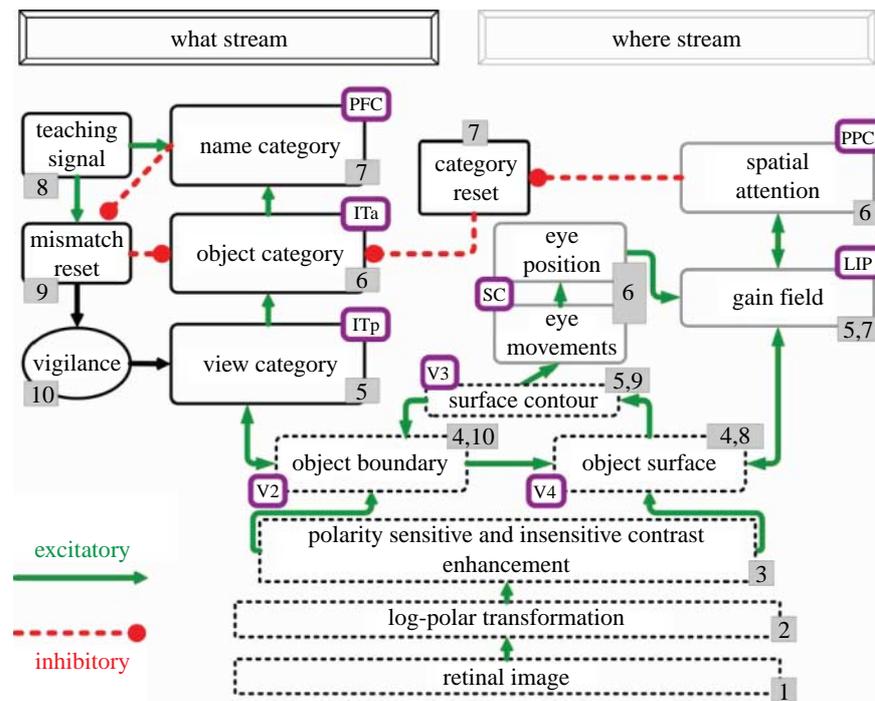


Figure 7. The ARTSCAN model: an active attentional shroud in PPC inhibits otherwise tonically active Category Reset inhibition. This enables the emerging view-invariant object category in ITa to stay active while view-specific categories in ITp are associated with it as the eyes scan a scene. Interactions between the object boundaries and the surfaces via a surface contour process are proposed to control eye movements on a surface whose shroud amplifies the corresponding object surface. (Adapted from [Fazl et al. \(2009\)](#)).

calcium signalling and mGluR in cerebellar adaptive timing ([Finch & Augustine 1998](#); [Takechi et al. 1998](#); [Ichise et al. 2000](#); [Miyata et al. 2000](#)). This model simulates both normal adaptively timed conditioning data and premature responding when cerebellar cortex is lesioned ([Perrett et al. 1993](#)). Autistic individuals with cerebellar malfunction also demonstrate prematurely released behaviours ([Sears et al. 1994](#); [Grossberg & Seidman 2006](#)).

Cerebellar adaptive timing hereby reconciles two potentially conflicting behavioural properties: fast allocation of attention to motivationally salient events via cortico-amygdala feedback versus adaptively timed responses to these events via cortico-cerebellar adaptively timed responding.

In order for adaptively timed responding to be effective, motivated attention needs to persist long enough to support the read-out of adaptively timed motor commands, and to prevent irrelevant events from prematurely resetting these commands. The START model ([Grossberg & Merrill 1992, 1996](#)) proposes how hippocampal dentate-CA3 circuits can do this ([figure 5](#)). Without these hippocampal mechanisms, a novel event could easily reset motor commands prematurely. Indeed, if a top-down prototype and bottom-up sensory input mismatch too much for resonance to occur, then the orienting system can be activated and reset active categories ([figure 2](#)). The hippocampal system and non-specific thalamus are proposed to be part of this mismatch-activated orienting system *A*. The thalamo-cortical and corticocortical mismatches that activate hippocampus or non-specific thalamus are not, however, sensitive to whether the novel event that caused the mismatch is task relevant. The START model clarifies

how mismatches may be modulated by task relevance in an adaptively timed way.

In particular, [figure 5](#) suggests how adaptively timed activity (*T* in [figure 5](#)) can inhibit *A* during an interval wherein a valued and predictable goal is being acted upon. *T* models adaptively timed activity in hippocampal dentate-CA3 cell firing during the rabbit nictitating membrane response ([Berger et al. 1986](#)). In summary, the START model enables three key properties to simultaneously coexist.

- *Fast motivated attention*. Rapid focusing of attention on motivationally salient cues occurs from regions such as the amygdala to prefrontal cortex (pathway $D \rightarrow S^{(2)}$ in [figure 5](#)). Without further processing, fast activation of the CS-activated $S^{(2)}$ sensory representations could prematurely release motor behaviours (pathway $S^{(2)} \rightarrow M$ in [figure 5](#)).
- *Adaptively timed responding*. Adaptively timed read-out of responses via cerebellar circuits (pathway *M* in [figure 5](#)) enables learned responses to be released at task-appropriate times, despite the fact that CS cortical representations can be quickly activated by fast motivated attention.
- *Adaptively timed duration of motivated attention and inhibition of orienting responses*. Premature reset of active CS representations by irrelevant cues during task-specific delays is prevented by adaptively timed inhibition of mismatch-sensitive cells in the orienting system of the hippocampus (pathway $T \rightarrow D \rightarrow A$ in [figure 5](#)). This inhibition is part of the competition between consummatory and orienting behaviours ([Staddon 1983](#)). Adaptively timed incentive motivational feedback ($D \rightarrow S^{(2)} \rightarrow S^{(1)}$ in [figure 5](#)) simultaneously maintains the CS

activation in short-term memory, so that the CS can continue to read out adaptively timed responses until they are complete. The contingent negative variation event-related potential is predicted to be a neural marker of adaptively timed motivational feedback. Many additional data have been explained using these circuits, including data from delayed non-match to sample experiments wherein both temporal delays and novelty-sensitive recognition processes are involved (Gaffan 1974; Mishkin & Delacour 1975). Similar adaptive timing mechanisms seem to operate in basal ganglia (Brown *et al.* 1999).

10. LAMINAR CORTICAL DYNAMICS OF WORKING MEMORY, LIST CHUNKING AND PERFORMANCE

The above mechanisms do not explain how the brain responds selectively to *sequences* of events. Predictive behaviour depends upon the capacity to think about, plan, execute and evaluate such event sequences. In particular, multiple events in a specific temporal order can be stored temporarily in *working memory*. As event sequences are temporarily stored, they are grouped, or chunked, through learning into unitized plans, or list chunks, and can later be performed at variable rates under volitional control. Here, the term ‘working memory’ is used to describe brain processes that temporarily store the *temporal order of several events*, not merely persistence of individual events.

Grossberg (1978*a,b*) introduced a model of working memory and list chunking, which proposed how the working memories are designed to enable list chunks to be stably learned and remembered. Inputs to this working memory are unitized *item categories* of individual events or objects (§2) that have enough adaptively timed, incentive motivational support (§7) to be persistently stored and transferred into the working memory. Item representations are stored in the working memory as a temporally evolving spatial pattern of activity across working memory cells. The *relative activity* of different cell populations codes the temporal order in which the items will be rehearsed, with the largest activities rehearsed earliest; hence, the name *Item and Order working memory* for this class of models. A more recent name is *competitive queuing* (Houghton 1990). The LIST PARSE model (Grossberg & Pearson 2008) built on this foundation to predict how laminar circuits in ventrolateral prefrontal cortex embody a cognitive working memory and list chunk learning network that interacts with a motor working memory in dorsolateral prefrontal cortex and a basal ganglia adaptively timed volitional control system.

Accumulating neurobiological data support the view that visual and verbal object categories may be learned in temporal and ventromedial prefrontal (e.g. orbitofrontal) cortex, with the latter responding to combined item and motivational signals, followed by the loading of these item representations into a sequential working memory that codes temporal order information in ventrolateral and/or dorsolateral prefrontal cortex (e.g. Goldman-Rakic 1987; Barbas

2000; Petrides 2005; Ranganath & D’Esposito 2005). These temporally evolving working memory patterns are, in turn, categorized by list chunks, or sequential plans, which can be used to predict subsequent expected events.

A full review of the LIST PARSE model goes beyond the scope of this paper. Here, it suffices to note that LIST PARSE unifies the explanation of cognitive, neurophysiological and anatomical data from humans and monkeys concerning how predictive, sequentially organized behaviours are controlled. Its laminar cognitive prefrontal circuits are variations of laminar circuits in visual cortex (§6). Thus, both vision and cognition seem to use variations of a shared laminar cortical design to rapidly learn stable categories with which to predict a changing world. In particular, LIST PARSE quantitatively simulates human cognitive data about immediate *serial* recall and immediate, delayed and continuous-distracter *free* recall, as well as the monkey neurophysiological data from the prefrontal cortex obtained during sequential sensory-motor imitation and planned performance. It hereby clarifies how both spatial and non-spatial working memories may share the same laminar cortical circuit design.

11. BALANCING REACTIVE VERSUS PLANNED BEHAVIOURS: BASAL GANGLIA GATING

Complementary orienting versus attentional systems search for and learn new recognition codes (§5). They are subsumed by a larger complementary brain system that balances reactive versus planned behaviours. Rapid reactive movements, such as orienting movements, facilitate survival in response to unexpected dangers. Planned movements, which involve focused attention, often take longer to select and release. How does the brain prevent premature reactive movements towards objects in situations where a more slowly occurring planned movement is more adaptive?

Movement *gates* (cf. §9) can inhibit a reactive movement command until a planned movement can effectively compete with it. Then, a planned command can open its gate and launch its movement. The basal ganglia carry out such a gating function. Movement gates overcome a potentially devastating problem: a movement gate must be opened to release *any* movement. How does the brain know that a plan is emerging *before* it is fully formed, so that it can inhibit the gate that would otherwise have prematurely released a faster reactive movement? The TELOS model (Brown *et al.* 2004) predicts how frontal–parietal interactions prevent a reactive movement command from opening its gate before a planned movement command is ready, yet also allows a reactive movement command to open its gate quickly when no planned movement command is being formed. TELOS predicted that a frontal–parietal resonance occurs when this competition is resolved, and lets the appropriate gate open. Such a resonance has recently been reported (Buschman & Miller 2007). Miller’s laboratory has also reported the expected timing of frontal and basal ganglia activations (Pasupathy & Miller 2002).

12. SPATIALLY INVARIANT RECOGNITION CODES CONTROL SPATIALLY PRECISE ACTIONS

Conditional movements towards valued goal objects cannot be made until goal objects are recognized and selected, and their spatial locations specified. As noted in §1 and [figure 1](#), the ‘what’ stream learns object representations that are increasingly independent of object position and size, whereas the ‘where’ stream represents the object positions and how to move. ‘What’–‘where’ stream interactions overcome these complementary informational deficiencies to generate movements towards recognized objects.

Whereas object representations in posterior inferotemporal cortex (ITp) combine feature and positional information, object representations in ITa are more positionally invariant. These two types of representations are linked by reciprocal learned connections, as described by ART. ITp representations also project to the posterior parietal cortex (PPC) as the target locations of an object. Consider what happens when multiple objects in a scene all try to activate their corresponding ITp and ITa representations. Suppose that a particular ITa category represents a valued goal object in that situation. As noted in §7, the ITa representation can get amplified by an inferotemporal–amygdala–orbitofrontal resonance. When this happens, the amplified ITa representation can better compete for object attention, and can send larger top-down priming signals to its ITp representations. The ITp representation that corresponds to the valued object is thereby selectively amplified, and sends an amplified signal to the parietal cortex, where its target location can win the competition for where the next movement will go ([figure 6](#)). This scheme can help to solve the ‘Where’s Waldo’ problem.

13. LEARNING VIEW- AND POSITION-INVARIANT OBJECT CATEGORIES USING ATTENTIONAL SHROUDS

How are positionally invariant and view-invariant categories learned by the brain? To understand how this happens, several basic questions need to be answered: what is an object? How does the brain learn what an object is under both unsupervised and supervised learning conditions? How does the brain learn to bind multiple views of an object into a view-invariant and positionally invariant object category while scanning its parts with eye movements?

To answer these questions, one also needs to solve the following problem: as 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, even before the brain knows what the object is?

The ARTSCAN model ([figure 7](#)) clarifies how the brain uses scanning saccadic eye movements to learn view-invariant object categories ([Fazl et al. 2009](#)). The discussion about ART above considered only object attention ([Posner 1980](#)) in the ‘what’ cortical stream. ARTSCAN explains how object attention works

with spatial attention ([Duncan 1984](#)) in the ‘where’ cortical stream to direct eye movements that explore object surfaces. As the eyes move around an object surface, multiple view-specific categories are learned of the object (e.g. in ITp) and are associated with an emerging view-invariant object category (e.g. in ITa). How does the brain know which view-specific categories should be associated with a given view-invariant category?

ARTSCAN predicts that a *pre-attentively* formed surface representation activates an *attentional shroud* ([Tyler & Kontsevich 1995](#)), or form-fitting distribution of spatial attention, even before the brain can recognize the surface as representing a particular object. This shroud persists within the ‘where’ stream during active scanning of an object. The shroud protects the view-invariant category from getting reset, even while view-specific categories are reset, as the eyes explore an object. The shroud does this by inhibiting the ITa reset mechanism ([figure 7](#)).

How does the shroud persist during active scanning of an object? A *surface-shroud resonance* arises owing to feedback interactions between a surface representation (e.g. in area V4) and spatial attention (e.g. in PPC), and focuses spatial attention upon the object to be learned. When the shroud collapses as the eyes move to another surface, its view-invariant object category is reset as well. Many paradoxical data are explained by these concepts, including how spatial attention can increase the perceived brightness of a surface ([Carrasco et al. 2000](#); [Reynolds & Desimone 2003](#)), and what sort of category invariance can be learned ([Zoccolan et al. 2007](#)).

14. INHIBITORY MATCHING AND MISMATCH LEARNING OF SENSORY MOTOR MAPS AND GAINS

As noted in §§1 and 2, learning of object representations in the ‘what’ stream uses excitatory matching and match-based learning to solve the stability–plasticity dilemma. ‘Where’ stream learning, by contrast, often uses inhibitory matching and mismatch-based learning. Inhibitory matching is often between brain representations of a *target position* and the *present position* of a motor effector. Inhibitory matching computes a *difference vector* that represents the distance and direction of an intended movement. The difference vector is volitionally gated (see §11) by a GO signal that determines when and how fast the movement will occur ([Bullock & Grossberg 1988](#); [Bullock et al. 1998](#)). 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 eliminate the source of the mismatch through time by recalibrating system maps and gains. Neural models predict how mismatch learning may tune spatial representations and adaptive motor gains in basal ganglia, cerebellum, motor cortex, parietal cortex and prefrontal cortex ([Guenther et al. 1994](#); [Fiala et al. 1996](#); [Brown et al. 1999, 2004](#); [Grossberg & Paine 2000](#)).

In summary, perceptual/cognitive processes often use excitatory matching and match-based learning to create stable predictive representations of objects and

events in the world. Complementary spatial/motor processes often use inhibitory matching and mismatch-based learning to continually update spatial maps and sensory motor gains. Together, these complementary predictive and learning mechanisms create a self-stabilizing perceptual/cognitive front end for activating the more labile spatial/motor processes that control our changing bodies as they act upon objects in the world.

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REFERENCES

- Aggleton, J. P. 1993 The contribution of the amygdala to normal and abnormal emotional states. *Trends Neurosci.* **16**, 328–333. (doi:10.1016/0166-2236(93)90110-8)
- 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. (doi:10.1016/S0896-6273(01)00224-0)
- Barbas, H. 1995 Anatomic basis of cognitive–emotional interactions in the primate prefrontal cortex. *Neurosci. Biobehav. Rev.* **19**, 499–510. (doi:10.1016/0149-7634(94)00053-4)
- Barbas, H. 2000 Connections underlying the synthesis of cognition, memory and emotion in primate prefrontal cortices. *Brain Res. Bull.* **52**, 319–330. (doi:10.1016/S0361-9230(99)00245-2)
- Baxter, M. G., Parker, A., Lindner, C. C. C., Izquierdo, A. D. & Murray, E. A. 2000 Control of response selection by reinforcer value requires interaction of amygdala and orbital prefrontal cortex. *J. Neurosci.* **20**, 4311–4319.
- Berger, T. W., Berry, S. D. & Thompson, R. F. 1986 Role of the hippocampus in classical conditioning of aversive and appetitive behaviors. In *The hippocampus*, vol. 4 (eds R. L. Isaacson & K. H. Pribram), pp. 203–239. New York, NY: Plenum Press.
- Berke, J. D., Hetrick, V., Breck, J. & Greene, R. W. 2008 Transient 23–30 Hz oscillations in mouse hippocampus during exploration of novel environments. *Hippocampus* **18**, 519–529. (doi:10.1002/hipo.20435)
- Brown, J. W., 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**, 502–511.
- 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. (doi:10.1016/j.neunet.2003.08.006)
- Buffalo, E. A., Fries, P. & Desimone, R. 2004 Layer-specific attentional modulation in early visual areas. *Soc. Neurosci. Abstr.* **30**, 717–6.
- Bullier, J., Hupé, J. M., James, A. & Girard, P. 1996 Functional interactions between areas V1 and V2 in the monkey. *J. Physiol. (Paris)* **90**, 217–220. (doi:10.1016/S0928-4257(97)81426-X)
- 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. (doi:10.1037/0033-295X.95.1.49)
- Bullock, D., Cisek, P. & Grossberg, S. 1998 Cortical networks for control of voluntary arm movements under variable force conditions. *Cereb. Cortex* **8**, 48–62. (doi:10.1093/cercor/8.1.48)
- Buschman, T. J. & Miller, E. K. 2007 Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* **315**, 1860–1862. (doi:10.1126/science.1138071)
- Caputo, G. & Guerra, S. 1998 Attentional selection by distractor suppression. *Vision Res.* **38**, 669–689. (doi:10.1016/S0042-6989(97)00189-2)
- Carpenter, G. A. & Grossberg, S. 1987 A massively parallel architecture for a self-organizing neural pattern-recognition machine. *Comput. Vis. Graph. Image Process.* **37**, 54–115. (doi:10.1016/S0734-189X(87)80014-2)
- Carpenter, G. A. & Grossberg, S. 1992 A self-organizing neural network for supervised learning, recognition, and prediction. *IEEE Commun. Mag.* **30**, 38–49. (doi:10.1109/35.156802)
- Carpenter, G. & Grossberg, S. 1993 Normal and amnesic learning, recognition, and memory by a neural model of cortico-hippocampal interactions. *Trend Neurosci.* **16**, 131–137. (doi:10.1016/0166-2236(93)90118-6)
- Carrasco, M., Penpeci-Talgar, C. & Eckstein, M. 2000 Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Res.* **40**, 1203–1215. (doi:10.1016/S0042-6989(00)00024-9)
- Damasio, A. R. 1999 *The feeling of what happens: body and emotion in the making of consciousness*. New York, NY: Harcourt Braces.
- Desimone, R. 1998 Visual attention mediated by biased competition in extrastriate visual cortex. *Phil. Trans. R. Soc. B* **353**, 1245–1255. (doi:10.1098/rstb.1998.0280)
- Downing, C. J. 1988 Expectancy and visual-spatial attention: effects on perceptual quality. *J. Exp. Psychol. Hum. Percept. Perform.* **14**, 188–202. (doi:10.1037/0096-1523.14.2.188)
- Dranias, M. R., Grossberg, S. & Bullock, D. 2008 Dopaminergic and non-dopaminergic value systems in conditioning and outcome-specific revaluation. *Brain Res.* **1238**, 239–287. (doi:10.1016/j.brainres.2008.07.013)
- Duncan, J. 1984 Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* **113**, 501–517. (doi:10.1037/0096-3445.113.4.501)
- Engel, A. K., Fries, P. & Singer, W. 2001 Dynamics predictions: oscillations and synchrony in top-down processing. *Nat. Rev. Neurosci.* **2**, 704–716. (doi:10.1038/35094565)
- 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. (doi:10.1016/j.cogpsych.2008.05.001)
- 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.
- Finch, E. A. & Augustine, G. J. 1998 Local calcium signalling by inositol-1,4,5-triphosphate in Purkinje cell dendrites. *Nature* **396**, 753–756. (doi:10.1038/25541)
- Frank, L. M., Stanley, G. B. & Brown, E. N. 2004 Hippocampal plasticity across multiple days of exposure to novel environments. *J. Neurosci.* **24**, 7681–7689. (doi:10.1523/JNEUROSCI.1958-04.2004)
- Gaffan, D. 1974 Recognition impaired and association intact in the memory of monkeys after transection of the fornix. *J. Comp. Physiol. Psychol.* **86**, 1100–1109. (doi:10.1037/h0037649)
- Goldman-Rakic, P. S. 1987 Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In *Handbook of physiology* (eds F. Plum & V. Mountcastle), pp. 373–417. Bethesda, MD: American Physiological Society.
- Gorchetnikov, 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. (doi:10.1016/j.neunet.2006.11.007)

- Gove, A., Grossberg, S. & Mingolla, E. 1995 Brightness perception, illusory contours, and corticogeniculate feedback. *Visual Neurosci.* **12**, 1027–1052.
- Grossberg, G. 1972a A neural theory of punishment and avoidance. I. Qualitative theory. *Math. Biosciences* **15**, 39–67. (doi:10.1016/0025-5564(72)90062-4)
- Grossberg, G. 1972b A neural theory of punishment and avoidance. II. Quantitative theory. *Math. Biosciences* **15**, 253–285. (doi:10.1016/0025-5564(72)90038-7)
- Grossberg, S. 1975 A neural model of attention, reinforcement, and discrimination learning. *Int. Rev. Neurobiol.* **18**, 263–327. (doi:10.1016/S0074-7742(08)60037-9)
- Grossberg, S. 1978a A theory of human memory: self-organization and performance of sensory-motor codes, maps, and plans. In *Progress in theoretical biology*, vol. 5 (eds B. Rosen & F. Snell), pp. 233–374. New York, NY: Academic Press. (Reprinted by Grossberg, S. *Studies of mind and brain*, pp. 500–639. Boston, MA: Reidel 1982.)
- Grossberg, S. 1978b Behavioral contrast in short-term memory: serial binary memory models or parallel continuous memory models? *J. Math. Psychol.* **17**, 199–219. (doi:10.1016/0022-2496(78)90016-0)
- Grossberg, S. 1980 How does a brain build a cognitive code? *Psychol. Rev.* **87**, 1–51. (doi:10.1037/0033-295X.87.1.1)
- Grossberg, S. 1982 Processing of expected and unexpected events during conditioning and attention: a psychophysiological theory. *Psychol. Rev.* **89**, 529–572. (doi:10.1037/0033-295X.89.5.529)
- Grossberg, S. 1999 How does the cerebral cortex work? Learning, attention and grouping by the laminar circuits of visual cortex. *Spatial Vis.* **12**, 163–186. (doi:10.1163/156856899X00102)
- Grossberg, S. 2000a How hallucinations may arise from brain mechanisms of learning, attention, and volition. *J. Int. Neuropsychol. Soc.* **6**, 579–588. (doi:10.1017/S135561770065508X)
- Grossberg, S. 2000b The complementary brain: unifying brain dynamics and modularity. *Trends Cogn. Sci.* **4**, 233–246. (doi:10.1016/S1364-6613(00)01464-9)
- Grossberg, S. 2000c The imbalanced brain: from normal behavior to schizophrenia. *Biol. Psychiatry* **48**, 81–98. (doi:10.1016/S0006-3223(00)00903-3)
- Grossberg, G. 2003 How does the cerebral cortex work? Development, learning, attention, and 3-D vision by laminar circuits of visual cortex. *Behav. Cogn. Neurosci. Rev.* **2**, 47–76. (doi:10.1177/1534582303002001003)
- Grossberg, S. Submitted. Beta oscillations and hippocampal place cell learning during exploration of novel environments.
- Grossberg, S. & Levine, D. S. 1987 Neural dynamics of attentionally modulated Pavlovian conditioning: blocking, inter-stimulus interval, and secondary reinforcement. *Appl. Opt.* **26**, 5015–5030.
- 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. (doi:10.1016/0926-6410(92)90003-A)
- Grossberg, S. & Merrill, J. W. L. 1996 The hippocampus and cerebellum in adaptively timed learning, recognition, and movement. *J. Cogn. Neurosci.* **8**, 257–277. (doi:10.1162/jocn.1996.8.3.257)
- Grossberg, S. & Myers, C. W. 2000 The resonant dynamics of speech perception: interword integration and duration-dependent backward effects. *Psychol. Rev.* **107**, 735–767. (doi:10.1037/0033-295X.107.4.735)
- 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. (doi:10.1016/S0893-6080(00)00065-4)
- 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. (doi:10.1037/a0012618)
- Grossberg, S. & Schmajuk, N. A. 1987 Neural dynamics of attentionally-modulated Pavlovian conditioning: conditioned reinforcement, inhibition, and opponent processing. *Psychobiology* **15**, 195–240.
- Grossberg, G. & Schmajuk, N. A. 1989 Neural dynamics of adaptive timing and temporal discrimination during associative learning. *Neural Networks* **2**, 79–102. (doi:10.1016/0893-6080(89)90026-9)
- Grossberg, S. & Seidman, D. 2006 Neural dynamics of autistic behaviors: cognitive, emotional, and timing substrates. *Psychol. Rev.* **113**, 483–525. (doi:10.1037/0033-295X.113.3.483)
- Grossberg, S. & Versace, M. 2008 Spikes, synchrony, and attentive learning by laminar thalamocortical circuits. *Brain Res.* **1218**, 278–312. (doi:10.1016/j.brainres.2008.04.024)
- Grossberg, S., Govindarajan, K. K., Wyse, L. L. & Cohen, M. A. 2004 ARTSTREAM: a neural network model of auditory scene analysis and source segregation. *Neural Networks* **17**, 511–536. (doi:10.1016/j.neunet.2003.10.002)
- Grossberg, S., Bullock, D. & Dranias, M. R. 2008 Neural dynamics underlying impaired autonomic and conditioned responses following amygdala and orbitofrontal lesions. *Behav. Neurosci.* **122**, 1100–1125. (doi:10.1037/a0012808)
- 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. (doi:10.1162/jocn.1994.6.4.341)
- Hafting, T., Fyhn, M., Molden, S., Moser, M. B. & Moser, E. 2005 Microstructure of the spatial map in the entorhinal cortex. *Nature* **436**, 801–806. (doi:10.1038/nature03721)
- Houghton, G. 1990 The problem of serial order: a neural network model of sequence learning and recall. In *Current research in natural language generation* (eds R. Dale, C. Mellish & M. Zock), pp. 287–319. London, UK: Academic Press.
- Hupé, J. M., James, A. C., Girard, D. C. & Bullier, J. 1997 Feedback connections from V2 modulate intrinsic connectivity within V1. *Soc. Neurosci. Abstr.* **23**, 1031.
- Ichise, T., Kano, M., Hashimoto, K., Yangihara, D., Nakao, K., Shigemoto, R., Katsuki, M. & Aiba, A. 2000 mGluR1 in cerebellar Purkinje cells essential for long-term depression, synapse elimination, and motor coordination. *Science* **288**, 1832–1835. (doi:10.1126/science.288.5472.1832)
- Kamin, L. J. 1969 Predictability, surprise, attention and conditioning. In *Punishment and aversive behavior* (eds B. A. Campbell & R. M. Church), pp. 279–296. New York, NY: Appleton-Century-Crofts.
- Kastner, S. & Ungerleider, L. G. 2001 The neural basis of biased competition in human visual cortex. *Neuropsychologia* **39**, 1263–1276. (doi:10.1016/S0028-3932(01)00116-6)
- LeDoux, J. E. 1993 Emotional memory systems in the brain. *Behav. Brain Res.* **58**, 69–79. (doi:10.1016/0166-4328(93)90091-4)
- Mishkin, M. & Delacour, J. 1975 An analysis of short-term visual memory in the monkey. *J. Exp. Psychol. Anim. Behav. Process.* **1**, 326–334. (doi:10.1037/0097-7403.1.4.326)
- Miyata, M. et al. 2000 Local calcium release in dendritic spines required for long-term synaptic depression. *Neuron* **28**, 233–244. (doi:10.1016/S0896-6273(00)00099-4)
- Mounts, J. R. W. 2000 Evidence for suppressive mechanisms in attentional selection: feature singletons produce inhibitory surrounds. *Percept. Psychophys.* **62**, 969–983.

- Muller, R. A. 1996 A quarter of a century of place cells. *Neuron* **17**, 813–822. (doi:10.1016/S0896-6273(00)80214-7)
- Pasupathy, A. & Miller, E. K. 2002 Different time courses of learning-related activity in the prefrontal cortex and striatum. *Nature* **433**, 873–876. (doi:10.1038/nature03287)
- Pavlov, I. P. 1927 *Conditioned reflexes*. Oxford, UK: Oxford University Press.
- Perret, S. P., Ruiz, B. P. & Mauk, M. D. 1993 Cerebellar cortex lesions disrupt learning-dependent timing of conditioned eyelid responses. *J. Neurosci.* **13**, 1708–1718.
- Petrides, M. 2005 Lateral prefrontal cortex: architectonic and functional organization. *Phil. Trans. Soc. B* **360**, 781–795. (doi:10.1098/rstb.2005.1631)
- Posner, M. I. 1980 Orienting of attention. *Quart. J. Exp. Psychol.* **32**, 3–25. (doi:10.1080/00335558008248231)
- Raizada, R. & Grossberg, S. 2003 Towards a theory of the laminar architecture of cerebral cortex: computational clues from the visual system. *Cereb. Cortex* **13**, 100–113. (doi:10.1093/cercor/13.1.100)
- Ranganath, C. & D'Esposito, M. 2005 Directing the mind's eye: prefrontal, inferior and medial temporal mechanisms for visual working memory. *Curr. Opin. Neurobiol.* **15**, 175–182. (doi:10.1016/j.conb.2005.03.017)
- Reynolds, J. H. & Desimone, R. 2003 Interacting roles of attention and visual salience in V4. *Neuron* **37**, 853–863. (doi:10.1016/S0896-6273(03)00097-7)
- Reynolds, J., Chelazzi, L. & Desimone, R. 1999 Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.* **19**, 1736–1753.
- Schoenbaum, G., Setlow, B., Saddoris, M. P. & Gallagher, M. 2003 Encoding predicted outcome and acquired value in orbitofrontal cortex during cue sampling depends upon input from basolateral amygdala. *Neuron* **39**, 855–867. (doi:10.1016/S0896-6273(03)00474-4)
- Schultz, W. 1998 Predictive reward signals of dopamine neurons. *J. Neurophysiol.* **80**, 1–27.
- Sears, L. L., Finn, P. R. & Steinmetz, J. E. 1994 Abnormal classical eye-blink conditioning in autism. *J. Autism Dev. Disord.* **24**, 737–751. (doi:10.1007/BF02172283)
- Sigala, N. & Logothetis, N. K. 2002 Visual categorization shapes feature selectivity in the primate temporal cortex. *Nature* **415**, 318–320. (doi:10.1038/415318a)
- Sillito, A. M., Jones, H. E., Gerstein, G. L. & West, D. C. 1994 Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature* **369**, 479–482. (doi:10.1038/369479a0)
- Smith, A. T., Singh, K. D. & Greenlee, M. W. 2000 Attentional suppression of activity in the human visual cortex. *Neuroreport* **11**, 271–278. (doi:10.1097/00001756-200002070-00010)
- Smith, M. C. 1968 CS-US interval and US intensity in classical conditioning of the rabbit's nictitating membrane response. *J. Comp. Physiol. Psychol.* **66**, 679–687. (doi:10.1037/h0026550)
- Somers, D. C., Dale, A. M., Seiffert, A. E. & Tootell, R. B. 1999 Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proc. Natl Acad. Sci. USA* **96**, 1663–1668. (doi:10.1073/pnas.96.4.1663)
- Staddon, J. E. R. 1983 *Adaptive behavior and learning*. New York, NY: Cambridge University Press.
- Steinman, B. A., Steinman, S. B. & Lehmkuhle, S. 1995 Visual attention mechanisms show a center-surround organization. *Vision Res.* **35**, 1859–1869. (doi:10.1016/0042-6989(94)00276-R)
- Takechi, H., Eilers, J. & Konnerth, A. 1998 A new class of synaptic response involving calcium release in dendritic spines. *Nature* **396**, 757–760. (doi:10.1038/25547)
- 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.
- Thompson, L. T. & Best, P. J. 1990 Long-term stability of the place-field activity of single units recorded from the dorsal hippocampus of freely behaving rats. *Brain Res.* **509**, 299–308. (doi:10.1016/0006-8993(90)90555-P)
- 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 *Classical conditioning* 3rd edn. (eds I. Gormenzano, W. F. Prokasy & R. F. Thompson), pp. 371–399. Hillsdale, NJ: Erlbaum Associates.
- Tyler, C. W. & Kontsevich, L. L. 1995 Mechanisms of stereoscopic processing: stereoattention and surface perception in depth reconstruction. *Perception* **24**, 127–153. (doi:10.1068/p240127)
- Vanduffel, W., Tootell, R. B. & Orban, G. A. 2000 Attention-dependent suppression of metabolic activity in the early stages of the macaque visual system. *Cereb. Cortex* **10**, 109–126. (doi:10.1093/cercor/10.2.109)
- Wilson, M. A. & McNaughton, B. L. 1993 Dynamics of the hippocampal ensemble code for space. *Science* **261**, 1055–1058. (doi:10.1126/science.8351520)
- Zoccolan, C., Kouh, M., Poggio, T. & DiCarlo, J. J. 2007 Trade-off between object selectivity and tolerance in monkey inferotemporal cortex. *J. Neurosci.* **27**, 12 292–12 307. (doi:10.1523/JNEUROSCI.1897-07.2007)