

# **Cortical and Subcortical Predictive Dynamics and Learning during Perception, Cognition, Emotion, and Action**

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September 10, 2008

Invited article for a special issue on:

Predictions in the brain: Using our past to generate a future

Philosophical Transactions of the Royal Society of London

**Key Words :** complementary cortical streams, invariant recognition learning, cognitive-emotional dynamics, adaptive timing, working memory, laminar cortical circuits, Adaptive Resonance Theory

\*Supported in part by the National Science Foundation (SBE-0354378)

**Abstract**

An intimate link exists between 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 current article reviews and synthesizes data and models of these processes, and outlines a unified theory of predictive brain processing.

## 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, 2000b). 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. The present article reviews and synthesizes data and models of these processes, and outlines a unified theory of predictive brain processing.

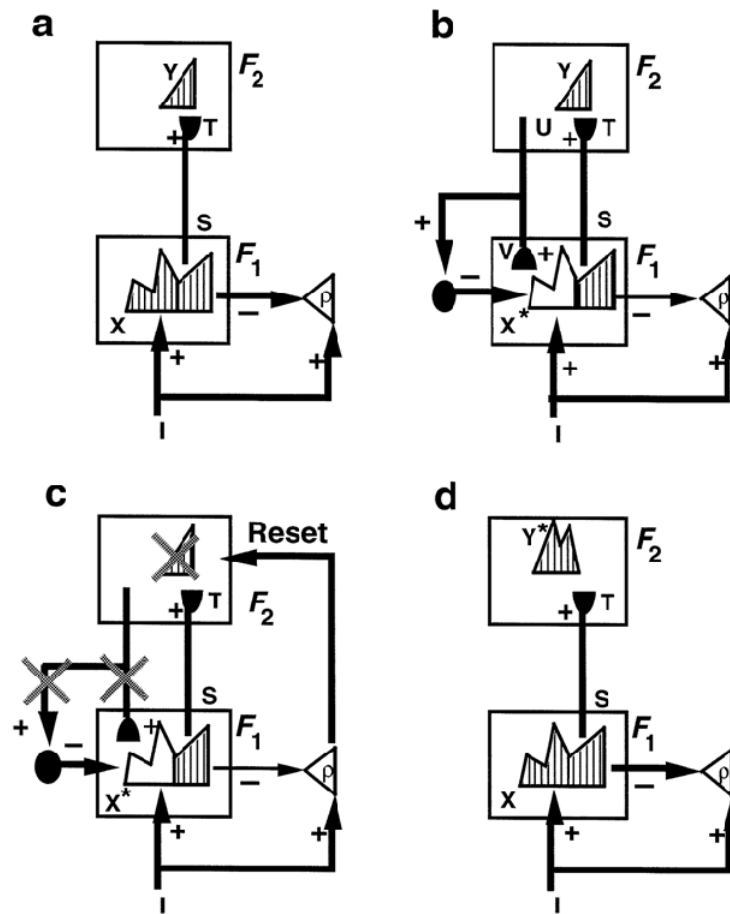
	<b>WHAT</b>	<b>WHERE</b>
	Spatially-invariant object learning and recognition	Spatially-variant reaching and movement
	Fast learning without catastrophic forgetting	Continually update sensory-motor maps and gains
	<b>IT</b>	<b>PPC</b>
	<b>WHAT</b>	<b>WHERE</b>
<b>MATCHING</b>	EXCITATORY	INHIBITORY
<b>LEARNING</b>	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.

## 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 exhibits such invariance (Bar et al., 2001; Sigala and Logothetis, 2002; Tanaka et al., 1991; Zoccolan et al., 2007), which helps to prevent a combinatorial explosion in 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 and 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 upon 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,



**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

nonspecifically activates the orienting system  $A$  with gain  $\rho$ .  $X$  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,  $A$  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).]

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 Section 13) and *one-to-many maps* (representations that enable us to expertly know many things about individual objects and events); see Carpenter and 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 support this prediction; e.g., Engel, Fries, and Singer (2001).

### **3. Expectations and Biased Competition: Modulatory On-Center, Off-Surround Network**

How are What stream top-down expectations computed? Carpenter and Grossberg (1987) mathematically proved that the simplest network that solves the stability-plasticity dilemma is a *top-down, modulatory on-center, off-surround network*, which provides excitatory priming of features in the on-center, and driving inhibition in the off-surround. The modulatory on-center emerges from a balance between top-down excitation and inhibition. Subsequent modeling studies provide additional evidence for such a circuit (e.g., Dranias, Grossberg, and Bullock, 2008; Gove, Grossberg, and Mingolla, 1995; Grossberg et al., 2004; Grossberg and Myers, 2000), and laminar cortical models predict identified cell types (Grossberg, 1999; Grossberg and Pearson, 2008; Grossberg and Versace, 2008; Raizada and Grossberg, 2003). Many anatomical and neurophysiological experiments support this prediction (e.g., Bullier, Hupé, James, and Girard, 1996; Caputo and Guerra, 1998; Downing, 1988; Hupé *et al.*, 1997; Mounts, 2000; Reynolds, Chelazzi, and Desimone, 1999; Sillito, Jones, Gerstein, and West, 1994; Smith, Singh, and Greenlee, 2000; Somers, Dale, Seiffert, and Tootell, 1999; Steinman, Steinman, and Lehmkuhle, 1995; Vanduffell, Tootell, and Orban, 2000), which is more qualitatively called “biased competition” (Desimone, 1998; Kastner and 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-center 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-center,

then read-out of a top-down expectation from a recognition category can fire cells in the on-center 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 like 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 vs. Unexpected Events**

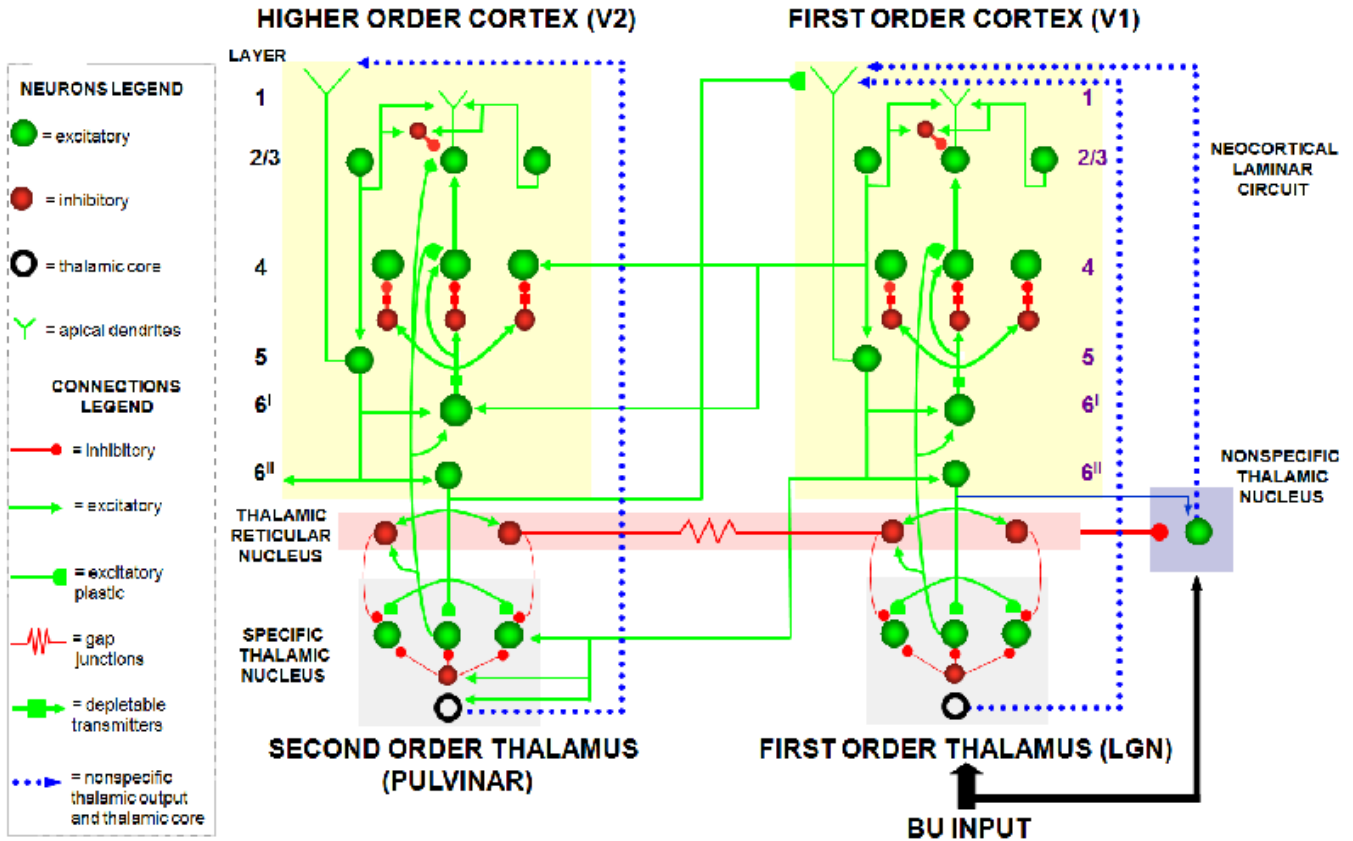
How does a brain learn about unexpected and unfamiliar events, such as novel objects to recognize, without causing catastrophic forgetting? Within ART, this is achieved by a memory search, or hypothesis testing, process that discovers the recognition category that best matches an event or object. Figure 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 (see Figures 2c and 2d).

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 SMART model (Figure 3) predicts how finer details about 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 (STDP), and acetylcholine modulation; detailed laminar thalamic 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.



**Figure 3.** The SMART model clarifies how laminar neocortical circuits in multiple cortical areas interact with specific and nonspecific thalamic nuclei to regulate learning on multiple organizational levels, ranging from spikes to cognitive dynamics. ART top-down modulatory on-center, off-surround networks occur in both corticocortical and corticothalamic circuits. For example, layer 6<sup>II</sup> of cortical area V2 sends top-down outputs to cortical area V1 via layer 1, where they activate apical dendrites of layer 5 cells. Layer 5, in turn, activates layer 6<sup>I</sup>, which sends modulatory on-center, off-surround signals to layer 4. In addition, layer 5 cells activate layer 6<sup>II</sup>, which sends top-down modulatory on-center off-surround signals to LGN. These pathways help to regulate stable learning in laminar thalamocortical circuits. [Reprinted with permission from Grossberg and Versace (2008).]

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:

(1) Buffalo, Fries, and Desimone (2004) have reported beta oscillations in deeper cortical layers.

(2) Buschman and Miller (in preparation) have reported beta oscillations during spatial attention shifts in parietal cortex.

(3) Berke et al. (2008) have reported beta oscillations during hippocampal place cell learning in novel environments.

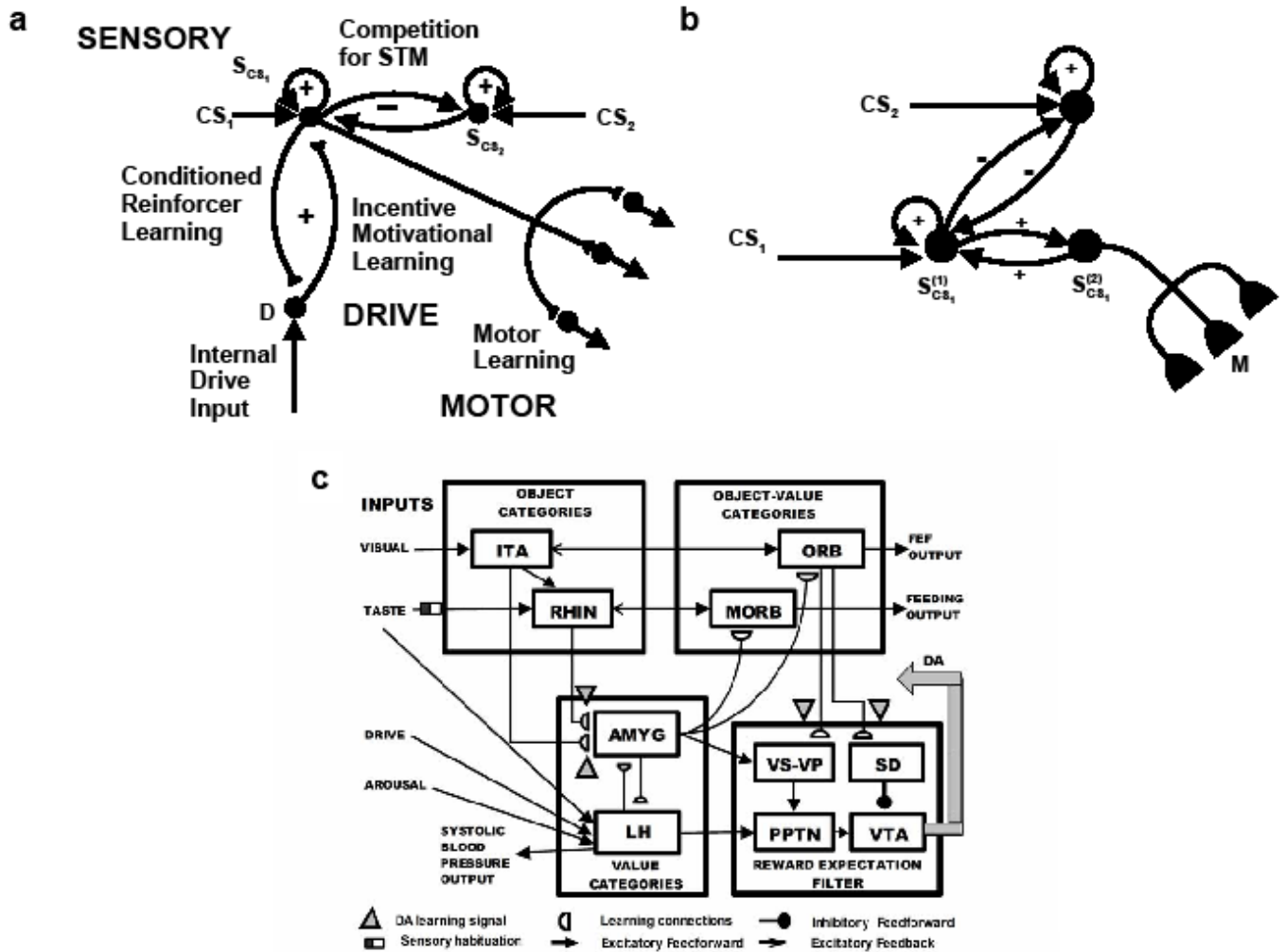
Place cells can develop within seconds to minutes, and can remain stable for months (Thompson and Best, 1990; Wilson and McNaughton, 1993; Muller, 1996; Frank et al., 2004). Place cell learning thus seems to have solved the stability-plasticity dilemma. Are place cells learned using ART dynamics? The 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 two minutes 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, 2008): Gorchetchnikov and Grossberg (2007) modeled 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 learning of a new category (Carpenter and 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 reset 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 choice and release of actions that realize valued goals in a context-sensitive way.

In Figures 4a and 4b, 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 behavior can be constrained by such external sensory options and internal emotional and motivational requirements.



**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 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. [Reprinted with permission from Grossberg and 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. [Reprinted with permission from Dranias, Grossberg, and Bullock (2008)]

The amygdala is a drive representation (e.g., Aggleton, 1993; LeDoux, 1993). Reinforcement learning (Figures 4a and 4b) 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 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 regions of prefrontal cortex ( $S_{CS_2}^{(1)}$ ), such as orbitofrontal cortex. The amygdala (D) also sends projections to orbitofrontal cortex (Barbas, 1995; Grossberg, 1975, 1982). Reinforcement learning can hereby strengthen amygdala-to-orbitofrontal 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 ( $S_{CS_2}^{(1)}$ ) 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 basic consciousness of goals and feelings (Damasio, 1999; Grossberg, 1975, 2000a), 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 Figures 4a and 4b predicted and functionally explained these processes with increasing precision and predictive range since its introduction in Grossberg (1972a, 1972b, 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 (Grossberg, 1975; Grossberg and Levine, 1987; Kamin, 1969; Pavlov, 1927). 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 and Seidman, 2006).

The MOTIVATOR model (Dranias, Grossberg, and Bullock, 2008; Grossberg, Bullock, and Dranias, 2008) further develops the CogEM model, just as SMART further develops ART; see Figure 4c. In addition, MOTIVATOR unifies the CogEM and TELOS models (Brown, Bullock, and Grossberg, 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 vs. 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 behavior, 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 behavior 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* behavior, which may discover novel sources of reward, and *consummatory* behavior, which may acquire expected sources of reward. A human or animal needs to suppress exploratory behavior and focus attention upon an expected source of reward when the reward is expected. The Spectral Timing model (Brown, Bullock, and Grossberg, 1999; Fiala, Grossberg, and Bullock, 1996; Grossberg and Merrill, 1992, 1996; Grossberg and Schmajuk, 1989) 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 reset of working memory, attention shifts, emotional rebounds, and exploratory behaviors. 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 optimal at a range of positive interstimulus intervals (ISI) between the conditioned stimulus (CS) and 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 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 (Fiala, Grossberg, and Bullock, 1996; Grossberg and Merrill, 1992, 1996; Grossberg and Schmajuk, 1987). 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 CS and 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 fiber/Purkinje cell synapses depresses the tonically active output from cerebellar Purkinje cells to cerebellar nuclei. LTD hereby disinhibits target cerebellar nucleus sites which read out adaptively timed learned movement gains at around the time when the US is expected.

Fiala, Grossberg, and Bullock (1996) modeled how the metabotropic glutamate (mGluR) receptor system may create the spectrum of delays during cerebellar adaptively timed learning. Subsequent experiments confirmed a role for calcium signalling and mGluR in cerebellar adaptive timing (Finch and Augustine, 1998; Ichise *et al.*, 2000; Miyata *et al.*, 2000; Takechi, Eilers, and Konnerth, 1998). This model simulates both normal adaptively timed conditioning data and premature responding when cerebellar cortex is lesioned (Perrett, Ruiz, and Mauk, 1993). Autistic individuals with cerebellar malfunction also demonstrate prematurely released behaviors (Grossberg and Seidman, 2006; Sears *et al.*, 1994).

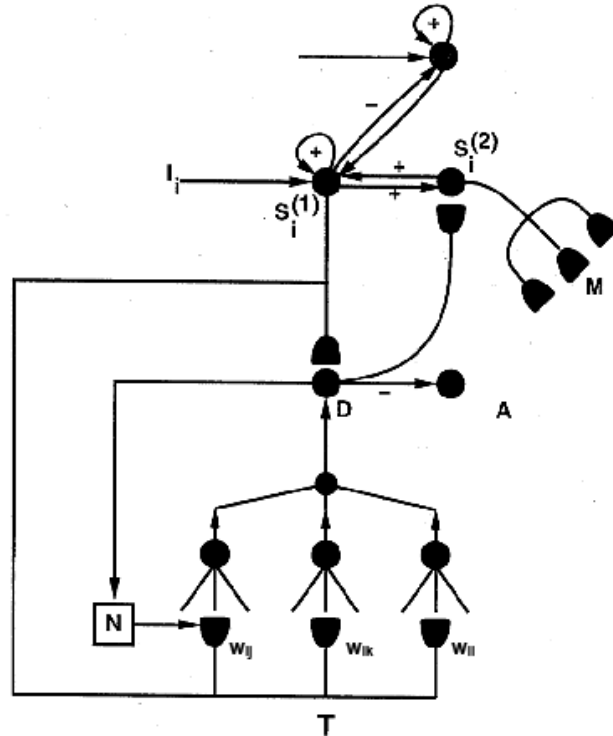
Cerebellar adaptive timing hereby reconciles two potentially conflicting behavioral properties: Fast allocation of attention to motivationally salient events via cortico-amygdala feedback vs. adaptively timed responses to these events via cortico-cerebellar adaptively timed responding.

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 and 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 nonspecific thalamus are proposed to be part of this mismatch-activated orienting system A. The thalamocortical and corticocortical mismatches that activate hippocampus or nonspecific 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, Berry, and Thompson, 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 like 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 behaviors (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.



**Figure 5.** 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. [Reprinted with permission from Grossberg and Merrill (1992).]

*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 behaviors (Staddon, 1983). Adaptively timed incentive motivational feedback ( $D \rightarrow S_i^{(2)} \rightarrow S_i^{(1)}$  in Figure 5) simultaneously maintains 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, or CNV, 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 (DNMS) experiments wherein both temporal delays and novelty-sensitive recognition processes are involved (Gaffan, 1974; Mishkin and Delacour, 1975). Similar adaptive timing mechanisms seem to operate in basal ganglia (Brown, Bullock, and Grossberg, 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 behavior 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 (1978a, 1978b) introduced a model of working memory and list chunking, which proposed how 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 (Section 2) that have enough adaptively timed, incentive motivational support (Section 7) to be persistently stored and transferred into working memory. Item representations are stored in 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 and 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., Barbas, 2000; Goldman-Rakic, 1987; 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 article. 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 behaviors are controlled. Its laminar cognitive prefrontal circuits are variations of laminar circuits in visual cortex (Section 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 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 vs. Planned Behaviors: Basal Ganglia Gating**

Complementary orienting vs. attentional systems search for and learn new recognition codes (Section 5). They are subsumed by a larger complementary brain system that balances reactive vs. planned behaviors. Rapid reactive movements, such as orienting movements, facilitate survival in response to unexpected dangers. Planned movements, that 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?

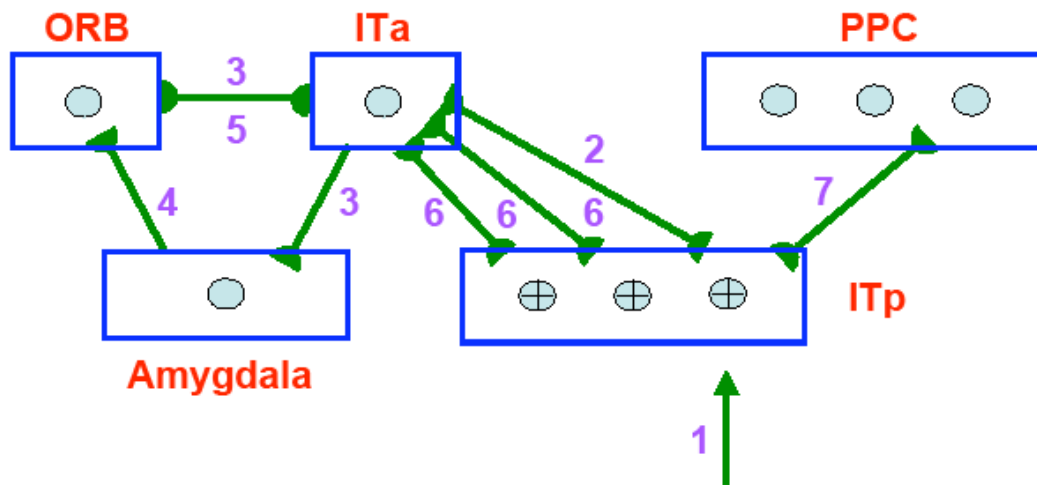
Movement *gates* (cf. Section 9) can inhibit a reactive movement command until a planned movement can effectively compete with it. Then a planned command can open its gate and launch its movement. The basal ganglia carry out such a gating function. Movement gates overcome a potentially devastating problem: 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, Bullock, and Grossberg, 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 and Miller, in preparation). Miller's lab has also reported the expected timing of frontal and basal ganglia activations (Pasupathy and 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 Section 1 and Figure 1, the What stream learns object representations that are increasingly independent of object position and size, whereas the Where stream represents 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 anterior inferotemporal cortex (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 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 Section 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. See Figure 6. This scheme can help to solve the Where's Waldo problem.



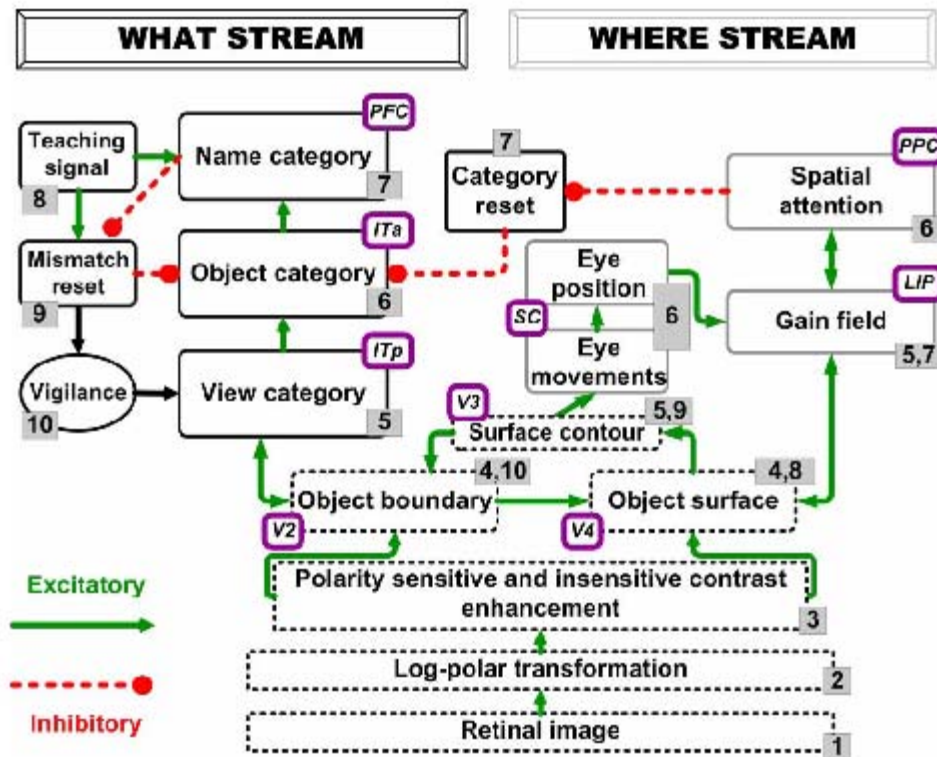
**Figure 6.** Linking What stream recognition to Where stream action: Interactions between cortical areas ITp, ITa, amygdala, orbitofrontal cortex (ORB), and posterior parietal

cortex (PPC) can bridge the gap between invariant ITa categories and 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.

### 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?



**Figure 7.** 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 object boundaries and surfaces via a surface contour process are proposed to control eye movements on a surface whose shroud amplifies the corresponding object surface. [Reprinted with permission from Fazl, Grossberg, and Mingolla, 2008].

The ARTSCAN model (Figure 7) clarifies how the brain uses scanning saccadic eye movements to learn view-invariant object categories (Fazl, Grossberg, & Mingolla, 2008). 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 and 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 due to feedback interactions between a surface representation (e.g., in area V4) and spatial attention (e.g., in posterior parietal cortex), 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, Penpeci-Talgar and Eckstein, 2000; Reynolds and 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 Section 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, in 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 Section 11) by a GO signal that determines when and how fast the movement will occur (Bullock and Grossberg, 1988; Bullock, Cisek, and Grossberg, 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 (Brown, Bullock, and Grossberg, 1999, 2004; Fiala, Grossberg, and Bullock, 1996; Grossberg and Paine, 2000; Guenther et al., 1994).

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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