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Laminar Cortical Dynamics of Cognitive and Motor Working Memory, Sequence Learning and Performance: Toward a Unified Theory of How the Cerebral Cortex Works

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ABSTRACT

How do the layered circuits of prefrontal and motor cortex carry out working memory storage, sequence learning, and voluntary sequential item selection and performance? A neural model called LIST PARSE is presented to explain and quantitatively simulate cognitive data about both immediate serial recall and free recall, including bowing of the serial position performance curves, error-type distributions, temporal limitations upon recall, and list length effects. The model also qualitatively explains cognitive effects related to attentional modulation, temporal grouping, variable presentation rates, phonemic similarity, presentation of non-words, word frequency/item familiarity and list strength, distracters and modality effects. In addition, the model quantitatively simulates neurophysiological data from the macaque prefrontal cortex obtained during sequential sensory-motor imitation and planned performance. The article further develops a theory concerning how the cerebral cortex works by showing how variations of the laminar circuits that have previously clarified how the visual cortex sees can also support cognitive processing of sequentially organized behaviors.

1. INTRODUCTION

Intelligent behavior depends upon the capacity to think about, plan, execute, and evaluate sequences of events. Whether we learn to understand and speak a language, solve a mathematics problem, cook an elaborate meal, or merely dial a phone number, multiple events in a specific temporal order must somehow be kept in mind temporarily in working memory. Once events are stored temporarily in a working memory, they are then grouped, or chunked, through learning into unitized representations that encode whole sequences of events; e.g., word and action sequences. How these working memory sequences and unitized plans interact during cognitive information processing and motor performance remains one of the most important problems confronting cognitive scientists and neuroscientists.

This article introduces the LIST PARSE (Laminar Integrated Storage of Temporal Patterns for Associative Retrieval, Sequencing and Execution) model, which proposes how the layered circuits of prefrontal and motor cortex may be organized to achieve processes of working memory storage, sequence learning, and motor planning and execution during both cognitive and sensory-motor tasks. A schematic of the model is shown in Figure 1. The model makes predictions about the laminar organization of such cortical circuits that go beyond present neurophysiological and anatomical knowledge. It formulates these predictions by integrating several sorts of convergent constraints: extensive behavioral and neuroimaging data about cognitive information processing in humans; behavioral and neurobiological data about sensory-motor storage and performance of familiar sequential actions in monkeys; anatomical data about the laminar circuits that are shared by granular neocortical areas and connectivity specific to the lateral prefrontal cortex; laminar models of visual cortex that can explain and quantitatively simulate neurobiological and perceptual data about visual perception; and properties of non-laminar models of cognitive and sensory-motor processing that have been used to explain and simulate behavioral and neurobiological data in these domains over a period of thirty years. This synthesis has led to the LIST PARSE laminar cortical model that is reported herein, and that enables explanations and simulations of a larger cognitive, neurobiological, and sensory-motor database than has previously been possible.

The LIST PARSE model illustrates how variations on laminar cortical circuits that have been able to quantitatively simulate data about such *spatial* processes as visual cortical perception, development, learning, and attention, can also quantitatively simulate challenging data about *temporal* processes such as the temporary storage of events, or items, in short-term working memory, their coding as sequence chunks in long-term memory, and their sequential motor performance either via imitation or from a previously learned plan. Of course, vision and cognitive information processing are both spatio-temporal processes, even though one is more SPATIO-temporal and the other more spatio-TEMPORAL. The article illustrates how a unified theory of neocortex may be developed in which seemingly qualitatively different behaviors may all be controlled by variations on a common laminar cortical design. This new paradigm, which promises to revolutionize our understanding of intelligent computation, is called Laminar Computing (Grossberg, 2003a).
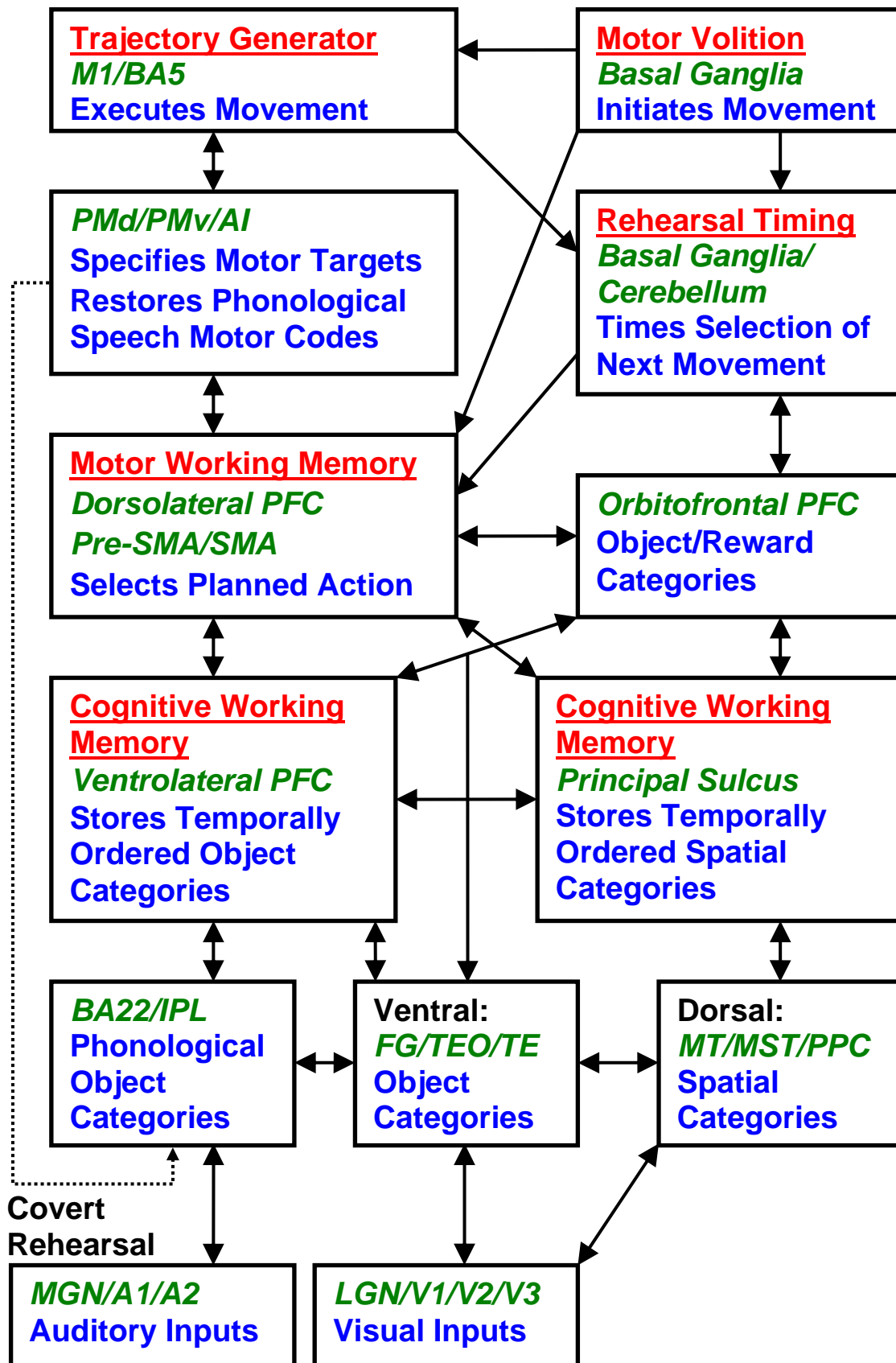
Figure 1. Schematic of the LIST PARSE model with proposed regional localizations in green italics. The proposed function of each region is shown in plain blue text and names of components that are modeled in this paper are red underlined text. Model connectivity has been simplified. A more detailed specification is provided in Sections 4 and 5 and in Figure 2. Abbreviations: MGN, thalamic medial geniculate nucleus; A1/A2, core and extended auditory cortex in the superior temporal gyrus; LGN, thalamic lateral geniculate nucleus; V1/V2/V3, early visual processing occurring in the occipital lobe; BA22, Brodmann's area 22 in the superior temporal gyrus, corresponding to Wernicke's Area in the left hemisphere; IPL, areas in the inferior lateral parietal lobule, including the posterior sylvian fissure near the temporal-parietal boundary (area Spt); Ventral: FG/TEO/TE, portions of the ventral "what" processing stream in the inferotemporal (IT) cortex including areas of the Fusiform Gyrus; Dorsal: MT/MST/PPC, portions of the dorsal "where" processing stream including the posterior middle temporal gyrus and the posterior parietal cortex, including Brodmann's areas 7a,c,ip,m; VLPFC, ventrolateral prefrontal cortex (specifically areas 44, 45 and 47/12); Principal Sulcus, portions of the dorsolateral prefrontal cortex corresponding to the depths of the principal sulcus in the macaque monkey (portions of areas 46, 9/46v,d); Dorsolateral PFC, the remainder of the dorsolateral prefrontal cortex (8, 9, and portions of 46, 9/46v/d); pre-SMA/SMA, pre-Supplementary Motor Area and Supplementary Motor Area; Orbitofrontal PFC, orbitofrontal prefrontal cortex; PMd/PMv, dorsal and ventral portions of the lateral premotor cortex; AI, anterior insula; M1, primary motor cortex; BA5, Brodmann's area 5 in the parietal lobe.

The LIST PARSE model proposes mechanisms (see Figure 2) by which dynamic cycles of short-term item storage, learned grouping of sequential information into list chunks or unitized sequential plans, resetting of item storage in working memory, and updating information from long-term memory may occur within the cognitive and sensory-motor systems. The model additionally proposes how variable-speed rehearsal from motor working memory may be volitionally controlled, notably how the cortex can automatically prepare the next action in the sequence to be rehearsed in an appropriately timed manner despite the volitionally-determined variability of performance speed through time. These mechanisms give rise to smooth performance curves of novel action sequences at variable performance rates.

In particular, the LIST PARSE model proposes a unified account of a wide-range of cognitive data about both immediate serial recall and free recall. Among the data for which the LIST PARSE model provides a quantitative account are: bowing of serial position performance curves (serial recall: Cowan, Nugent, Elliott, Ponomarev & Saults, 1999; Henson, Norris, Page, & Baddeley, 1996; free recall: Tan & Ward, 2000), error type distributions (Henson et al., 1996), list length effects (Baddeley, Thompson & Hitch, 1975; Crannell & Parrish, 1957), and temporal limitations upon recall (Murdoch, 1961). The model also provides a conceptual framework within which explanations can be provided for many additional data, including: effects of attention upon serial performance curves (Cowan, Nugent, Elliott, Ponomarev & Saults, 1999), temporal grouping effects (Hitch, Burgess, Towse & Culpin, 1996; Ryan, 1969), presentation variability (Knoedler, Hellwig & Neath, 1999; Tan & Ward, 2000), phonemic similarity effect (Baddeley, 1986), non-word lexicality (Besner & Davelaar, 1982), word frequency/item familiarity and list strength effects (DeLosh & McDaniel, 1996; Ratcliff, Clark & Shiffrin, 1990), distracter protocols (Watkins, Neath & Sechler, 1989) and modality effects (Baddeley, 1986; Crowder, 1978). See Tables 1 and 2.

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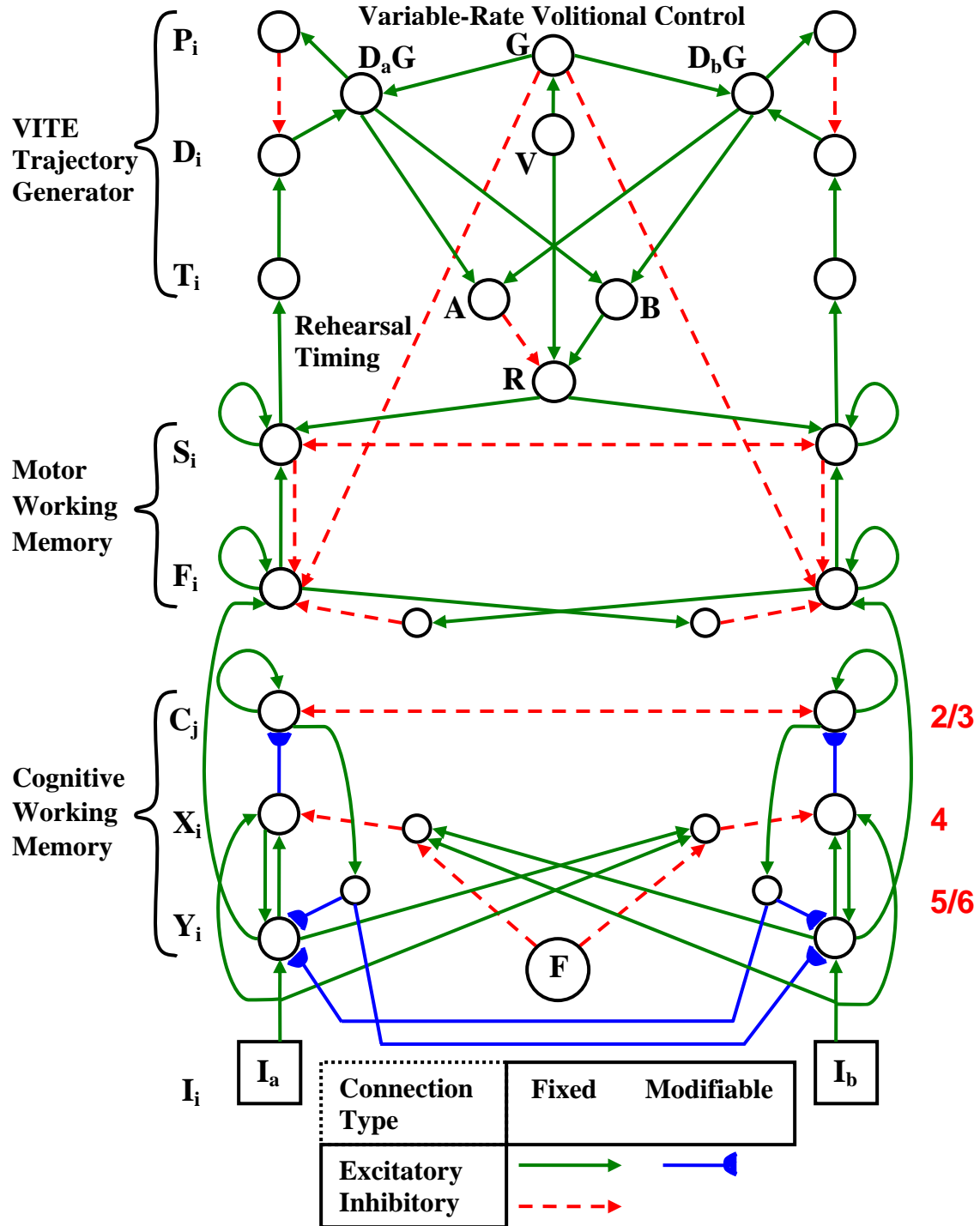
Figure 2. Circuit diagram of the LIST PARSE model. Solid green arrows indicate fixed excitatory connections. Solid blue lines with hemi-disks indicate modifiable (i.e., learned) connections. Dashed red arrows indicate fixed inhibitory connections. This convention is maintained throughout the remainder of the circuit diagrams. Only 1-item chunks (C) are shown, whereas the model uses chunks of various sizes in layer 2/3. Also, only the excitatory projections from cognitive working memory to the motor plan field ($Y \rightarrow F$) are shown. A more detailed treatment of these circuits is provided in Section 4.

Table 1. Psychophysical phenomena observed in both immediate serial recall and immediate free recall protocols for which the LIST PARSE model gives a quantitative account:

Bowing of serial position performance curves: For a presented list, the first few items have an advantage in recall (primacy effect), though they are likely not the most recently rehearsed in either protocol. The last item(s) tend to have advantages in recall (recency effect) although they are commonly recalled last especially in the ISR task and often not recalled first in the IFR task (e.g., object serial recall: Hulme, Roodenrys, Schweickert, Brown, Martin & Stuart, 1997; spatial serial recall: Jones, Farrand, Stuart and Morris, 1995; free recall: Tan & Ward, 2000).

Error type distributions: Item recall errors like omissions, insertions and repetitions, occur in both protocols. However, order errors largely consisting of transpositions of neighboring items tend to make up the majority of errors at span length in the ISR task while they are not typically regarded as errors in the IFR task (e.g., Henson, Norris, Page & Baddeley, 1996).

Word length and list length effects: Performance for lists with words that take longer to articulate or with more items tend to be more poorly recalled that lists with shorter words or fewer items. Additionally, the span (length of lists subjects are able to recall correctly) tends to scale linearly with articulation rate (e.g., Baddeley, 1986; Baddeley, Thompson, & Hitch, 1975; Cowan et al., 1992; Crannell & Parrish, 1957; Hulme et al., 1997).

Temporal limitations upon recall: Increasing retention interval without rehearsal decreases list performance. Representations of portions of unrehearsed lists of items at span length are rendered irrecoverable by delays of as little as two to three seconds under most protocols and stimulus types (e.g., Baddeley, 1986). However, memory for sub-span lists may persist to some extent for non-rehearsed periods far exceeding those intervals (Murdoch, 1961).

Table 2. Psychophysical phenomena observed in both immediate serial recall and immediate free recall protocols for which the LIST PARSE model gives a qualitative account:

Effects of attention: In tasks where attentional resources are diverted, there are enhanced recency effects (e.g., Cowan, Nugent, Elliott, Ponomarev & Saults, 1999).

Temporal grouping effects: Inserting pauses between groups of items creates primacy and recency gradients within groups (e.g., serial recall: Henson et al., 1996; Ryan, 1969).

Presentation variability: Faster presentation rates (reduced IOIs) result in enhanced recency effects and diminished primacy effects. Increasing the delay after list presentation enhances primacy effects at the expense of recency effects, even in cases where rehearsal is not likely to be a significant factor (e.g., Watkins, Neath & Sechler, 1989; Tan & Ward, 2000).

Phonemic similarity effect: Performance in recalling a list composed of items that are phonologically confusable, such as the rhyming letter names B, D, C and G, is worse than for low-confusability stimuli (e.g., Baddeley, 1986).

Non-word lexicality: Maximum number of items recalled (span) increases for non-words that sound like words relative to those that do not, regardless of the use of articulatory suppression, techniques aimed at restricting the ability to phonologically rehearse a list (e.g., Besner & Davelaar, 1982).

Word frequency/item familiarity and list strength effects: Maximum number of items recalled (span) increases with item familiarity. With items of differing retention strength (familiarity), weak items are recalled better in lists of strictly weak items, whereas strong items are recalled less well in pure-strong lists than in mixed lists (e.g., DeLosh & McDaniel, 1996; Ratcliff, Clark & Shiffrin, 1990).

Distracter protocols: Adding a distracter task at the end of list presentation greatly reduces the recency effect. However, also adding a distracter task between each word presentation (called the continuous distracter protocol) largely reinstates the recency effect (Watkins, Neath & Sechler, 1989).

Modality effects: Auditory list presentation tends to produce slightly more extended recency portions of the serial performance curve than visual presentation when subvocal rehearsal is prevented (Baddeley, 1986). However, an irrelevant auditory item presented at the end of the list largely eliminates the modality difference (suffix effect: Crowder, 1978).

The model describes both cognitive and sensory-motor processes that involve working memory, sequence learning, and performance. In particular, it proposes a unified explanation of data that have been collected by electrophysiological recording studies in monkeys performing a sequential movement task (Averbeck et al., 2002, 2003a, 2003b) and functional imaging studies of humans conducting various working memory tasks (e.g., Braver, Barch, Kelley, Buckner, Cohen, Miezin, Snyder, Ollinger, Akbudak, Conturo & Petersen, 2001; Chein & Fiez, 2001; D'Esposito, Aguirre, Zarahn, Ballard, Shin & Lease, 1998; Fletcher & Henson, 2001; Marshuetz, Smith, Jonides, DeGutis & Chenevert, 2000; Paulesu, Frith & Frackowiak, 1993; Poeppel, 1996; Smith, Jonides, Marshuetz & Koeppe, 1998; Ranganath, Johnson & D'Esposito, 2003). It is now widely-held, based upon these and other studies (for review: Passingham, 1993), that a set of interconnected cortical structures in the granular lateral prefrontal cortex (PFC), supplementary motor area (SMA), pre-SMA, and posterior and inferior parietal and temporal lobes, along with basal gangliar (BG) and cerebellar structures, largely subserve these cognitive and motor functions.

2. MODELING BACKGROUND

Storing Temporal Order as a Spatial Activity Gradient: Short-Term Working Memory Enables Stable List Learning and Memory. LIST PARSE implements in model laminar cortical circuits a proposal about the neural mechanism of working memory and sequence chunking that was first made in Grossberg (1978a), an article that, along with Grossberg (1976a, 1976b, 1980), introduced a number of core cognitive models, including the interactive activation, competitive learning, and competitive decision making models that were later utilized and elaborated by the Parallel Distributed Processing (PDP) group (McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982; Rumelhart & Zipser, 1986; Usher & McClelland, 2001). In addition, Grossberg (1978a), and the companion article Grossberg (1978b), introduced and mathematically characterized a neural design for an Item and Order working memory for short-term storage of event sequences. This working memory was designed to be able to support the *stable learning and long-term memory* of sequential chunks, or plans, that are activated by sequences of the items that are stored in working memory. Grossberg noted that a short-term working memory would be useless if it could not support learning of sequential plans since, otherwise, every event sequence would always seem to be novel.

The key innovations of the Item and Order model of working memory, which was later refined and renamed the STORE (Sustained Temporal Order REcurrent) model were (see Figure 3) to propose: (1) how a working memory encodes a series of events occurring sequentially in time as an evolving *spatial* pattern of activation in parallel across content-addressable cells, rather than as binary activations of a series of linearly ordered "slots" wherein each item moves to the next slot as additional items are stored, as the popular model of Atkinson and Shiffrin

(1968, 1971) had proposed; (2) how this temporal-to-spatial recoding can support the stable learning and long-term memory of sequential chunks or plans, including plans that represent supersets of already familiar plans (e.g., how to learn a chunk for MYSELF without forcing unselective forgetting of the already familiar chunks for MY, SELF, and/or ELF); (3) that a volitionally-controlled, nonspecific rehearsal wave activates read-out from all of the working memory cells to initiate recall, with the most active cell generating its output first; (4) that each rehearsed cell output activates a recurrent inhibitory interneuron that shuts off the item being rehearsed and thereby causes inhibition-of-return, so that less active items can then be rehearsed in order, and perseveration on a single item is prevented; and (5) how the stored pattern of cell activations can renormalize itself as items are rehearsed. These hypotheses have formed the foundation of ordinal models of serial representation and competitive queuing models of sequential planning as developed in many later modeling studies; e.g., Boardman & Bullock, 1991; Houghton & Hartley, 1996; Page & Norris, 1998; Rhodes et al., 2004.
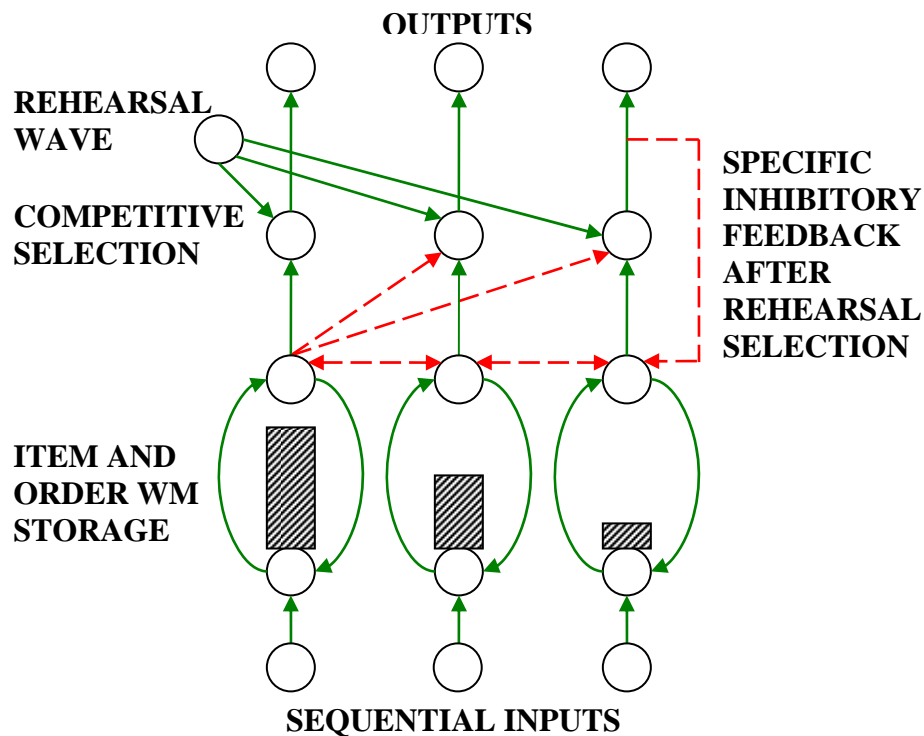
Figure 3. General framework for ordinal theories of serial order and competitive-queuing models of motor planning: temporal sequence of inputs creates a spatial activation pattern among STM activations, often a primacy gradient (height of hatched rectangles is proportional to cell activity). Relative activation level among items in STM codes for item and order. A rehearsal wave (global signal) allows item activations to compete before the maximal item elicits an output signal and self-inhibits via feedback inhibition. The process then repeats itself. (Adapted from Figures 20 and 34 in Grossberg, 1978b).

Categorizing Individual Events: Priming, Attention, and Synchrony. In the family of STORE models, individual items (events, objects) are categorized, or unitized, at an earlier processing stage. Related modeling work developed Adaptive Resonance Theory, or ART, to explain how these unitized categories may be learned through interactions between several cortical regions (sensory, temporal, parietal, prefrontal), interacting with the hippocampal system, and how the

top-down expectations from the prefrontal cortex of these categories can help to stabilize category learning and long-term memory (e.g., Bradski & Grossberg, 1995; Brown, Bullock & Grossberg, 2004; Carpenter & Grossberg, 1991, 1993; Grossberg & Merrill, 1996; Grossberg, 1978a, 1980, 1999a, 2003a; also see reviews in Engel, Fries & Singer, 2001 and Pollen, 1999). These top-down expectations attentively modulate or prime during a delay period, and match, synchronize, and amplify the bottom-up distributed features that their categories learn to bind. The match/mismatch operations between top-down expectations and bottom-up features also permit discrimination between familiar and novel events, can drive reset of an active category and its top-down expectation during a mismatch, and trigger selection of a better-matching category during the next time interval.

Posterior parietal association areas in (a) the inferior parietal lobule, (including the supramarginal and angular gyri) and areas of the sylvian fissure near the parietal-temporal boundary overlapping into the superior temporal sulcus (including area Spt; Hickok & Poeppel, 2004), and (b) Brodmann's areas 7a,c,ip,m are likely locations for high-level category storage operations for phonological (for review: Goldman-Rakic, 1987; Hickok & Poeppel, 2004) and spatial (e.g., dorsal "where" visual processing stream; Ungerleider & Mishkin, 1982) information, respectively. More specifically, Brodmann's area 22 in the superior temporal gyrus (termed Wernicke's area in the left hemisphere of the human) and the phonological areas of the inferior parietal lobe project extensively through the arcuate fasciculus to portions of the ventrolateral prefrontal cortex (e.g., areas 44 and 45, including portions of anterior Broca's area in the left hemisphere of the human). Visuospatial information from areas 7a,c,ip,m in the parietal lobe target largely distinct and localized portions of areas 9/46v,d and 46 (Petrides & Pandya, 1994) in and around the principal sulcus of the dorsolateral prefrontal cortex (for review: Goldman-Rakic, 1987). Object (e.g., semantic) category information from auditory (for review: Hickok and Poeppel, 2004) and visual (e.g., the ventral "what" visual processing stream; Ungerleider & Mishkin, 1982) presentation are likely to involve the anterior superior temporal sulcus and inferotemporal region (e.g., areas TEO and TE) respectively. These areas are known to be reciprocally connected with ventrolateral prefrontal cortex (Brodmann's areas 47/12 and 45; for review: Barbas, 1992). Regional localizations of the lower-level portions of the auditory and visual "What" and "Where" processing streams, which are collapsed across in Figure 1, are well established (Constantinidis & Procyk, 2004; Kandel, Schwartz & Jessel, 2000). Aside from the consistent connectivity patterns, similar activity patterns between these areas and their prefrontal targets in a variety of protocols (e.g., Chafee & Goldman-Rakic, 2000; D'Esposito et al., 1998) are consistent with the hypothesis that, among other possible functions, these areas represent high-level categorical information which is then fed into lateral prefrontal cortical working memory centers.

Motivationally Salient Object Categories and Adaptively Timed Delay Activity. Another line of modeling work developed the CogEM and START (e.g., Grossberg & Seidman, 2006) models to clarify how these learned categories can attract attention when they are motivationally salient, and how attention can be maintained during an adaptively timed delay interval. CogEM predicts how reinforcement learning enables categories in temporal cortex to activate the amygdala (and related reward-related brain regions) via conditioned reinforcer signals, and the amygdala, in turn, to activate orbitofrontal projections of the temporal categories via incentive motivational signals, thereby giving rise to the object/reward-sensitive cells of the orbitofrontal cortex (e.g., Grossberg, 1971, 1982, 2000; Grossberg & Levine, 1987; Grossberg & Seidman, 2006). In

particular, learned incentive motivational signals from regions such as the amygdala enhance the activation of these category cells in orbitofrontal cortex.

The hypothesis that motivationally salient object and event categories are represented in the orbitofrontal cortex is consistent with neurophysiological experiments (for reviews: Rolls, 2004; Schoenbaum & Roesch, 2005; Schoenbaum & Setlow, 2001). These motivationally salient categories and incentive value representations can bias category representations in prefrontal cortex in favor of stimuli and motor plans that are task-relevant. These interactions can also serve to bias, via top-down attentive expectations, the representations in lower-levels of the sensory/cognitive processing hierarchy (Barbas, Medalla, Alade, Suski, Zikopoulos & Lera, 2005).

The START model extended the CogEM model to propose how motivated attention can maintain the activity of these orbitofrontal categories during a task-appropriate delay interval using adaptively timed signals from the hippocampal system (Grossberg & Merrill, 1992, 1996; Grossberg & Schmajuk, 1989; Grossberg & Seidman, 2006).

Many laboratories have reported that prefrontal cells can retain their activation during a delay interval after their eliciting sensory stimuli terminate (e.g., Curtis & D'Esposito, 2004; Curtis, Rao & D'Esposito, 2003; D'Esposito & Postle, 1999; Funahashi, Bruce & Goldman-Rakic, 1989, 1990, 1991; Funahashi, Inoue & Kubota, 1993, 1997; Fuster, 1973; Fuster & Alexander, 1971; Fuster, Bauer & Jervey, 1985; Kubota & Niki, 1971; Mechelli, Price, Friston & Ishal, 2004; Miller, Erickson & Desimone, 1996; Niki, 1974; Ranganath & D'Esposito, 2005; Stern, Sherman, Kirchhoff & Hasselmo, 2001). This delay period activity, as such, has sometimes been called a form of "working memory". In this article, consistent with the broader psychological concept of a temporary workspace that supports mental manipulations, the term working memory is used to describe brain processes and regions that are capable of simultaneously storing the temporal order of *several* such high-level categories. This distinction differentiates *working memory* from the *short-term memory* processes associated with the early sensory cortices (e.g., visual persistence phenomena). As noted above, other model mechanisms have been identified for bridging temporal gaps throughout the neocortex, typically for the sustained processing of a given event (e.g., via ART-like top-down expectations to, say, the temporal or parietal cortices from prefrontal stored categories), or for prediction of an anticipated event over a delay period (e.g., via START-like adaptively timed feedback that is proposed to be mediated by the hippocampus). One goal of computationally precise neural models is to distinguish the mechanisms and functions of these several different types of delay activity processes.

Storing Temporal Order of Item Category Lists using Spatial Activity Gradients. With this precise concept of working memory in mind, the model proposes that each motivationally-salient object or verbal category may activate an *item representation* in working memory, depending on multiple contextual factors (Cohen & Grossberg, 1986; Cohen, Grossberg & Stork, 1988; Grossberg, 1978a, 1986a). The term "item" is used to denote a categorical, or unitized, representation of a spatial pattern of features that occurs at an earlier processing level within a short time interval.

As successive categories are activated, they may store their item representations in working memory and thereby alter the total spatial pattern of activation across the entire working memory. As a sequence of items is stored, it creates an evolving pattern of stored activity across the working memory cell populations (Figure 2) in which the *relative activity* of different cell populations codes the order in which the items will be rehearsed, with the items having the

largest activities being rehearsed first (Grossberg, 1978a, 1978b). Hence, the original name Item and Order working memory for this class of models.

There is accumulating neurobiological evidence for the interactions predicted by ART, CogEM, and STORE. 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 (Barbas, 2000; Bor, Cumming, Scott & Owen, 2003; Browning, Inoue & Hernadi, 2005; Chafee & Goldman-Rakic, 2000; Frey, Kostopoulos & Petrides, 2004; Goldman-Rakic, 1987; Hasegawa, Blitz & Goldberg, 2004; Kostopoulos & Petrides, 2003; Ninokura, Mushiake, & Tanji, 2004; Petrides, 1991, 2005; Petrides, Alivisatos & Frey, 2002; Ranganath & Blumenfeld, 2005; Ranganath & D'Esposito, 2005; Ranganath, Johnson & D'Esposito, 2003; Rolls, 2004; Schoenbaum & Roesch, 2005; Schoenbaum & Setlow, 2001). Under this view, one can expect lateral prefrontal cortex to be relatively insensitive to low-level features but to show load-effects as more items are simultaneously stored, even when there are no learning effects. This prediction is consistent with several recent experiments (Habeck, Rakitin, Moeller, Scarmeas, Zarahn, Brown & Stern, 2005; Narayanan, Prabhakaran, Bunge, Christoff, Fine & Gabrieli, 2005; Ranganath, DeGutis & D'Esposito, 2004; Rypma, Berger & D'Esposito, 2002, Song & Jiang, 2005; Woodward, Cairo, Ruff, Takane, Hunter & Ngan, 2005). Additionally, the proposal that multiple item storage in lateral prefrontal cortex is inherently sequential in nature implies that even with similar amount of information, one can expect to see increased activity of lateral prefrontal cortex if grouping of multiple items, especially on the basis of temporal order, is a central requirement (Bor, Cumming, Scott & Owen, 2004; Bor, Duncan, Wiseman & Owen, 2003).

Given the extensive interconnectivity among all regions of prefrontal cortex (for review: Barbas, 2000) and between these higher-level parietal and temporal association cortices, neurons responsive to multiple modalities and category-types are found in all of these locations (e.g., Rao, Rainer & Miller, 1997). However, lesions to the areas of prefrontal cortex receiving extensive bottom-up projections or the areas projecting to them would effectively cut off a majority of the direct category-specific information to the prefrontal cortex and would be expected to result in category-type selective impairments to working memory functionality.

In fact, lesion studies provide another compelling source of evidence for these functional localizations (for reviews: Curtis & D'Esposito, 2004; Goldman-Rakic, 1987; Passingham, 1993). Monkeys with dorsolateral prefrontal lesions show severe *specific* impairment in a wide range of tasks that require monkeys to retain spatial information in memory over a delay period (Goldman & Rosvold, 1970; Goldman, Rosvold, Vest & Galkin, 1971; Jacobsen, 1936; Levy & Goldman-Rakic, 1999; Mishkin, 1954; Mishkin & Pribram, 1954, 1955, 1956; Mishkin, Vest, Waxler, & Rosvold, 1969; Petrides, 1991, 1995, 2000a; Pribram & Mishkin, 1956), particularly for stimuli presented in the contralateral visual field (Funahashi, Bruce & Goldman-Rakic, 1993). However, lesions confined to the principal sulcus typically produce deficits in spatial working memory of similar severity to much larger dorsolateral lesions (which include the principal sulcus) and lesions to areas of dorsolateral prefrontal cortex which leave the depths of the principal sulcus intact do not produce the typical general spatial working memory impairments (e.g., Goldman & Rosvold, 1970; Goldman, Rosvold, Vest & Galkin, 1971; Petrides, 2000a). These studies, and the localized projections of dorsal "where" stream centers (e.g., Goldman-Rakic, 1987), specifically implicate the principal sulcus in the maintenance of

spatial information (in particular, stimulus cues) across a delay, a finding further supported by numerous electrophysiological recording studies during oculomotor working memory tasks (e.g., Funahashi et al., 1989, 1990, 1991). In contrast, lesions to the lateral prefrontal cortex that include the ventrolateral prefrontal cortex (in addition to the dorsolateral prefrontal cortex) result in an additional deficit in object alternation tasks (Mishkin & Pribram, 1955, 1956; Mishkin, Vest, Waxler & Rosvold, 1969; Pribram & Mishkin, 1956; Petrides, 1995) and selective lesions to areas ventral to the principal sulcus result in impairment on *non-spatial* working memory tasks which localized principal sulcal lesions do not impair (Mishkin & Manning, 1978; Passingham, 1975).

Lesions to Broca's area (which frequently include caudal portions of ventrolateral prefrontal cortex, ventrolateral premotor cortex and anterior insula; Dronkers, 1996; Hillis, Work, Barker, Jacobs, Breese & Maurer, 2004) in humans classically produce a type of speech aphasia in which patients, aside from having profound articulation difficulty, typically have difficulty with word naming, produce sentences of two, or sometimes one, words and have dramatically impaired spontaneous speech and repetition competency (Goodglass & Kaplan, 2001). In contrast, transcortical motor aphasia, which occurs following lesions slightly superior and anterior to Broca's area, likely partially severing its connections with portions of the supplementary motor area, premotor cortex and dorsolateral prefrontal cortex, results in difficulty initiating and organizing structured responses but notably preserves repetition and cue-based (confrontational) naming (Goodglass & Kaplan, 2001).

In addition, model mechanisms may help to clarify why neuroimaging data show that ventrolateral prefrontal cortex is activated when a decision needs to be made regarding the relative familiarity of stimuli, whereas dorsolateral prefrontal cortex may be more active in a monitoring condition wherein a non-familiar stimulus must be chosen (Petrides, 2005); see Section 4.

Stable Learning Implies Primacy, Recency, and Bowed Gradients. Grossberg (1978a, 1978b) mathematically derived STORE working memories from two postulates, which are called the LTM Invariance Principle and the Normalization Rule. These postulates assume merely that the representations of items stored in working memory (a) closely preserve their relative activations, or ratios, throughout their retention time to enable stable learning, and (b) item representations are approximately normalized such that total activity is redistributed when new items are encoded. Taken together, these simple rules generate working memories that can support stable learning and long-term memory of sequence, or list, chunks. List chunks categorize sequences of stored items and their temporal order. In particular, it was mathematically proved that, under constant attentional conditions, the pattern of activation that evolves in a STORE working memory is typically one of three types:

(1) A *primacy gradient*, in which the first item to be stored has the largest activity and the last item to be stored has the smallest activity. A primacy gradient allows the stored items to be rehearsed in their correct order.

(2) A *recency gradient* stores the first item with the smallest activity and the last item with the largest activity. Rehearsal of a recency gradient recalls the most recent item first and the first item last.

(3) A *bowed gradient* may be stored, in which the first and last items to be stored have larger activities, and thus are earlier rehearsed, than the middle of the list. It was also proved that, as more and more items are stored, a primacy gradient always becomes a bowed pattern.

In other words, in order to be able to stably learn and remember list chunks or plans based on short-term working memory storage of a sequence of events, the brain is limited in the number of items that can be recalled in the correct order from the working memory, due to the development of a bow in the stored gradient.

Stable Learning Implies the Magical Numbers Four and Seven. This result provided a conceptually satisfying explanation of the well-known *immediate memory span* (Miller, 1956), and was used to explain data about free recall and related paradigms in which bowing effects are observed (Grossberg, 1978b). Indeed, because relative activity translates into both relative order and probability of recall (bigger activities can provide more reliable recall in a noisy brain), such a model helps to explain why, say, items from the beginning and end of a list in free recall may be recalled earlier and with larger probability (Murdoch, 1962). Transposition errors also have a natural explanation in such a working memory, since stored items with similar activity levels will transpose their relative activities, and thus their rehearsal order, more easily than items with very different activity levels if noise perturbs these levels through time. Grossberg (1978a, 1978b) also proved that, if attention varies across items, then multi-modal bows, or Von Restorff (1933) effects, can obtain by altering the relative sizes of stored activities.

Finally, the Grossberg (1978a) analysis distinguished between the classical *immediate memory span* (IMS) of Miller (1956) and a (then) new concept called the *transient memory span* (TMS). The IMS was predicted to be the result of a read-out from short-term working memory after it is already influenced by read-out of long-term memory from learned chunks that interact with the working memory. That is, the extent of the IMS was proposed to be a result of long-term memory chunks biasing the pattern of activity stored in working memory toward an extended primacy gradient. The TMS was predicted to be just the result of short-term working memory recall without a significant long-term memory component. Grossberg (1978b) proved that the TMS is smaller than the IMS. Estimating the IMS at 7, he predicted that the TMS would be around 4. Experimental results reviewed in Cowan (2000) suggesting the existence of a 4+/-1 working memory capacity limit are consistent with this prediction.

Working Memories from Recurrent On-Center Off-Surround Networks. The STORE models provide a satisfying answer to the following perplexing question: How could evolution have been so intelligent as to discover a brain design for something that seems as sophisticated as a working memory? Grossberg (1978a, 1978b) predicted how a ubiquitous and ancient brain circuit design can be specialized to realize the properties that are needed in an Item and Order working memory; namely, a *recurrent on-center off-surround network* of interactions among cells that obey the membrane, or shunting, equations that neurons are known to obey (Grossberg, 1973, 1980; Hodgkin & Huxley, 1952; see equation (1) in Appendix). In other words, feedback (*recurrent*) connectivity that is self-excitatory (*on-center*) from the cells to themselves (that maintain activation after an external input shuts off), balanced by competitive (*off-surround*) signals to other cells in the working memory, can store a sequence in working memory in a manner that obeys the LTM Invariance Principle and the Normalization Rule; see Bradski, Carpenter, & Grossberg (1992, 1994) for mathematical analyses of STORE model properties in a recurrent shunting on-center off-surround network.

Other Related Modeling Studies. Since the 1970's, models of working memory have undergone significant development. The seminal work of Baddeley & Hitch (1974) and Baddeley (1986) on the phonological loop in working memory has had a particularly large impact. More recent authors have often called Item and Order working memories by the name of Competitive Queuing, or CQ, models, to capture the idea that they are storing and rehearsing

queues of items in working memory using competitive interactions (Houghton, 1990). Given that all sequential working memories need to be able to support stable learning and memory of sequence chunks or plans, it is not surprising that this sort of model has been able to explain and simulate several different types of data, including the learning of musical sequences (Mannes, 1994; Page, 1994), speech perception and word recognition (Cohen & Grossberg, 1986, 1987; Grossberg, 1978b, 1986; Grossberg, Boardman, & Cohen, 1997; Grossberg & Myers, 2000; Grossberg & Stone, 1986b), attention shifting during working memory storage (Grossberg & Stone, 1986a), control of cursive handwriting (Bullock, Grossberg & Mannes, 1993), and reaction time data during skilled typing (Boardman & Bullock, 1991; Rhodes et al., 2004).

A particularly relevant recent contribution to the LIST PARSE model, that built upon the Grossberg (1978a, 1978b) analysis, was done by Page & Norris (1998), who used a primacy gradient in working memory to explain and simulate a broad array of cognitive data about immediate serial order working memory, notably: word and list length, phonological similarity, and forward and backward recall effects. More recently, Farrell and Lewandowsky (2004) have directly tested whether activation gradients store event sequences in working memory by examining the latency of responses following serial performance errors. They concluded that (p. 115): "Several competing theories of short-term memory can explain serial recall performance at a quantitative level. However, most theories to date have not been applied to the accompanying pattern of response latencies, thus ignoring a rich and highly diagnostic aspect of performance. This article explores and tests the error latency predictions of four alternative mechanisms for the representation of serial order. Data from three experiments show that latency is a negative function of transposition displacement, such that list items that are reported too soon (ahead of their correct serial position) are recalled more slowly than items that are reported too late. We show by simulation that these data rule out three of the four representational mechanisms. The data support the notion that serial order is represented by a primacy gradient that is accompanied by suppression of recalled items."

The LIST PARSE model builds upon this scholarly background. It further elaborates how laminar cortical circuits can realize parallel storage of item and order information as a spatial gradient of activation across item representations, can learn sequence chunks or plans of these stored gradients, and can recall both novel and planned sequences of stored events. To realize these capabilities, the LIST PARSE model joins together a cognitive working memory, a motor working memory, a motor trajectory generator, and a volitional controller (see Figure 1) that coordinates the variable-rate recall of both novel sequences and previously learned sequences as they are read-out into sequential action from a cognitive plan. The neurophysiological data of Averbeck et al. (2002, 2003a, 2003b; also see Rhodes et al., 2004) directly support the prediction that activation gradients control the read-out of sequences of actions from working memory through recordings in the peri-principalis region of dorsolateral prefrontal cortex in macaque monkeys. The model simulates key neurophysiological data from these experiments. Model interactions between these working memories and motivational and volitional processes that help to control various monitoring functions may suggest new experiments to more directly probe the underlying cortical mechanisms and their precise cortical localization.

Given its ability to link neurophysiological, anatomical, cognitive, and sensory-motor data, the LIST PARSE model has a broader explanatory and predictive range than traditional models in the literature. Despite widespread interest in working memory related tasks, the first conceptual models arose relatively recently (Atkinson & Shiffrin, 1968, 1971; Baddeley & Hitch, 1974; Estes, 1972; Grossberg, 1978a, 1978b; Lee & Estes, 1977). Detailed mathematical

models attempting to account for large cross-sections of the known properties of a particular working memory task have been an even more recent advent (e.g., Anderson & Matessa, 1997; Brown, Preece & Hulme, 2000; Burgess & Hitch, 1999; Farrell & Lewandowsky, 2002; Henson, 1998b; Howard & Kahana, 2001; Lewandowsky, 1999; Lewandowsky & Murdock, 1989; Nairne, Neath, Serra & Byun, 1997; Page & Norris, 1998; Ratcliff, 1978, 1981; Rhodes et al., 2004). Limitations of these models are one or more of the following: they attempt to model aspects of only one working memory experimental protocol; they fail to use self-organizing constraints that show how the model can learn in real time; and/or they do not use biologically plausible mechanisms that may be interpreted in terms of known cortical properties.

3. EXPERIMENTAL BACKGROUND

This section reviews key experimental data that the LIST PARSE model can explain. Given that working memory allows the temporary retention of sequences of events, thereby enabling the performance of delayed response tasks or learning to recall the information for use at a much later time, working memory functionality is theorized to underlie aspects of nearly every non-reactive behavioral task and all forms of skilled action. It is therefore not surprising that these working memory competencies have long interested cognitive psychologists (Nipher, 1878) and that extensive data sets on short-term memory behavioral phenomena have been developed.

3.1 Immediate Serial Recall and Immediate Free Recall Experiments. The two most extensive literatures to be addressed by an integrated model of working memory function are those of the immediate serial recall (ISR) task (e.g., Henson, Norris, Page & Baddeley, 1996) and the immediate free recall (IFR) task (e.g., Tan & Ward, 2000). In the ISR protocol, a series of items (typically words, letters, numbers or spatial targets) are presented (either auditory or visual) in succession, with identical stimulus durations and inter-stimulus intervals followed by a brief retention interval. Participants are then cued to recall the list of items in the same serial order in which they were presented (see Figure 4). In the IFR protocol, also a series of items (typically words, letters, numbers or spatial targets) are presented (either auditory or visual) in succession with identical durations and inter-stimulus intervals followed by a brief retention interval. However, participants are then cued to recall the list of items presented in any order they choose (see Figure 4).

A number of significant complications hamper analysis and comparison of the ISR and IFR task literatures. Among these are: differences in the definition of errors, difficulty in isolating long-term memory influences and chunking, and difficulty in monitoring or preventing rehearsal.
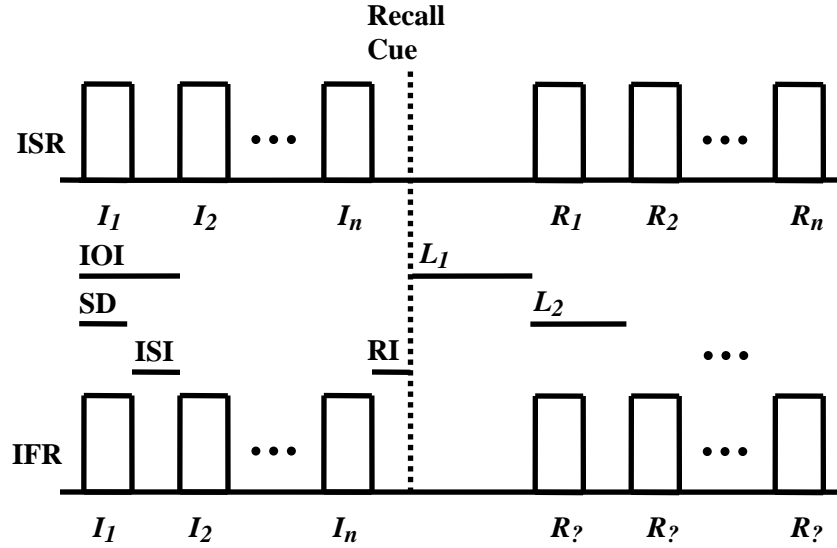
Figure 4. The immediate serial recall (ISR) and immediate free recall (IFR) protocols both consist of a series of n item inputs (I_1, …, I_n), typically with the same stimulus duration (SD) and inter-stimulus interval (ISI). The inter-onset interval (IOI) equals the sum of SD and ISI. A brief retention interval (RI) occurs before a cue is presented to begin recall. In the ISR protocol, participants make responses (R_1, …, R_n) corresponding to stimuli in their presented order. In the IFR protocol, participants make responses corresponding to the stimuli in any order they choose. Subject responses occur with variable latency times (L_1, L_2, …, L_n).

Different Experimental Definitions. The most fundamental difficulty in comparing the data between the ISR and IFR tasks are that many of the definitions used in the two tasks result in different experimental protocols being used in the two literatures. The resulting difficulties range from increased degrees of freedom due to non-overlapping experimental protocols to different data being presented with the same labeling. For instance, span length for a given inter-stimulus interval (ISI), stimulus duration (SD), and retention interval (RI) (see Figure 4) refers to the list length at which a participant makes some percentage of list recall errors and is commonly the length of list studied. However, the methods of computing this span, even within a protocol (e.g., the ISR task) are experimenter-specific, ranging from the maximum list length at which a subject can perform two consecutive lists correctly (Cowan et al., 1999) to variations upon the number of items that yield approximately 50% of lists recalled correctly (Hulme, 1991). This leads to different numbers of items and levels of performance being taken to represent "span," which hampers comparisons between studies even within the same protocol.

The use of these span definitions across protocols creates a more serious complication when taken together with differing definitions of what constitutes an error in each protocol. In the IFR protocol, item errors are the only error types, including *intrusions* of items that were not in the presented list and *omissions* of items that were presented. Item errors like omissions and intrusions occur in the ISR task as well, but order errors also occur in which an item from the list is successfully recalled but is recalled in the wrong serial position (or is erroneously repeated). Studies of both tasks commonly only report percentage of total correct responses (or percentage of total errors) versus serial position for each experimental condition, thereby averaging across the variety of possible error types that occur in each of the protocols.

In the ISR protocol, Henson et al. (1996) did perform an analysis of the types of errors observed and found the vast majority of errors for lists of span length (or shorter) consist of order errors, primarily transpositions. Thus, the majority of errors in the ISR protocol at span would not be considered errors if they were given as responses in an IFR task, making the use of total list error rate (span) in determining experimental parameters a major confound that complicates comparison across experimental studies of the two tasks. That is, identical presentation protocols for ISR and IFR tasks result in dramatically different total error rates with their serial position performance curves, leading to potential floor effects in the ISR or ceiling effects in the IFR task. Thus, the difficulty in finding identical presentation schedules across experimental task complicates informative comparison.

Long-term Memory Influences and Chunking. Another complication to testing short-term memory performance regardless of task is the difficulty of factoring out long-term memory and chunking influences, whether volitionally controlled or otherwise. A common presumption has been that during *immediate* recall protocols these effects are minimal, but some recent analyses (e.g., Cowan, 2000) have contended that these effects are in fact so common among the typical experimental protocols that they have masked a limited (four plus or minus one chunk) constant capacity underlying all short-term memory operation; cf., a similar claim in Grossberg (1978b).

Cowan's analysis has clear parallels to the classic finding by Miller (1956) of a "magical number seven plus or minus two" chunks that can be stored in working memory at any time, although Miller suggested that this capacity limit may emerge as a by-product of other factors. Cowan suggests that this larger capacity was in fact an artifact of experimental protocols which allow easy learned unitization of items (e.g., digits with which subjects have extensive experience) into sequence, or list, chunks, thereby allowing the apparent extension of the four plus or minus one limit to approximately seven or more items through chunking. The LIST PARSE model builds upon the STORE model analyses of why such chunk capacity limits exist, and are in fact necessary for stable learning and memory of order information in long-term memory.

More recent studies of the properties of these list chunks have provided evidence that they encode not only item but order information. In a study by Cowan, Chen & Rouder (2004), associative pairs were presented with varying frequencies across trials (0-4 exposures) within the context of an 8-item ISR task. Subjects not only recalled more items when a test list contained some of the previously seen paired-associates but performance scaled with increasing amounts of prior exposure to the paired-associates. Even more, subjects showed nearly identical item and total (item plus order) error improvement with increasing exposure. That is, prior exposure to paired items resulted in subjects remembering more items in lists that included them but those additional recalled items did not result in any additional order errors implying that the sequential order of the paired-items was intrinsic to their learning. Other studies have provided some evidence that subjects may also process statistical item-position associations in long-term memory as part of the learning of items in hierarchical structure; for review, see Conway & Christiansen (2001).

Controlling Rehearsal Strategy. Another complication when analyzing the experimental literatures of the ISR and IFR tasks is the need to adequately control, monitor, or prevent, participant covert or overt rehearsal during the list presentation. Four common approaches to addressing this problem are: (1) overt rehearsal protocols in which subjects are instructed to vocally rehearse between stimulus presentations so that these rehearsals can be analyzed, (2) articulatory suppression protocols in which subjects are instructed to mouth, or even vocalize,

some repetitive phrase (such as "the") when stimuli are presented and between pauses, (3) rapid list presentation which limits the amount of time that covert rehearsal can occur, and (4) distracter protocols in which subjects are required to perform a concurrent task either during the retention interval or throughout the task. Without the benefit of these protocols, an accurate analysis of the representations of items throughout task performance is difficult to conduct.

Despite these complications, the only inherent difference between the two experimental protocols is that participants recall items in their presented order after the recall cue in the ISR task (Figure 4). Given the striking experimental similarity of the tasks, it seems plausible that working memory storage in the two tasks involves similar neural processing mechanisms. The similarity of a wide range of performance characteristics between the two tasks (Tables 1 and 2) supports this hypothesis. However, the data across tasks also differ in several important respects that complicate a unified theory of the data.

Bowing of Serial Position Performance Curves. Nipher (1878) already noted bowing of the serial position error curves, which needs to be explained in any model of working memory. Both ISR and IFR protocols exhibit bowed error curves with a *primacy* portion at the beginning of the list, in which errors increase with item position, and a *recency* portion at the end of the list, in which errors decrease with serial position. Various differences across the ISR and IFR paradigms need, however, to be noted.

The typical serial position curve for the ISR protocol at approximately span list length (often the length resulting in approximately 50% of lists being recalled entirely correctly) consists of an extended primacy portion showing approximately linear increases in errors with item position and a recency portion. With auditory presentation, the recency portion may extend to several items at the end of the list depending upon experimental design (Figure 5b, c). With visual list presentation, the recency portion is often just one item long (Figure 6, circles). These one or two item error patterns are not universal (Drewnowski, 1980; Drewnowski & Murdock, 1980), as some modelers (Page & Norris, 1998) have suggested, however, and their shape can be susceptible to alteration due to experimental variables like attentional modulation (Figure 5c). This fact calls into question the sufficiency of models for explaining recency gradients that do not incorporate effects of attentional manipulations (e.g., Page & Norris, 1998).
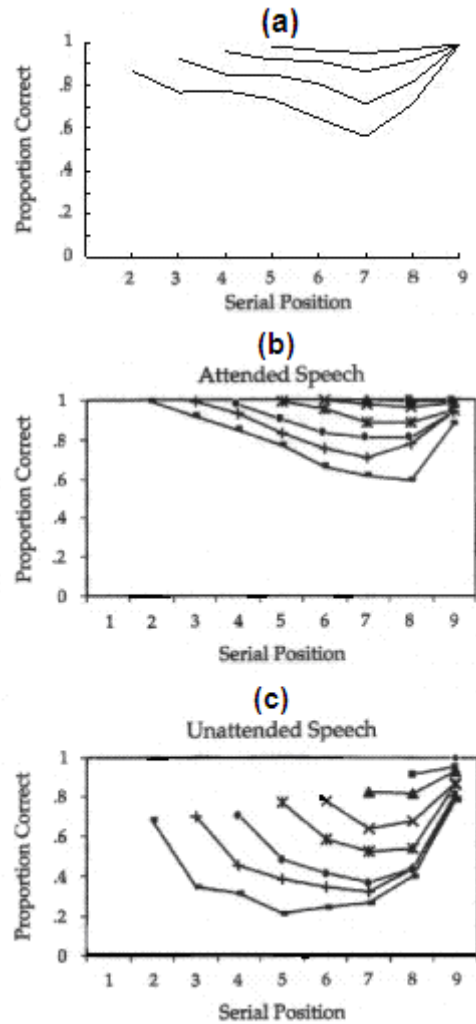
Figure 5. (a) Simulations of proportion correct vs. serial position by the LIST PARSE model for auditory presentation of various list lengths. (b) Observed mean proportion of items correct in attended speech (auditory presentation) ISR task vs. serial position at various list lengths. (c) Observed mean proportion of items correct in unattended speech (auditory presentation) ISR task vs. serial position at various list lengths. Note: all graphs are shifted rightward to avoid overlaps. (Data reprinted with permission from Cowan et al., 1999).

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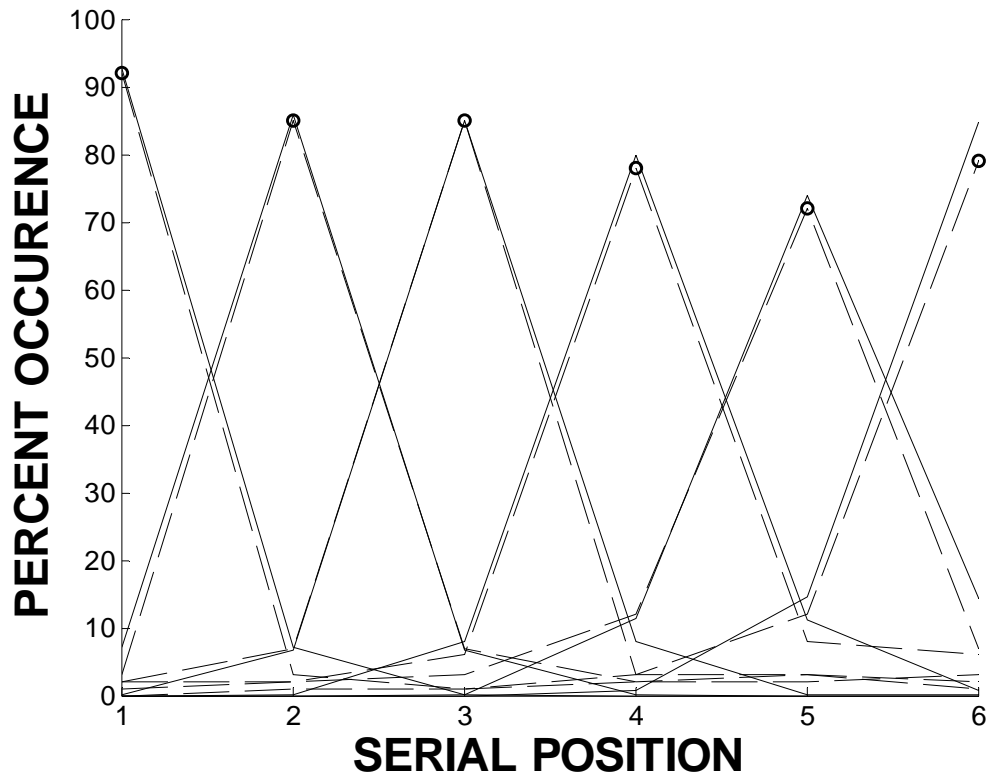
Figure 6. Percentage of recalls at each item *recall* serial position vs. item *presentation* serial position. Solid Lines: Simulations by LIST PARSE model. Dashed lines: Data from Experiment 1 in Henson et al., 1996. Circles: Percentage of correct responses for each serial presentation position. (Data reprinted with permission from Henson et al., 1996).

In the IFR protocol, the serial position curve tends to have a more rounded shape and a substantially longer recency gradient than in the ISR task, regardless of presentation modality (Figure 7c). The differences in shape of these serial position curves have been taken to be evidence that different mechanisms underlie the two tasks (e.g. Tan & Ward, 2000). However, as discussed previously, experimental confounds exist between ISR and IFR tasks that may cause such differences without a change of underlying mechanisms. The LIST PARSE model suggests how this can happen.
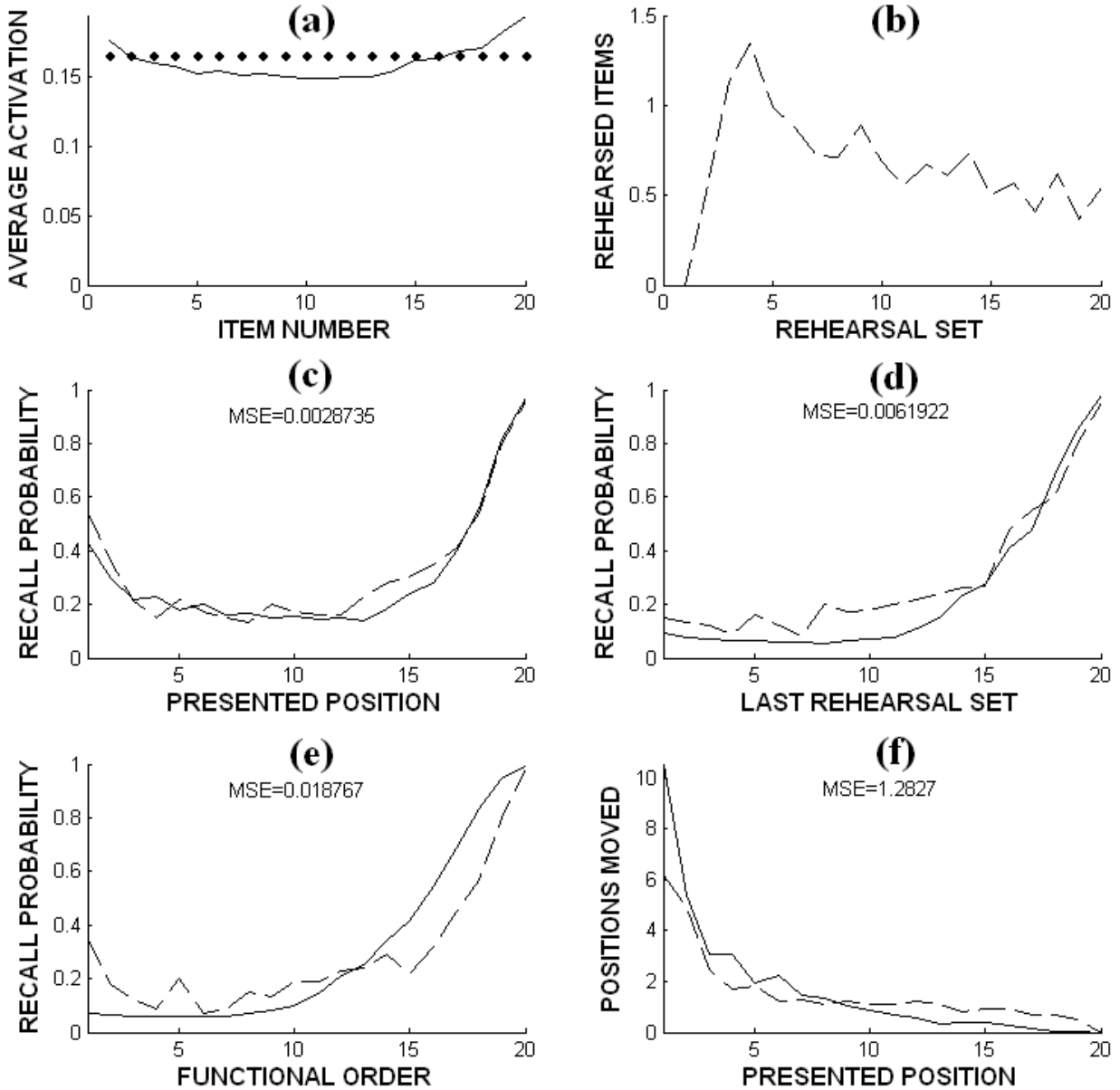
Figure 7. Solid lines: Simulations of performance measures during an IFR task by the LIST PARSE model. Dashed lines: Data from the fast condition of Experiment 1 in Tan & Ward, 2000. (a) Average activation of Y_i cells representing each item when errors were assessed and omission threshold (dotted line). (b) Observed number of rehearsals of distinct previous items during each rehearsal interval in Tan & Ward (2000). (c) Probability of recall vs. presented (nominal) serial position; that is, the standard serial position performance curve. (d) Probability of recall vs. set in which items were last vocalized. (e) Percentage of recall vs. (functional) order of last rehearsal. (f) Difference between set in which an item was last vocalized (rehearsed) and its presentation set. (Data reprinted with permission from Tan & Ward, 2000).

Error Type Distributions. Although few analyses (e.g., Drewnowski, 1980) of ISR or IFR data study the different types of error comprising the serial position curve, Henson, Norris, Page & Baddeley (1996) demonstrated the power of such an approach. Their analyses showed that (a) for sub-span and span length lists, omissions monotonically increased with input serial position; (b) order errors comprised the vast majority of errors in an ISR task for lists approximately at span; (c) within these order errors, transposition errors (i.e., swapping of item serial positions) caused the majority of these errors; (d) transpositions of neighboring items were far more likely than interchanges at more distant recall positions (Figure 6); and (e) when an item is not recalled in its correct serial position (i.e., an item later in the list is recalled in its serial position), the displaced item is by far the most likely item to be recalled in the next position, a property that Norris, Page & Baddeley (1994) termed *filling-in* (not to be confused with lightness or color filling-in in the context of visual perception).

With respect to item errors, the observed monotonic increase in item errors with serial position is typical in sub-span (or span). However, there is significant evidence that this pattern of errors does not extend to super-span lists for auditory presentation (which could potentially be explained by a specialized echoic memory) or visual presentation (Drewnowski, 1980; Drewnowski & Murdoch, 1980; Watkins & Watkins, 1980), where recency effects in item errors may occur. This recency effect in item errors when list length exceeds span is a failing of every other model of serial order, which all assume item errors to be monotonically increasing with serial position or flat, with one known recent exception (Henson, 1998b). This pattern of item errors was, in fact, mathematically proved in Grossberg (1978a, 1978b) to be an inevitable result when a sufficient number of items are stored by a pattern of activity that obeys the LTM Invariance Principle and the Normalization Rule within a recurrent shunting on-center off-surround neural network; see Section 2. As shown below, these item error recency effects for super-span lists are a natural consequence of the competitive dynamics within the cognitive working memory of the LIST PARSE model.

List Length Effects. Other things being equal, lists with more items are more poorly recalled, as are phonological lists with items that take longer to articulate than those with shorter items (Figures 8a; for review: Baddeley, 1986). Baddeley and colleagues (Baddeley et al., 1975; Baddeley, 1986) have proposed that the maximum list length of phonological material that can be correctly recalled (list span) in the ISR task is limited to the number of items that can be pronounced in approximately 1.5 - 2 seconds, thus scaling linearly with articulation rate. These findings have been extended to a variety of item types and across languages (e.g., Schweickert & Boruff, 1986; Zhang & Simon, 1985).
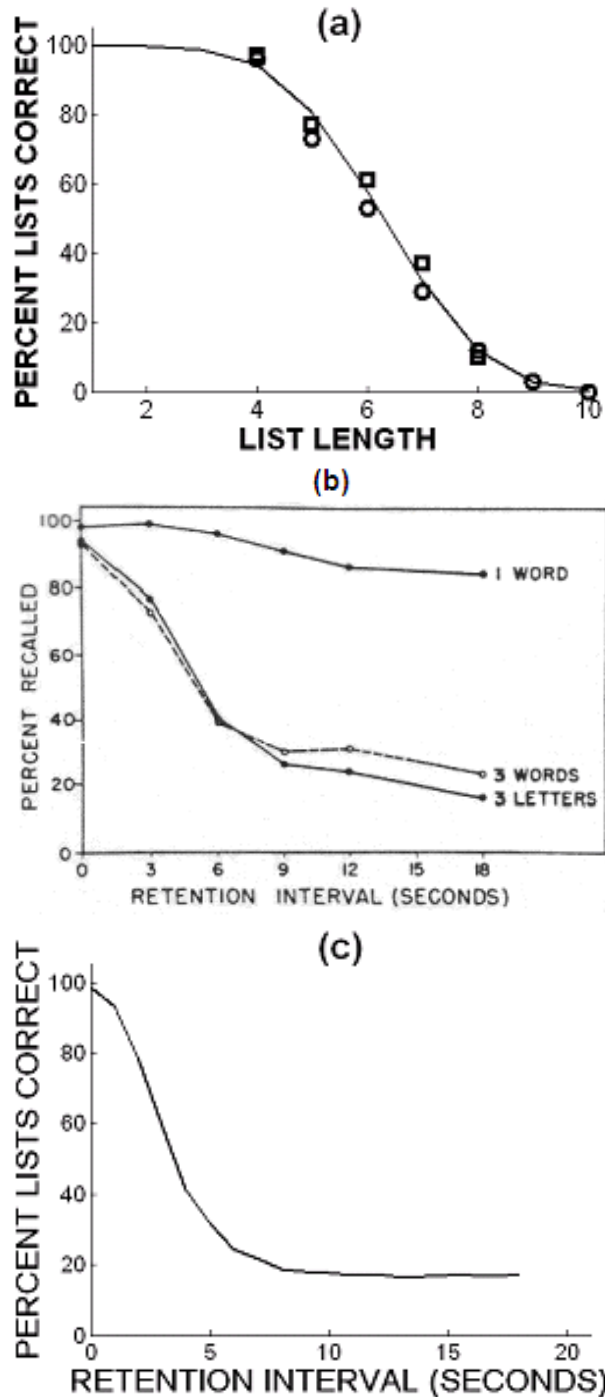
Figure 8. (a) Percentage of lists recalled correctly during immediate serial recall tasks for various list lengths. Solid line: Simulation of LIST PARSE model for lists of varying numbers of items. Circles: data averaged over limited and unlimited letter conditions from Crannell & Parrish, 1957. Squares: data reprinted with permission from Baddeley & Hitch, 1975. (b) Percentage of lists recalled correctly after extended distracter-filled retention intervals (data from Murdoch, 1961). (c) Simulations of LIST PARSE model for 3 item lists with various filled (no rehearsal) retention intervals. (Reproduced with permission from Baddeley & Hitch, 1975, Crannell & Parrish, 1957, and Murdoch, 1961).

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Temporal Limitations Upon Recall. Delays in recall of as little as two to three seconds can render portions of unrehearsed lists of items at span length irrecoverable (e.g., Baddeley, 1986; Baddeley & Scott, 1971; Baddeley, Thompson & Hitch, 1975; Cowan, Day, Saults, Keller, Johnson, & Flores, 1992b). Even for lists of items of sub-span length (in an *immediate* serial recall), a retention interval that is filled with a distracting task that prevents rehearsal can greatly reduce recall accuracy (Figure 8b).

However, the facts that (a) span seems to be closely related to articulation rate and/or output time and (b) unrehearsed delays hinder list recall only imply that recall performance is to some extent *time-dependent*. It does not necessarily mean that there is a simple *temporal decay* process underlying these phenomena. In fact, the explanations given for limitations in working memory performance are nearly as numerous as the experimental protocols used to explore them. Cowan (2000) proposed that at least seven different approaches to the limited capacity of working memory exist, but the largest dichotomy seems to concern whether time (*temporal decay*) or the amount (and type) of information being simultaneously stored (*interference*) principally limits accurate recall capability.

Interference versus Pure Temporal Decay. Thus, a lingering debate in the working memory literature is whether working memory limitations are due to (a) temporal decay mechanisms, in which the ability to recall items declines solely due to time held in memory prior to an item's recall, or (b) interference, in which distracters or other items in the list decrease the ability to recall an item correctly (including pure capacity limits). Various proposals have been made for the mechanisms underlying these perspectives (e.g., Cowan, 2000; Jensen & Lisman, 1996; Lewandowsky, 1999; Lewandowsky & Murdock, 1989; Nairne, 1990; Neath & Nairne, 1995; Schweickert & Boruff, 1986; Service, 1998, 2000) but much recent research has examined the *time-dependence* of performance declines.

Several researchers have made a strong case for temporal decay processes of some sort as the primary bases for recall performance limits. By carefully monitoring the timing of items throughout list presentation and recall, their analyses show that the time (articulation time: Cowan et al., 1992; or total output time: Dosher & Ma, 1998) taken to recall an item from the beginning of the recall period so strongly correlates with decreased recall performance that decay during this delay period may be sufficient to account for nearly all of the observed errors. The Cowan et al. (1992) study in particular found that performance of lists declined when words that took longer to articulate were located in the early portion vs. the later portion of the list. This conclusion is consistent with much of the articulatory loop literature which emphasizes an articulation time account (Baddeley, 1986; Baddeley & Hitch, 1974; Jarrold, Hewes & Baddeley, 2000; Schweickert & Boruff, 1986). Similarly, Henry (1991) and Avons, Wright & Pammer (1994) used probed recall paradigms to explore word length effects and proposed the diminished word length effects in probed recall versus serial recall reflected the shorter output time necessary to complete the task.

Cowan et al. (1992b) studied the responses of persons with differing spans in Cowan (1992a), and found that larger item span correlated with larger temporal extent of inter-response intervals. Cowan concluded that, rather than a single rate of decay occurring during the recall period (i.e., total output time dependence), there may be multiple rates of decay and reactivation depending upon whether articulation or an inter-response pause is occurring. To explain their data, Cowan (1992a) proposed an account in which item representations are partially restored

(the authors remained agnostic as to mechanisms) during inter-response periods to compensate for the decays during articulation of other items (a so-called Decay-and-Reactivate process).

Such studies have not ended the debate in favor of purely temporal decay (particularly articulation time) accounts. Service (1998, 2000) and Lovatt, Avons & Masterson (2000, 2002) have instead asserted the importance of phonological complexity and error recovery to explain the observed correlation performance declines with total output time (Dosher & Ma, 1998), rather than articulation time. For instance, the Lovatt et al. (2000, 2002) studies used different sets of di-syllabic words than were used in previous studies which showed a correlation between performance and articulation time (e.g., Baddeley et al., 1975; Caplan, Rochon & Waters, 1992; Cowan, 1992), and also controlled for the numbers of errors in the first half of list recall. They observed no effect of articulation time (word length) when lists were controlled for error rates. Thus, the previously reported effect of articulation time (as opposed to purely output time) upon recall performance could be an artifact of the particular data set, in which words with longer articulation time inherently had a higher propensity for errors (see also, Hulme, Suprenant, Bireta, Stuart & Neath, 2004).

In perhaps the classic demonstration of interference effects, Waugh & Norman (1965) used a probed serial recall protocol to show that the number of items in a list was strongly negatively related to probability of probed recall, with temporal factors playing only a minor role. Cowan, Wood, Nugent & Treisman (1997b) found dissociable effects of duration (implying temporal effects) and complexity (implicating interference effects) using lists of variable word length in an ISR task. More pointedly, the Baddeley et al. (1975) articulation rate vs. list span finding itself points to the importance of interference, since it establishes a specific maximal capacity (number of items) that can be correctly recalled for a given articulation rate, rather than establishing an amount of time that an arbitrary amount of information can be maintained in memory, an additional proposal that was subsequently made in Schweikert & Boruff (1986).

In fact, when sub-span lists are used, participants can retain this information across filled retention intervals (which presumably prevent rehearsal) for times that far exceed the few second (span length) interval (Figure 8b; Murdoch, 1961). Additionally, there have been reports that for sub-span lists, a positive asymptote in performance level (i.e., correct recall percentage plateaus rather than dropping to zero) can result over the extended observed intervals (Figure 8b). These findings seem to be inconsistent with a simple temporal decay account in which an unrehearsed item decays continuously, losing its ability to be recalled after a few seconds, regardless of the concurrent load in memory. The failures to consistently record and report order of recall in the IFR task and to time participant responses during the recall phase of both tasks have hindered a more complete resolution of this debate across paradigms.

An approach that partially combined temporal decay and interference processes to account for list and word length effects was employed by Page & Norris (1998) in the primacy model. Specifically, order information was proposed to be maintained by relative activation levels which exponentially decay and compress (i.e., become closer together) over unrehearsed delays and during recall. Initial item activation level was mathematically specified to be limited by the presence of previous items in working memory. A similar account that synthesizes both interference and temporal decay evolves naturally from the interactions of the LIST PARSE model: (1) representations of items converge (reducing their distinctiveness and increasing the probability of order errors) with increasing time without rehearsal in cognitive working memory, and (2) the presence of other items in working memory competitively limits the amount of activation that each item has in the self-normalizing motor working memory, a property that

follows naturally in the LIST PARSE model from the real-time dynamics of shunting recurrent on-center off-surround networks (Bradski, Carpenter & Grossberg, 1984; Grossberg, 1973).

Similarities between Spatial and Non-spatial Processing. Another lingering question concerns whether spatial and non-spatial material is retained and processed similarly in working memory, given that there is evidence for relatively distinct processing localizations even within granular prefrontal cortex (see Section 2 and Figure 1). At least for sequential processing, evidence exists to suggest shared neural mechanisms, even if they are occurring in relatively distinct cell populations in cortex. For instance, Jones, Farrand, Stuart and Morris (1995) conducted a spatial task in which visual target locations were sequentially presented and subjects subsequently recalled the locations in their presented order (i.e., spatial serial recall). The authors reported strikingly similar results to those seen in the non-spatial (e.g., auditory or visual object serial recall) literature including: similar serial position bows, list length effects including similar measures of span capacity, interference effects including from items and actions in different modalities, and retention interval effects. Additionally, Agam, Bullock and Sekuler (2005) sequentially presented spatial targets and instructed subjects to manually imitate the sequence. The authors reported that subjects not only made errors that closely resembled the bowed (1-item recency) shape of the serial position performance curves, but the majority of sequential errors were transpositions of neighboring movements, mimicking a central property of the error-type distribution of non-spatial ISR (e.g. Henson et al., 1996).

3.2 Sequential Movement Neurophysiology. An issue intimately linked with the representation of items in working memory during any task is the means by which the items are selected for output during the recall phase of that task. The neurophysiological basis of these mechanisms was probed using extra-cellular recording from the areas near the caudal portions of the principal sulcus of macaque monkeys during the performance of a sequential motor task (Averbeck et al*.,* 2002, 2003a, 2003b). The monkeys copied concurrently presented geometrical shapes on an LCD screen using an X-Y joystick in a prescribed order (counter-clockwise starting at the top middle of each shape; Figure 9a). These experiments demonstrated for the first time: (a) simultaneous representation of all items in a planned sequence (parallel planning) prior to sequence initiation, with relative activity of item representations being highly predictive of eventual sequential order; and (b) strongest coding within this parallel representation for the item to-be-performed next throughout sequence performance. Both of these properties are central predictions of competitive-queuing models of serial order (Grossberg, 1978a, 1978b; Houghton & Hartley, 1996).
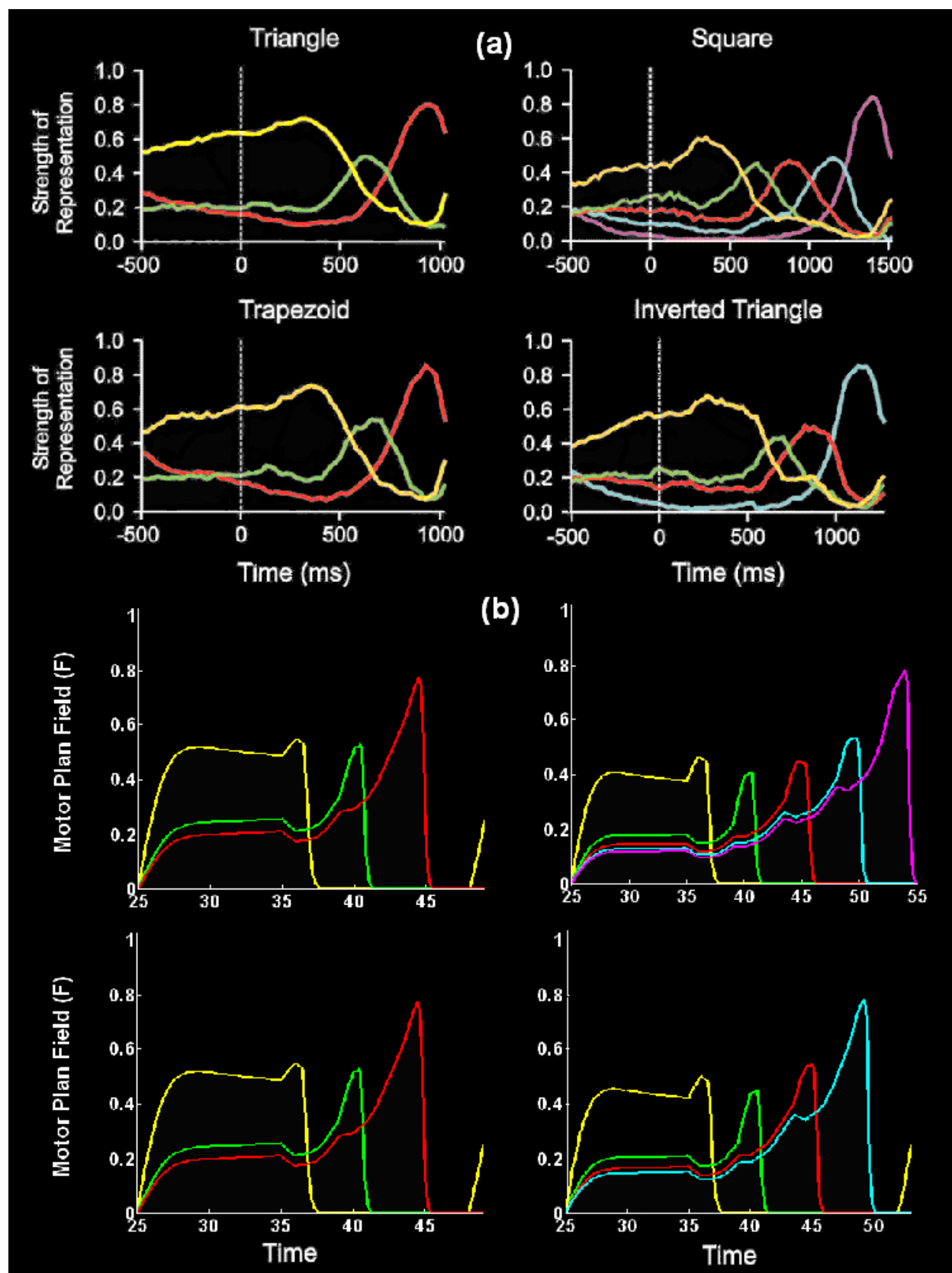
Figure 9. (a) Plots of relative strength of representation (a complex measure of cell population activity, as defined by Averbeck et al., 2002) vs. time for four different produced geometric shapes. Each plot shows the relative strength of representation of each segment for each time bin (at 25ms) of the task. Time 0 indicates the onset of the template. Lengths of segments were normalized to permit averaging across trials. Plots show parallel representation of segments before initiation of copying. Further, rank order of strength of representation before copying corresponds to the serial position of the segment in the series. The rank order evolves during the drawing to maintain the serial position code. (b) Simulations of item activity across the motor plan field of the LIST PARSE model for 3, 4, and 5 item sequences vs. simulation time. In both (a) and (b), line colors correspond to representations of segments as follows: yellow, segment 1; green, segment 2; red, segment 3; cyan, segment 4; magenta, segment 5. (Reproduced with permission from Averbeck et al., 2002).

At least four phases of the Averbeck et al. (2002; Figure 9a) curves should be noted: (1) presence of a primacy gradient; that is, greater relative activation corresponds to earlier eventual execution in the sequence during the period prior to the initiation of the movement sequence (period -500 to 400ms); (2) contrast enhancement of the pattern to favor the item to be performed (greater proportional representation of the first item) prior to first item performance (period ~100 to 400ms); (3) reduction of item activity just prior to its performance and preferential relative enhancement of the representation of the next item to be preformed such that it becomes the most active item prior to its execution (period ~400ms to near sequence completion); and (4) possible re-establishment of the gradient just prior to task completion. Similar dynamics are exhibited by the activation levels of the motor plan storage cell populations, F_i, of the LIST PARSE model (Figure 9b).

4. LIST PARSE MODEL

This section provides an intuitive functional explanation of the various processes modeled by the LIST PARSE model and their interactions. Figure 2 summarizes these processes and interactions, as do several subsequent Figures in greater detail. Mathematical equations and parameters are provided in the Appendix.

The Baddeley (1986) model of working memory has remained an effective framework for organizing cognitive research since its proposal and has received significant support from the rapidly expanding functional imaging experimental literature (e.g., Braver et al., 2001; Chein & Fitz, 2001; Marshuetz et al., 2000; Paulesu et al., 1993; Poeppel, 1996; Smith et al., 1998). The Baddeley model proposes that working memory function can best be described as a central executive controlling two subsystems that are specialized by the information they represent; namely, the phonological loop and visuospatial sketchpad. The phonological loop has historically received the majority of investigation by both psychophysical and functional imaging studies, whereas electrophysiological studies have generally focused upon the processing of visuospatial information. The LIST PARSE model may be seen as providing a computational account of the functionality of the phonological loop and visuospatial sketchpad along with volitional executive functions such as non-specific gain control mechanisms and task performance gating, as dictated by task stimulus cues (e.g., a recall cue), underlying working memory storage, learning, and sequential rehearsal of items.

4.1 Cognitive Working Memory

Unitized Category Inputs to Layers 6 and 4. The inputs I_i to the LIST PARSE model represent familiar object or event categories that have been unitized through previous learning. These categories are henceforth called *items*, and are designated as Item Category Inputs in Figure 10a.
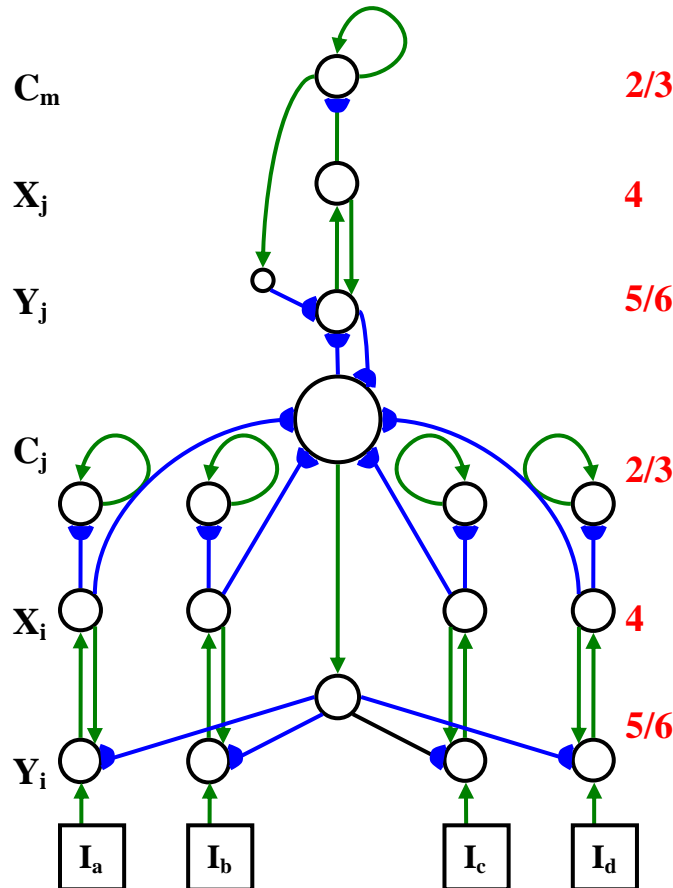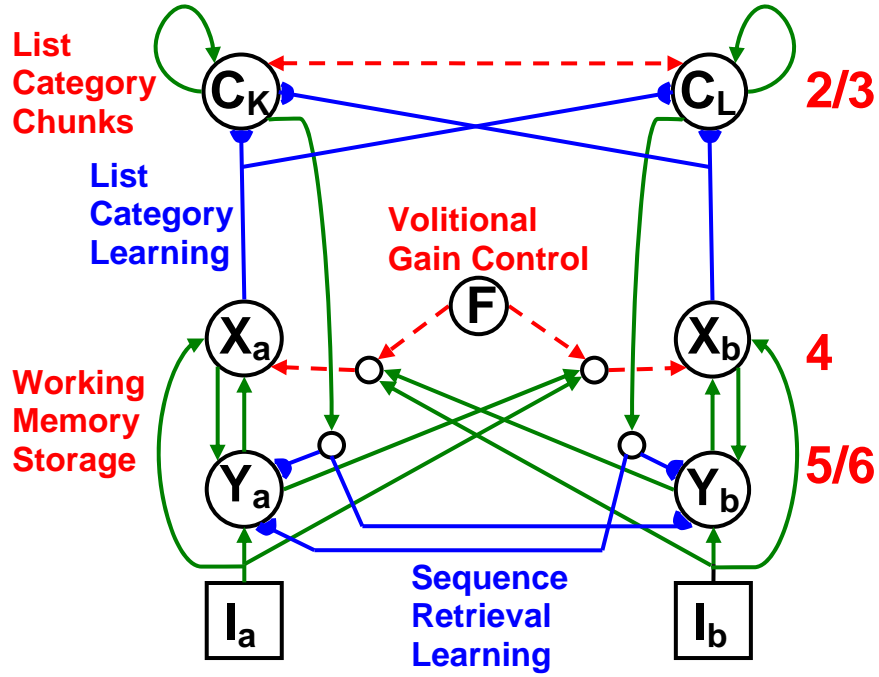
Figure 10. (a) Two columns (a and b) of the cognitive working memory circuit. Given a temporally separated sequence of inputs (*I*), layers 4 (*X*) and 6 (*Y*) form a positive feedback loop that sustains an activity gradient that codes both item and order information. This stored pattern can be modulated by a volitional gain control (*F*) which serves to alter the level of cross-columnar competition within this loop. Stored item subsequences (*X*) learn to activate layer 2/3 list category chunks (*C*) via a learned layer 4-to-2/3 adaptive filter. These list categories (*C*) bias the working memory pattern (in *Y*) and learn to re-institute (retrieve) their coded pattern through learned top-down expectations (sequence retrieval learning) from layer 2/3-to-5/6. (b) Interactions between two processing levels in a hierarchical working memory. In the lower level, four simultaneously active items (*X_i* and *Y_i* loops) are unitized into a chunk (*C*) that codes for all four items through learned feedforward and feed-back connections. This larger chunk differs from the one-item chunks shown only in the number of inputs it receives and in the strength of its competitive connections with other chunks in layer 2/3. This unitized chunk serves as bottom-up input to a higher-level cognitive working memory as an item representation, where it too can be combined with other items into a unitized list chunk. Competitive interactions among the list chunks (*C*) and the inhibitory off-surround connections between layer 4 and 6 are omitted.

The model assumes that these unitized items generate stereotyped transient, or pulse, inputs to the LIST PARSE working memory. In particular, all the inputs I_i to the cognitive working memory network in Figures 2, 10, and 11a have the same fixed duration (1 simulation time unit for convenience) and the same magnitude (.1). These assumptions allow the working memory to use the relative activities of the stored items to code their *temporal order* with as little bias as possible.

Working Memory in Layers 6/4. The LIST PARSE model proposes how the temporal order information of sequences of items may be stored in working memory by recurrent on-center off-surround shunting networks between layers 6 and 4 (6/4) of ventrolateral prefrontal cortex and the depths of the principal sulcus; see variables X_i (layer 4) and Y_i (layer 6) in Figures 2, 10a and 11a. Storage of items in working memory is accomplished by an evolving spatial pattern of item activities—that is, an activity *gradient*—which simultaneously codes item and order information of the stored items. In particular, the item representations for a temporally ordered sequence of n inputs I_1, I_2, …., I_n are maintained through the relative activities $Y_1, Y_2, …, Y_n$, where Y_i is the activity of the cell population in layer 6 that represents the ith item category. These item activations are distributed spatially across a cortical area. As noted above, correct storage of item temporal order is realized by a primacy gradient wherein $Y_1 > Y_2 > … > Y_n > 0$.
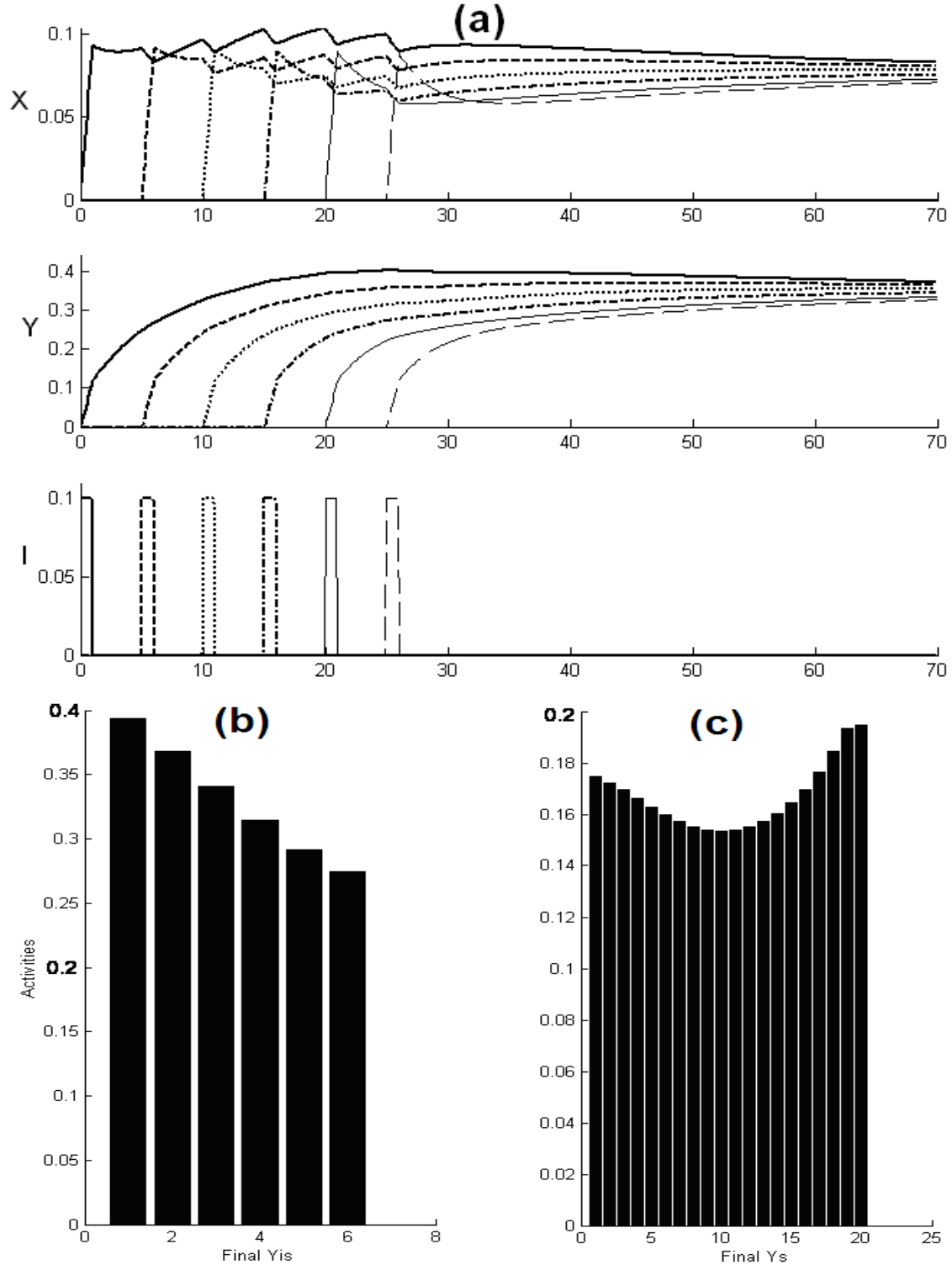
Figure 11. (a) Simulation of the development of a primacy gradient: activation across time of cells in layers 4 (*X*) and 5/6 (*Y*) of the cognitive working memory results from the presentation of a 6 input (*I*) list with 5 simulation time unit IOIs. Cells coding for each item channel are represented as follows: item 1, dark solid line; item 2, dark dashed line; item 3, dotted line; item 4, dash-dot alternating line; item 5, light solid line; item 6, light dashed line. This convention for

displaying multiple stored item activations in parallel is maintained through the remainder of the paper. (b) Simulation of the same primacy gradient as in (a) across the layer 5/6 cells (*Y*) of the cognitive working memory 5 simulation time units after last item IOI when a sub-span list of 6 items. (c) Simulation of a bowed gradient (with extended recency) in response to a super-span list of 20 items presented with 5 simulation time unit IOIs.

Learned Grouping of Item Sequences by List Chunks in Layers 2/3. The model proposes how the items that are coded in the working memory may be grouped through learning into list chunks, or unitized sequence codes, in layers 2/3; see variable C_j in Figures 2 and 10b. In all, the model proposes that: (a) the temporal order of item sequences is stored via recurrent on-center off-surround interactions in the deeper layers 6 through 4 (6/4); (b) that learned list chunks are found in the superficial layers 2/3; (c) that learned interactions from layers 4/6-to-2/3 are a bottom-up category learning adaptive filter whereby the list categories are learned (see the pathways labeled List Category Learning in Figure 13); and (d) that learned interactions from layers 2/3-to-5/6 are top-down learned expectations whereby a list chunk can read-out (retrieve) into short-term working memory the pattern of temporal order information across items that is stored in its adaptive weights, or long-term memory traces (see the pathways labeled Sequence Retrieval Learning in Figure 10a).

The list chunking network in layers 2/3 is also defined by a recurrent on-center off-surround shunting network. This network contains cells of multiple sizes such that the larger cells selectively code longer lists. Such a network was introduced in Grossberg (1978a), where it was called a *masking field* because the larger cells can "mask" or inhibit the activities of the smaller cells, more than conversely. This property was able, for example, to naturally explain the Magical Number 7 of Miller (1956). A number of authors have subsequently used masking field networks or variations upon this architecture (e.g., Cohen & Grossberg, 1986, 1987; Grossberg & Myers, 2000; Nigrin, 1993; Page, 1994).

Cohen and Grossberg (1987) provided the first simulations of how cells in a masking field can learn to selectively respond to different sequences of items. This demonstration used hard-wired inputs. The LIST PARSE model shows how a laminar realization of masking field dynamics enables the cells in layer 2/3 to learn to become list chunks in response to dynamically evolving patterns of activity in layers 4/6. In particular, stored activity patterns in layer 4 (with activities X_i) project to layer 2/3 via an adaptive filter; see the pathways labeled List Category Learning in Figure 10a. Excitatory and inhibitory feedback within layer 2/3 in response to these input patterns from layer 4 contrast-enhances the activity of some layer 2/3 cells while inhibiting the activities of all other layer 2/3 cells. The winning layer 2/3 cells drive learning by the adaptive weights within the layer 4-to-2/3 pathways. After learning occurs, different stored sequences in layers 4/6 activate different masking field list chunks.
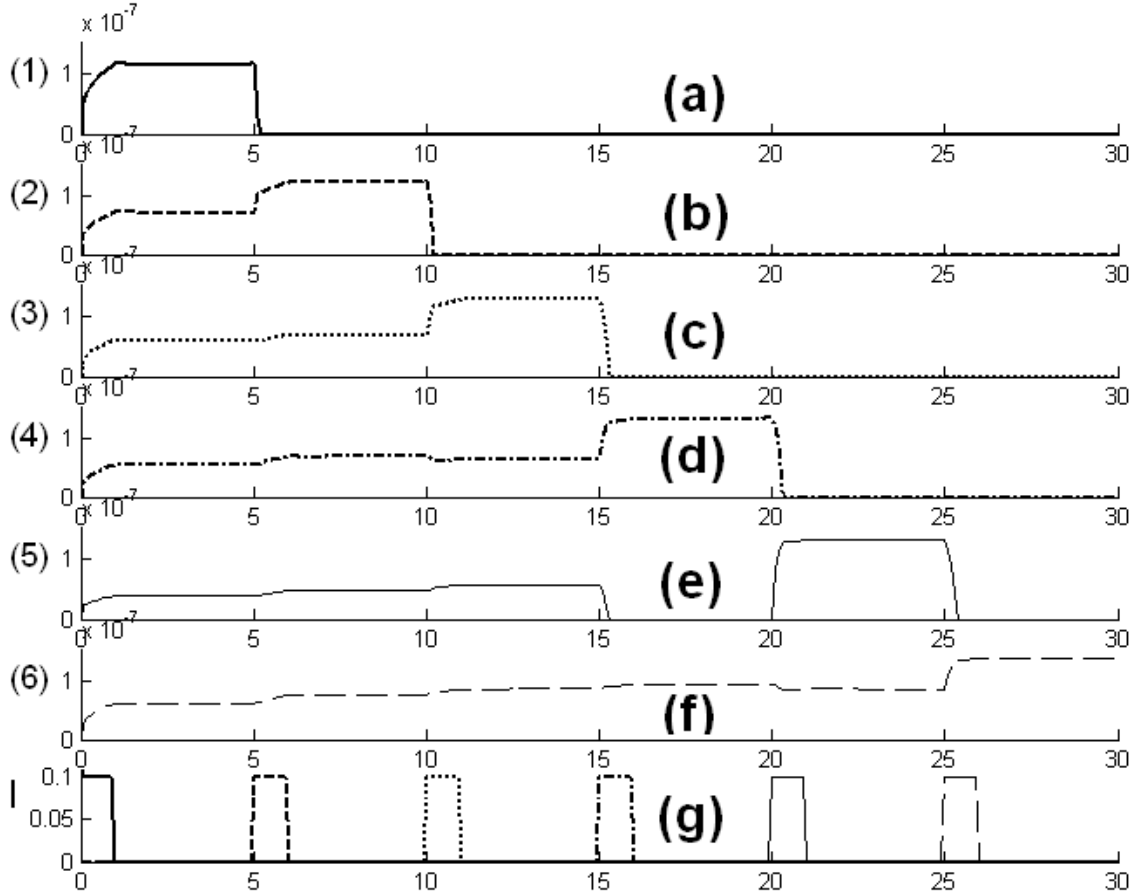
Figure 12. List chunk activations across time of layer 2/3 cells (*C*) coding for different length subsequences of a presented list of 6 items, with 5 simulation time unit IOIs. (a) Connected only to the first item in the sequence. (b) Connected only to the first 2 items. (c) Connected only to the first 3 items. (d) Connected only to the first 4 items. (e) Connected only to the first 5 items. (f) Connected to all of the 6 items in the presented list. (g) The inputs to the cognitive working memory.

The competitive dynamics in layers 2/3 enable: (a) partial activation (priming) when the items in working memory form a subset of the list that a list chunk has learned to code, but (b) strong competitive suppression when another chunk is activated that codes for a larger subset of the sequence of items (Figure 12). The priming effect illustrates the *sequence selectivity* of a masking field: it prevents the prior learning of a list sequence (for instance, a word like "myself") from suppressing the activation of a cell that has learned to code a subsequence of this list (for instance, the words "my," "self," or "elf") when only that subsequence is presented. In contrast, the strong suppressive action of cells coding for longer sequences (when these larger sequences are actually active; e.g., "myself") upon those coding for subsequences (e.g., "my") prevents the erroneous association of these subsequences with the larger list chunk, which could easily prevent the larger chunks from learning their own meanings. Said in another way, a masking field selects those list chunks that best predict the entire temporal context of events that have recently occurred. With this property ensured, other crucial properties follow, such as the selective association of predictive list chunks with the rewards or punishments that may obtain after the actions that their sequences control.

Top-Down Learning from List Chunks to Working Memory Items. As noted above, the list chunks are self-organized by bottom-up learning from the item sequences stored in layers 4/6 via the adaptive filter from layers 4/6-to-2/3. This bottom-up learning occurs simultaneously with top-down learning from the emerging list chunks to the item sequences stored in working memory via learned expectation pathways from layers 2/3-to-4/6. This top-down learning helps to stabilize the bottom-up learning via general rules of Adaptive Resonance Theory, or ART (Carpenter and Grossberg, 1991; Grossberg, 1980, 2003a). Top-down learning also enables selective activation of a list chunk (e.g., of a learned word) to read-out its learned weights and activate items in working memory through long-term memory retrieval, thereby leading to their fluent execution via the Motor Working Memory; see Figure 2 and the pathways labeled Sequence Retrieval Learning in Figure 10a. In other words, triggered by the activation of list chunk cells, learned LTM feedback projections to the working memory network provide a means of (a) reactivating these items from LTM, and (b) boosting currently active working memory activations and creating a resonance based upon the strength of the item sequence's learned familiarity.

Such a read-out from long-term sequence memory can also bias stored working memory activity patterns in layers 4/6 towards representing more extended primacy portions. Put simply, the earlier in a presented sequence context an item enters the cognitive working memory storage network (layers 4/6), the longer the top-down weights have to learn upon these items in the gradient, and thus there is a tendency for these items to be more strongly coded. As a result, the primacy-dominant gradient that is typically stored in cognitive working memory may be somewhat extended when learned by the top-down weights (i.e., there tends to be more items in the primacy gradient that is stored in these long-term weights than is present in the working memory network taken separately). The tendency of the serial position curve for a list to tend toward primacy with increasing post-presentation delays, even in cases where rehearsal is deemed impossible (e.g., Knoedler et al., 1997), may be explained by a learned primacy gradient in the LTM feedback from activated list chunks to the working memory representations. This top-down read-out property was also the basis whereby Grossberg (1978a) distinguished the TMS, which operates without LTM read-out and predicted the Magical Number 4 (Cowan, 2000), from the IMS, which operates with LTM read-out and explained why a larger Magical Number 7 is often observed (Miller, 1956).

Higher-Order Cognitive Invariants: Chunks of Chunks. Figure 10b shows how the list chunks in one region of prefrontal cortex can be the inputs to a successive region of cortex, whose "items" are list chunks and whose "list chunks" are chunks of chunks. Such a hierarchical organization allows higher-level chunks to represent increasingly large temporal contexts, such as sequences of words, and thereby to more reliably predict meaning and future action. In Figure 15, outputs from the list chunks of layers 2/3 in a given cortical area input to layers 6 and 4 of the next cortical area to activate the list chunk "items" that are stored in this higher-order working memory. In other words, the list chunks provide "bottom-up" inputs to the higher chunking area.

Laminar Cortical Circuits for Both Temporal and Spatial Processing. The LIST PARSE prediction about different roles for the lower and upper layers of ventrolateral prefrontal cortex goes beyond known neurophysiological data. On the other hand, it is a testable prediction which, if true, would show that a *temporal* working memory and list chunking network may be viewed as a variation on the same sorts of circuits that are better known in the visual cortex, where the representations are more *spatial* in character. This similarity in proposed function is paralleled by their highly granular (i.e. having a well-developed granule cell layer IV) six-layered

cytoarchitectures (e.g., Barbas & Pandya, 1989; Barbas & Rempel-Clower, 1997; Calloway, 1998). In particular, recurrent layer 4/6 interactions in cortical area V1 seem to play an important role in controlling the development and maintenance of visual cortical maps of ocular dominance and orientation tuning (e.g., Grossberg & Seitz, 2003; Kayser & Miller, 2002; Olson & Grossberg, 1998), whereas layer 2/3 includes depth-selective complex cells (e.g., Hubel & Wiesel, 1968; Poggio, 1972; Poggio & Fischer, 1977; Poggio & Talbot, 1981; Smith et al., 1997; modeled in Cao & Grossberg, 2005; Grossberg, 2003a; Grossberg & Howe, 2003; Grossberg & Swaminathan, 2003). Feedforward interactions from layers 6/4-to-2/3 of cortical area V1 are modeled in Grossberg & Howe (2003) and Cao & Grossberg (2005) as an adaptive filter that helps to create depth-selective complex cells in layers 2/3, which also interact recurrently to begin to form perceptual groupings. Feedback interactions from layers 2/3-to-6/4 are predicted to help to select the monocular cells that are consistent with winning binocular cells in layers 2/3. Inputs from cortical area V1 to V2 lead to the formation of long-range perceptual groupings in layers 2/3 of V2, which may be interpreted as the higher-order chunks of V1; see Grossberg and Raizada (2000) and Raizada and Grossberg (2003) for simulations and supportive data.

Analogous to this line of reasoning, Felleman and Van Essen (1991) proposed a hierarchical framework of cortical organization in which feedforward projections tend to originate primarily in the supragranular layers of a lower cortical area and to terminate in layer IV of a higher area, while feedback connections tend to originate primarily in the infragranular layers of a higher area and to terminate in layer I, and possibly layer VI, of the lower area. Barbas and colleagues have extended this framework demonstrating in a multitude of structures the importance of laminar definition in establishing the connectivity patterns between cortical areas (e.g., Barbas & Rempel-Clower, 1997; Dombrowski, Hilgetag & Barbas, 2001; Hilgetag, Dombrowski & Barbas, 2002; Rempel-Clower & Barbas, 2000). In particular, Barbas & Rempel-Clower (2000) established that projections from a range of prefrontal areas, particularly area 46, terminate primarily in the supragranular areas of anterior temporal lobe area TE, and resemble the feedback pathways in early sensory cortical areas. Confirmation of this pattern of hierarchical connectivity between the posterior parietal lobes and the lateral prefrontal cortex has been previously reported (Goldman-Rakic, 1987). Similar feedback pathways were reported to exist in the projections from prefrontal area 8 to posterior visual areas MT and MST (Cusick, Seltzer, Cola & Griggs, 1995). These frameworks of organization are generally consistent with the connectivity between the hierarchical layers of cognitive working memory in the LIST PARSE model (Figures 1, 2, and 10b).

Working Memory Storage and Reset by Volitional Gain Control. The cognitive working memory circuit includes a Volitional Gain Control mechanism (see variable *F* in Figures 2 and 10a) that maintains items in working memory under volitional control, and enables all current item activations to quickly decay in order to store subsequently presented items, or re-presentations of earlier items. In Figure 10a, this is modeled as a nonspecific inhibition of the recurrent inhibitory interneurons in the on-center off-surround working memory circuit. When volition is turned on, the gain of the inhibitory interneurons is reduced, thereby enabling storage. When volition is shut off, inhibitory gain increases. Inhibition then overwhelms excitation and the stored activities collapse. This is not the only way in which the balance between excitatory and inhibitory feedback in the working memory circuit can be controlled to achieve storage and reset. Anatomical experiments need to be carried out to study the locus of such a nonspecific gain control mechanism.

A Homolog Between Working Memory Storage and Visual Imagery and Fantasy. The anatomical site of this volitional inhibitory gain, at the inhibitory interneurons within layer 4, is consistent with the hypothesis that a similar volitional circuit occurs in the visual cortex. Here, increasing the volitional gain is predicted to enable top-down expectations to generate suprathreshold conscious percepts of visual imagery and fantasy, rather than merely modulatory attentional feedback. When this type of phasic volitional control over visual imagery and fantasy is replaced by tonic hyperactivity of the gain control source, hallucinations can occur that have many of the properties of schizophrenic hallucinations (Grossberg, 2000a). If these predictions are supported, then they provide another example whereby homologous mechanisms within a similar underlying neocortical circuit design can carry out seemingly quite different functions: working memory storage in prefrontal cortex vs. visual imagery and fantasy in visual cortex.

As shown below, the simple circuit comprising the variables X_i, Y_i, F, and their interactions in Figures 2 and 10a can simulate a wide range of serial position curve data.

4.2 Motor Working Memory

The cognitive working memory activates cells in the motor working memory; see Figures 2 and 13a. The items in the motor working memory are learned motor plans that are associated through learning with the items in the cognitive working memory. This learning process is not modeled here. Rather, it is assumed for simplicity that each cognitive item in layer 6 (with activity Y_i) can activate a corresponding motor item (with activity F_i). As a result, the spatial pattern of items stored in the cognitive working memory can be transferred and stored in the motor working memory. For example, read-out of a cognitive list chunk can activate its cognitive working memory pattern which, in turn, can activate the corresponding motor working memory pattern. The model proposes below how rehearsal of working memory items can elicit recall of a sequence of items that are currently stored in the cognitive working memory, or that are volitionally read-out from a cognitive list chunk.

Rehearsal of a sequence of items from motor working memory requires that each motor working memory activity is inhibited as it is chosen for performance, as explained below, in order to prevent perseveration of a single item; also see Section 2. Reset of the motor working memory does not, however, require reset of the cognitive working memory. Because of the distinction between cognitive and motor working memories, items that remain stored in the cognitive working memory can be rehearsed multiple times.

A volitional GO signal (*G* in Figures 2 and 13a) gates read-out from the cognitive working memory into the motor working memory at times when recall from the motor working memory occurs. The model predicts that the same volitional GO signal that gates *on* motor performance also gates *off* read-out from the cognitive working memory to the motor working memory (see Appendix). Volitional gating enables feedback from motor performance to the cognitive working memory via the environment to take place without forcing reinstatement of an inhibited working memory item right after it is performed.
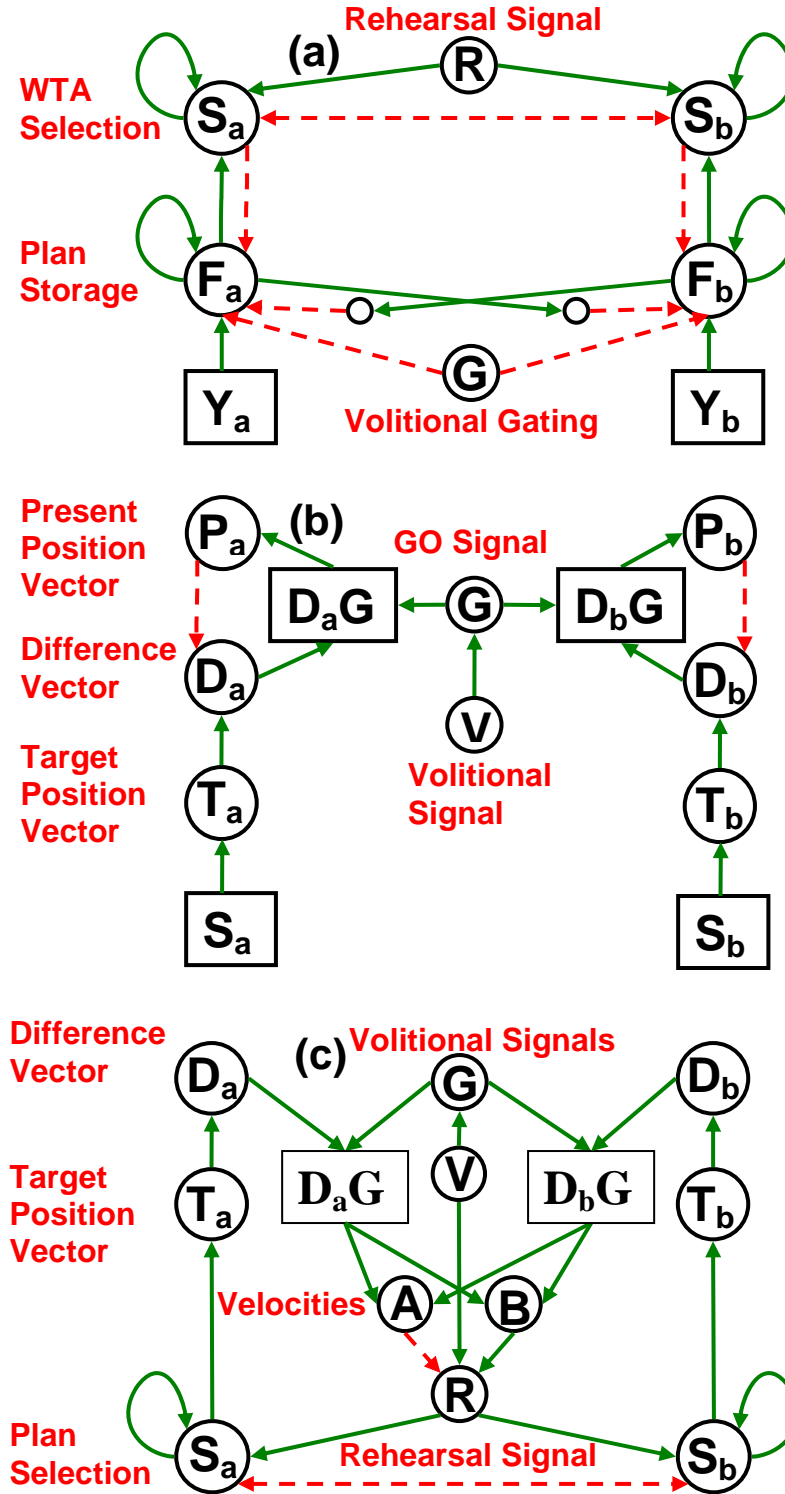
Figure 13. (a) Two columns in the motor working memory. Inputs from cognitive working memory (*Y*) are stored in the self-normalizing motor plan storage network (*F*). When a rehearsal signal (*R*) is active (above a zero threshold level), these parallel motor plans are instated in a plan selection layer (*S*). When a plan becomes super-threshold, it inhibits other plans, thereby preventing simultaneous execution of multiple plans, and sends self-inhibitory feedback to its

representation in the motor plan storage network, thereby preventing perseveration. (b) Two columns in the trajectory generator circuit. Inputs from the plan selection field (S) of the motor working memory system establish a desired (target, T) configuration of the relevant motor effectors. The system maintains a representation of the present configuration (P) of these motor effectors. Trajectories are generated at a volitionally scaled rate (G) through a negative feedback loop that reduced the difference (D) between these two configurations. (c) The signals influencing the rehearsal signal (R). Selection of the next item in the plan selection field (S) is gated by the rehearsal signal. The rehearsal signal is activated by volitional signals (V) indicating that the circuit is in the recall phase of the task. The rehearsal signal is also modulated by a deceleration estimate ($B - A$) from slow (B) and fast (A) cells that time-average outflow velocity signals at different rates.

One possible anatomical substrate of the non-spatial cognitive working memory in the primate is in the ventrolateral prefrontal cortex, whereas motor working memory may be stored in the dorsolateral prefrontal cortex and medial premotor cortex (e.g., supplementary motor area (SMA) and pre-SMA). Under these assumptions, lesions to the ventrolateral prefrontal cortex would be likely to detrimentally effect the learned association of high-level stimulus cues and their planned motor response. In fact, just such a selective deficit in visuo-motor association learning is observed from localized bilateral ventrolateral prefrontal cortical lesions (Bussey, Wise & Murray, 2001; Wang, Zhang & Li, 2000) as well as lesions that remove the connectivity between inferotemporal cortical centers in one hemisphere and ventrolateral prefrontal cortices in the other (Eacott & Gaffan, 1992; Parker & Gaffan, 1998; for a review: Curtis and D'Esposito, 2004).

In contrast, lesions to the mid-dorsolateral prefrontal cortex that spare the depths of the principal sulcus produce deficits in both spatial and non-spatial object tasks that require complex "monitoring" (e.g., updating of working memory representations), rather than simple maintenance, of information in working memory (Petrides, 1991, 1995, 2000a). In particular, the self-ordered task that is often used to demonstrate deficits in non-spatial tasks from dorsolateral prefrontal lesions (Petrides 1991, 1995) typically requires the monkey to remember its previous *movements*. The dorsolateral prefrontal cortex has been implicated by numerous electrophysiological recording studies in the representation of prospective movement sequences based upon past reward experience (Barraclough, Conroy, & Lee, 2004; Averbeck, Sohn & Lee, 2006). The medial premotor cortex (e.g., SMA and pre-SMA) has been linked in electrophysiological recordings to the preparation of motor response sequences based upon stimulus cues and/or the selection of motor responses maintained in working memory (Shima & Tanji, 1998, 2000). In addition, several studies have found serial order dependent-firing for movements within an eventual sequence among wide cross-sections of cells in both pre-SMA and SMA (e.g., Clower & Alexander, 1998; Isoda & Tanji, 2004; Shima & Tanji, 2000). Some subset of these cells may provide a substrate for explicit positional coding of some nature that is strongly suggested by secondary error effects like across-trial and across-position positional intrusions, but which are not modeled herein (for reviews: Henson, 1998b, 2001).
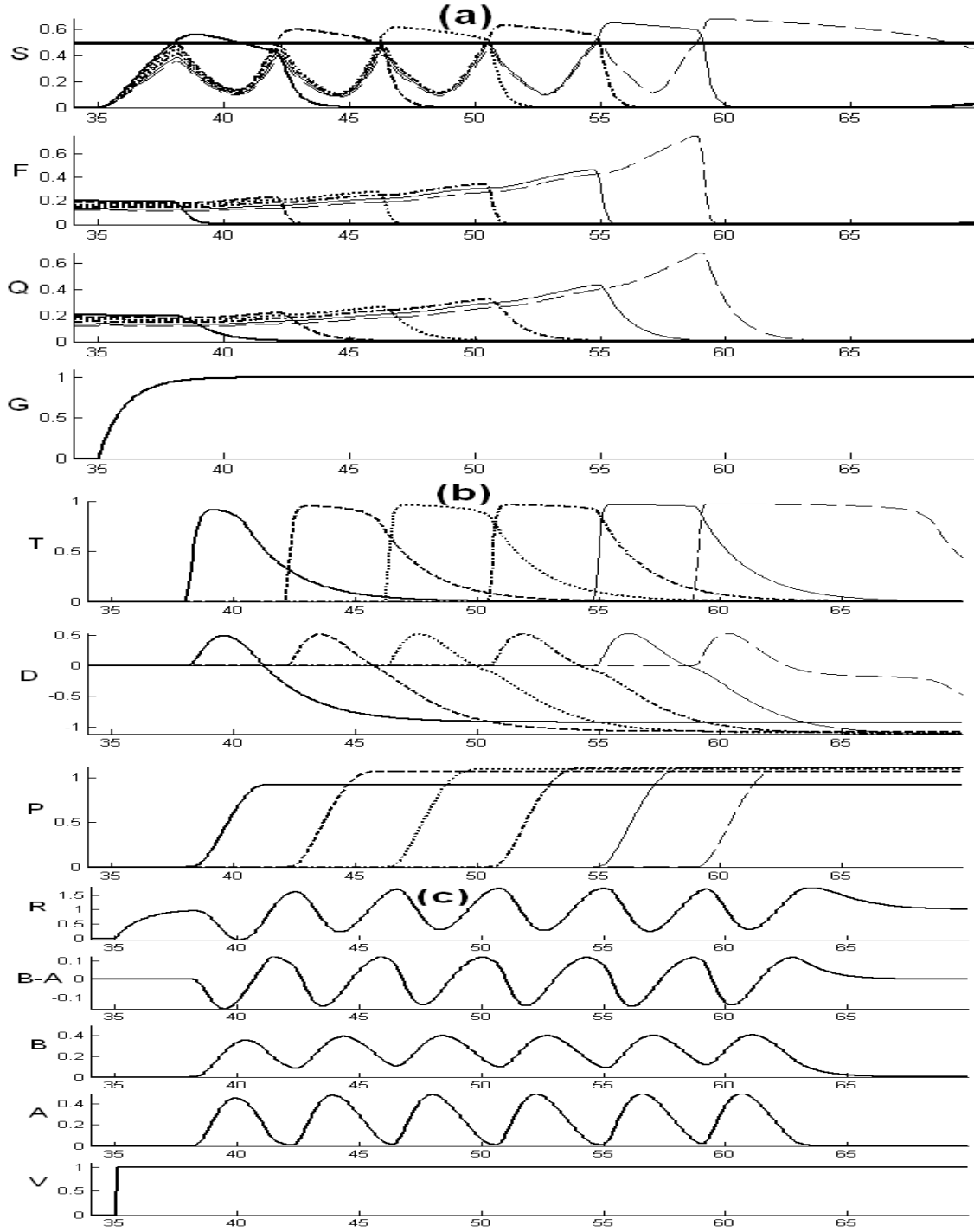
Figure 14. (a) Simulation of the motor working memory circuit when presented with a 6 item list with 5 simulation time unit IOIs. Inputs from cognitive working memory (*Y*) transfer an activation gradient to the motor plan storage network (*F*) and then are gated off by a volitional GO signal (*G*). The motor plan storage cells compete among themselves by sending inhibitory signals by way of inhibitory interneurons (*Q*). A rehearsal signal (*R*) allows read-out of the activity gradient by the plan selection layer (*S*), where a winner-take-all competition takes place. The winning cell activates a motor target (*T*) and sends feedback to inhibit its bottom-up motor plan (*F*). (b) Activities of the VITE trajectory generation circuit when presented with a 6 item list

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with 5 simulation time unit IOIs. Target position cell (T) is activated by a plan selection cell (S). An outflow representation of present position (P) is subtracted from the target position to compute a position difference (D) that represents the distance and direction the motor effectors must move. A volitional GO signal (G), which scales with desired rate of movement (V), gates the position difference (DG) representation before it is integrated by the present position (P). Thus DG represents outflow velocity. This velocity signal is sent to cells A and B which time-average them at different rates. See Figure 14a. (c) Variable-rate rehearsal control circuit when presented with a 6 item list with 5 simulation time unit IOIs. The rehearsal signal (R) which gates the read-out of the motor plan gradient into the plan selection layer (S) receives volitional input that scales with performance rate (V), excitatory input from slow integrating velocity cells (B) and inhibitory input from fast velocity cells (A).

Sequential Rehearsal of Motor Plans. Many of the control structures for rehearsal that are summarized in Figures 1 and 2 are predicted to take place within motor working memory circuits. These control structures are, we would argue, among those needed to realize the monitoring functions that are known to occur in dorsolateral prefrontal cortex (e.g., Petrides, 2005). In particular, a nonspecific rehearsal wave (R in Figures 2, 13a and 14c) activates read-out of the motor plan activation gradient from a layer of cells (with activities F_i in Figure 2, 13a and 14a) into a plan selection layer of cells (with activities S_i in Figures 2, 13a, c and 14a). A recurrent on-center off-surround shunting network in this plan selection circuit carries out a winner-take-all (WTA) choice of the most highly activated item from the motor working memory, with selection occurring when a motor plan's activity level exceeds a fixed threshold (for neurophysiological evidence see: Hanes & Schall, 1996). How such a WTA recurrent network can be designed was first proved mathematically in Grossberg (1973); see Grossberg (1980, 1988) for reviews.

In order to prevent perseveration during performance of each item, the chosen activity S_i both elicits performance of its plan and self-inhibits its input source F_i (Figures 2, 13a and 14a). Taken together, the motor working memory storage, plan choice, and self-inhibition mechanisms implement a variation of an Item and Order, or Competitive-Queuing, working memory which has been previously used to model motor planning in a wide variety of contexts (Boardman & Bullock, 1991; Grossberg 1978a, 1978b; Houghton & Hartley, 1996; Page & Norris, 1998; Rhodes et al., 2004). The properties of the LIST PARSE motor working memory simulate neurophysiological data collected during macaque motor performance from the dorsolateral prefrontal cortex (Averbeck et al., 2002, 2003a, 2003b); see Figure 9 and the exposition below. As noted above, Competitive-Queuing models of motor planning have received extensive support from movement latency data in a wide variety of tasks; see Farrell & Lewandowsky (2004) and Rhodes et al. (2004) for reviews.

4.3 Trajectory Generator

The selected plan is transformed into a motor action via a trajectory generator (see Figures 2, 13b,c and 14b). The trajectory generator that is used in the LIST PARSE model is a variant of the Vector Integration To Endpoint, or VITE, family of models that was introduced by Bullock & Grossberg (1988a). Increasingly realistic versions of the model have, since that time, been successfully applied to explain movement kinematics for activities as wide-ranging as planned arm movements, speech articulator movements, cursive handwriting, ball catching, and piano performance (Bullock, Bongers, Lankhorst, & Beek, 1999; Bullock & Grossberg, 1988a, 1988b, 1989, 1991; Bullock, Cisek, & Grossberg, 1998; Bullock, Grossberg, & Guenther, 1993;

Bullock, Grossberg, & Mannes, 1993; Cisek, Grossberg, & Bullock, 1998; Dessing, Peper, Bullock, & Beek, 2005; Grossberg & Paine, 2000; Guenther, 1994, 1995; Guenther, Ghosh & Nieto-Castanon, 2003; Guenther, Hampson & Johnson, 1998; Jacobs & Bullock, 1998; Paine, Grossberg, & Van Gemmert, 2004).

The chosen motor plan (with activity S_i in Figures 2, 13a, c, and 14a) activates a Target Position Vector, or TPV (T_i in Figures 2, 13a, c, and 14b) which represents a target configuration of motor effectors; that is, where the effectors are commanded to move. This target vector is compared with an outflow representation of the Present Position Vector, or PPV (P_i in Figures 2, 13b, and 14b) which represents the present configuration of the motor effectors. The Present Position Vector is subtracted from the Target Position Vector to compute a Difference Vector, or DV (D_i in Figures 2, 13b, c, and 14b) which computes the direction and distance that the motor effectors need to move in order to realize the Target Position Vector. A volitional GO signal gates, or multiplies, the DV before it is integrated by the PPV; that is, the PPV integrates (GO)(DV), see D_iG in Figures 2, and 13 b, c. In this way, a new TPV can prime a DV before the volitional GO signal initiates movement. Increasing the GO signal increases movement speed. The PPV always approaches the TPV when the GO signal is positive, no matter how large the GO signal is chosen, because the GO signal multiplies the DV, which approaches zero as the PPV approaches the TPV. It is worth noting that, because the PPV integrates (GO)(DV), this product represents the instantaneous commanded movement speed.

A VITE circuit naturally embodies the Three S's of movement trajectory control: Synergy, Synchrony, and Speed (Bullock & Grossberg, 1988a). When the same GO signal multiplies a DV that controls a prescribed set of muscles (i.e., a synergy), those muscles contract in equal time (i.e., synchrony) and reach their respective TPV targets no matter how large the GO signal may be chosen (i.e., variable speed). Bullock & Grossberg (1988a) proved how such a trajectory controller can generate the bell-shaped velocity profiles that are ubiquitous in biological movement control, among many other properties of neurobiological and psychophysical movement data. Subsequent models have built upon this foundation to explain even more data in a self-consistent way.

Neurophysiological correlates of TPV, PPV, and DV computations have been reported in Brodmann's area 4 (primary motor cortex) and area 5 of the parietal lobe. These data are simulated and reviewed in Bullock, Cisek, & Grossberg (1998). Evidence for GO signal properties have been reported in the basal ganglia by Horak & Anderson (1984a, 1984b), among others. Brown, Bullock, & Grossberg (1999, 2004) review many data about basal ganglia gating in the context of a detailed model of how basal ganglia gating balances between reactive and planned movements, while regulating how planned movements may be learned (e.g., Alexander, & Crutcher, 1990a, 1990b; Alexander, Crutcher, & DeLong, 1990; Alexander, DeLong, & Strick, 1986; Hikosaka & Wurtz, 1989; Redgrave, Prescott, & Gurney, 1999).

4.4 Variable-Rate Volitional Control

Coordinating Variable-Rate Rehearsal and Performance at Multiple Sites. Volitional signals control variable-rate rehearsal and recall of action sequences. Given that the internal organization of stored knowledge (e.g., the items and their order stored in cognitive working memory) is not known at the source of the volitional signal, these signals are *nonspecific*; that is, a signal of equal size influences *all* of its target cells. These signals need to target all possible movement sites and the internal structure of the system as a whole translates these nonspecific volitional signals into contextually appropriate planned sequential behaviors.

Multiple stages of the system need to be coordinated by such volitional signals so that fluent variable-speed performance is achieved. For example, the volitionally triggered onset of a movement from the motor working memory needs to be coordinated with the gating off of output signals from the cognitive working memory to the motor working memory.

First, in Figures 2 and 13a, onset of the GO signal, G, inhibits read-out of the cognitive working memory activities, Y_i, to the motor working memory activities, F_i. The last cognitive working memory activities to have been loaded into the motor working memory are thus those that will be performed while G is on. In other words, the sequence to be performed by the motor working memory is now fixed.

Second, the rate with which items are read-out from motor working memory needs to be coordinated with the rate at which individual items are performed by the VITE trajectory generator. In Figures 2 and 13a, even as G inhibits read-out from the cognitive working memory, it increases the gain of the activities that are already stored in the motor working memory. A larger G implies a faster integration rate within the motor working memory, so that it can keep up with the faster rate of performance.

Third, the GO signal, G, in the trajectory generator is coordinated with the read-out of the next item for performance from the motor working memory by rehearsal wave activity R. The model proposes that the same volitional signal V activates both the rehearsal wave activity R, which begins the read-out of motor plans from the motor working memory, and the GO signal G, which supports the execution of each motor command in the trajectory generator. In order to test this prediction, one would seek a common basal ganglia source (of V) for inputs to dorsolateral prefrontal cortex (to control R) and also to cortical area 4, (to control G; see data and simulations in Bullock, Cisek, & Grossberg (1998)).

Fourth, the model can anticipatorily select the next motor plan in a sequence and prepare its execution prior to the successful completion of the preceding movement. As noted by Lashley (1951), in the absence of such anticipation, the performance of any novel sequence of movements (for which learned compensatory mechanisms would be ineffective) would degenerate into a procession of disjointed individual movements separated in time by at least two transmission delays: one when a sensory cue of movement completion is sent to the brain, and the other when transmission of the next motor command is sent from the brain to the motor effectors.

Distance and Speed Estimates Are Not Sufficient. What signals can be used to control variable-rate anticipatory timing of sequential performance? Perhaps the simplest cue, an estimated distance to target, while valuable, is insufficient for the task of anticipatorily timing movements because it yields essentially identical information irrespective of: (a) the speed of execution of the movement, and (b) the size of movement involved, such that the same distance to target could indicate the end of a large movement or the beginning of a small one. Other cues are needed to compensate for those limitations.

Other things being equal, faster sequence execution requires faster selection of the next movement in order to maintain seamless performance of a movement sequence. A velocity-sensitive cue may help to compensate for limitation (a) above. As noted above, the processing stage that computes (DV)(GO) represents the instantaneous commanded movement velocity. This velocity function has a unimodal Inverted-U shape (usually called a "bell-shaped velocity profile") as the DV is integrated through time until PPV equals TPV. This bell-shaped velocity profile is problematic as a timing cue for at least two reasons: (1) it is close to zero both near the beginning and end of a movement, which leaves limitation (b) unaddressed; and (2) smooth

movement sequencing implies that velocity does not necessarily approach zero between movements, except at the completion of the entire sequence, thereby eliminating a near zero crossing as an anticipatory cue.
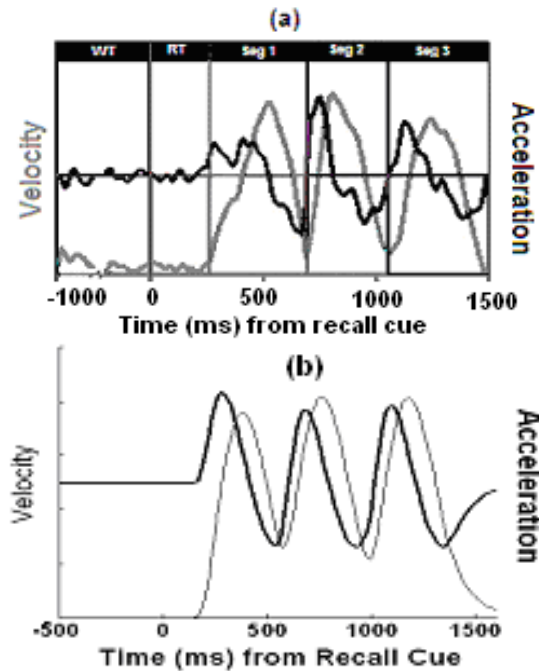

Figure 15. (a) Profile of movement kinematics (velocity and acceleration) from performance of a triangle during a monkey sequential copying task. (b) Internal estimates of velocity (*B*) and acceleration (*A* - *B*), based upon outflow velocity signals from the VITE trajectory generator, used by LIST PARSE model to construct the rehearsal signal (*R*). Note: in both graphs, the X-axis labels have been shifted so that 0 ms corresponds to the recall cue presentation time and the acceleration graphs have been shifted upward in both (a) and (b) to more easily portray the phase differences with the velocity graphs. (Adapted with permission from Averbeck et al., 2003a)

Using Acceleration/Deceleration Estimates to Control Volitional Signals. Kinematic factors that *are* capable of anticipating movement completion are the acceleration and/or deceleration of movement commands. Given a typical bell-shaped velocity profile (Figure 15a), the acceleration function is positive for the first part of a movement, negative for the last part of a movement and, for smooth movements, tends to approach (but not equal) zero near movement completion. This asymmetry between acceleration at movement initiation and completion provides information that may be used to resolve limitation (b). Given that movement plans do not seem to explicitly compute accelerations and decelerations, but rather difference vectors and outflow velocity estimates, the question remains of how a central movement planning mechanism can compute and use movement acceleration and deceleration estimates.

The LIST PARSE model proposes that acceleration and deceleration estimates are derived from the bell-shaped velocity profile. These estimates scale with changes in the actual speed of movement execution. The model proposes that this is accomplished in the following simple way: In addition to sending signals to the PPV stage, where they are integrated into outflow present position commands, the (DV)(GO) stage also sends signals to two parallel cell populations that time-average the velocity signals at different rates. Said in another way, the (DV)(GO) stage

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sends signals to three processing stages, one of which, the PPV stage, has a very small decay rate.

The cells that time-average the velocity signal more quickly are called *fast cells* (with activity A in Figures 14c), and those that time-average the velocity signals more slowly are called *slow cells* (with activity B in Figures 14c). During the beginning of a movement, the bell-shaped velocity curve increases. Hence the fast cells generate a larger activity A than the activity B of the slow cells, because the fast cells better track the increasing velocity signal, whereas the slow cells still remember the smaller velocity signals. At the end of a movement, the bell-shaped velocity curve decreases. Here, the fast cells generate a smaller activity A, because they better track the smaller velocities. The slow cells generate a larger activity B, because their time-average still remembers the larger velocities from when the bell-shaped velocity profile was still increasing. Thus, at the beginning of the movement, the difference $(B - A)$ (shown in Figure 14c) is negative, whereas at the end of the movement $(B - A)$ is positive. The model proposes that activity B excites the rehearsal cell activity R, whereas activity A inhibits the rehearsal cell activity. Because $(B - A)$ is positive towards the end of movement, and is sensitive to the rate of movement by being derived directly from the bell-shaped velocity profile, it can excite R before the present movement is over, and thereby enables the next movement command to be released in anticipation of completion of the present movement.

Thus, when a volitional signal V turns on, it excites the rehearsal wave R, which gates *on* the selection of the next motor item to be performed in a movement sequence (see S_i and R in Figures 14a, c). Read-out of this motor item activates the TPV of the trajectory generator (see S_i and T_i in Figure 14a, b) which, in turn, creates a non-zero DV. The volitional signal V also excites the GO signal G which begins the movement by gating the difference vector DV into a positive outflow velocity vector signal (DV)(GO) that is integrated by the PPV until it reaches the TPV (see V, G, D_i, P_i, and T_i in Figures 13b and 14a, b, c). This outflow velocity vector signal also activates the acceleration-sensitive signal $(B - A)$, which initially turns off R, thereby preventing the premature read-out of the next motor item (see S_i and R in Figure 14a, c, and A and B in Figure 14c). As the movement starts to decelerate, $(B - A)$ becomes positive, thereby making R positive, and enabling the next motor item to be read out before the previous command has been completed. In this way, successive motor items are read out in anticipation of completing the present motor command, thereby leading to seamless variable-speed performance of a sequence of movements.

Alternate approaches to the anticipatory initiation of selection in the context of prospective motor control for piano key presses and visually guided catching or hitting have recently been proposed that utilize an explicit computation of an estimated time-to-contact (TC) signal (e.g., Bullock et al., 1999; Dessing, Caljouw, Peper & Beek, 2004; Dessing et al., 2005; Jacobs & Bullock, 1998; Lee, 1976). While remaining agnostic as whether such a signal is computed in the brain, the LIST PARSE model utilizes a somewhat more direct means of controlling motor plan selection in which movement kinematics (velocity outflow signals) produce a deceleration computation that directly drive the gating of plan selection by way of the rehearsal signal (R).

5. RESULTS: DATA EXPLANATIONS AND SIMULATIONS

Variation in Simulation Protocol Between Experimental Paradigms. Presentations for the ISR simulations occurred every 5 simulation time units corresponding to the 500ms IOIs (see Figure 4) used in all of the modeled ISR tasks (1 simulation time unit = 100ms). These data were chosen for simulation because they reasonably could be assumed to minimize or eliminate covert

rehearsals and the associated confounds. That is, the very short ISIs in all experiments, the presence of distracter tasks in several (e.g., Cowan, 1999; Murdoch, 1961), and the explicit instruction not to rehearse given in several of the experiments (e.g., Cowan, 1999) serve to limit the likelihood of rehearsals.

Presentations of new items in the IFR simulations occurred every 12.5 simulation time units, corresponding to the 1.25 second IOIs (1 simulation time unit = 100 ms) used in the fast condition of experiment 1 in Tan & Ward (2000). In the IFR task, it has been established clearly (Brodie & Prytulak, 1975; Tan & Ward, 2000; Kahana & Howard, 2005) that rehearsal distribution can be widely variable between trials and/or subjects and is an essential consideration when assessing the typical shape of the serial position curve. A rehearsal consisted of a re-presentation of the item selected (rehearsal selection procedure discussed below) with the same stimulus duration (one simulation time unit) and magnitude (.1) as the ordinary stimulus inputs (I_i), at an interval evenly spaced between two presentations (i.e., 6.25 simulation time units after the most recent item presentation onset). For sub-span lists or lists with large inter-stimulus intervals (e.g., slow condition of Tan & Ward, 2000), there is some evidence that participants mimic sequential (ISR) rehearsal strategies; that is, rehearse as many items in presentation order, starting from the beginning of the list, as possible during each rehearsal period. However, for super-span lists and short inter-stimulus intervals, as modeled herein, such a strategy would result in rehearsal of only the first item or two every rehearsal period and it appears subjects use different rehearsal strategies (Tan & Ward, 2000). Due to these differing rehearsal strategies, the LIST PARSE model assumes two differences in the manner in which rehearsal and item storage takes place in the simulations of the serial recall and super-span, short-IOI IFR tasks: (a) given that veridical order information is irrelevant in the IFR task, subjects are assumed not to reset the cognitive working memory during rehearsal allowing for better item retention, at the expense of order, and (b) selection of an item for rehearsal in the IFR task is assumed to be probabilistic with the likelihood of selection at any time point being dependent upon the item's relative activation strength.

This probabilistic selection process was mathematically specified as follows. A re-analysis of the Tan & Ward (2000; figure 7b) data showed that the likelihood of a rehearsal of a previously presented item during a given rehearsal interval was load-dependent; that is, subjects were far less likely to rehearse previous items during rehearsal periods near the end of a list, when more items had been presented. Thus, at the designated time of a given rehearsal (6.25 simulation time units after the most recent item presentation onset), it was first determined whether any rehearsal at all would take place during this rehearsal period. In order to algorithmically capture this load-dependence, the likelihood of rehearsals seen in the data for a given rehearsal period (Figure 7b) was compared against a uniformly distributed random variable between 0 and 1 chosen at each rehearsal point in each trial. If the random variable fell below (within) the data-specified likelihood of rehearsals for a given rehearsal period, a previous item was selected for rehearsal; if the random variable exceed this number, then no rehearsal took place. In this way, the total probability of rehearsal for a given rehearsal sets was limited to correspond to the data. If an item rehearsal was designated to take place, the item selection was specified by adding a uniformly distributed (between 0 and .2) random amount of activation to the currently active item activations. The item with the largest activation above a fixed threshold (.5) was then chosen for rehearsal.

This algorithmic process can be understood biologically and within the context of the model diagram as follows. Each item's activity prior to selection can be interpreted as its starting position when it enters the selection process (*S*). During the stochastic selection process, random amounts of activation are added to the item starting positions so that one item maximally exceeds a fixed threshold and is selected. Items that have higher starting positions (initial activations) thus have a proportionate advantage in exceeding the threshold and being selected. If one were to additionally assume that this stochastic additive selection process takes longer the more activity it has to add to exceed threshold, we have a parsimonious explanation for the observed load effects in the IFR task within the LIST PARSE model context. That is, given that the activations of items are partially normalized, the average activation levels of items entering the selection circuit are less when more items are being retained and thus have farther to go to exceed the fixed threshold. The latency of the first item selection would be greater with a larger working memory load, and thus a higher probability of "no rehearsals" within the fixed time intervals would occur near the list end. Simulations of similar load latency effects observed in sequential tasks (e.g. Sternberg, Monsell, Knoll & Wright, 1978) by normalizing competitive-queuing networks using such assumptions have previously been demonstrated (Boardman & Bullock, 1991; Rhodes et al., 2004).

The probabilistic nature of rehearsal order in the IFR task simulations (i.e., subjects may rehearse a different order and number of items each trial) creates wide variation in the activation levels of individual items at the time of recall from trial to trial. Thus 250 separate trials (Monte Carlo simulations), for which error proportions were computed separately and averaged across trials for each serial position, were conducted to capture a broad distribution of possible rehearsal patterns. Otherwise, the simulation techniques described below were the same across the ISR and IFR task simulations.

Modality Effects. Page & Norris (1998) suggested that modality-related recency effects (e.g., the advantage in recall for the last one or two items for audibly presented lists as compared with visually presented lists) may occur because, during auditory list presentation, the last presented item is recalled from a reliable independent processing stage (e.g., the pre-categorical acoustic store of Crowder & Morton, 1968). Not only is the last item recalled more reliably from this store but the lack of its interference with other items in the list can improve their performance as well, particularly the last few items in the list which are most likely to interchange with this last item. Watkins & Watkins (1980) provided evidence that such a reliable limited capacity store may persist for more than four seconds. This assumption provides an expedient explanation for the suffix effect (Crowder, 1978), in which the addition of a single irrelevant auditory item greatly attenuates modality differences, and is shared by the LIST PARSE model. Thus, for audibly presented lists that use written recall, the last presented item is presumed to be recalled nearly perfectly, due to being stored in a separate echoic memory buffer, and is not present in the competitive working memory stage of the model. Read-out from this echoic memory is performed algorithmically in the present version of the model. The lower echoic processing level from which the last item is read-out into motor production is hypothesized to be part of the auditory perception/production loop that is learned through imitation of other speakers (Cohen, Grossberg & Stork, 1988; Grossberg, 2003b)

Error Simulation Assumptions. As described above, the parallel activation gradient of items above threshold in cognitive working memory is loaded into motor working memory where upon the largest motor plan activity is selected and suppressed. The process is then iterated until all associated motor plans above threshold in motor working memory have been selected and

suppressed. Within this modeling framework, order errors (which are only meaningful during the ISR task) occur when a motor plan representing an inappropriate item (typically another item in the list that should be recalled later) has the largest representation at the time of a particular serial position's recall. Such distortion of the primacy gradient is presumed to be due to noise that distorts the activation gradients of the cognitive working memory or the motor working memory. Item errors occur when the activation level of an item in motor working memory falls below a threshold level of activation prior to being selected, or the activity level of an item in cognitive working memory does not exceed a threshold in order to become instantiated in motor working memory.

Some simplifying assumptions with respect to the influence of noise were made in order to reduce the time necessary to perform circuit simulations: (a) Order errors in the serial recall simulations in (Figures 5a, 6, and 8a, c) were assumed to occur as a result of distortions due to Gaussian noise within the activation gradient of the cognitive working memory. (b) Rather than having noise operate continuously in time, zero mean Gaussian noise (with a variance of .015) was added to the activations in cognitive working memory (Y_i) at a single time point, five simulation time units after the time of the recall cue. The recall cue in all *immediate* serial and free recall simulations (Figures 5a, 6, 7, and 8a) occurred five simulation time units after the onset of the last item in each simulation. In Figure 8c, which demonstrates delayed recall performance, the recall cue presentation time was chosen to be consistent with the variable retention intervals in the data with a conversion of 1 simulation time unit = 100ms. (c) Omissions of items was taken to occur if the activation level of items after the inclusion of noise failed to exceed an output threshold (.165). In other words, the simplifying assumption was made that omissions were the result of items in cognitive memory (Y_i) failing to exceed the output threshold when entering motor working memory (in F_i) rather than activity being also continually assessed to see if it falls below threshold within motor working memory. This simplification allowed for the computed activation levels prior to noise addition to be held static and 100,000 separate noise additions ("trials") to be averaged to obtain stable average network performance. Running a comparable number of full network simulations in which stochastic processes continuously operated at multiple levels in the network was computationally infeasible.

Although these simplifying assumptions were made for computational ease, the resulting error patterns should not differ significantly from those of a more realistic stochastic simulation. The most compelling reason is that errors were assessed at the time they are most likely to occur. The inputs from Y_i continuously compress throughout time, becoming more susceptible to order errors the longer multiple items are simultaneously held, and they drive the activity levels in motor working memory, F_i, until they are gated off by the initiation of motor responses, G. Noise influences this late activity pattern. Subsequently, the self-normalizing dynamics in motor working memory make additional item and order errors progressively less likely, because as items are selected and suppressed their activity is redistributed to the remaining items, thereby expanding the range of activation between them. Thus, the majority of errors in the model are due to confusions during encoding in cognitive and motor working memory prior to first item selection. Model parameters relevant to order error production (see Gaussian noise variance, and variables *b*, *e*, and *F* in Appendix equations (2) and (3)) were selected to provide a best fit for the performance curves in Experiment 1 of Henson et al. (1996, Figure 6) and the omission threshold, relevant to item errors, was selected to provide a best fit for the performance curves in

Experiment 1 (fast condition) in Tan & Ward (2000). All parameters were identical for all cognitive simulations (Figures 5, 6, 7, and 8).

Primacy and Bowing of Serial Position Gradient. Most ordinal models of sequence representation (e.g., Farrell & Lewandowsky, 2002; Page & Norris, 1998) assume a primacy gradient and then use it to explain cognitive data. These models naturally have decreased order error rates for the first and last items in a list due to end effects (Page & Norris, 1998). That is, order errors are generally explained as noise causing an item to become more or less activated than another item, leading to its selection earlier or later than is appropriate. Items with the largest and smallest activation have fewer items with similar activation levels to their own with which to have interchanges. The one-item recency portions observed in the sub-span ISR protocols simulated in Figure 5a and in the peaks (circles) of Figure 6 may be attributed to these end effects.

Figure 5a demonstrates simulations of the serial position performance curves (Figure 5b) of Cowan et al. (1999) which used quickly presented (two per second; 500ms IOI) auditory lists of 5-8 items and a visual distracter task to prevent rehearsal. As described above, simulations of all the ISR tasks were produced by presenting inputs (I_i) of one simulation time unit duration and magnitude = .1 every five simulation time units to the noiseless cognitive working memory circuit (see Figure 11). Given that these were auditory lists that required written recall, the last item in the list was assumed to be recalled nearly perfectly and kept separate from the competitive working memory interactions. Gaussian noise was then applied to this gradient five simulation time units after the recall cue, as an indication of the pattern of activity that is transferred to the motor working memory just before being gated off during motor performance. Order and omission errors for each serial position were calculated based upon this noisy activation gradient and 100,000 iterations of this noise application and error assessment were conducted and averaged to obtain a stable picture of model performance.

Performance was nearly perfect for shorter lists in both the data and model simulations, and thus were omitted for clarity of representation. The simulations provided a close match to the data for all of the list lengths in the attended speech condition of the Cowan et al. (1999) study, with the most significant departure being that subject performance of the first item of every list length tested was perfect. These fits are particularly impressive given that the ISR task that the model parameters were selected to fit (Experiment 1 of Henson et al., 1996, Figure 6) only studied one list length (six visually presented items) and, despite having an identical IOI of 500ms, performance for the first item in this list length was significantly below 100 percent. Thus, a more precise fit of this aspect of the Cowan et al. (1999) study was not to be expected, and model parameters were not specifically tailored to this task in the interest of showing the main effect. One possible difference between the two tasks was the presence of a two second retention interval in the task used by Cowan et al. (1999) which could potentially have been used to covertly selectively rehearse the first couple of items immediately before recall.

In contrast to other ordinal models (e.g., Page & Norris, 1998), the LIST PARSE model maintains that these end effects, in addition to a mechanism to account for omissions, are only part of the explanation for the recency portion of the ISR or IFR serial position performance curves. Purely end effect accounts would seem to be contradicted by the existence of recall protocols in which a recency portion of more than one or two items appear (e.g., verbal ISR: Cowan et al., 1999; spatial ISR: Jones, Farrand, Stuart & Morris, 1995; IFR: Tan & Ward, 2000). In the LIST PARSE model, the inherent dynamics of the cognitive working memory may yield a variety of bow configurations depending upon a number of experimental parameters, particularly

number of items, rehearsal schedule and volitional gain control which influence the working memory competition. In this way, the same neural dynamics that produce a primacy gradient for short lists (Figure 11b) produce bowed activity gradients with extended recency portions for lists well beyond the length for which ISR tasks can be performed veridically, but which are typical of the IFR task (Figure 11b).

The shape of the activation gradient in cognitive working memory for short and long lists is determined as follows (see Figure 11). Brief bottom-up excitatory inputs are received in the cognitive working memory by layer 4 cells (with activities, X_i, in equation (2) of the Appendix) and layer 6 (with activities, Y_i, in equation (3) of the Appendix). Due to the shunting on-center off-surround competitive dynamics of the cells in layer 4 and the parameters (b and F in equation (2)) chosen, the cells partially normalize activity across the network and respond rapidly and strongly to alterations in bottom-up stimulus input. Thus, while these brief pulses are active, they are typically sufficient to make the activation level of cells receiving these inputs in layer 4 larger than the activations levels of cells not receiving inputs, regardless of the number of active cells. However, the lack of similar competitive dynamics in layer 6 and different parameters (e in equation (3)) leads these cells to behave essentially as leaky integrators. The bottom-up inputs merely partially activate the cells in layer 6 to which they are directed and, while the bottom-up inputs are being presented, the most recently activated item is typically also the least active. Between presentations of items, or after presentation of the list, the layer 4 and 6 cells serve as a positive feedback loop in which the somewhat different representations in the two layers influence one another. The slow changing gradient, for short lists, that typifies layer 6 cell activity becomes instituted in the layer 4 cells and the normalized activities in the layer 4 cells sustain the activations in layer 6. Thus, for short lists, the activations in layer 6 are largely dictated by the length of time they have been integrating the activities in layer 4 and so primacy dominates.

As more items enter the working memory network (i.e., when lists become long), the average activation level of cells in layer 4 continues to decrease due to the self-normalizing dynamics of the network. Combined with the partially normalizing shunting term in the layer 6 cells (see Appendix), these cell activations cannot sustain the high firing rates of the layer 6 cells and the average activity level of layer 6 cells drops. When a sufficient number of items are presented to the cognitive working memory, corresponding approximately to span list length in the ISR paradigm, the average activation levels of layer 6 cells are small enough that the strong bottom-up pulse inputs drive the incoming item to have an activity level greater than at least one of these stored items (i.e., a recency portion is instituted). When the bottom-up pulse ceases, similar dynamics diminish this new item's representation so that, when the next item is presented, it has a greater activation than the last item (i.e., extended recency). Thus, the same dynamics that produce a clear primacy gradient for short lists can produce extended recency effects as more items enter the competition.

In addition, an inhibitory volitional gain control signal, F (see equation (2) in the Appendix), serves to modulate the level of competitive interaction that occurs within the network. If a strong inhibitory signal is present (e.g., large parameter F in equation (2) due to a lack of volitional support), then this strong competitive influence will make it difficult for items to become significantly activated in layer 4; a medium gain signal allows a few items to become significantly active but limits the average activity level in layer 4, which in turn leads to an early onset of recency (i.e., reduced ISR span); a weak inhibitory signal allows for many items to become significantly active and enables the accurate retention of their order information in a

primacy gradient (i.e., strong volitional support, for instance due to attentional focus, can lead to larger memory spans; see Figures 2 and 11b).

These bowed gradients naturally lead to a higher probability of recall for the final items in extended lists and thus an extended bow in *item* errors. However, assuming a competitive-queuing self-inhibitory mechanism operating on such a gradient to produce output, the LIST PARSE model predicts that these items would tend to be recalled earlier in the list than is desirable in the ISR task, resulting in pronounced *order* errors for these items. Thus, for super-span ISR tasks, the dynamics which produce a bowed activation gradient predict significant recency portions of the *item* serial position curve, with less prominent *order* and *total* (item and order errors) serial position performance curves. This pattern of error distributions is, in fact, observed in subject performance of super-span ISR tasks (Drewnowski, 1980; Drewnowski & Murdoch, 1980; Watkins & Watkins, 1980; for a review: Henson, 1998b). An additional consideration is that experimental protocols in which the subject is aware of the number of items in the list (e.g., blocked list length paradigms) or actually provided with this information during recall (e.g., use of visible blanks that responses are placed in) may allow subjects to use compensatory output strategies to simply place the final remembered items at the known end of the list, leading to artificially high serial position performance on these items.

Figure 7 demonstrates model simulations of the serial position performance curves and aspects of the overt rehearsal distribution obtained for a 20 item IFR task in the fast condition of Experiment 1 of Tan & Ward (2000). In this task, words were visually presented every 1.25 seconds and subjects were instructed to read the word aloud and to rehearse previously presented words overtly while being tape recorded. Subjects were then required to write down as many words as they could recall for one minute following a recall cue. As described above, simulations of the IFR tasks were produced by presenting inputs (I_i) of one simulation time unit duration and magnitude = .1 every 12.5 simulation time units to the noiseless cognitive working memory circuit. Depending upon the likelihood of rehearsing a previously presented item seen in the data (Figure 7b), a single additional "rehearsal", consisting of a re-presentation of a probabilistically (based upon relative activity level) chosen previously presented item, was performed 6.25 simulation time units after each new item presentation onset (i.e., evenly spaced between novel item presentations). After presentation (and rehearsal) of the entire list, Gaussian noise was then applied to the gradient five simulation time units after the recall cue, just as in the ISR simulations. Omission errors for each serial position were calculated based upon whether an item's noisy activation level exceeded the output threshold and 100,000 iterations of this noise application and error assessment were conducted and averaged across to gain a stable picture of model performance given the particular rehearsal sequence used. The above simulation process was conducted 250 times in order to gain a broad distribution of the possible rehearsal orders that the system might produce and all of the results were averaged together to produce the average performance characteristics shown in Figure 7.

The LIST PARSE model provides remarkably close fits to these IFR data given that the model parameters were chosen to fit a six item ISR task without rehearsal (as described above) and limited additional assumptions were made to specifically model it. To the authors' knowledge, the LIST PARSE model is the first cognitive neural model to provide quantitative simulations of both free and serial recall performance data. Within Figure 7, panel (a) shows the average activation of the Y_i cells at the time that errors were assessed as well as the omission threshold. Panel (b) plots the likelihood that a previously presented item was rehearsed during each rehearsal set; that is, during the inter-stimulus interval after each novel item presentation.

To obtain this measure, a re-analysis of the Tan & Ward (2000) data was conducted in which the percentage of trials on which each item was rehearsed during each rehearsal set (defined as the items overtly rehearsed between the onset of a one stimulus and the presentation of the next) was summed and the percentage of rehearsals of the item that was presented on the screen during each rehearsal set (~100%) was omitted; that is, the instructed reading aloud of the item presented on the screen which occurred on essentially all trials was omitted in order to identify the rehearsals that occurred during the ISI). For panel (c), the probability that an item was recalled was plotted against its presented order; that is, the standard serial position performance curve, termed nominal serial position in Tan & Ward (2000). For panel (d), the last rehearsal set in which each item was read aloud or rehearsed was calculated and performance was averaged across the items in each set, providing a rough estimate of performance versus time of last vocalization. In panel (e), the last time each item was vocalized, either during a rehearsal or presented on the screen, was calculated and the items, and their associated probability of recall, were arranged on the x-axis based upon this order of last presentation (termed *functional* order in Tan & Ward, 2000). While the information contained in panels (d) and (e) are similar, panel (e) describes probability of recall based upon the *order* in which items were last rehearsed, whereas panel (d) describes the probability of recall based upon a coarse measure of how long ago (i.e., *time*) they were last rehearsed. Finally, panel (f) shows the difference between the set in which an item was last rehearsed and the set in which it was first presented.

Error Type Distributions. Simulations of the error distribution in the ISR task from Experiment 1 in Henson et al. (1996), which used six item visually presented lists of letters with 500ms IOIs and written recall, are presented in Figure 6. This simulation was created using the same procedure, including five simulation unit IOIs and assumed lack of covert rehearsal, as used to simulate the Cowan et al. (1999) data in Figure 5a, with the exception that this task involved visually presented 6 item lists, so no advantage for the final list item was assumed. The calculated serial position of each recalled item (or lack of such a position in the rare case of omissions), as indicated by the Gaussian noise distorted activation gradient, was recorded across the 100,000 trials, averaged and plotted.

This simulated task was used to specify the values of the relevant model variables used by all of the ISR and IFR simulations in this paper (see *b*, *e*, and *F* in Appendix equations (2) and (3)). Simulations and resulting error distributions were performed for all values of: *b*, from .1 to 2 with step size of .1; *e*, from .05 to 1 with step size of .05; *F*, from .25 to 20 with step size of .25; and Gaussian noise variance from .01 to .025 with .001 step size. The values that provided the best fit to the data in this task (*b* = .7; *e* = .05; *F* = 1.25; Gaussian noise variance = .015) were then chosen. Given the rarity of omissions in the task, the output threshold, applied to determine if an item was recalled or omitted, was determined by obtaining a best fit to the free recall data. For the serial recall tasks modeled herein, this output threshold preferentially causes omissions of the last and penultimate items due to their having the least activity in the primacy gradient and was chosen to be at the level (.165).

In the absence of noise, item activities representing neighboring sequential recall positions naturally have less difference in their activation levels than more distant items (see Figure 11b, left panel). The addition of Gaussian noise to this activation gradient will thus tend to increase interchanges of items in neighboring serial positions preferentially (Figure 6). Should an item from later in the list erroneously acquire the largest activation and be selected, the remaining items are still biased toward a primacy gradient (which the noise originally served to obscure)

and thus the most likely item to be selected will be the skipped item (i.e., the model framework naturally produces fill-in effects; Norris, Page, & Baddeley, 1994).

List Length Effects. The fact that increasing the number of items to be retained has a negative influence upon the ability to remember the entire list is well established. Crannell & Parrish (1957) used visually presented lists to show that increasing list length actually produces an S-shaped curve in the ability to *correctly recall entire lists*. Simulations of these list length effects are presented in Figure 8a. These simulations were created using the same procedure used to simulate the Henson et al. (1996) data in Figure 6, with the addition that simulations were performed for lists of five, six, seven, eight, nine, and ten items. Additionally, correct performance of the entire list is at issue in the Crannell & Parrish (1957) and Baddeley & Hitch (1975) data, so only simulated recall trials that produced correct recall *of the entire list* were counted as correct. The percentage of trials at each list length that produced accurate recall of the entire list was then plotted (Figure 8a).

Longer lists resulted in increased list errors for a number of reasons in the LIST PARSE model. For instance, the additional items themselves provide increased opportunities for interchanges, and thus order errors, due to noise. Also, the time needed to present the additional items (while maintaining the same IOIs) results in longer intervals of time that the first items must be stored and thus more time for their representations to compress together.

Temporal Limitations Upon Recall. The imposition of a delay prior to recall during which rehearsal is prevented (i.e. a filled retention interval) dramatically reduces the ability to correctly recall a list. Simulations of these delay effects as shown in a serial recall task using sub-span length lists by Murdoch (1960) are presented in Figure 8c. These simulations were created using the same procedure used to simulate the Crannell & Parrish (1957) and Baddeley & Hitch (1975) data in Figure 8a, with the caveats that simulations were performed only for lists of three items and performance was assessed after unrehearsed retention intervals of 1-24 seconds (with the convention used throughout the ISR simulations of 1 simulation time unit = 100ms). The percentage of trials at each retention interval that produced accurate recall of the entire list was then plotted (Figure 8c).

After approximately 9 seconds in both the data and simulations, performance plateaus at approximately 20% (see Figure 8b). Although Murdoch (1960) did not present separate results for item and order errors in this task, the LIST PARSE model predicts that for sub-span lists (three items in this task) unrehearsed retention intervals have a particularly detrimental effect with respect to order retention. That is, unrehearsed retention intervals result in increased list errors due to the increased time that item representations have to compress, or become more similar in activation level (see Figure 11a). The observed performance plateau corresponds to a situation in which the activation levels of the three items have become so similar that noise dominates the recalled order of the list. Assuming that subjects largely retain item information for *sub-span* lists in the absence of rehearsal (which is anecdotally suggested by the high level of performance in the one item condition, which eliminates all order information, in the left panel of Figure 2), pure chance for the ordering of three items would indicate a plateau performance level of 16.7% (1 out of 6 possible orderings of 3 items).

The simulations presented above provide quantitative fits to a wide range of phenomena from immediate serial recall, delayed serial recall and immediate free recall under simplifying assumptions (listed above) that limits noise-based error modeling to cognitive working memory (see equations (2) and (3) in the Appendix). The circuit is only part of a larger functional architecture (Figures 1 and 2) which is needed to perform even the most basic sequential motor

performance tasks. For instance, when operating with the motor plan selection and execution modules (specified below), the cognitive working memory can sequentially perform a list of actions and on-the-fly rehearsals, by which the items are effectively re-presented to the cognitive working memory. When operating in conjunction with the cortical list chunking circuitry (specified below), the cognitive working memory has a means of storing extended sequences of items and recalling them from memory. These additional circuits were not included in the simulations above for computational ease. This simplification eliminated additional degrees of freedom that could aid in fitting the data, but had the additional cost of not incorporating mechanisms needed for the brain to perform the tasks, which are also missing in all previous models of these tasks. Simulations of data constraining aspects of these performance circuits are provided below.

Sequential Movement Neurophysiology. As noted in Section 3.2, neurophysiological recordings from the dorsolateral prefrontal cortex of monkeys demonstrated a parallel activation gradient of sequential movements with larger total activation corresponding to earlier sequential performance; a primacy gradient of planned movements (Averbeck et al., 2002, 2003a, 2003b). Simulations of the Averbeck et al. (2002; Figure 9a) data by cell responses, F_i, in the motor working memory are shown in Figure 9b. The cells in F_i interact within a recurrent shunting on-center off-surround network, or recurrent competitive field, which has the property of self-normalization; i.e., the total activation across the network is approximately the same over time (Grossberg, 1973, 1980). Thus, reduced activation of one cell population leads to an increase in activation of other active cells in the network.

The simulations of these data by the cell population activities in the plan storage field, F_i, of motor working memory (Figure 9b) were produced by presenting 3, 4, and 5 input sequences with 5 simulation time unit IOIs, identical to the methodology used in the serial recall simulations (Figures 5, 6, and 8). The motor plan field activities were algorithmically held at zero until the 25th simulation time unit across all list lengths, at which point the activations in cognitive working memory were allowed to flow into the motor plan field. This procedure was used to capture the qualitative effect of buffer loading from cognitive into motor working memory without the additional degrees of freedom that an separate volitional buffer loading parameter would allow. The pattern that is stored in motor working memory at the time of the recall cue (at the 35th simulation time unit) is the same whether this algorithmic buffer loading procedure is used or items are continuously loaded from cognitive working memory.

As task performance proceeds through each phase, as discussed in Section 3.2, the following response properties of F_i arise: (1) The primacy gradient of item representations present in cognitive working memory, Y_i, is transferred to their associated motor plans in motor working memory, F_i, prior to the initiation of the first movement; (2) this primacy gradient is contrast-enhanced to favor the item to be performed (i.e., greater relative representation of the most active item) prior to item performance. This enhancement is due to GO-based gain enhancement and a visual feedback signal generated by the eye movement that precedes the arm movement, consistent with the monkeys' reported eye movement patterns (Averbeck et al., 2003a, p. 132): "The monkeys generally made a saccade to the template after it appeared [in the representative figure, the monkey foveated the first segment of the eventual movement sequence]. They then made a saccade back to the drawing area as drawing began, followed by a sequence of smaller saccades falling near the advancing copy trajectory as this progressed;" (3) just prior to performance of an arm movement, the maximally activated plan, S_i, is amplified above threshold and selected. This selected plan is forwarded to a motor target position representation, T_i, and

feedback inhibition (S_i to F_i) suppresses the chosen representation in F_i. The self-normalizing dynamics of the plan network in F_i enhances the activities of the other plans and prevents perseveration; (4) the data are ambiguous as to whether there is a natural re-establishment of the primacy gradient when all of the items in the sequence have been selected; see right-hand sides of the data traces in Figure 9. The self-normalizing dynamics of the cells in F_i would result in such a re-establishment and re-performance of the list unless the volitional signal, V, to continue rehearsing is turned off.

Different parameters were needed to fit human cognitive data and monkey sensory-motor data. The shape of the motor working memory primacy gradient prior to initiation of the monkey movement sequence (Figure 9) differs from that of the cognitive working memory used to fit the human cognitive data (Figures 11). At least three possible reasons for this difference are: (1) the different species of subjects: macaque monkeys vs. humans; (2) different movement tasks: arm control during copying of a concurrently presented figure versus visual or verbal recall of sequentially presented items; and (3) different levels of learning: the monkeys in the copying task knew which shape would need to be copied and performance of the sequence was well-learned and practiced, whereas the cognitive tasks involved novel sequences of familiar items. Any of these reasons, even assuming shared brain mechanisms between tasks and across species, could account for something as simple as different levels of attention which could distort the gradient in cognitive and motor working memory. While remaining agnostic as to the reasons for the difference in gradient shape, the variables of the cognitive working memory which determine this gradient shape ($b = 2$, $e =. 2$ and $F = 15$ in equations (2) and (3) of the Appendix) were hand-chosen to fit the gradient in F_i at the marked time (Figure 9b) for the triangle in the Averbeck et al. (2002) data. These parameters were then used to produce the simulations for the four (inverted triangle) and five (square) item sequences in Figure 9b.

Velocity and Acceleration Approximations. The LIST PARSE model proposes that internal estimates of velocity (DV)(GO) and deceleration ($B - A$) are computed from neural outflow movement signals and used to anticipatorily time rehearsal of even novel sequences of well-learned movements. The pattern of these internal representations of velocity and acceleration (Figure 15b) closely match the observed kinematics recorded from monkeys performing the copying task described above (Figure 15a). Note that the acceleration signal that is used by the LIST PARSE model to time rehearsal is most appropriately described as a *de*celeration ($1 -$ acceleration), whereas the observed *ac*celeration is plotted in Figure 15b.

Explanations of Other Data Properties within the LIST PARSE Framework. The LIST PARSE model provides a conceptual framework within which several groups of working memory phenomena can be qualitatively explained and neurally interpreted (Figure 1). Included in these phenomena are presentation modality effects, discussed in the modality effects section (above), and temporal grouping effects (Ryan, 1969). Items that enter cognitive working memory at nearly the same time (i.e., are temporally grouped by having short IOIs) are integrated in the cognitive working memory, Y_i, for similar amounts of time and hence have similar levels of activation. Inserting a long pause (larger IOI) in the middle of a sequence results in significantly different integration times for the items in working memory before the pause and those after the pause. This results in a large difference between activations of these two groups of items. Therefore, the dynamics of the cognitive working memory imply that (a) order errors between temporally grouped items are more likely than errors across temporal groups, and (b) end effects (and thus bows) occur within temporal groups due to the unlikelihood that the smallest item of one group will interchange with the very different level of activity of the largest item in other

temporal groups. Properties (a) and (b) are both well-established effects of temporal grouping (e.g., Ryan, 1969). Simulations of the relative *order error proportions* produced by the LIST PARSE model when a six item list with 500 ms IOIs has an additional pause of 200 ms inserted between the presentations of the third and fourth item are provided in Figure 16a. All of the other simulation protocols (e.g., stimulus duration, magnitude of stimulus, noise variance, etc.) were identical to those used in the simulations of the Henson et al. (1996) data in Figure 6.
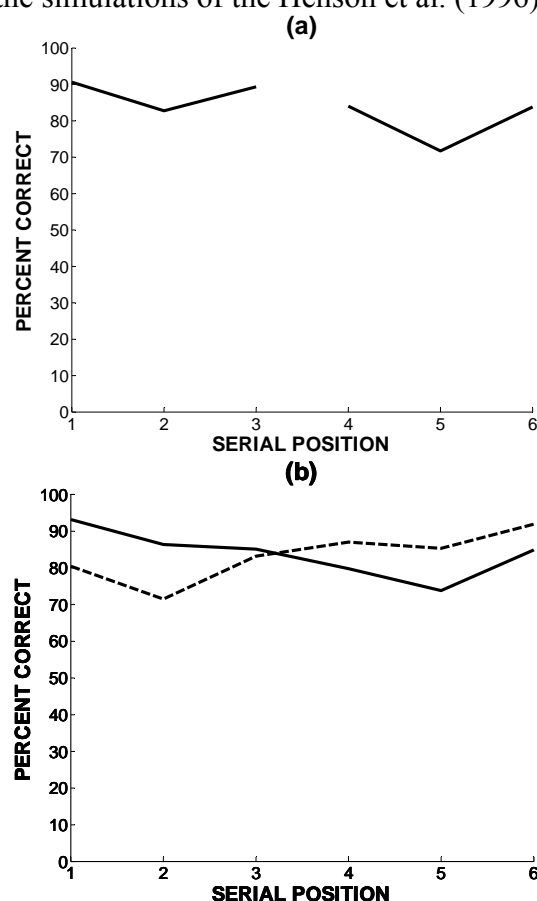

Figure 16. Simulation of the proportion of order errors vs. serial position for 6 item lists with: (a) an extended pause (IOI equal to 7 time units) between the third and fourth items, and IOIs of 5 simulation time units between other items, and (b) IOIs of 5 (solid) and 10 (dashed) simulation time units between all items.

Variations in experimental protocols (e.g., IOI) can have dramatic effects upon the distribution of errors even when rehearsal is prevented. However, few studies have applied long IOIs while simultaneously employing distracter tasks that could realistically be expected to prevent (both phonological and attentional) covert rehearsal during these delay periods (one example in the free recall paradigm is: Watkins, Neath & Sechler, 1989). The LIST PARSE model predicts that extended IOIs in which all forms of rehearsals can be convincingly prevented would preferentially decrease performance at the beginning of the list (reduced primacy) but may improve performance of the ends of the list. In effect, increased IOIs cause the beginning items in the list to experience competitive working memory interactions for much longer before the recall period actually begins, resulting in more compression of their activations and a loss of order information to noise. The extended IOIs between recently presented items in the list

however result in their having more difference in their integration times, and thus more distinct activation levels and order retention, than they would have with shorter IOIs. Thus the LIST PARSE model predicts that, for short lists, longer delays between items would be beneficial to working memory performance due to improved order encoding (in contrast to the predictions of pure temporal decay accounts of working memory). Simulations of the *order errors* predicted in each serial position by the LIST PARSE model for serial recall of a six item list with ten simulation time unit IOIs (with no rehearsals) are presented in Figure 16b. All of the other simulation procedures were identical to those used in the simulations of the Henson et al. (1996) data in Figure 6.

The effects of phonemic similarity of items has been modeled (Page & Norris, 1998; Henson, 1998b) through the addition of a second stage of processing after item selection for recall in which phonological codes are reconstructed for motor output and confusions occur between active phonemically similar items. These data are not simulated herein due to the similarity of the LIST PARSE model account to the one in Page & Norris (1998), except to say that an analogous process of phonological reconstruction is presumed to occur in the stage that transforms speech plans between the point when they are selected (stage *S* of the model) and specific motor targets, *T*, are specified in the trajectory generation circuitry; see Figures 1 and 2. "Saw tooth" error patterns, in which phonologically confusable items are less likely to be recalled in their correct serial position due primarily to transpositions with phonemically similar items, are the natural result of this second processing stage (see Page & Norris (1998) for a review of this phenomenon and its modeling).

6. COMPARATIVE ANALYSIS OF WORKING MEMORY MODELS

The most influential general framework for the functional organization of human working memory is that elaborated by Baddeley (1986) which combines a "central executive" (controlling a wide range of "higher cognitive" functions) and two separate slave subsystems. One of those subsystems, termed the *phonological loop*, uses a volatile *phonological store* to passively store auditory information and an *articulatory control process* for the manipulation of phonological information. A set of processes are presumed to perform analogous function for visuo-spatial information through the *visuo-spatial sketchpad* subsystem. Within this widely-held general conceptual framework, various approaches to the modeling of working memory phenomena (including those of free recall and serial recall) have been taken.

6.1 Free Recall Modeling

Although order information is not conceptually necessary for rote free recall performance, free recall modeling has the dual confound of needing to address (a) the extent to which subjects use order information during performance, and (b) the potentially more complex rehearsal strategies that are likely to be employed in free recall, since the most conceptually simple strategies (e.g., repetitively rehearsing in serial order from the start of presentation list or repetitively rehearsing the last presented items) are not necessarily either optimal strategies or the way that subjects actually rehearse items. Few, if any models, have attempted to provide detailed accounts of the rehearsal strategies that subjects use during free recall except to note that most studies of rehearsals in free recall (e.g., Tan & Ward, 2000) rule out repetitive rehearsal completely and serial order rehearsal for lists with short to medium length IOIs and many items.

Among the most successful classes of free recall models are the distinctiveness models (e.g., Bjork & Whitten, 1974; Crowder, 1976; Howard & Kahana, 2002; Murdoch, 1960; Nairne, 1990; Tan & Ward, 2000). Among these models, the *temporal distinctiveness models* typically

propose that the ratio of the time between instances of item rehearsals (e.g., between the first and last rehearsal, ΔT; see Figure 7f) and the time from the last rehearsal of a particular item before the beginning of recall, T (see Figure 7d), largely accounts for the item's likelihood of recall. Detailed neural mechanisms which may underlie such a distinctiveness account have not yet, to the authors' knowledge, been detailed. A common analogy used to illustrate the model (e.g., see Tan & Ward, 2000) is that of a line of telephone poles separated by a distance, ΔT, with a separation between the observer and the last of these poles given by T. The smaller the distance, ΔT, between a pole and one of its duplicates, the more difficult it is to distinguish any particular instance of it. In contrast, the larger the distance, T, between the observer and the last pole the greater the difficulty of identification of any one of them is, because of the smaller perceived distance between the poles. The explanatory capabilities of these theories, given their relative simplicity, make them an appealing metaphorical explanation of free recall data and beyond (for a review: Tan & Ward, 2000), but they have not been generalized to perhaps the fundamental working memory protocol, the ISR task.

The LIST PARSE model provides an alternative neurally-specified variation of the temporal distinctiveness "ratio rule" that Tan & Ward (2000) used to account for these distribution curves. In the LIST PARSE model, for all but the last rehearsed (or presented) items in a span or super-span list, the longer an item goes unrehearsed in the presence of other items, the less likely it is to be recalled because competitive dynamics continually push items toward a sub-threshold equilibrium point. This tendency roughly correlates with the detrimental effect of increasing "retention interval (T)" in the ratio rule of Tan & Ward (2000). With short retention intervals (e.g., items rehearsed at the ends of long lists), however, there are strong recency effects because these recently presented items have had less time to "decay" and still retain much of the activation they acquired at last presentation (e.g., see the gradients in Figures 7a and 11c).

The rehearsal of an item in the LIST PARSE model significantly boosts its activity relative to the other items in the list, and this boosted activity makes it more likely that this item will be rehearsed again later in the list. Items at the beginning of lists therefore have a natural tendency to be rehearsed more often and further down the list relative to their starting position than other items (see Figure 7f), because they have fewer items competing with them to be rehearsed early in the list, and these early rehearsals boost their representations relative to the items that come in the middle of the list. Therefore, we see extended primacy effects (due to extensive rehearsal of the first items in the list) in the performance curves as well. These effects roughly correlate with the "ΔT" effects of the ratio rule of Tan & Ward (2000).

Finally, even some of the secondary factors noted by Tan & Ward (2000) to have an influence upon probability of recall, like the influence of rehearsal grouping, have clear correlates in the LIST PARSE model. The competitive dynamics of the cognitive working memory assure that the relative boost in activation due to the rehearsal of an item that is already highly active is less than that for an item with lower activation. Therefore, several rehearsals of an item that are temporally close together will have less net effect in keeping the item's activity large (and increasing probability of eventual recall) than the same number of rehearsals more evenly spaced throughout the list.

6.2 Serial Recall Modeling
The various neural modeling approaches to serial recall (particularly the ISR task) can generally be placed into three general schools: associative chaining, positional, and ordinal (for a more general review: Henson, 1998b).

Associative Chaining Theories. Associative chaining theories, for example TODAM (Lewandowsky & Murdock, 1989), Jordan's (1986) compound-chaining model or Elman's (1990) simple recurrent model, rely principally upon associative links between ordered items to produce serial responses. While interitem associations certainly play a role in list learning across multiple trials (e.g., Klein, Addis & Kahana, 2005), and these models are conceptually simple, using mechanisms that are well-known to exist in at least some neural contexts (e.g., simple associative learning and priming mechanisms), their mechanical simplicity also leaves them with little hope of accounting for several central competencies of working memory function. Perhaps the most famous counter-evidence for an associative chaining account of serial performance is Lashley's (1951) analysis of typing errors and kinematics, in which he found that (a) his own typing errors tended to be transpositions of neighboring items (for a more rigorous analysis of typing errors: see MacNeilage, 1964), and (b) by analyzing the response times of experienced typists, he concluded that feedback signals of completion of a keypress could not be the central signal to cue the next keypress. Under his reasoning, nerve fiber signal conduction is too slow and many actions must have central parallel "partially activated or readied" representations that can be anticipatorily queued. In response to these well-accepted limitations, all modern chaining theories incorporate central planning mechanisms. For a more extensive review of the evidence for limitations of associative chaining and discussion of possible alternatives, see Hartley & Houghton (1996) and Henson et al. (1996). In fact, Item and Order working memories were derived from an analysis of limitations of associative chaining theories and of how both sorts of mechanisms could be joined together for cognitive and sensory-motor control into *context-sensitive avalanches* (Grossberg, 1978a).

Positional Theories. The second class of models of serial ordering is positional theories (e.g., Burgess, 1995; Burgess & Hitch, 1992, 1999; Henson, 1998b; Johnson, 1991). Here, positional information (either absolute or relative to the beginning and/or end of lists) is directly maintained to establish recall order. These models have the advantage of being able to account conceptually for certain data that simple models of other types cannot easily explain at present; e.g., an increased likelihood of intrusions at similar list positions across trials, or of interchanges in similar within-group positions in the same list when using temporal grouping protocols (Burgess & Hitch, 1999; Henson, 1998b). Among the most common weaknesses of these models are that: (a) the source of the positional data used in the model is often difficult to biologically implement or justify (e.g., the cues' implementation in neural processes are often unclear); (b) order information often does not emerge in an self-organizing context (e.g., some models require knowledge that an item is the end of a list in order to accurately calculate the end-of-list positional cues, while others use attentional activation windows which presumably must have learned to accurately store relative positional information across a wide spatial distribution of cells); (c) they do not scale well to account for multi-level serial order storage (e.g., they require the use of higher-level attentional windows to provide positional information which presumably must be used at all levels of the learning process); and (d) they typically do not treat repetitions of items. It should be noted that some recent positional models (e.g. Henson, 1998) use item representation gradients to maintain positional information (e.g., primacy gradients representing position relative to list start and recency gradients for position relative to list end). As such, there is some question as to the basis that such relative positional models should be classified as positional versus ordinal.

Ordinal Theories. The third class of models, ordinal theories (e.g., Bradski et al., 1994; Cohen & Grossberg, 1987; Farrell & Lewandowsky, 2002; Grossberg, 1978a, 1978b; Hartley & Houghton, 1996; Nigrin, 1993; Page, 1994; Page & Norris, 1998), represent both order and item information concurrently with temporal order based upon relative item activation (typically a primacy gradient). This class of models, of which the LIST PARSE model is an example, has the advantages of being able to naturally account for certain data sets (e.g., response latency data; for a review: Farrell & Lewandowsky, 2004) that other models are incapable of accommodating, being conceptually simple, capable of self-organizing in a neural network context, and enjoying straight-forward biological interpretations. However, these models tend to (a) lack full treatments of item repetition phenomena (e.g., the Ranschburg effect, in which repeated items separated by more than one item are less likely to be recalled than distinct items, whereas less separation increases probability of recall, reviewed in Kahana & Jacobs, 2000, and Henson, 1998a; however, see Bradski et al., 1994 for a partial treatment of repetition), and (b) fail to handle some of the positional error data for which other (positional) models have more ready explanations (e.g., the ability of Burgess & Hitch (1999) and Henson (1998b) to treat positional item interchanges across trials or temporal groupings). The limitations in (b) suggest that direct positional information of some sort may indeed be used in the coding of temporal order in the brain. However, what mechanisms and processing levels may be used to implement such information, and how such information may complement the type of temporal order storage that is described herein, and for which there is accumulating behavioral and neurobiological evidence, remain open questions.

6.3 Advances of the LIST PARSE Model

The extensive interest in working memory function by cognitive psychologists over at least the past century has generated a wide-range of established phenomena across a variety of experimental tasks. As a result of this effort, working memory models of how these properties can be realized have been developed, including many that attempt to incorporate biologically plausible mechanisms (e.g., Baddeley, 1986; Boardman & Bullock, 1991; Bradski, Carpenter & Grossberg, 1994; Burgess & Hitch, 1999; Cohen & Grossberg, 1986; Dreher & Burnod, 2002; Durstewitz & Seamans, 2002; Farrell & Lewandowsky, 2002; Gillund & Shiffrin, 1991; Grossberg, 1978a, 1978b; Grossberg & Myers, 2000; Grossberg & Stone, 1986a; Gupta & MacWhinney, 1997; Mannes, 1994; Page & Norris, 1998; Rhodes et al., 2004). Taken together, these models have begun to explain large cross-sections of the cognitive, neurophysiological and functional imaging working memory data. Despite the growing competency of these models within the domains of their target paradigms, a more comprehensive treatment of working memory function must address all of these data sets, including cognitive data from both the IFR and ISR protocols given that both protocols almost certainly require at least some of the same working memory mechanisms. To the present, the LIST PARSE model is the first model to provide a unified quantitative account for all these classes of data using the laminar circuits that are prominent in the lateral prefrontal cortex.

Thus, among the advances of the LIST PARSE model beyond previous ordinal and competitive queuing models of which it is an example are that, (a) whereas the primacy model (Page & Norris, 1998) mathematically specified initial item activations and decay functions, the LIST PARSE model's parallel cognitive working memory gradients arise dynamically from real-time self-organizing network operations; (b) the LIST PARSE model offers the first unified quantitative account by any neural processing model of known properties from both ISR and IFR protocols; (c) rather than conceptually reiterating how competitive queuing assumptions could

allow sequential selection of items from a primacy gradient, the LIST PARSE model implements a competitive queuing architecture in testable neurobiologically plausible circuits and illustrates how observed neurophysiological recording data correspond to the dynamics of item selections from a motor working memory; and (d) the LIST PARSE model proposes how variations of laminar cortical circuits that have explained and predicted many data about how visual cortex sees (Grossberg, 2003a; Raizada and Grossberg, 2003), can also be used to predict how lateral prefrontal cortex stores sequential information in a temporally evolving working memory and learns them as sequential plans that can be read-out as sequences of actions or cognitive operations. Additionally, the model simulates electrophysiological data concerning the mechanisms that the primate brain uses to perform sequential actions (Averbeck et al., 2002) through a competitive selection architecture in motor planning working memory, as first proposed by Grossberg (1978a) and later termed a competitive queuing (CQ) system (for reviews, see: Bullock & Rhodes, 2003; Rhodes et al., 2004; Houghton & Hartley, 1996). The LIST PARSE model hereby makes detailed predictions about how granular neocortical circuits may be specialized to learn and carry out a wide range of intelligent tasks, and substantially advances the program of developing a unified theory of how the neocortex works.

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APPENDIX

A.1 Cell Membrane Equations

Model cell dynamics obey membrane, or shunting, equations that interact (Hodgkin & Huxley, 1952; Grossberg, 1973). Each model cell possesses a single voltage compartment with membrane potential, $V(t)$, given by an equation of the form:

$$C_m \frac{d}{dt} V(t) = -\left(V(t) - E_{leak}\right)\gamma_{leak} - \left(V(t) - E_{inhib}\right)\gamma_{inhib}(t) - \left(V(t) - E_{excit}\right)\gamma_{excit}(t). \qquad (1)$$

In (1), the time-varying conductances $\gamma_{excit}(t)$ and $\gamma_{inhib}(t)$ represent, respectively, the total excitatory and inhibitory inputs, as described by the model architecture (Figures 2, 10, and 13), in addition to a constant leakage conductance, γ_{leak}, which maintains a resting membrane potential in the absence of inputs. Reversal potentials are set to: $E_{excit} = 1$, $E_{inhib} = -1$, $E_{leak} = 0$ except where otherwise indicated. These continuous-time differential equations were numerically integrated using a fourth-order Runge-Kutta algorithm and implemented in C++.

A.2 Simulation Conventions

Inputs to the cognitive working memory system, I_n, were pulse inputs arbitrarily taken to be of magnitude .1 and 1 simulation time unit duration. For all tasks, 1 simulation time unit was equivalent to 100ms within the experimental protocol. Thus, items were presented every five simulation time units to correspond to the 500ms IOIs (Figure 4) used in all serial recall tasks and presented every 12.5 simulation time units to correspond to the 1.25 second IOIs used in the free recall task. The recall cue in the ISR and IFR tasks (Figures 5, 6, 7 and 8a) occurred one IOI after the onset of the last item presentation. In the delayed serial recall task (Figure 8c), the same time conversion (1 simulation time unit = 100ms) was used to compute the appropriate delays for each of the retention intervals (Figure 8b) before presentation of the recall cue.

For all cognitive data error simulations (Figures 5, 6, 7, and 8), at 5 simulation time units after the time of the recall cue, zero mean Gaussian noise with standard deviation .015 was applied to all cognitive working memory item activations, Y_i. This method of simulating noise was selected for computational ease in order to capture, in the simplest possible way, the effects of internal system noise. However, similar results would be expected if the noise were more realistically applied continuously during pattern storage. Also for computational ease, no noise was applied in the motor working memory. Thus, any noise-dependent distortions of output order were inherited by the motor working memory from the cognitive working memory. The output signals, $f_5(Y_i)$ (see equation 13), from cognitive working memory to motor working memory in equation (10) includes a threshold (.165) that determines whether the corresponding activities are omitted or recalled.

At the designated time of a potential rehearsal in the free recall task (6.25 simulation time units after the most recent item presentation), a uniformly distributed random variable between 0 and 1 was compared that to the corresponding likelihood of rehearsing a previous item in the given rehearsal set in the data (Figure 7b) to determine whether a rehearsal should occur. If a rehearsal was chosen to occur, the item to be rehearsed was specified by adding a uniformly distributed random amount of activation (between 0 and .2) to the current item activations. The item with the largest activation above a fixed threshold (.5) was chosen for rehearsal. Rehearsal consisted of a re-presentation (an input of .1 magnitude and duration of 1 stimulus time unit) of this item to the circuit.

A.3 Cognitive Working Memory

Working Memory Storage of Activity Gradients. The cognitive working memory consists of a recurrent on-center off-surround shunting network that includes two layers of interacting cells (layers 6 and 4) that store an activity gradient.

Layer 4. The activity X_i of the ith layer 4 cell obeys the shunting on-center off-surround equation:

$$\frac{d}{dt}X_i = -.1X_i + (1 - X_i)(I_i + e[Y_i]^+) - FX_i \sum_{k \neq i}(I_k + e[Y_k]^+).$$ (2)

As in equation (1), the three terms on the right hand side of (2) are the passive decay, excitatory, and inhibitory terms, respectively. Excitatory inputs are the bottom-up inputs, I_i, from the ith item category and from positive activation of the ith layer 6 cell output signal $[Y_i]^+$. Off-surround inhibitory inputs come from all the other bottom-up input channels ($k \neq i$) from item categories, I_k, and layer 6 output signals $[Y_k]^+$. Parameter F measures the effect of volitional gain control; see Figures 2 and 10a. For human cognitive data simulations, $e = .05$ and $F = 1.25$; for monkey neurophysiological data simulations, $e = .2$ and $F = 15$.

Layer 6. The activity Y_i of the ith layer 6 cell obeys a shunting equation:

$$\frac{d}{dt}Y_i = -.1Y_i + (1 - Y_i)(I_i + b[X_i]^+ + \sum_j f_1(C_j)M_{ji}),$$ (3)

where

$$f_1(C_j) = \frac{C_j^3}{(.000001)^3 + C_j^3}.$$ (4)

Equation (3) contains only passive decay and excitatory terms. Excitatory inputs to the ith layer 6 cell are the bottom-up inputs, I_i, from the ith item category, top-down intracortical feedback from the positive layer 4 output signal $[X_i]^+$, and top-down intracortical sigmoid feedback, $f_1(C_j)$, from layer 2/3 cells. These signals are multiplicatively gated by the adaptive weights, or long-term memory traces, M_{ji} that enable list chunks to read-out into the cognitive working memory the pattern of item categories that they represent. For human cognitive data: $b = .7$; for monkey neurophysiological data: $b = 2.3$.

A.4 List Chunks and Masking Field Networks

Layer 2/3. Item sequences that are stored in the cognitive working memory are grouped, or categorized, through learning into list chunk cells in layer 2/3 by a *masking field* network. A masking field is a self-similar, multiple-scale, recurrent on-center off-surround network (Cohen & Grossberg, 1987; Grossberg, 1978a; Grossberg & Myers, 2000). The activity of the jth list chunk is C_j. List chunks obey dynamics that allow for (a) partial activation of a list chunk when the items in cognitive working memory form a subset of the list that a chunk has learned to code, but (b) strong competitive suppression, or masking, of chunks that code smaller sequences by the chunk whose optimal item sequence is presently active in working memory. By property (a), list chunk activities reflect the "amount of evidence" for the list that they code; they predictively prime the future by becoming more active as the amount of evidence for them increases. By property (b), list chunk activities enable the network to make the "best prediction" that can be based upon the current temporal context; see Figure 12. List chunks also gradually learn to reactivate the pattern of items in the cognitive working memory that activated them, so that their activation can control unitized read-out of a sequence of items into the cognitive working memory system. The masking field equations for list chunks, C_j, are:

$$\frac{d}{dt}C_j = -.1C_j + (1 - C_j)\left[\frac{20}{10 + J}\sum_i [X_i]^+ W_{ij} + .001(J)f_1(C_j)\right]$$
$$-2[1 + C_j]\frac{\sum_k f_1(C_k)K(1 + (K \wedge J))}{\sum_k K(1 + (K \wedge J))},\tag{5}$$

where

$$f_1(C_j) = \frac{C_j^{\ 3}}{(.000001)^3 + C_j^{\ 3}}.\tag{6}$$

The masking field contains passive, excitatory, and inhibitory inputs. These inputs obey a *self-similarity* property whereby larger scales have more weight in the cooperative-competitive struggle for cell activation. The excitatory input consists of two terms: (1) Positive inputs, $[X_i]^+$, from layer 4 that are normalized by *1/(10 + J)*, which increases with the number *J* of inputs converging on list chunk *j,* and filtered by learned bottom-up adaptive weights, or long-term memory traces, W_{ij}, that enable the list chunk to be selectively activated due to learning; and (2) self-excitatory feedback sent through a sigmoid signal function, $f_1(C_j)$, that helps to store list chunk activity in working memory and whose strength increases with the number *J* of cortical inputs that the cell receives.

Inhibitory inputs, $\dfrac{\sum_k f_1(C_k)K(1 + (K \wedge J))}{\sum_k K(1 + (K \wedge J))}$, balance the excitatory ones. Layer 2/3 cells have

different sizes and interactions whose strengths scale with cell size. Terms *J* and *K* refer to the number of inputs that cells C_j and C_k receive, respectively, and $K \wedge J$ refers to the number of inputs that the two cells C_j and C_k share. Thus, larger cells *K* inhibit a neighboring cell *J* more than smaller cells, and the strength of competition depends upon how many working memory items $K \wedge J$ are shared by *K* and *J*. The sum, $\sum K(1 + K \wedge J)$, in the denominator normalizes the total strength of inhibitory connections to each cell to equal 1. For simplicity, each possible sequence of items in cognitive working memory was represented by one list chunk.

A.5 Bottom-up and Top-Down Cognitive Learning

Layer 6-to-2/3 Adaptive Filter. The bottom-up adaptive weight, W_{ij}, from the ith item in layer 4 to the jth list chunk in layer 2/3 is defined by the self-normalizing instar learning equation:

$$\frac{d}{dt}W_{ij} = a_1 f_2(C_j)\left[(1 - W_{ij})d_1 X_i - h_1 W_{ij}\sum_{k \neq i} X_k\right],\tag{7}$$

where

$$f_2(Z) = \frac{Z^3}{(.00001)^3 + Z^3}.\tag{8}$$

(Carpenter & Grossberg, 1987). In (7), activity of the list chunk C_j opens a learning gate $f_2(C_j)$ that enables weight W_{ij} to track X_i. Due to the excitatory term, $(1 - W_{ij})d_1 X_i$, each item *i* attempts to code a proportion of the total weight 1. The inhibitory term $h_1 W_{ij}\sum_{k \neq i} X_k$ ensures that these learned weights are competitively distributed among all the items that succeed in activating C_j. Biologically, the connections between cells in layer 4 and layer 2/3 are assumed to be widely distributed, with each C_j receiving connections from a limited subset of possible X_is. For the

simulation in Figure 12, however, connections were chosen such that each of the C_j cells was connected to a different size subset of the items in the presented sequence. All weights were initially taken to have the same small initial value (.001). In all simulations, $a_1 = 1$, $d_1 = 1$, and $h_1 = 2$.

Layer 2/3-to-6 Top-Down Expectations. The top-down weight, M_{ij}, from the jth list chunk in layer 2/3 to the ith item in layer 6 is defined by the outstar learning equation:

$$\frac{d}{dt}M_{ji} = a_2 f_2(C_j)\left[Y_i - M_{ji}\right]. \tag{9}$$

(Grossberg 1968, 1980). In (9), activity of the list chunk C_j opens a learning gate, $f_2(C_j)$, that enables weight M_{ji} to track Y_i. This connectivity completes a functional loop within the cognitive working memory, in which a stored pattern in working memory activates list category chunks with activities C_j that code for that pattern through the learned layer 4-to-2/3 adaptive filter and send top-down learned expectations back to working memory through layer 2/3-to-6 connections. In this way, the partial activation of a list category chunk (for instance, due to activation of a portion of the list it codes) may prime other items that have accompanied this list in the past. Biologically, these connections are presumed to be widely distributed, with each C_j sending connections to a large subset of the Y_i. For simplicity, the connections from each C_j were assumed to connect with each Y_i and to start with a small initial adaptive weight, $M_{ji} = .001$. In all simulations, $a_2 = 1$.

Layer 5 interneurons are presumed to be part of this feedback connectivity (as shown in Figures 2 and 10; and are known to exist in visuo-cortical areas: Briggs & Callaway, 2001; Callaway & Wiser, 1996), but were omitted from the simulations in Figure 11 since layer 5 acts primarily as a relay from layer 2/3-to-6 in the model.

A.6 Motor Working Memory

Working Memory Storage and Selection of Motor Plans. The motor working memory consists of a network with two layers of interacting cells, a motor plan field (F_i) that stores motor plans as an activation gradient and a plan selection field (S_i) that selects the most active motor plan and forwards it to the trajectory generator. The motor plan selection circuit implements a self-normalizing variation of a competitive-queuing architecture (Grossberg, 1978a; Hartley and Houghton, 1996).

Motor Plan Field. The activity F_i of the ith motor plan field cell obeys the recurrent competitive field equation:

$$2\frac{d}{dt}F_i = -.1F_i + (1 - F_i)\left[(1 + G)f_3(F_i) + E_i + (1 - f_4(G))f_5(Y_i)\right]$$

$$- F_i\left[100\left[S_i - .5\right]^+ + (1 + G)\sum_{k \neq i}f_3(Q_k) + \sum_{k \neq i}E_k + (1 - f_4(G))\sum_{k \neq i}f_5(Y_k)\right], \tag{10}$$

where

$$f_3(Z) = \frac{Z^{1.2}}{.8^{1.2} + Z^{1.2}}, \tag{11}$$

$$f_4(Z) = \frac{Z^2}{.02^2 + Z^2}, \tag{12}$$

and

$$f_5(Z) = \left[Z - .165\right]^+. \tag{13}$$

The three terms on the right hand side of (10) are the passive decay, excitatory, and inhibitory terms, respectively. The excitatory inputs are a contrast-enhancing self-excitatory feedback term, $f_3(F_i)$, boosted by the presence of a GO signal (G), a selective boost (e.g., in the monkey copying task; see Figure 9) of visual attention, E_i, associated with eye movement and a thresholded bottom-up input, $f_5(Y_i)$, from the ith layer 6 cell in the cognitive working memory system, which is gated off by the presence of the volitional GO signal, $(1-f_4(G))$. The inhibitory inputs are derived from the excitatory inputs in the form of off-surround signals that balance the excitatory input and prevent saturation of cell activities (Grossberg, 1973). A strong specific inhibitory feedback signal, $100[S_i-.5]^+$, from supra-threshold activation of the ith plan in the plan selection field, S_i, prevents perseveration by inhibiting an item from the motor plan field after it is selected for motor output ("inhibition of return"). Off-surround ($k \neq i$) recurrent inhibitory signals, $\sum_{k \neq i} f_3(Q_k)$, come from other plans whose activity is processed by inhibitory interneurons with activities, Q_k, before being contrast-enhanced via signal, $f_3(Q_k)$. As for the excitatory on-center input, the inhibitory inputs are boosted by the GO signal. The other inputs are similar, namely the eye movement related attentional boost signals, E_k, and bottom-up inputs, $\sum_{k \neq i} f_5(Y_k)$, from layer 6 cells of cognitive working memory.

The attentional boost signals, E_k, are assumed to be pulses of duration 1 and magnitude .4 and occur two simulation time steps before item selection (in the plan selection field, S_i) during the monkey copying task. These signals are assumed to be received from a similar motor working memory that controls eye movements operating in parallel to the arm movement control system (e.g., from FEF or SEF), but for simplicity, such a parallel system is not modeled herein. They contribute to the enhancement of chosen movement commands seen in the data. The recurrent competition between items in the motor plan field is processed through inhibitory interneurons with activities, Q_i, that time-average the motor plan field activities, F_i:

$$\frac{d}{dt}Q_i = F_i - Q_i .\tag{14}$$

Time-averaging imposes a slight lag in inhibition and leads to smoother activity profiles in the motor plan field.

Plan Selection Field. The activity S_i of the ith plan selection field cell obeys the winner-take-all recurrent competitive field equation:

$$\frac{d}{dt}S_i = -.1S_i + (1 - S_i)([R]^+ F_i + [S_i - .5]^+) - 20S_i \sum_{k \neq i}[S_k - .5]^+ .\tag{15}$$

The three terms on the right hand side of (15) are the passive decay, excitatory, and inhibitory terms, respectively. The excitatory inputs, $([R]^+ F_i + [S_i - .5]^+)$, are a bottom-up input, F_i, from the ith cell in the motor plan field gated on by a positive rehearsal signal, $[R]^+$, and a self-excitatory feedback term when the cell exceeds an activity threshold, $[S_i - .5]^+$. Strong off-surround inhibitory signals, $20S_i \sum_{k \neq i}[S_k - .5]^+$, come from cells in other plan selection channels ($k \neq i$). The threshold-linear self-excitatory feedback, together with threshold-linear competitive inhibition of other cells when a cell exceeds that threshold, allows only one cell to become super-threshold (i.e., winner-take-all; Grossberg, 1973, 1980). The winning cell activates the trajectory generator through output to T_i in equation (16), and sends self-inhibitory feedback that suppresses its bottom-up input, F_i in (10), thereby preventing perseveration when the rehearsal signal again gates on bottom-up inputs, F_i, for the selection of the next motor plan.

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A.7 VITE Trajectory Generator

The motor Target Position (T), Position Difference (D), Outflow Velocity ($[D]^+G$), and Present Position (P) fields correspond to the Target Position Vector (TPV), Difference Vector (DV), Outflow Velocity ($[DV]^+GO$), and Present Position Vector (PPV), respectively, of the Vector-Integration-To-Endpoint, or VITE, model (Bullock & Grossberg, 1988a, 1991; Cisek et al., 1998).

Target Position. The activity T_i of the ith target motor position cell obeys the network equation:

$$\frac{dT_i}{dt} = -.5T_i + (1 - T_i)(100[S_i - .5]^+) . \tag{16}$$

The two terms on the right-hand side of (15) represent passive decay and excitatory terms, respectively. Equation (16) simplifies the idea that $[S_i - .5]^+$ activates a learned target position. Passive decay via term, $-.5T_i$, quickly removes the target when it is no longer supported by activity in the plan selection field. See Gaudiano and Grossberg (1991) for an analysis of how a TPV can be learned.

Position Difference. The activity D_i of the ith motor position difference cell obeys the following equation:

$$\frac{dD_i}{dt} = -D_i + [T_i]^+ - P_i . \tag{17}$$

The three terms on the right-hand side of (17) represent a passive decay, excitatory, and inhibitory terms, respectively. This cell receives excitatory input from a positive target motor position, $[T_i]^+$, and inhibitory input representing the current motor position, $-P_i$. Thus, the Motor Position Difference field (D) serves as an internal estimation of the distance between the current motor position (P) and the target motor configuration (T).

Outflow Velocity. The activity of the Position Difference field, $[D_i]^+$, is gated by the volitional GO signal, G. This gated signal, $[D_i]^+G$, scales the rate at which the Present Position, P_i, approaches the Target Position, T_i, as well as driving the differential integration-rate velocity cells, A and B, which in turn gate the selection of the next movement.

Present Position. The activity P_i of the ith present position cell obeys the following equation:

$$\frac{dP_i}{dt} = [D_i]^+ G . \tag{18}$$

Here, P_i, integrates the rectified difference, $[D_i]^+$, between present and target positions at a rate, $[D_i]^+ G$, that is determined by the volitional GO signal, G.

A.8 Motor Volition

Volitional Signal. A volitional signal, V, coordinates all the performance read-out processes and scales the desired rehearsal rate with the rate at which movement occurs. The volitional signal serves as excitatory input to the GO signal, G, and rehearsal signal, R. For all tasks, $V = 0$ during the presentation phase of the task, and 1 during the recall phases of the tasks, as indicated by the recall cue.

GO Signal. The activity, G, of the GO signal cells obey the leaky integrator equation:

$$\frac{dG}{dt} = -G + V . \tag{19}$$

The two terms on the right hand side of (19) are passive decay and excitatory terms, respectively. The GO signal (G) time-averages the excitatory input it receives from the volitional signal, V, making it positive when recall is desired and scaled by the desired performance speed. GO signal

cells modulate the speed of trajectory generation via the present position cells, *P* in (18), and close the cognitive-to-motor read-out gate from the cognitive working memory system, *Y*, to the motor plan field, *F*, during rehearsal (see (10)). These signals also modulate the rate of plan selection during rehearsal, as noted below.

A.9 Variable-Rate Rehearsal

Performance Rate Estimators. The activities, *A* and *B*, of the fast and slow performance rate estimator cell populations obey the leaky integrator equations:

$$\frac{dA}{dt} = \phi\left[-.1A + G\sum_i [D_i]^+ \right],$$ (20)

and

$$\frac{dB}{dt} = \theta\left[-.1B + G\sum_i [D_i]^+ \right],$$ (21)

respectively. The two terms on the right hand sides of (20) and (21) are passive decay and excitatory inputs, respectively. These cells are excited by the same outflow velocity signals as the speed-sensitive cells (see (18)) and time-average these inputs at fast, ϕ, and slow, θ, rates. As a result, *A* and *B* lag the current outflow velocity signals by different degrees, so that their difference, *B - A*, approximately indicates the phase (increasing or decreasing portion) of a bell-shaped velocity performance curve (see Figure 15). Integration rates of the cell activities *A* and *B* (parameters ϕ and θ in equations (20) and (21), respectively) were selected so that items were selected at a rate of approximately 500ms each (consistent with the rate of presentations in the ISR simulations). For all tasks: $\phi = 3$; $\theta = 1$.

Rehearsal Signal. The activity, *R*, of the rehearsal signal cells obey the following equation:

$$\frac{dR}{dt} = -R + V + 10(B - A).$$ (22)

The three terms on the right hand side of (22) are passive decay, an excitatory volitional term, *V*, and a term, *B − A*, that may be either excitatory or inhibitory, depending upon task dynamics. In particular, the rehearsal signal, *R*, receives excitatory input from the volitional signal, *V*, indicating that the system is in the recall phase of the task. The rehearsal signal also receives excitatory input from slowly integrating velocity cells, *B*, and inhibitory inputs from quickly integrating velocity cells, *A*. During the initial phase of a movement, the fast cells, *A*, are more active as they closely track the bell-shaped velocity performance curve, causing inhibition by (*B − A)* of the rehearsal signal. As the movement nears completion, the fast cells, A, closely track the decline in velocity at the end of the bell-shaped velocity curve while the slow cells, *B*, still encode the peak velocity, so the net effect on (*B − A*) is excitatory. A net positive rehearsal signal (*R*) opens the rehearsal gate in equation (15), thereby allowing inputs from the motor plan field (*F*) to update the plan selection field (*S*), and initiates selection of the next movement before current movement completion (i.e., achieves anticipatory movement selection).