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Memory for serial order across domains: An overview of the literature and directions for
future research



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Abstract

From vocabulary learning to imitating sequences of motor actions, the ability to plan, represent, and recall a novel sequence of items in the correct order is fundamental for many verbal and nonverbal higher-level cognitive activities. Here, we review phenomena of serial order documented across the verbal, visual, and spatial short-term memory domains, and interpret them with reference to the principles of serial order and ancillary assumptions instantiated in contemporary computational theories of memory for serial order. We propose that functional similarities across domains buttress the notion that verbal, visual, and spatial sequences are planned and controlled by a competitive queuing (CQ) mechanism in which items are simultaneously active in parallel and the strongest item is chosen for output. Within the verbal short-term memory CQ system, evidence suggests that serial order is represented via a primacy gradient, position marking, response suppression, and cumulative matching. Evidence further indicates that output interference operates during recall, and that item similarity effects manifest both during serial order encoding and retrieval. By contrast, the principles underlying the representation of serial order in the visual and spatial CQ systems are unclear, largely because the relevant studies have yet to-be-performed. In the spatial domain, there is some evidence for a primacy gradient and position marking, whereas in the visual domain there is no direct evidence for either of the principles of serial order. We conclude by proposing some directions for future research designed to bridge this and other theoretical gaps in the literature.

Memory for serial order across domains: An overview of the literature and directions for future research

In a seminal article, Karl Lashley (1951) drew attention to the fact that a fundamental requirement for most if not all behaviors is the ability to process serial order information. The capacity is central to verbal behaviors ranging from speech perception and generation to vocabulary acquisition and spelling, as well as nonverbal behaviors ranging from motor control to planning, and goal-directed action. Lashley dubbed the problem of how behaviors are sequenced in these and other domains as *the problem of serial order in behavior* and he declared it to be one of the most important problems in psychology.

This article is concerned with one instantiation of this general problem—the problem of serial order in short-term memory. Applied to this domain, the problem of serial order is to specify how a novel sequence of items or events is stored and recalled in the correct order. This problem has fascinated experimental psychologists ever since the time of Ebbinghaus (1964) and it has been the subject of a wealth of research, largely owing to a conviction that memory for serial order is crucial for various higher-level cognitive activities. For example, in the verbal domain, memory for serial order is thought to be a basic requirement for vocabulary learning (Baddeley, Gathercole, & Papagno, 1998; Page & Norris, 2009), since the learning of a new word depends crucially on being able to remember the phonemes that make up that word in their correct order (for evidence consistent with this view see Baddeley et al., 1998; Gathercole & Baddeley, 1990; Leclercq & Majerus, 2010; Majerus, Poncelet, Greffe, & Van der Linden, 2006). In the nonverbal domain, memory for serial order is thought to be important for the acquisition of many motor skills and social behaviors, which are often learned by observing and imitating sequences of actions performed by others (Agam, Bullock, & Sekuler, 2005; Agam, Galperin, Gold, & Sekuler, 2007; Baddeley, 2007). The presumed importance of

memory for serial order is further underscored by evidence that people exhibit a preference to recall information from memory in forward serial order even when the task demands do not require it (Bhatarah, Ward, Smith, & Hayes, 2009; Bhatarah, Ward, & Tan, 2006, 2008; Grenfell-Essam & Ward, 2012; Howard & Kahana, 1999; Kahana, 1996; Ward, Tan, & Grenfell-Essam, 2010), suggesting that forward ordered recall may be a general principle of memory.

The problem of serial order has been studied extensively in verbal short-term memory using the task of serial recall in which participants are given short sequences of familiar verbal items (e.g., letters, digits, or words) that they must subsequently recall in order. Much of this research has been interpreted within the framework of the working memory model of Baddeley and Hitch (1974; see also Baddeley, 1986, 2000, 2007), which comprises (amongst other components) a subsystem for the retention of verbal information known as the phonological loop, complemented by a subsystem for the retention of visual and spatial information known as the visuospatial sketchpad. The phonological loop has been successful in explaining a wealth of serial recall data at a qualitative level, including the effects of phonological similarity, word length, articulatory suppression, presentation modality, and the complex interplay between these four variables. This explanatory success notwithstanding, as noted by Burgess and Hitch (1992), a major shortcoming of the phonological loop is that it lacks any detailed mechanism(s) for the retention of serial order.

This omission highlights a need for more formal accounts of serial recall. Accordingly, building on earlier attempts to model serial order (e.g., Estes, 1972), a number of researchers have developed computational models of verbal short-term memory that explain serial recall phenomena at a quantitative level using well-specified principles for representing serial order. Some of these theories have been couched in terms of the phonological loop construct (e.g., Burgess & Hitch, 1992, 1999, 2006; Page & Norris,

1998), essentially supplementing Baddeley's verbal-conceptual theory with an explicit mechanism for ordering, whilst others have been framed within alternative theoretical perspectives (e.g., Botvinick & Plaut, 2006; Brown, Neath, & Chater, 2007; Brown, Preece, & Hulme, 2000; Farrell & Lewandowsky, 2002; Grossberg & Pearson, 2008; Henson, 1998a; Lewandowsky & Farrell, 2008a). Recently, comparisons of these models on their core assumptions have identified a number of principles that contribute to the representation of serial order in verbal short-term memory (Farrell, 2006; Farrell & Lelièvre, 2009; Farrell & Lewandowsky, 2004; Hitch, Fastame, & Flude, 2005; Lewandowsky & Farrell, 2008a, 2008b).

Like its phonological loop counterpart, the visuospatial sketchpad lacks any detailed mechanism(s) for the retention of serial order. However, in contrast to the wealth of data and theoretical progress relating to verbal short-term memory, there has been comparatively less research exploring the problem of serial order in the visuospatial domain. This is partly attributable to experimental convenience: It is generally easier to construct, manipulate, and test memory for serial order using verbal than visuospatial stimuli. Encouragingly, however, recent years have seen increased interest in visuospatial short-term memory for serial order, and where there was once only a trickling of studies, there now exists a substantive empirical database and a steady influx of new research. These studies have shown that short-term memory for various kinds of nonverbal stimuli exhibit a number of phenomena of serial order that have until recently been thought to be emblematic of verbal short-term memory. These stimuli include sequences of visual-spatial locations (e.g., Farrand, Parmentier, & Jones, 2001; Jones, Farrand, Stuart, & Morris, 1995; Smyth & Scholey, 1996), auditory-spatial locations (e.g., Parmentier & Jones, 2000; Parmentier, Maybery, & Jones, 2004; Tremblay, Guérard, Parmentier, Nicholls, & Jones, 2006), visual-spatial movements (e.g., Agam et al., 2005; Agam et al., 2007), novel visual patterns (e.g., Avons, 1998; Avons & Mason, 1999) and unfamiliar faces (e.g., Smyth, Hay,

Hitch, & Horton, 2005; Ward, Avons, & Melling, 2005).

These functional similarities notwithstanding, computational theories that attempt to account for empirical data on visuospatial short-term memory for serial order are currently lacking, and the principles underlying the representation of serial order in this domain remain unspecified. One objective of this review is to explore the possibility that the commonalities between domains can be explained by recourse to the hypothesis that principles of serial order proposed to explain verbal short-term memory for order are extensible to visuospatial short-term memory for order. It is of course possible that distinct principles underlie the representation of serial order in different domains, and it would be premature to rule out this possibility. However, given the existence of a common set of behavioral features, it is clearly more parsimonious to assume that at least some core sequencing principles exist which apply across domains. If this is indeed the case then it would not compromise the assumption of distinct verbal and visuospatial short-term memory subsystems, as specified by the working memory model, but suggest instead that the problem of serial order has been resolved in similar ways across systems.

Before proceeding, it is worth noting that there exist theories of short-term memory and working memory other than the working memory model (e.g., Barrouillet, Bernadin, & Camos, 2004; Cowan, 1999, 2005; Jones, Beaman, & Macken, 1996; Jones, Hughes, & Macken, 2006; Oberauer, 2009). However, we focus on the working memory model because the problem of serial order across domains is a core issue within this theory. In what follows, we seek to identify some fundamental principles of serial order in short-term memory, and to establish whether these principles are the same in the verbal and visuospatial domains. The structure of the remainder of this article is as follows: We begin by describing the evidence for separate verbal and visuospatial short-term memory systems as well as evidence for a further fractionation of visuospatial short-term memory into separate visual and spatial sub-components. We then describe the kinds of tasks and

stimuli that have been used to examine memory for serial order in the verbal, visual, and spatial domains, before describing some of the major empirical phenomena of memory for serial order witnessed in each. This analysis identifies a number of features in the data common to the three domains, as well as several phenomena that have hitherto only been investigated in the verbal domain. Next, we describe the principles of serial order and ancillary assumptions that have been instantiated in historic and contemporary computational theories of verbal short-term memory for serial order. We subsequently review the evidence (or lack thereof) for the operation of each of those theoretical constructs in the verbal, visual, and spatial domains. After summarizing the major findings of our analysis, we propose some avenues for future research.

The case for separate verbal and visuospatial short-term memory systems

By way of introduction, we begin by considering whether there is any need to posit separate verbal and visuospatial short-term memory sub-systems, as is assumed within the working memory framework (Baddeley, 1986, 2000, 2007; Baddeley & Hitch, 1974). Such a fractionation is supported by at least three lines of converging evidence. First, dual-task studies have shown that verbal short-term memory tasks are susceptible to interference from verbal, but not visuospatial secondary tasks, whereas visuospatial short-term memory tasks are susceptible to interference from visuospatial, but not verbal secondary tasks (Alloway, Kerr, & Langheinrich, 2010; Farmer, Berman, & Fletcher, 1986; Guérard & Tremblay, 2008; Lange, 2005; Logie, Zucco, & Baddeley, 1990; Meiser & Klauer, 1999). Second, some neuropsychological patients exhibit impairments in verbal short-term memory, but not visuospatial short-term memory, whereas other patients exhibit the converse pattern of preservation and impairment (De Renzi & Nichelli, 1975; Hanley, Young, & Pearson, 1991; Vallar & Baddeley, 1984). Third, neuroimaging studies have

shown that verbal and visuospatial short-term memory tasks recruit different neural networks in the brain, with verbal tasks recruiting a predominantly left lateralized neural network and spatial tasks recruiting a predominantly right lateralized neural network (Awh, Jonides, Smith, Schumacher, Koeppe, & Katz, 1996; Smith & Jonides, 1997; Smith, Jonides, & Koeppe, 1996). These double dissociations provide compelling evidence for distinct verbal and visuospatial short-term memory sub-systems.

It has also been suggested that visuospatial short-term memory may not be a unitary system—as originally envisaged by Baddeley and Hitch (1974)—but one that is fractionated into separate visual and spatial sub-components. For example, Logie (1995) proposed that visuospatial short-term memory consists of a passive perceptual input store—the “visual cache”—that deals with static properties of visual images, such as color, shape, luminance and form, combined with an active spatial rehearsal mechanism—the “inner scribe”—that processes dynamic information about the movements of objects in space. Two lines of evidence support this fractionation of visuospatial short-term memory. First, dual-task studies have shown that short-term memory tasks that are primarily visual in character are more vulnerable to disruption by visual than spatial secondary tasks, whereas short-term memory tasks that are primarily spatial in character are more susceptible to interference from spatial than visual secondary tasks (Klauer & Zhao, 2004; Logie & Marchetti, 1991; Tresch, Sinnamon, & Seamon, 1993; although see Vergauwe, Barrouillet, & Camos, 2009 for an exception). Second, neuropsychological patients have been identified that exhibit impairments on visual, but not spatial short-term memory tasks, whereas other patients have been identified that exhibit the converse pattern of preservation and impairment (Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999). This theoretical fractionation of visuospatial short-term memory is relevant because it has influenced the kinds of tasks that have been used to study memory for serial order in the visuospatial domain. We turn to this issue in the next section.

Assessing memory for serial order

Memory for serial order has typically been examined using the *serial recall* task in which participants are given short sequences of items that they are subsequently required to recall in order. A related task is that of *serial reconstruction* (Healy, 1982; Healy, Fredrich, Cunningham, & Till, 1987) in which the items in the sequence are simultaneously re-presented at recall in a random arrangement and the participant must sort them back into their presentation order. In studies of verbal short-term memory for order, the stimuli employed typically consist of sequences of familiar verbal items, such as digits, letters, or words presented orally, or visually in the center of a computer display. Serial recall has been the dominant recall method, with participants being required to write, speak, or type (using the computer keyboard) their responses, although serial reconstruction is also frequently employed.

In studies of spatial short-term memory for order, sequences of discrete two-dimensional spatial locations presented on a computer display have typically been employed as stimuli. For example, in computerized versions of the Corsi blocks test—a popular test used to assess spatial short-term memory—the locations are represented by nine squares arranged haphazardly on a display screen and the order of a sequence is denoted by a transitory change in the color of each location, or a sub-set of those locations. In a variant of this test—known as the dots test (Jones et al. 1995)—the locations are represented by dots presented within an invisible matrix. Unlike the Corsi test, the locations are not simultaneously visible during the presentation of the sequence. Instead, each location is presented in isolation. Moreover, the locations are not fixed, as is the case in the Corsi test, but instead vary randomly from trial to trial. In most studies employing either test, the presented locations are simultaneously visible during the recall phase and participants must reproduce the order of the sequence using the method of serial reconstruction by clicking on the locations using a mouse-driven pointer (e.g.,

Avons, 2007; Jones et al., 1995; Smyth & Scholey, 1996). On occasion, a serial recall procedure has been employed: At recall, the locations are concealed from view and participants must point to the coordinates of the locations, as well as indicate their serial order (e.g., Farrand & Jones, 1996; Farrand et al., 2001; Guérard & Tremblay, 2008).

As well as the above tests employing sequences of seen spatial locations as stimuli, other studies, conducted by Agam and his colleagues (e.g., Agam et al., 2005; Agam, et al., 2007), have examined memory for sequences of seen spatial directional movements. In the spatial memory test employed by these authors, a disc initially located in the central screen position moves along a trajectory that is divided into a number of linear connected directional movement segments. A serial recall procedure is employed during the test phase in which the participant must draw the sequence of movements of the disc with a stylus on a graphics tablet or imitate the sequence via hand and arm gestures.

Although most studies of spatial short-term memory for order have employed visual-spatial stimuli, a few studies have utilized auditory-spatial stimuli consisting of sequences of heard spatial locations (e.g., Groeger, Banks, & Simpson, 2008; Parmentier & Jones, 2000; Tremblay et al., 2006). In this test, a series of bursts of white noise are emitted from a number of speakers arranged in azimuth space ahead of the participant. In the recall phase, a serial reconstruction procedure is most often employed: A row of response boxes is presented on a computer display, each corresponding to a location in the sequence, and participants must click on the locations in order using a mouse-driven pointer.

Finally, studies of visual short-term memory for order have used sequences consisting of novel visual patterns, created by randomly filling the cells of visual matrices (e.g., Avons, 1998; Avons & Mason, 1999), or unfamiliar faces (e.g., Smyth et al., 2005; Ward et al., 2005) presented from a constant (central) spatial position. Due to the absence of a natural response mode for visual, non-spatial stimuli, these studies have

necessarily used serial reconstruction as the recall method.

Major phenomena of memory for serial order

This section presents an overview of phenomena of serial order in short-term memory documented using the tasks described in the preceding section. In particular, we focus on eight benchmark findings and sub-findings from verbal short-term memory that are well replicated, are particularly relevant to the problem of serial order, and for the most part have also been documented in the visual or spatial short-term memory domains. Note, however, that some of the phenomena have yet to be examined using visual and spatial memoranda, and we show later that this renders the task of identifying the preferred principles of serial order in visual and spatial short-term memory more difficult than in verbal short-term memory.

We deal with serial order in short-term memory tasks where sequential redundancy plays only a minor role. Thus, the tasks typically involve the ordered recall of random or pseudo-random sequences sampled from a small set of familiar items. In the verbal domain, this restriction excludes memory for meaningful phrases or sentences, where syntactic and semantic constraints complicate the empirical pattern (see e.g., Baddeley, Hitch, & Allen, 2009). We also exclude memory for sequences of nonwords where constraints on the ordering of phonemes within the syllable play a crucial role in supporting recall (e.g., Treiman & Danis, 1988). This restriction in the scope of our analysis is an accurate reflection of the wealth of the empirical research on short-term memory and, with few exceptions (e.g., Hartley & Houghton, 1996), computational theories of serial order do not yet specify how such constraints influence short-term order recall. Finally, we omit a number of benchmark findings from verbal short-term memory including the effects of *word length* (sequences of words with short pronunciation durations are recalled better than sequences of words with long pronunciation durations; Baddeley,

Thomson, & Buchanan, 1975), *articulatory suppression* (repeating a verbal token or a sequence of verbal tokens aloud during the encoding of a verbal sequence impairs order recall accuracy; Macken & Jones, 1995; Murray, 1967), and *word frequency* (sequences of high frequency words are recalled better than sequences of low frequency words; Hulme, Roodenrys, Schweickert, Brown, Martin, & Stuart, 1997). We do so on account that these phenomena are not directly relevant to the problem of serial order *per se* and it is, as yet, unclear whether analogues of these effects exist in the nonverbal domain.

The eight phenomena that are the subject of our review include the serial position curves associated with (1) forward recall and (2) backward recall, (3) the sequence length effect, (4) patterns of errors underlying the forward recall serial position curve, (5) temporal grouping effects, (6) item similarity effects, (7) the Ranschburg effect, and finally (8) the Hebb repetition effect. Table 1 lists those phenomena—initially observed in verbal short-term memory—and highlights the short-term memory domains in which they have been documented. The reader is invited to inspect this table in order to obtain an overview of those results that have been shown to extend to the visual and spatial domains, and those that remain to be investigated. The data listed in Table 1 are primarily based on response probabilities but also include response timing data which have been collected in recent studies using keyboard serial recall (with verbal memoranda) and serial reconstruction (with verbal and spatial memoranda).

A description of the phenomena of serial order now follows.

1. *Forward serial position curves*

The serial position curve plots recall accuracy as a function of the serial positions of items. When people are required to recall verbal sequences in forward order, the resulting accuracy serial position curve is characterized by two canonical effects that have been replicated across countless studies: First, there is a sharp monotonic decrease in recall

accuracy extending from the first position onwards known as the *primacy effect*. Second, there is a small upturn in performance for the final serial position known as the *recency effect*.¹ These effects are illustrated graphically in Figure 1A.

Forward accuracy serial position curves exhibiting effects of primacy and recency are not confined to verbal memoranda. The forward serial position curves associated with the recall of sequences composed of various different types of nonverbal stimuli have been shown to exhibit an extensive primacy effect accompanied by a one-item recency effect. These stimuli include visual-spatial locations (Avons, 2007; Farrand et al., 2001; Guérard & Tremblay, 2008; Jones et al., 1995; Smyth & Scholey, 1996; Tremblay et al., 2006), visual-spatial movements (Agam et al., 2005; Agam et al., 2007; Agam, Huang, & Sekuler, 2010), auditory-spatial locations (Groeger et al., 2007; Parmentier & Jones, 2000; Tremblay et al., 2006), visual matrix patterns (Avons, 1998; Avons & Mason, 1999), and unfamiliar faces (Smyth et al., 2005; Ward et al., 2005).

Forward serial position curves can also be plotted using inter-response time as the dependent measure. Recall timing studies have shown that the latency to initiate recall of the first item in a verbal sequence is considerably longer than that for any other item, with latencies for subsequent serial positions following an inverted U shaped profile (Anderson, Bothel, Lebiere, & Matessa, 1998; Farrell, 2008; Farrell & Lewandowsky, 2004; Farrell, Wise, & Lelièvre, 2011; Haberlandt, Lawrence, Krohn, Bower, & Thomas, 2005; Maybery, Parmentier, & Jones, 2002; Parmentier & Maybery, 2008; Thomas, Milner, & Haberlandt, 2003). A typical latency serial position curve for forward recall is shown in Figure 1B. Studies by Parmentier, Andrés, Elford, & Jones (2006; see also Parmentier, Elford, & Maybery, 2005) and Parmentier, King, and Dennis (2006) have extended these latency-pattern observations with verbal sequences to the recall of sequences of visual-spatial and auditory-spatial locations, respectively.

2. Backward serial position curves

The requirement to recall verbal sequences in the backward direction qualitatively alters the shape of the accuracy serial position curve. Numerous studies have shown that backward recall enhances the recency effect, but diminishes the primacy effect (Anderson et al., 1998; Farrand & Jones, 1996; Hulme et al., 1997; Li & Lewandowsky, 1993, 1995; Madigan, 1971).² This empirical pattern is illustrated in Figure 1A. Backward recall also exerts systematic effects on response time patterns (Haberlandt et al., 2005; Thomas et al., 2003). As can be seen in Figure 1B, people leave a long pause prior to the first item to be output—in this case the last item in the sequence—as in forward recall. The penultimate item is then emitted rapidly, after which the recall latency for the antepenultimate item increases considerably. Thereafter, recall latencies become gradually quicker across earlier serial positions. In general, it can be seen that recall latencies are longer in backward than forward recall, particularly at medial positions. To explain the backward recall latency data, it is assumed that recall of the final item is delayed due to time required to plan the sequence for output. The penultimate item is then recalled rapidly, by virtue of being recent. Subsequently, backward recall is accomplished by covertly recalling the sequence in forward order, overtly recalling the last item, and repeating this process until the first item is retrieved—the *multiple-scan* strategy (Haberlandt et al., 2005; Thomas et al., 2003).

A few studies have compared forward and backward recall employing sequences of visual-spatial locations as stimuli (Cornoldi & Mammarella, 2008; Farrand & Jones, 1996; Mammarella & Cornoldi, 2005). However, with the exception of the study by Farrand and Jones (1996), the above studies only reported aggregate levels of recall performance, but did not report serial position data. Farrand and Jones (1996) compared forward and backward recall of auditory-verbal and visual-verbal sequences, with sequences of visual-spatial locations. They found that when serial recall was employed as the recall method (Experiments 2, 3, and 4), the backward recall curves witnessed for all three types

of stimuli exhibited enhanced recency, but diminished primacy effects.

However, it is noteworthy that the same authors found that when serial reconstruction was employed (Experiment 1), the backward recall curves for all three types of stimuli resembled those obtained with forward recall. They reasoned that the different backward recall patterns observed with serial recall and serial reconstruction are attributable to the different demands placed by the two tasks on item and order memory: Serial recall requires retrieval of item as well as order information, whereas serial reconstruction only requires retrieval of order information. However, recent studies that have compared forward and backward recall of verbal sequences using serial reconstruction have revealed the typical pattern of results, with backward recall enhancing the recency effect, but reducing the primacy effect (Guérard & Saint-Aubin, 2012; Guérard, Saint-Aubin, Burns, & Chamberland, 2012).

3. Sequence length effect

Forward recall accuracy for verbal sequences decreases with increasing sequence length (Anderson et al., 1998; Crannell & Parrish, 1957; Maybery et al., 2002). This *sequence length effect* has also been documented with sequences of visual-spatial locations (Jones et al., 1995; Smyth, 1996; Smyth, Pearson, & Pendleton, 1989; Smyth & Scholey, 1994, 1996), visual-spatial movements (Agam et al., 2005, Agam et al., 2007), visual matrix patterns (Avons, 1998), and unfamiliar faces (Smyth et al., 2005; Ward et al., 2005).

4. Error patterns

Errors in serial recall can be transposition errors or item errors. A transposition occurs when an item from the study sequence is recalled in the wrong position. When plotted over serial position, transpositions in the recall of verbal sequences obey an inverted U shaped trend, with most occurring at medial sequence positions (Henson, 1996;

Henson, Norris, Page, & Baddeley, 1996). The incidence of transpositions in the recall of sequences of visual-spatial locations (Guérard & Tremblay, 2008) and visual matrix patterns (Avons & Mason, 1999) has also been shown to conform to this inverted U shaped function. Transpositions are typically the only errors possible in serial reconstruction.

Transpositions can be classified according to their displacement, which refers to the numerical difference between an item's presentation and recall positions. Transpositions with negative displacement values are known as *anticipation* errors and correspond to items recalled ahead of their correct positions. Transpositions with positive displacement values are known as *postponement* errors and correspond to items recalled after their correct positions. Items recalled in their correct positions are represented by a displacement value of zero. Transpositions are typically measured in terms of transposition gradients which plot the probability of transpositions as a function of displacement. Typical transposition gradients for the forward recall of verbal sequences are shown in Figure 2A from which it can be seen that the probability of an error decreases as the absolute displacement value increases; thus, when an item is recalled in the wrong position it will tend to be close to its correct position. This tendency for transpositions to cluster around their correct recall positions is known as the *locality constraint* (Henson, 1996). The locality constraint is not confined to verbal memoranda. Transposition gradients for sequences consisting of visual-spatial locations (Parmentier, Andrés et al., 2006; Smyth & Scholey, 1996), auditory-spatial locations (Groeger et al., 2007; Parmentier & Jones, 2000; Parmentier, King, & Dennis, 2006), visual-spatial movements (Agam et al., 2005), novel visual patterns (Avons & Mason, 1999), and unfamiliar faces (Smyth et al., 2005) have also been shown to display this fundamental property.

Transposition gradients for verbal sequences are accompanied by a systematic pattern of recall latencies. Farrell and Lewandowsky (2004) have shown that when the latency of transpositions is plotted as a function of displacement, anticipations are slower

than postponements, as illustrated in Figure 2B. Additionally, it can be seen that transposition displacement has different effects on the recall latencies for anticipations and postponements: Latencies for anticipations increase as an approximately linear function of displacement, whereas latencies for postponements are generally invariant with respect to displacement. The dynamics of transpositions have not yet been examined for sequences of visual or spatial stimuli. However, as we show later, transposition latencies carry diagnostic information about the principles underlying the representation of serial order in short-term memory.

A final feature of transpositions has also turned out to be important for identifying computational principles underpinning memory for serial order. This is that transposition errors in recalling sequences of verbal stimuli are characterized by a particular pattern of sequential dependency. Specifically, if an item i is recalled a position too soon, recall of item $i-1$ is more likely at the next output position than item $i+1$. To explain, given the sequence ABC, if B is recalled at the first output position then a *fill-in error*, reflected by the recall of A at the next output position, is more likely than an *infill error*, reflected by the recall of C. Available data on these errors suggests that fill-in errors outweigh infill errors by a ratio of approximately 2:1 (Farrell, Hurlstone, & Lewandowsky, 2013; Henson, 1996; Page & Norris, 1998; Surprenant, Kelley, Farley, & Neath, 2005).³ Guérard and Tremblay (2008) have shown that this fill-in tendency extends to the ordered recall of sequences of visual-spatial locations and it obeys the 2:1 ratio observed with verbal material.

Item errors can be divided into *intrusion*, *omission*, and *repetition* errors. An intrusion occurs when an item is recalled that was not part of the study sequence. In verbal serial recall, intrusions often involve the recall of an item on trial n that occurred in the same within-sequence position on trial $n-1$ (Conrad, 1960; Henson, 1999a). These position-preserving intrusions are known as *protrusions* (Henson, 1996). An omission

occurs when an item is not recalled, whilst a repetition occurs when an item is recalled on more than a single occasion despite being presented only once in the study sequence.

Repetitions are rare and widely separated in verbal serial recall. For sequences composed of unique items, repetitions account for approximately 2% (Henson, 1996) to 5% (Vousden & Brown, 1998) of all responses and are separated by an average distance of 3-4 positions (Henson, 1996).

In verbal serial recall, item errors are less common than transposition errors, accounting for around 20% of total errors (Aaronson, 1968), and their incidence has been shown to increase across serial positions (Henson, 1996). Guérard and Tremblay (2008) have shown that item errors are also less frequent than transpositions in the serial recall of sequences of visual-spatial locations and that the incidence of intrusions and omissions (the only item errors reported in their study) increases across serial positions. Avons and Mason (1999) observed a similar pattern for sequences consisting of visual matrix patterns using a serial reconstruction method that permitted the recording of transpositions and intrusions. Protrusions and repetitions have yet to be studied with visual and spatial memoranda.

5. *Temporal grouping effects*

Differentiating a verbal sequence into sub-groups by inserting extended temporal pauses after every few items—known as *temporal grouping*—has been shown to exert a number of systematic effects on ordered recall which are illustrated in Figure 3. First, grouping enhances recall accuracy (Frankish, 1985, 1989; Henson, 1996; 1999a; Hitch, Burgess, Towse, & Culpin, 1996; Maybery et al., 2002; Ng & Maybery, 2005; Ryan, 1969a, 1969b) and produces effects of primacy and recency within each sub-group (Figure 3A), giving the accuracy serial position curve for grouped sequences a scalloped appearance (Frankish, 1985, 1989; Hitch et al., 1996). Second, grouping modifies the pattern of errors

by reducing the number of transpositions overall, and between groups in particular. However, one type of between group transposition actually increases in grouped sequences: These *interpositions* are transpositions between groups that preserve their positions within groups (Henson, 1996, 1999a; Ng & Maybery, 2002, 2005; Ryan, 1969a). For example, if a 9-item sequence is organized into three groups of three, interpositions are indicated by an increase in the probability of ± 3 and ± 6 transpositions (Figure 3B). A third feature of grouping is that it modifies the shape of the response latency serial position curve (Figure 3C): As well as leaving a long pause prior to outputting the first item in the sequence, participants leave long pauses prior to outputting the first item of each sub-group (Anderson et al., 1998; Anderson & Matessa, 1997; Farrell, 2008; Farrell & Lewandowsky, 2004; Farrell et al., 2011; Maybery et al., 2002; Parmentier & Maybery, 2008).

With the exception of the increase in interpositions, the effects of temporal grouping documented above using verbal memoranda have also been witnessed in the ordered recall of temporally grouped auditory-spatial (Parmentier, Maybery, & Jones, 2004) and visual-spatial (Parmentier, Andrés et al., 2006; Experiment 3) sequences of locations. However, grouping phenomena have yet to be investigated in visual short-term memory.

6. *Item similarity effects*

A classic and robust finding in the verbal short-term memory literature is that sequences of phonologically similar sounding items (e.g., *B D G P T V*) are recalled less accurately than sequences of phonologically dissimilar sounding items (e.g., *F K L R X Y*; Baddeley, 1966, 1968; Conrad, 1964; Wickelgren, 1965a, 1965b). This *phonological similarity effect* (Baddeley, 1986) is also observed when sequences are constructed by alternating phonologically dissimilar and similar items (e.g., *F B K G R T*). Such mixed sequences engender a saw-toothed accuracy serial position curve characterized by peaks corresponding to the recall of dissimilar items and troughs corresponding to the recall of

similar items (Baddeley, 1968; Farrell, 2006; Farrell & Lewandowsky, 2003; Henson et al., 1996; Lewandowsky & Farrell, 2008b). Representative data for this mixed-sequence phonological similarity effect are displayed in Figure 4.

Item similarity effects have also been documented using visual memoranda. Avons and Mason (1999) found that sequences of similar matrix patterns were recalled less accurately than sequences of dissimilar matrix patterns, whilst Smyth et al. (2005) found that sequences of similar unfamiliar faces were recalled less accurately than sequences of dissimilar unfamiliar faces. Jalbert, Saint-Aubin, and Tremblay (2008) have shown an item similarity effect using spatial memoranda. They found that sequences of spatial locations presented in the same color hue were recalled less accurately than sequences of locations presented in different color hues. These studies show that the standard item similarity effect observed with sequences of purely dissimilar and similar items extends to the use of visual and spatial memoranda. However, no studies have examined item similarity effects in the visual and spatial domains using sequences in which similar and dissimilar items are intermixed.

7. *Ranschburg effect*

The *Ranschburg effect* (named after its founder: Pablo Ranschburg)—also known as the phenomenon of *repetition inhibition*—occurs when two conditions are compared in the serial recall of verbal sequences: In the repetition condition, the sequences presented for recall contain two occurrences of the same item separated by a number of intervening items, whilst in the control condition, the sequences always contain unique items. The typical finding is that recall of the second occurrence of a repeated item is impaired relative to items in corresponding positions in the control condition (Crowder, 1968; Duncan & Lewandowsky, 2005; Henson, 1998b; Jahnke, 1969; Kahana & Jacobs, 2000; Vousden & Brown, 1998). A violation of this general pattern occurs when the two

occurrences of a repeated item are presented within close proximity—adjacent or separated by a single position. Under these conditions, recall of both occurrences of a repeated item is often enhanced relative to items in corresponding positions in the control condition—a phenomenon known as *repetition facilitation* (Crowder, 1968). The Ranschburg effect has not yet been investigated using visual or spatial memoranda.

8. *Hebb repetition effect*

Hebb (1961) introduced a procedure for simultaneously studying short-term serial recall and sequence learning within the same experiment. The procedure involves a multi-trial serial recall task in which, unbeknownst to the participant, the same sequence is repeated every few trials. The typical finding is that recall of the repeated sequence, but not the novel filler sequences, improves gradually over successive presentations, a result dubbed the *Hebb repetition effect*. Since Hebb employed sequences of familiar items (digits) it follows that what participants learned was the order of the items in the sequence. The Hebb repetition effect is therefore considered to be a vehicle for investigating the mechanisms underlying the long-term learning of serial order.

The Hebb repetition effect has been documented in numerous studies of verbal short-term memory (e.g., Bower & Winzenz, 1969; Couture, Lafond, & Tremblay, 2008; Cumming, Page, & Norris, 2003; Hitch, Fastame, & Flude, 2005; Hitch, Flude, & Burgess, 2009; Page, Cumming, Norris, Hitch, & McNeil, 2006). One key result is that the integrity of the start of the repeated sequence is an important determinant of whether a Hebb repetition effect is observed. Schwartz and Bryden (1971) found that the effect disappeared if the first two items in the repeated sequence were changed on each presentation, whereas the effect was still obtained when the last two items in the sequence changed. Also important to the demonstration of a Hebb repetition effect is the integrity of the temporal structure of the repeated sequence. It has been shown that when the

repeated sequence is temporally grouped, but the grouping pattern changes on each presentation, the Hebb repetition effect is either removed completely or greatly reduced, whereas the usual effect is obtained if the grouping pattern remains constant (Bower & Winzenz, 1969; Hitch et al., 2009). In contrast to the above results, Hitch and colleagues (Hitch et al., 2009) have shown that the Hebb repetition effect is insensitive to the phonological similarity of items. In their study, the rate of learning of a repeated sequence of phonologically similar items was found not to differ from a repeated sequence of phonologically dissimilar items, even though similarity had its usual large detrimental effect on immediate recall.

The Hebb repetition effect is not restricted to the use of verbal memoranda: Recently, a Hebb repetition effect has been shown using sequences of visual-spatial (Couture & Tremblay, 2006) and auditory-spatial (Parmentier, Maybery, Huitson, & Jones, 2008) locations, as well as visual sequences of unfamiliar faces (Horton, Hay, & Smyth, 2009) or pictorial stimuli (Page et al., 2006). However, studies of the Hebb repetition effect in the visual and spatial domains have not yet examined the impact of partial repetition, changes in temporal grouping, and item similarity on repetition learning.

Summary

In summary, we have briefly described eight core phenomena relating to short-term memory for serial order information, noting a number of points of similarity across the verbal, visual, and spatial domains. However, although each phenomenon is well established in the verbal domain, evidence in the other two domains is much less complete, often because the relevant studies have yet to be carried out.

Computational approaches to serial order

In this section, we describe computational approaches to modeling short-term memory for serial order and evaluate their ability to account for the phenomena delineated above, as well as some phenomena not yet mentioned. Although developed as accounts of serial order in verbal short-term memory, the principles and assumptions underlying these theories are extensible to the processing of visual and spatial material, amongst others. We begin by describing a once popular approach to serial order that shaped initial theoretical developments in this field, namely associative chaining, and we argue that several of the phenomena reviewed in the previous section militate against a role for chaining in the verbal, visual, and spatial domains. Next, we describe the principles of serial order underlying a new generation of computational theories that eschew the chaining notion and we identify evidence for the operation of those principles in the three domains.

Associative chaining

Associative chaining is the oldest approach to serial order in short-term memory (e.g., Ebbinghaus, 1964) and serial behavior more generally (e.g., Lashley, 1951). It is mentioned for historic purposes, since the dominant view at present is that chaining is inadequate as a solution to the problem of serial order in short-term memory (e.g., Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a; Page & Norris, 1998). The basic premise behind chaining is that serial order is encoded by forming associations between items. Ordered recall is accomplished by traversing these associations which act as the retrieval cues for sequence production. This constitutes a *serial representation of order*, because the information necessary for producing a sequence is not simultaneously accessible, rather it emerges dynamically as recall unfolds.

The mechanism of associative chaining appears in various theories of memory (e.g., Ebbinghaus, 1964; Jones et al., 1996; Kieras, Meyer, Mueller, & Seymour, 1999;

Lewandowsky & Murdock, 1989; Murdock, 1993, 1995; Wickelgren, 1965b). However, the most successful application of the chaining approach to short-term serial recall is the Theory of Distributed Associative Memory (TODAM) model (Lewandowsky & Murdock, 1989). TODAM is a formal model of verbal short-term memory in which items are represented as vectors of random elements and order information is represented by merging the vectors of pairs of contiguous items. In TODAM, the item vectors are taken to represent verbal items, such as letters, however they could equally be taken to represent visuospatial items, such as visual patterns or spatial locations. Sequence information is encoded by adding the item and associative vector representations one by one to a common memory vector. Serial recall is initiated by probing the memory vector with a start marker that is linked to the initial item. The first item recalled is then used to cue the second item, which is used to cue the third item, and so on and so forth.

One major objection to simple chaining models of this kind, in which order is encoded solely by contiguous associations between items, is that if recall should fail mid-sequence then the chain is broken and recall must necessarily cease. However, TODAM manages to circumvent this shortcoming using the following recall procedure. Due to its use of distributed representations, the output of TODAM in response to a recall cue is not an exact copy of an item, but rather a blurry approximation. To recover the item representation, the noisy output vector must first be deblurred by determining which of a pool of experimental vocabulary items it approximates best. If this process is successful then the deblurred item is retrieved and used to cue the next response. However, if this process fails then the associative chain is not necessarily broken, because the blurry output vector can still be used as a retrieval cue, often successfully retrieving the correct next item.

Lewandowsky and Murdock (1989) show that TODAM can reproduce effects of primacy and recency of the forward serial position curve. The recency effect is a

consequence of retroactive interference during the encoding of item and associative information, as well as the removal of each item from the competitor set once recalled which reduces the number of competitors towards the end of the sequence. In contrast, the primacy effect is attributable to an ad hoc assumption introduced specifically to accommodate this effect: The weighting of the encoding strength of each successive association decreases exponentially rendering errors more probable towards the end than near the beginning of the sequence.

One major shortcoming of TODAM is that it has difficulties explaining transpositions. Specifically, the model cannot produce positional exchange errors whereby two items swap positions with one another, nor can it accommodate the locality constraint underlying movement errors more generally. Murdock (1995) has presented a complex chaining instantiation of TODAM that incorporates remote (non-adjacent) as well as contiguous associations, the strengths of which decrease as a function of the distance between items (cf. Ebbinghaus, 1964). According to Murdock (1995), this version of TODAM qualitatively meets these shortcomings.

Nevertheless, some of the core phenomena described in the previous section are problematic for TODAM and associative chaining accounts more generally. First, chaining accounts have difficulties explaining the pattern of findings associated with the recall of sequences containing repeated items. For example, given the sequence $A B A C$, chaining accounts predict that recall of B and C will be compromised, because they share the same retrieval cue. However, the Ranschburg effect shows that it is the recall of the second occurrence of the repeat that is impaired, not the items following the repeats. Second, a related problem occurs when participants are given sequences containing alternating phonologically similar and dissimilar items, such as the sequence $B K P R$. Chaining accounts predict that recall of the dissimilar items K and R should be impaired, because they possess similar (confusable) retrieval cues. However, as we have seen, this prediction

is contrary to the data (Baddeley, 1968; Henson et al., 1996) which shows that dissimilar items on mixed sequences are recalled as effectively as items in corresponding positions on pure dissimilar sequences, if not more so (see e.g., Farrell, 2006; Farrell & Lewandowsky, 2003; Lewandowsky & Farrell, 2008b). Third, chaining accounts predict more infill than fill-in errors, because an item recalled too soon will subsequently cue the item that followed it in the input sequence more strongly than any other by virtue of its direct associative link with that item. This prediction is antithetic to the data (Farrell et al., 2013; Henson et al., 1996; Page & Norris, 1998; Surprenant et al., 2005). Finally, a study by Hitch et al. (2005) casts doubt on the viability of a chaining account of the Hebb repetition effect. In their study, participants were presented with sequences of variable length that contained a repeated fragment whose positioning varied from one sequence to the next. This meant that the associations between items and positions (item-position associations) in the repeated fragment changed over trials, whereas the associations between the items themselves (item-item associations) were preserved. Accordingly, chaining models predict that despite the changes in the serial positions of the items, sequence learning should still take place. However, Hitch and colleagues failed to observe any such learning, suggesting that the Hebb repetition effect is not driven by the reinforcement of item-item associations.

These shortcomings are endemic to all associative chaining accounts of serial order in short-term memory including a recent theoretical attempt to revive the chaining notion by Solway et al. (2012). To date, no chaining model has been developed that can account for these phenomena. In light of this claim, the serial recall model of Botvinick and Plaut (2006) merits brief comment. These authors show that an Elman (1990) recurrent neural network, once trained to perform serial recall, is able to meet the abovementioned shortcomings of chaining models. This accomplishment is noteworthy, because neural network models of this kind have previously been disregarded as candidate models of

serial recall on account that they operate through chaining (Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a). This is because the output of such networks is determined by a cue that is a compound of their past contextual states. That the Botvinick and Plaut (2006) model can explain these results is a consequence of its extensive training regime during which it essentially learns not to use chaining, and instead develops some form of positional representations which are similar to those employed in models that we describe in the next section. Precisely what these representations are and how they emerge is not yet clear. In our view, however, the explanatory success of the Botvinick and Plaut model is not attributable to a chaining-based representation of serial order.

The empirical findings reviewed above are forceful in ruling out a role for associative chaining in the representation of serial order in verbal short-term memory. In visual and spatial short-term memory, no studies have yet examined the recall of visual and spatial sequences containing repeated items nor sequences in which visually similar and dissimilar items are intermixed. Similarly, the possible role of item-item associations during the learning of visual and spatial sequences in the Hebb repetition paradigm has yet to be investigated. However, Guérard and Tremblay (2008) have shown that fill-in errors are more likely than infill errors in the recall of sequences of visual-spatial locations, a result that appears to cast doubt on the viability of a chaining account of serial order in spatial short-term memory. Moreover, it seems unlikely, given the functional similarities between verbal, visual, and spatial short-term memory for serial order, combined with the lack of evidence for chaining in the verbal domain, that chaining would operate in the visual and spatial domains. Indeed, as we will see shortly, there exist alternative principles of serial order that provide a more powerful and parsimonious account of phenomena of memory for serial order witnessed in the verbal and nonverbal domains.

Before closing, objections to chaining as a general approach to serial order briefly merit comment. In his seminal article, Lashley (1951) integrated evidence from a variety

of domains to highlight the inadequacies of chaining. He noted that the ease with which phonemes can be combined to form new words, and words to form new sentences, is too flexible for chaining. The preponderance of anticipation errors in speech and typing, he argued, suggest that ‘prior to the overt enunciation of the sentence, an aggregate of word units is partially activated or readied’ (p.19), signifying that sequence information is activated in parallel, not serially as posited by chaining theories. The need for a parallel representation of serial order is evident in skilled behavior where many actions such as the finger strokes of a musician, Lashley noted, are performed too quickly for feedback from each response to serve as the cue for the next. Lashley concluded that serial behavior cannot be explained by a single mechanism based upon associative chaining, proposing instead a two-stage mechanism wherein the first stage all acts to be performed are simultaneously activated, whilst in the second stage a scanning mechanism selects their serial order. As we shall see in the next section, many recent computational theories of verbal short-term memory use a mechanism known as competitive queuing which provides a computational instantiation of the parallel response activation and sequential selection process envisaged by Lashley.

Principles of serial order in contemporary theories

Following the demise of chaining theory, a new generation of computational theories of verbal short-term memory for serial order has emerged in recent years. The wealth and complexity of contemporary theories means that a thorough treatment of each is not possible. Moreover, a focus on the detailed properties of specific models can obscure important commonalities between them. Fortunately, there is some convergence amongst theories and several principles of serial order have now been identified which are commonly employed. Accordingly, we classify theories according to the core principles on which they rely to produce their behavior (for a similar approach, see Lewandowsky & Farrell, 2008a).

A list of recent models of short-term memory, the principles of serial order they instantiate, and the supplemental assumptions to which they appeal is shown in Table 2.

As can be seen from inspection of this table, current theories of short-term memory generate serial order using one or more of the following principles: (a) a competitive queuing sequence planning and control mechanism, (b) position marking, (c) a primacy gradient of activation levels, (d) response suppression, (e) cumulative matching. Some theories additionally accord a role for: (f) output interference during recall, and postulate that (g) the effects of item similarity are localized solely at retrieval or that item similarity additionally exerts an effect during serial order encoding. Below, we describe the different principles and assumptions of these theories, before evaluating supporting evidence for their role in verbal, visual, and spatial short-term memory.

Competitive Queuing

Most contemporary models of verbal short-term memory generate serial order using a response selection mechanism pioneered by Grossberg (1978a, 1978b) and subsequently dubbed by Houghton (1990) as competitive queuing (CQ). The popularity of this mechanism is underscored by the fact that it is instantiated in ten of the fourteen models listed in Table 2. This mechanism, which is buttressed by recent neurophysiological evidence from monkeys (Averbeck, Chafee, Crowe, & Georgopoulos, 2002)—described later in this article—is closely related to Lashley’s (1951) general theory of serial behavior. Although popularized in models of verbal short-term memory, it has found application in computational theories of serial order generation spanning a variety of serial performance domains (see Glasspool, 2005 for a review).

A schematic of a generic CQ mechanism (e.g., Bullock, 2004; Bullock & Rhodes, 2003; Rhodes & Bullock, 2002) envisaged as a neural network model is illustrated in Figure 5. The model comprises two layers of localist item nodes: A parallel planning layer

and a competitive choice layer. The nodes in the parallel planning layer represent the pool of items from which sequences are generated. In theories of verbal short-term memory, these nodes correspond to verbal tokens such as phonemes or words, however they could equally represent visuospatial tokens such as spatial locations or visual patterns. Recalling a sequence is a two-stage process: In the first stage, an ordering mechanism activates in parallel a sub-set of the nodes in the parallel planning layer, with the relative strength of node activations coding the relative priority of items. This constitutes a *parallel representation of serial order* because all of the items in the sequence are simultaneously activated. In the second stage, the activations in the parallel planning layer elicited by the ordering mechanism are projected to corresponding nodes in the competitive choice layer. The node activations in this layer are governed by recurrent-competitive-field dynamics. Each item node excites itself and sends lateral inhibition to competitor nodes in the same layer. This sets-up a response competition and the item with the strongest activation level is chosen for recall, after which a feedback signal from the competitive choice layer inhibits its corresponding representation in the parallel planning layer. This maximum-finding selection and suppression process continues iteratively until all sequence items have been recalled. Note that if this mechanism is disrupted by perturbing the activations in one or both layers (through the addition of random noise to the item activations) then it predicts transposition errors akin to those observed in serial recall.

Models that utilize this sequence planning and control mechanism are jointly known as CQ models, because the activations in the parallel planning layer are organized in a competitive queue (Davelaar, 2007). There are several variations on the basic CQ mechanism described above. For example, not all CQ models are neural network based (e.g., Henson, 1998a) and whilst some models implement the competitive choice layer as a recurrent-competitive field (e.g., Burgess & Hitch, 1999; Farrell & Lewandowsky, 2004) others simply select the strongest item based upon the raw activations elicited by the

ordering mechanism (e.g., Henson, 1998a; Page & Norris, 1998). Models also critically differ in the mechanism that generates the activations in the parallel planning layer, with some models using a static ordering mechanism that generates a single activation gradient (viz., a primacy gradient, see below) and with other models employing a dynamic ordering mechanism that modulates the activation gradient over time (viz., position marking, see below). Finally, models differ in their degree of reliance on the post-output inhibition of items (viz., response suppression, see below), with such inhibition being a crucial ingredient in some CQ models (e.g., Grossberg & Pearson, 2008; Page & Norris, 1998), but less crucial in others (e.g., Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a).

Not all models utilize the CQ selection mechanism. For example, the Context-Serial-Order-in-a-Box (C-SOB) model (Farrell, 2006; Lewandowsky & Farrell, 2008a) utilizes a CQ-like selection mechanism, but differs critically in its use of distributed, rather than localist representations of items, combined with an (obligatory) iterative, dynamic selection process. In contrast, the Scale Invariant Memory, Perception and Learning (SIMPLE) model (Brown et al., 2007) utilizes the Luce choice rule (Luce, 1963) to select items. In this variant of the selection mechanism, recall probabilities are computed for each item, at each recall position, by dividing the activations generated by the ordering mechanism by their sum total. The item with the strongest recall probability is then chosen for recall.

Position marking

Position marking is an approach to representing serial order in which associations are formed between sequence items and some independent and varying contextual representation of their position. The positional representations are only approximate, meaning that the representations of neighboring positions overlap to some degree. At recall, the positional cues are reinstated in turn and each sequence item is activated to the

extent that the positional cue it was associated with during serial order encoding is similar to the current positional cue. Response selection proceeds by emitting the item activated most strongly in response to each positional cue.

Models of serial recall implementing position marking differ according to whether they represent positional information using temporal, absolute, or relative codes (Henson, 1999b). An example of a model relying on a temporal coding scheme is the Oscillator-Based Associative Recall (OSCAR) model (Brown et al., 2000). In this model, items are linked with the different states of a time-varying context signal driven by sets of temporal oscillators operating at different frequencies (Figure 6A). At recall the context signal is reset to its initial state before being replayed, with list items being activated through their original associations with the timing signal. The item activations elicited by the re-evolving context signal are processed by a CQ mechanism that emits the most actively cued items at different recall times. A similar, but more abstract, temporal coding scheme is utilized by the SIMPLE model (Brown et al., 2007).

Models employing an absolute coding scheme include C-SOB (Farrell, 2006; Lewandowsky & Farrell, 2008a) and the original Burgess and Hitch (1992) model. For example, in the latter model, items are associated with an event-driven context signal implemented as a vector of inactive nodes containing a dynamic window of active nodes (Figure 6B). The context vector changes gradually with the presentation of each item by sliding the attentional window from left to right by a constant one node per item. The same moving window scheme is employed in more recent instantiations of the model (Burgess & Hitch, 1999, 2006), except the context signal is driven by the passage of time, rather than by items, resulting in a temporal coding scheme.

An example of a model employing a relative coding scheme is the Start-End Model (SEM; Henson, 1998a; see also Houghton, 1990). In this model items are linked to the varying states of a context signal comprising two elements: A start marker that is

strongest for the first position and decreases exponentially in strength across positions and an end marker that is weakest for the first position and increases exponentially in strength across positions (Figure 6C). The relative strengths of the start and end markers provide an approximate two-dimensional representation of the position of each item relative to the start and end of a sequence.

Primacy gradient

A simpler scheme for representing serial order is in terms of a primacy gradient of activation levels whereby the first item is activated strongest and the activations of subsequent items decrease monotonically across positions (Figure 7A). When serial order is represented by a primacy gradient complemented by response suppression (see below), forward recall is accomplished via an iterative process of selecting the most active item for recall before suppressing its activation so the next strongest item can be emitted. This is the functional mechanism for ordered recall in the original competitive queuing model of Grossberg (1978a, 1978b), the primacy model (Page & Norris, 1998), the original Serial-Order-in-a-Box (SOB) model (Farrell & Lewandowsky, 2002), and the LIST PARSE (Laminar Integrated Storage of Temporal Patterns for Associative Retrieval, Sequencing and Execution) model (Grossberg & Pearson, 2008).

Some models that use position marking to represent order also incorporate a primacy gradient. For example, in OSCAR (Brown et al., 2000) and C-SOB, (Farrell, 2006; Lewandowsky & Farrell, 2008a), the primacy gradient is implemented as an exponential decrease in the strength of the associations between items and their position markers (similar comments apply to the start marker in Henson's SEM). In the Burgess and Hitch (1999) model, a primacy gradient is implemented through decaying inhibition of activated item nodes during sequence presentation. To elaborate, during presentation of a sequence each stimulus activates its corresponding item node after which it is inhibited.

Critically, this inhibition wears off gradually over time, meaning that once recall is initiated earlier items will have had more time for their activations to recover from inhibition. This sets up a primacy gradient of activations over the item nodes, with the outcome that the Burgess and Hitch (1999) model can accomplish forward recall even in the absence of its positional context signal (Page, 2005).

Thus, most models of short-term memory assume the presence of a primacy gradient at some level. The models differ, however, in terms of the underlying mechanism they adopt to explain the genesis of the primacy gradient. As noted above, in the Burgess and Hitch (1999) model, a primacy gradient arises due to the operation of decaying inhibition following item selection during serial order encoding. Page and Norris (1998) propose two mechanisms by which the primacy gradient might arise in their primacy model. On the one hand, in an activation-based conception of their model, the primacy gradient arises from the decaying activation of a modulating factor, which is, in turn, multiplied by the number of items already encoded into memory. The activity of the modulating factor is maximal upon presentation of the first item in the sequence and then decays exponentially with the passage of time, meaning that each incoming item is encoded with less strength than its predecessor. On the other hand, in a context-based conception of their model, the primacy gradient arises through the association of each incoming item with a start of sequence context, with the strength of the association decreasing with sequence position. This context cue is then reinstated at recall in order to retrieve the primacy gradient of activations over items.⁴ In the LIST PARSE model (Grossberg & Pearson, 2008; see also Bradski, Carpenter, & Grossberg, 1992, 1994), the primacy gradient arises because once the nodes representing items are activated during serial order encoding their activations gradually accumulate in strength. Since items encoded earlier in the sequence will have had more time for their activations to accumulate, primacy will dominate in the resulting activation gradient over item nodes. Finally, in the SOB model (Farrell & Lewandowsky,

2002) and its more recent extension, C-SOB (Lewandowsky & Farrell, 2008a), the primacy gradient is a consequence of an endogenous encoding process, exclusive to this model, known as *similarity-sensitive encoding*. This process determines the encoding strength of each study item by calculating its novelty with respect to existing information in memory. Items which are novel with respect to existing information are encoded strongly, whereas items which are similar are encoded less strongly. Crucially, because each new study item will bear some resemblance to existing information in memory this means that each item will be encoded with less strength than its predecessor, thereby generating a primacy gradient. However, as we will see later, encoding conditions exist in which SOB and C-SOB predict a non-monotonic rather than a monotonic primacy gradient.

Response suppression

Response suppression is the output-contingent inhibition of items, and is, as Table 2 indicates, a widespread assumption in models of short-term memory. In CQ models, response suppression is reflected by the inhibitory feedback signal from the competitive choice layer to the parallel planning layer following the retrieval of an item. It is considered to be a defining property of those models (Davelaar, 2007). However, it is more important in CQ models (and non-CQ models e.g., Farrell & Lewandowsky, 2002) that represent serial order via a primacy gradient than models that represent serial order through position marking. In the former models, response suppression is necessary to remove an emitted item from the competitive queue so that the next strongest item can be recalled (Figure 7B). Without response suppression, the response selection mechanism would perseverate on the initial response, which would always remain the most active. Response suppression is less important (but still employed) in models that represent serial order through position marking, because at recall the dynamically evolving positional context signal continuously modifies the competitive queue, thereby reducing the burden

on response suppression for sequencing. Another distinction between models employing response suppression concerns whether this suppression decays over time, so that the activation of a suppressed item can gradually recover from inhibition (e.g., Burgess & Hitch, 1999; Henson, 1998a; Page & Norris, 1998), or whether response suppression is time-invariant, with recovery from inhibition only occurring following recall of the entire sequence (e.g., Farrell, 2006; Farrell & Lewandowsky, 2002; Lewandowsky & Farrell, 2008a).

Cumulative matching

An important question for theories of short-term memory for serial order is how to account for the long-term learning of sequences—the transfer of order information from short-term to long-term memory—as witnessed in the Hebb repetition effect (Hebb, 1961). There is evidence (reviewed later) that in order to explain Hebb repetition learning, models of short-term memory must incorporate a recognition process for computing whether an incoming sequence is a novel sequence or one that has been encountered previously. Two of the models listed in Table 2, namely the most recent instantiation of the Burgess and Hitch (2006) model and the revised primacy model (Page & Norris, 2009), accomplish this using a process known as cumulative matching, whereby an incoming sequence is incrementally matched to the representations of previously presented sequences to establish whether it is familiar or not.

We illustrate the process of cumulative matching first using the mechanism instantiated in the Burgess and Hitch (2006) model as an example. As noted earlier, in the Burgess and Hitch (1999) model, serial order is represented by associating each item in a sequence to a set of context nodes with a pattern of activation that varies dynamically across positions. In that model, the same set of context nodes is used to encode all sequences to which the model is exposed. However, in the most recent version

of the model (Burgess & Hitch, 2006), multiple sets of context nodes are employed, with different sequences each recruiting a potentially unique context-set. In the revised model, context-item pairings have both short-term and long-term characteristics. When a sequence is presented, a matching process is initiated whereby each currently presented item is compared with the long-term item-context pairings of each of the different existing context-sets. A context-set receives a match value of 1 for each item in the sequence that matches the long-term item-context associations and a value of 0 otherwise. For each presented item in the sequence, the model calculates the cumulative match between the sequence so-far-presented and each context-set. The cumulative match is calculated by summing the number of matches and multiplying this value by $1/n$, where n is the number of items so-far-presented. If the cumulative match of a context set falls below a threshold value (set to 0.6 in the simulations of Burgess and Hitch) then it is dropped from the cohort of possible candidate context-sets. Thus, as more items in the sequence are conveyed, more and more context-sets will gradually be eliminated. Once the sequence has been presented, the remaining context-set with the best cumulative match is used to encode and recall the sequence. If no context-set remains active then a new context-set will be recruited instead.

A similar matching process operates in the revised primacy model of Page and Norris (2009). In their model, a sequence made familiar through repetition is represented by a single localist “chunk” node. This chunk node has connections to each of its constituent items that vary in strength according to a primacy gradient. For example, the chunk node for the familiar sequence YMCA would have a strong connection to the letter Y, a weaker connection to the letter M, a weaker connection still to the letter C, and so forth. This primacy gradient in the item-to-chunk node connections parallels the primacy gradient of activations over items used to represent order in short-term memory. When a sequence is conveyed, chunk nodes will fire according to the extent to which the incoming

short-term memory primacy gradient of activations matches the primacy gradient in the connections between chunk nodes and items. Thus, the YMCA node will fire maximally in response to the sequence YMCA, but less so in response to sequences such as YMAC, CAYM etc. If no chunk node fires during the presentation of a sequence then a new chunk node will potentially be established.

Output interference

A further assumption invoked by four of the models listed in Table 2 is that of output interference. This refers to the notion that the recall of an item from short-term memory interferes with the representations or accessibility of items that are yet to be recalled. This output interference manifests irrespective of whether or not a recalled item is subsequently suppressed and its effects accumulate as sequence production unfolds, meaning that the representations of items in the middle and towards the end of a sequence will be most impaired by its action. Accordingly, output interference is one mechanism by which the primacy effect in forward ordered recall might materialize.

In the OSCAR (Brown et al., 2000) and C-SOB (Lewandowsky & Farrell, 2008a) models, output interference is modeled by adding increasing amounts of Gaussian noise with each successive item recalled to the weight matrix encoding associations between items and their position markers. By contrast, in the SIMPLE model (see Lewandowsky, Duncan, & Brown, 2004), output interference is simulated by reducing the distinctiveness of the positional representations of yet to be recalled items by an amount which increases with each recalled item. The use of output interference in these models enables them to more accurately accommodate primacy and sequence length effects (see e.g., Brown et al., 2000).

Locus of similarity effects

Several theories additionally incorporate assumptions about the nature and locus of item similarity effects in short-term memory (Botvinick & Plaut, 2006; Brown et al., 2007; Burgess & Hitch, 1999; Farrell, 2006; Henson, 1998a; Lewandowsky & Farrell, 2008a; Page & Norris, 1998). These theories can be distinguished according to whether they explain similarity effects solely in terms of the stage of retrieving item information, or whether similarity also affects initial encoding.

According to retrieval-based accounts of similarity effects (Burgess & Hitch, 1999; Henson, 1998a; Page & Norris, 1998), ordered recall proceeds in (at least) two competitive stages. In the first, order-based competition stage, items are activated by the ordering mechanism driving recall and the strongest item is chosen. In the second, similarity-based competition stage, an item chosen from the first stage will undergo a further competition in which it is vulnerable to confusion with other items remaining to be recalled based upon its degree of similarity to those items. To elaborate, we illustrate the recall procedure underlying the primacy model (Page & Norris, 1998), which relies on a dual-stage procedure for recall. In the primacy model, items are activated according to a primacy gradient in the first stage and the item with the strongest activation is selected through competitive queuing. The recalled item is then passed on to a second stage wherein its activation is set equal to 1. Items which are similar to the recalled item are activated by an amount equal to the value of a parameter reflecting their degree of similarity, whereas items which are dissimilar to the recalled item have an activation equal to 0. The effect of this is to increase the likelihood that a similar item recalled from the first stage will be confused with another similar item in the second stage, thereby accommodating the poorer ordered recall of sequences of similar items.

Other theories (Botvinick & Plaut, 2006; Brown et al., 2007; Farrell, 2006; Lewandowsky & Farrell, 2008a; Nairne, 1990), by contrast, posit that the effects of

similarity do not occur solely during retrieval, but also occur during the encoding of serial order. For example, the C-SOB model (Farrell, 2006; Lewandowsky & Farrell, 2008a) has an initial serial ordering stage that involves context-item associations and a second retrieval stage in which a “noisy” item representation recovered from the first stage is converted into a recallable item. This latter “deblurring” stage uses long-term knowledge in order to reconstruct degraded representations of items retrieved from the first stage. C-SOB predicts an effect of similarity on serial order encoding by virtue of the similarity-sensitive encoding mechanism that underlies the generation of its primacy gradient. Recall from earlier that similarity-sensitive encoding determines the encoding strength of each successive study item by computing its similarity to the current contents of memory. Items that are dissimilar and novel with respect to existing information in memory are encoded strongly, whereas items that are similar are encoded less strongly. A natural consequence of this similarity-sensitive encoding process is that items in similar sequences will be encoded with less strength than items in dissimilar sequences, rendering the primacy gradient for similar sequences shallower than that for dissimilar sequences. In addition to its effect on encoding, similarity affects recall by reducing the accuracy of the deblurring process used to disambiguate retrieved items. Both the effects of similarity at encoding and during retrieval in C-SOB render errors more likely in similar sequences than in dissimilar sequences.

Selection of principles

We now review empirical evidence for the role of the principles of serial order and ancillary assumptions described above in verbal, visual, and spatial short-term memory, in an attempt to identify the theoretical constructs that are best suited to explaining memory for serial order in the three domains. Note that this is not a straightforward exercise, because many of the phenomena of serial order reviewed earlier are explicable in

terms of different combinations of the theoretical constructs. This is reflected by the fact that contemporary theories of memory for serial order, with their different architectural and representational commitments, can account equally well for many of the findings listed in Table 1 (see e.g., Lewandowsky & Farrell, 2008a). A particularly telling demonstration of this problem is provided in Figure 8, which shows the predictions of five models of serial order studied by Farrell and Lewandowsky (Farrell & Lewandowsky, 2004; Lewandowsky & Farrell, 2008a) that were built from different combinations of principles for representing serial order (representative of the combinations of principles employed by the models listed in Table 2).⁵ The models were implemented in a common, dynamic neural network architecture corresponding to the competitive choice layer in CQ models that permitted the generation of response probability and recall latency predictions. It is apparent from inspection of this figure that the five models predict qualitatively similar accuracy serial position curves (Figure 8A), transposition gradients (Figure 8B), and latency serial position curves (Figure 8C), rendering it impossible to distinguish between them on these measures. Fortunately, however, some of the phenomena listed in Table 1—as well as some new data that we introduce next—do provide direct support for the specific principles of serial order and ancillary assumptions illustrated in Table 2. We consider this evidence in the following sections.

Evidence for competitive queuing

Although human short-term memory studies have failed to provide direct evidence for CQ, there are nevertheless strong grounds for believing that the CQ mechanism is the central basis for sequence planning and control in the verbal, visual, and spatial short-term memory domains. The CQ mechanism provides a powerful and parsimonious account of a host of phenomena of memory for serial order that have been shown to be common to the three domains, most notably the greater incidence of transposition than item errors and

the locality constraint underlying transpositions, as well as other ancillary outcomes, such as effects of primacy and recency of the serial position curve and the sequence length effect. All CQ models predict that the most common errors will be movements and exchanges between items. This prediction is a natural consequence of the parallel sequence dynamics assumed by these models which when perturbed by noise will alter the relative priority of items. Near-neighbor transpositions predominate because the representation of serial order via an activation gradient necessarily implies that the strongest competitors to the target item at each recall position will be items from adjacent serial positions.

These predictions are not unique to CQ models. However, recent electrophysiological recording studies with monkeys have provided direct evidence for the dynamics assumed by the CQ mechanism (Averbeck et al., 2002; Averbeck, Chafee, Crowe, & Georgopoulos, 2003; Averbeck, Crowe, Chafee, & Georgopoulos, 2003). For example, in a study by Averbeck et al. (2002), macaque monkeys were trained to imitate geometric shapes (triangle, square, trapezoid, inverted triangle) made up of serial movement segments. They found that prior to sequence imitation a parallel representation of the sequence was present within prefrontal cortex (area 46). Each movement segment was represented by a distinct pattern of neural activity and their relative strengths of activation predicted their relative performance order. During copying, neuronal ensembles coding the forthcoming movement segment increased in firing rate until the movement was executed, after which the neural activity associated with the performed segment decreased sharply. Analyses of transposition errors revealed that near-neighbor transpositions were most frequent, and materialized when a neural ensemble coding a movement segment from an incorrect serial position was activated more strongly than the neural ensemble coding the movement segment for the current position. These neural response profiles were strikingly similar to those predicted by Houghton's CQ model (Houghton, 1990). These results, obtained with monkeys, confirm that the brain utilizes the parallel response

activation and sequential selection process postulated by the CQ mechanism. We take the preponderance of near-neighbor transposition errors in verbal, visual, and spatial serial order memory to be indirect behavioral signatures of their reliance on such a mechanism. More recently, Agam and colleagues (Agam et al., 2010; Agam & Sekuler, 2007) have extended some of these findings observed with monkeys to humans by taking event-related potential (ERP) recordings whilst participants observed and subsequently imitated sequences of visual-spatial movements. They found that the amplitude of the ERPs associated with each movement segment decreased as a function of their serial position within the sequence as in the study of Averbek et al. (2002) consistent with the activation gradient representation of serial order assumed by the CQ mechanism.

There are further grounds for supposing that a CQ selection process underpins verbal, visual, and spatial sequence planning and control. Specifically, there is mounting evidence to suggest that CQ is a general basis for all cognitive sequential behavior (Bullock, 2004; Bullock & Rhodes, 2003; Rhodes, Bullock, Verwey, Averbek, & Page, 2004). For example, computational models that utilize the CQ mechanism have been developed and successfully applied to data from a range of serial performance domains, including typing (Rumelhart & Norman, 1982), speech production (Bohland, Bullock, Guenther, 2009; Dell, 1986; Dell, Burger, & Svec, 1997; Hartley & Houghton, 1996; Houghton, 1990), sequence learning (Rhodes & Bullock, 2002; Rhodes et al., 2004), spelling (Glasspool & Houghton, 2005; Glasspool, Houghton, & Shallice, 1995; Glasspool, Shallice, & Cipolotti, 2006; Houghton, Glasspool, & Shallice, 1994), saccade generation (Brown, Bullock, & Grossberg, 2004; Silver, Grossberg, Bullock, Histed, & Miller, 2012), action planning (Cooper & Shallice, 2000), music performance (Palmer & Pfordresher, 2003), and of course short-term memory (Burgess & Hitch, 1992, 1999, 2006; Henson, 1998a; Page & Norris, 1998). The success of CQ models in these various domains is attributable to their ability to capture error patterns, such as transpositions, that appear

to be a characteristic of all serial behaviors.

Given the above precedents, we identify CQ as the preferred mechanism for sequence planning and control in verbal, visual, and spatial short-term memory.

Evidence for position marking

Theories that use position marking to represent order can account for many of the phenomena of memory for serial order observed in verbal, visual, and spatial short-term memory, including effects of primacy and recency of the accuracy serial position curve (Figure 8A), the sequence length effect, the locality constraint governing transpositions (Figure 8B), and the increase in omissions and intrusions observed over output positions (Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a; Lewandowsky & Farrell, 2008a). In all positional models, primacy and recency effects are partly, if not wholly, determined by “edge effects”: There are less opportunities for items near the beginning and end of a sequence to engage in movement errors, compared to items in the middle of the sequence. In some models (e.g., Brown et al., 2007; Henson, 1998a), an additional factor contributing to primacy and recency effects is the greater distinctiveness of position markers for terminal positions. For example, in Henson’s (1998a) SEM, neighboring states of the start and end markers are more distinctive at terminal than medial sequence positions bestowing the two-dimensional ordering mechanism with more discriminatory power in primacy and recency regions. Sequence length effects arise because the greater the number of items in the target sequence, the greater the probability of an error being committed. In some positional models (e.g., Henson, 1998a), an additional factor contributing to the sequence length effect is that the resolution of the positional codes for longer sequences is weaker than for shorter sequences, meaning that the probability of recalling an item at a given position on a long sequence will be lower than an item at the same position on a shorter sequence. The locality constraint arises because the position

markers for items at proximal positions are more similar than the markers for items at distant positions, rendering near-neighbor transpositions most frequent. Omission errors are accommodated by incorporating an output threshold that the strongest item must exceed in order to be recalled, whilst intrusion errors are modeled by weakly activating extra-sequence items to allow them to enter into the competition process. The increase in omissions and intrusions over output positions is attributable to the primacy gradient that virtually all positional models incorporate (Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a; Lewandowsky & Farrell, 2008a). The encoding strength of items decreases across serial positions rendering items towards the end of the sequence more likely to fall beneath the output threshold or encounter strong competition from extra-sequence items (by contrast, the increase in repetitions across output positions seen in the recall of verbal sequences arises because as output position increases there are more opportunities to produce these errors).

Positional models can also account for the inverted U shape of the latency serial position curve witnessed for the ordered recall of verbal, visual-spatial, and auditory-spatial sequences (Figure 8C; Farrell & Lewandowsky, 2004). As noted above, items near the beginning and towards the end of the sequence possess more distinctive position markers than items at medial sequence positions. Consequently, items at the sequence boundaries will encounter less competition during recall and this translates into faster recall latencies for these items. The extremely long initial recall latency is assumed to reflect the operation of set-up processes that prepare the sequence for output (cf. Sternberg, Monsell, Knoll, & Wright, 1978) but current theories of serial recall do not simulate these processes (i.e., they are assumed but not explicitly modeled). Furthermore, positional models can potentially explain the backward recall accuracy and latency serial position curves obtained using verbal and visual-spatial sequences. The enhanced recency effect would manifest because the last two items in the sequence, by virtue of being recent,

are well represented in memory. As in forward recall, the long recall time for the last item—the first to be output—would reflect set-up time required to prepare the sequence for output, whilst the fast recall time for the penultimate item would occur because it is still recent in memory. Thereafter, items would be retrieved using the multiple-scan strategy. This would be accomplished by covertly scanning through the position markers in forward order until the next item is reached. Once output, the item would be inhibited via response suppression and the scanning process would repeat until the first item is recalled. The reduced primacy effect and longer response time pauses in backward recall compared to forward recall would arise because the multiple scans generate extra processing requirements during output of the sequence.

Models that use position marking are also extensible to the Hebb repetition effect. For instance, in the Burgess and Hitch (1999) model, the Hebb repetition effect arises because following each presentation and attempt to recall the repeated sequence, the associations between the items in that sequence and the positional context signal used to represent order are gradually strengthened. However, a major shortcoming of the model is that the long-term learning of multiple sequences is not possible, because the use of a single context signal to encode all sequences causes interference. This inability of the model is inconsistent not only with everyday experience, but also with data showing that participants can learn multiple sequences in parallel during the course of a Hebb experiment (Cumming et al., 2003; Hitch et al., 2009). As noted earlier, in the most recent version of the model (Burgess & Hitch, 2006), multiple context signals are incorporated for representing different sequences in conjunction with a cumulative matching process. The use of multiple context signals enables the model to learn more than one sequence in parallel, whilst the matching process provides a mechanism for determining whether an incoming sequence is familiar or not. In the revised model, the Hebb repetition effect arises as a result of the repeated re-use of an old context signal for

the same (or a similar) sequence. A recall advantage is obtained through this context re-use, because each time the context signal is recruited, the long-term item-context connections will be strengthened, thereby reducing the likelihood of errors, and the more often the context-set has been recruited, the greater this recall benefit will be.

The above phenomena are not uniquely accountable in terms of theories that use position marking to represent serial order; they can also be accommodated by theories that invoke a primacy gradient as the functional basis for serial ordering (see below). However, there are two direct pieces of evidence for position marking in short-term memory. The first comes from the effects of temporal grouping documented in the ordered recall of verbal sequences (e.g., Frankish, 1985, 1989; Hitch et al., 1996; Maybery et al., 2002; Ryan, 1969a, 1969b) and sequences of visual-spatial (Parmentier, Andrés et al., 2006) and auditory-spatial (Parmentier et al., 2004) locations. Positional theories explain such effects by postulating that positional information in grouped sequences is represented on at least two dimensions, with one dimension representing the positions of items or groups within the sequence, and with the second dimension representing the positions of items within groups (Brown et al., 2007; Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a; Lewandowsky & Farrell, 2008a). This representational scheme has been shown to be both necessary and sufficient to accommodate the major effects of grouping on recall accuracy, latency, and errors (Brown et al., 2000; Henson, 1998a; Lewandowsky & Farrell, 2008a). Theories that rely solely on a primacy gradient to represent serial order cannot explain grouping phenomena, because the primacy gradient can only be used to represent order along a single dimension of activation strength.

The second piece of direct evidence for position marking comes from the existence of positional errors in verbal short-term memory, namely interpositions in temporally grouped sequences (Henson, 1996, 1999a; Ng & Maybery, 2002, 2005; Ryan, 1969a) and protrusions in ungrouped sequences (Conrad, 1960; Henson, 1999a). Theories that use

position marking to represent serial order predict interpositions in grouped sequences, because items in the same positions in different groups will possess similar within-group positional codes, rendering them vulnerable to positional confusions. Protrusions can be accommodated by assuming that items, as well as being coded for their position in a sequence, are coded for their position within a sequence of sequences (Burgess & Hitch, 1999; Henson, 1998a). Such errors manifest because items occupying the same sequence position on different trials will possess similar within sequence positional codes. Theories that represent serial order using a primacy gradient cannot accommodate protrusions, because the simple gradient-based representation of order does not provide any direct coding of positional information.

It is noteworthy that although Parmentier and colleagues have shown that short-term memory for visual-spatial (Parmentier, Andrés et al., 2006) and auditory-spatial (Parmentier et al., 2004) sequences of locations exhibit effects of temporal grouping on recall accuracy and latency similar to those witnessed with verbal sequences, they nevertheless failed to replicate one of the key aspects of grouping documented in verbal studies, namely the increased tendency of participants to produce interpositions in grouped sequences. The reason for this discrepancy is unclear. However, given that the elevated incidence of interpositions in grouped sequences is a key piece of evidence in support of the claim that positional information contributes to the representation of serial order in verbal short-term memory (e.g., Henson, 1996, 1999a, 1999b), the failure to observe an increase in these errors with grouped spatial sequences suggests that the evidence for position marking is less robust in the spatial domain. Studies of spatial short-term memory have yet to examine whether it exhibits the second class of error that is an empirical assay of position marking—namely protrusions. Neither temporal grouping effects nor positional errors have been examined using visual, non-spatial memoranda rendering it unclear whether position marking plays a role in the representation of serial

order in visual short-term memory.

Evidence for a primacy gradient

Theories that rely on a primacy gradient to represent order can also explain many of the phenomena of memory for serial order observed in the verbal, visual, and spatial short-term memory domains. When complemented with response suppression, these models can account for the extensive primacy and restricted recency of the accuracy serial position curve (Figure 8A), the sequence length effect, and the locality constraint (Figure 8B; Farrell & Lewandowsky, 2002, 2004; Page & Norris, 1998). The primacy effect materializes because the activations of items near the beginning of the sequence are more distinctive, meaning these items encounter less competition during recall than items towards the end of the sequence. By contrast, the recency effect manifests because as successive items are recalled and suppressed, the number of response competitors is gradually reduced. Thus, as the end of the sequence approaches, only one or two unsuppressed items will compete for recall in final sequence positions. The sequence length effect occurs because increases in the length of the target sequence will necessarily increase the probability of committing at least one error during recall, whilst the locality constraint arises because the disparity in activation between items is smallest for those at neighboring ordinal positions. Primacy gradient models can also account for the increase in omissions and intrusions across output positions observed with verbal, visual, and visual-spatial sequences (Farrell & Lewandowsky, 2002; Page & Norris, 1998), the mechanisms for accounting for these errors being the same as those described in the previous section on position marking.

Like positional models, primacy gradient models can also account for the inverted U shape of the latency serial position curve observed with verbal, visual-spatial, and auditory-spatial sequences (Figure 8C; Farrell & Lewandowsky, 2004). This pattern is

predicted because the relative differences in the activation levels of items decrease across input positions, meaning that competition amongst items increases over output positions, thereby yielding gradually longer recall latencies. However, the suppression of items once emitted means that the final item will encounter little competition during recall allowing that item to be recalled relatively quickly. As noted earlier, the pronounced initial recall latency is assumed to reflect the operation of general set-up processes that precede production of the first response, rather than a specific property of the representation of serial order. In addition, primacy gradient models can explain the backward recall accuracy and latency serial position curves in the same way as described for positional models, except that the multiple-scan strategy would be implemented by covertly scanning along the primacy gradient representation of order, rather than by traversing a series of position markers (cf. Page & Norris, 1998).

Page and Norris have illustrated how a primacy gradient model can additionally account for the Hebb repetition effect. In their revised primacy model (Page & Norris, 2009), when a previously unlearned sequence is presented, the short-term memory primacy gradient of activations over items is copied into the strength of connections between those items and a chunk node representing the entire sequence. When the sequence is presented a second time, the cumulative matching process will activate its chunk node representation, which in turn will activate its constituent items via the primacy gradient that has been partially learned in the item-to-chunk node connections. The resulting long-term memory primacy gradient is added to the primacy gradient of activations used to represent order in short-term memory, rendering it steeper and higher than when the sequence was recalled the first time. Because the relative activations of the short-term memory primacy gradient will now be wider apart than before, this will reduce the likelihood of committing a transposition. Furthermore, because the activations will also be stronger, this will reduce the likelihood of committing an omission. Thus, the

sequence should tend to be recalled more accurately on this second occasion, compared to the first. After the sequence has been presented and before it is output, the strength of the item-to-chunk node connections will be further strengthened by once again copying the primacy gradient of activations held in short-term memory into them. Subsequent presentations and recalls of the sequence will yield further improvements in recall accuracy—i.e., a Hebb repetition effect—as the long-term memory primacy gradient in the item-to-chunk node connections becomes increasingly stronger and more distinctive.

As already noted, the above phenomena are also explicable in terms of theories that use position marking to represent serial order. As such, they do not confer direct support for the involvement of a primacy gradient in the representation of serial order in short-term memory. However, there are two empirical findings that necessitate a direct role for a primacy gradient. First, a primacy gradient, complemented by response suppression, is necessary to accommodate the finding that fill-in errors are more frequent than infill errors in the recall of verbal sequences (Henson, 1996; Page & Norris, 1998; Surprenant et al., 2005) and sequences of visual-spatial locations (Guérard & Tremblay, 2008). Primacy models predict this empirical outcome, because if an item i is recalled a position too soon and then suppressed, item $i-1$ will be a stronger competitor at the next recall position than item $i+1$, because the former item, by virtue of being presented earlier in the sequence, will have been encoded more strongly on the primacy gradient. Although some theories that use position marking to represent serial order can also accommodate this result (Burgess & Hitch, 1999; Henson, 1998a), they do so either by incorporating a primacy gradient in conjunction with position marking (Burgess & Hitch, 1999) or by incorporating a primacy gradient as one component of the context signal responsible for coding positional information (Henson, 1998a).

Second, Farrell and Lewandowsky (2004) have shown that a primacy gradient is necessary to accommodate the pattern of transposition latencies witnessed in the recall of

verbal sequences. Figure 8D shows the transposition latencies predicted by the five models of serial order examined by Farrell and Lewandowsky (Farrell & Lewandowsky, 2004; Lewandowsky & Farrell, 2008a) whose predicted accuracy and latency serial positions curves, and transposition gradients were mentioned earlier. It can be seen from inspection of this figure that, in contrast to those initial predictions, there is considerable variability in the transposition latency predictions of the five models. Specifically, when serial order is represented on the basis of position marking alone (PM), the function relating recall latency to displacement exhibits a symmetric V-shaped function. When position marking is augmented with either response suppression (PM+RS) or output interference (PM+OI), the function relating recall latency to displacement is rendered partially asymmetric, due to postponements having slightly shorter recall latencies than anticipations of the same absolute displacement. In sharp contrast to the above models, the combination of a primacy gradient with response suppression (PG+RS) predicts a negative relationship between recall latency and displacement, with much faster recall latencies for postponements than for anticipations of the same absolute displacement. Finally, the model combining a primacy gradient, position marking, and response suppression (PG+PM+RS) also predicts a negative relationship between recall latency and displacement, but with a reduction in the slope of the function for postponements, compared to anticipations.

Farrell and Lewandowsky (2004) presented data from three experiments involving keyboard-timed serial recall of verbal sequences showing that recall latency is a negative function of transposition displacement but with a reduction in the slope of the function for postponements, compared to anticipations. As can be seen by comparison of representative data from their experiments in Figure 2B with the predictions of the models in Figure 8D, this error latency pattern is most compatible with the prediction of a mechanism combining a primacy gradient, position marking, and response suppression.

The characteristics of the function relating recall latency to transposition displacement have yet to be examined in visual and spatial short-term memory, rendering it unclear whether the same representational mechanism is implicated in these domains.

Evidence for response suppression

That response suppression contributes to verbal short-term memory for serial order is indicated by a number of indirect empirical precedents. First, as noted earlier, people struggle to recall an item twice when it was repeated in a sequence (the Ranschburg effect; Crowder, 1968; Duncan & Lewandowsky, 2005; Henson, 1998b; Jahnke, 1969; Vousden & Brown, 1998), an outcome which according to response suppression accounts is attributable to the suppression of the repeated item once it is recalled which renders it unlikely that it will be retrieved a second time. That this difficulty in recalling a repeated item twice is witnessed even when people can detect repetitions with a high level of accuracy (Henson, 1998b) suggests that response suppression is obligatory and not under volitional control. The operation of response suppression is further supported by the scarcity of erroneous repetitions in participants' recalls (Henson, 1996; Vousden & Brown, 1998). Indeed, such erroneous doublings of responses when they do occur tend to be spaced several positions apart (Henson, 1996) which is consistent with decaying inhibition accounts of response suppression, according to which response suppression wears off gradually over time (e.g., Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a). However, this assumption is contradicted by evidence showing that the Ranschburg effect is not modulated by the delay between recall of the first and second occurrence of a repeated item. Decaying inhibition accounts predict that the Ranschburg effect should be weaker with a long than with a short delay between recall of the first and second occurrence of a repeated item, because with a long delay the item will have had more time for its activation to recover from inhibition, thereby increasing the likelihood it will be

recalled a second time. Duncan and Lewandowsky (2005) empirically manipulated the delay time between recall of the two occurrences of a repeated item and found that the magnitude of the Ranschburg effect was unaffected, a finding at odds with decaying inhibition accounts of response suppression (Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998a), but consistent with time-invariant accounts of response suppression (Farrell & Lewandowsky, 2002; Lewandowsky & Farrell, 2008a) which assume partial and non-decaying response suppression. Note also that the results of Duncan and Lewandowsky (2005) are by extension incompatible with the decaying inhibition mechanism by which the Burgess and Hitch (1999) model generates its primacy gradient.

As well as incorporating response suppression to prevent perseveration on the same response during recall, many models rely on response suppression either partially (Brown et al., 2000; Burgess & Hitch, 1999; Henson, 1998; Lewandowsky & Farrell, 2008a) or entirely (Farrell & Lewandowsky, 2002; Grossberg & Pearson, 2008; Page & Norris, 1998) to produce recency. In those theories, response suppression contributes to recency by reducing the number of response competitors towards the end of the sequence, which increases the likelihood that the final item will be recalled in its correct position. A contribution of response suppression to recency in the forward recall of verbal sequences has been demonstrated in a conditional analysis of the recency effect by Farrell and Lewandowsky (2012). Across a large number of serial recall studies, these authors examined the accuracy of recall of the last item on those trials in which exactly two errors occurred in all but the final serial position. Specifically, they examined how the recency effect is modulated by three different combinations of errors, either: (1) two transpositions, (2) one transposition and one intrusion, or (3) two intrusions. In all instances, two errors are committed, but in (1) all items in the sequence have been recalled and hence suppressed, whereas in (2) the single intrusion leaves one item unrecalled and unsuppressed, whilst in (3) the two intrusions leave two items unrecalled

and unsuppressed. Farrell and Lewandowsky found that the magnitude of the recency effect was a function of the number of items that have putatively been suppressed, with recency strongest following two transpositions, weaker following a transposition and an intrusion, and weakest following two intrusions. This outcome suggests that response suppression contributes to recency in verbal short-term memory.

However, it is important to note that studies that have dissociated the input and output positions of items in serial recall have highlighted the potential importance of factors other than response suppression as determinants of recency. For example, in a study by Cowan, Saults, Elliott, and Moreno (2002) participants were presented with 9-item verbal sequences and were post-cued to commence serial recall either at input position 1, 4, or 7. When prompted to initiate recall from position 4 or 7, recall proceeded up until the end of the sequence and then wrapped back around to the beginning. The latter two conditions permitted an analysis of serial position effects when the input and output order of items was dissociated. If recency is attributable to response suppression alone, then a recency effect should be witnessed over the output position, but not the input position, of items. However, Cowan and colleagues observed a strong recency effect over the input position of items, a result that can be attributed variously to (a) an “edge effect” (see earlier), (b) a positional coding mechanism in which the position markers for items near the end of the sequence are more distinctive than for items near the middle of the sequence (e.g., Brown et al., 2007; Henson, 1998a), or (c) both factors. Similar results were obtained in a study by Oberauer (2003) using a different paradigm that also permitted a deconfounding of the input and output ordering of items. Like Cowan and colleagues, Oberauer observed a recency effect over the input positions of items, but additionally failed to observe such an effect over the output positions of items, a result at odds with response suppression accounts of recency. Taken together, the results of Farrell and Lewandowsky (2012), Cowan et al. (2002), and Oberauer (2003) suggest that

response suppression contributes to recency in the standard forward recall paradigm, but it is not the only contributing factor. Crucially, the results of Oberauer (2003) suggest that response suppression might be a bespoke mechanism employed in the standard forward recall paradigm that is abandoned in paradigms where recall must commence from different input positions.

The role (or lack thereof) of response suppression in visual and spatial short-term memory for serial order is presently unclear because the above phenomena have yet to be examined in these domains.

Evidence for cumulative matching

A key prediction of cumulative matching is that if the start of a repeated sequence changes appreciably from one presentation to the next, the Hebb repetition effect should be abolished. This is because the matching process is crucially dependent not only on the overall similarity of an incoming sequence to existing sequences, but crucially, similarity from the start of the sequence. This prediction is consistent with the finding of Schwartz and Bryden (1971) that the Hebb repetition effect is removed if the first two items of a repeated verbal sequence are changed on each presentation, whereas the effect remains when it is the last two items in the sequence that are changed. Note that, on the cumulative matching account, changing the last two items should not disrupt the Hebb repetition effect because the cumulative match to an existing sequence will already be sufficiently strong for it to be recognized as familiar before the novel items are conveyed.

Cumulative matching can also explain the findings from a study by Cumming et al. (2003) that tested the hypothesis that sequence learning in the Hebb repetition paradigm involves the learning of item-position associations. In their study, participants engaged in a Hebb repetition experiment and after a strong repetition effect was established, performance was evaluated on a transfer sequence that had not previously been presented.

Half of the items in this sequence maintained the same positions as in the repeated sequence, whereas the other half were assigned to different positions. Sometimes the items at odd positions in the repeated sequence were assigned to the same positions in the transfer sequence (e.g., S-D-S-D-S-D-S-D; where S = same position; D = different position) and sometimes items at even positions in the repeated sequence were assigned to the same positions in the transfer sequence (e.g., D-S-D-S-D-S-D-S). The key finding was that items that maintained their positions from the repeated sequence were recalled no better than items in control sequences occupying corresponding positions. Similar results were obtained in a study by Hitch et al. (2005) who also employed a transfer sequence methodology. At first blush, the absence of transfer of item-position associations in the above studies appears to rule out an account of the Hebb repetition effect in which repetition learning is driven by the reinforcement of item-position associations. However, the Burgess and Hitch (2006) model can accommodate this result, because the transfer sequences are sufficiently different from the repeated sequence that they will not be recognized as familiar by the cumulative matching process. Specifically, for both transfer sequences, the cumulative match to the repeated sequence after the fourth item has been conveyed will be .5, which is less than the threshold of .6 for retaining a context-set. Accordingly, a new context set should be recruited to encode and recall both transfer sequences and a benefit of repeating the item-position pairings from the repeated sequence should not be obtained.

Thus, the absence of item-position transfer in the above studies does not preclude the possibility that the Hebb repetition effect is attributable to the strengthening of item-position associations. Indeed, the finding that the Hebb repetition effect with verbal memoranda is disrupted when the temporal grouping pattern of the repeated sequence varies from one presentation of the sequence to the next (Bower & Winzenz, 1969; Hitch et al., 2009) lends credibility to the hypothesis that repetition learning in verbal

short-term memory does involve the strengthening of such associations. Qualified support for this claim is provided by the outcomes of a simulation reported by Burgess and Hitch (2006) in which they showed that their positional model of the Hebb repetition effect could account for the slower repetition learning observed when the temporal grouping pattern of the repeated sequence varies. In the Burgess and Hitch (2006) model, a temporally grouped sequence will recruit two sets of context units, one set for encoding the positions of items in the sequence and one set for encoding the positions of items within groups. When a context-set is re-used both components are employed and the re-use of a context-set depends upon the cumulative match provided by the combined input from the two context components. If a repeated sequence is presented using the same temporal grouping pattern, the cumulative match will be strong for both the position-in-sequence and position-in-group context components and so the previously used context-set will be recruited to encode and recall the sequence. However, if the sequence is presented using a different temporal grouping pattern from that used previously, although the cumulative match will still be strong for the position-in-sequence context component, it will be weak in the case of the position-in-group context component, as some items will have been presented at different within-group positions due to the new grouping structure. Since the re-use of a context-set depends upon the cumulative match from both context components, a poor match for the position-in-groups context component will reduce the likelihood that a context-set will be re-used, thereby accounting for the slower repetition learning observed when the temporal grouping structure of the repeated sequence varies. Note that this result cannot be explained by primacy gradient models because, as we have already noted, grouping effects are beyond the purview of such models. Thus, these data pose problems for the revised primacy model's account of the Hebb repetition effect (Page & Norris, 2009).

Studies of the Hebb repetition effect in the visual and spatial domains have not yet

examined the impact of partial repetition of a sequence or how changes in the temporal grouping structure of the repeated sequence impact on repetition learning. Accordingly, whether cumulative matching and position marking play a role in the Hebb repetition effect in these domains is currently unclear.

Evidence for output interference

A contribution of output interference to ordered recall would be reflected in the primacy effect. However, identifying such a contribution is rendered difficult by the fact that in the standard forward recall paradigm, the output order of items is perfectly correlated with their input order. Thus, the primacy effect may originate from input processes, such as a primacy gradient, output processes, such as output interference, or a combination of the two. As noted above, the studies of verbal serial recall conducted by Cowan et al. (2002) and Oberauer (2003) empirically dissociated the input-output ordering of items by having participants commence serial recall from different input positions. In both studies, a strong decrement in performance was observed over the output positions of items, suggesting that output interference is one source of the primacy effect in verbal short-term memory. However, it is noteworthy that in both studies a decrement in performance was also witnessed over the input positions of items, suggesting that a primacy gradient also contributes to the genesis of the primacy effect.

Since no studies have yet attempted to deconfound the contribution of input and output processes to serial position effects in visual and spatial short-term memory, whether or not output interference contributes to the genesis of the primacy effect in these domains is presently unclear.

Evidence on the locus of similarity effects

All accounts of item similarity effects have been designed to accommodate the classic phonological similarity effect in verbal short-term memory. It follows that the

different accounts cannot be distinguished on the basis of these data. However, adjudication becomes possible by considering their predictions concerning the effects of phonological similarity for sequences in which similar and dissimilar items are mixed together. Initial studies of this mixed-sequence phonological similarity effect showed that dissimilar items in mixed sequences are recalled with the same level of accuracy as items in corresponding positions in pure dissimilar sequences (Baddeley, 1968; Henson et al., 1996). This so-called *dissimilar immunity* finding (Farrell, 2006) was initially taken as evidence in favor of retrieval-stage accounts of item similarity effects, since in those theories the recall of dissimilar items is unaffected by whether or not they are surrounded by similar items.

However, recent studies have cast doubt on the validity of this dissimilar immunity finding (Farrell, 2006; Farrell & Lewandowsky, 2003; Lewandowsky & Farrell, 2008b). In the first of a series of studies, Farrell and Lewandowsky (2003) showed that the absence of a difference in the recall accuracy of dissimilar items on pure and mixed sequences is a consequence of a failure to equate the stimulus ensemble sizes for the two sequence-types. In early studies (Baddeley, 1968; Henson et al., 1996), the stimulus ensembles for mixed sequences contained double the number of items used in the pure dissimilar and similar sequence stimulus ensembles. Farrell and Lewandowsky showed that the effect of this imbalance is to increase the number of omissions and intrusions in mixed sequences. When the greater incidence of these errors in mixed sequences was abolished by equating the stimulus ensemble sizes for the two sequence types, Farrell and Lewandowsky found that dissimilar items on mixed sequences were recalled with greater accuracy than their counterparts on pure dissimilar sequences. This so-called *mixed-sequence advantage*—illustrated graphically in Figure 9—is of considerable empirical generality, having been witnessed using: (a) immediate serial recall (Farrell, 2006; Farrell & Lewandowsky, 2003; Lewandowsky & Farrell, 2008b) and serial reconstruction (Farrell & Lewandowsky, 2003), (b) delayed serial recall (Farrell, 2006), (c) blocked (Farrell, 2006;

Farrell & Lewandowsky, 2003) and random presentation (Lewandowsky & Farrell, 2008b) of pure and mixed sequences, and (d) mixed sequences containing equal numbers of dissimilar and similar items or a single dissimilar item appended to a sequence of otherwise similar items (Farrell, 2006; Farrell & Lewandowsky, 2003; Lewandowsky & Farrell, 2008b).

The mixed-sequence advantage for dissimilar items is incompatible with theories that rely solely on the retrieval stage of recall for simulating the effects of item similarity. Qualified support for this claim was provided by Farrell and Lewandowsky (Farrell, 2006; Lewandowsky & Farrell, 2008b) who showed by simulation that two such theories, namely SEM (Henson, 1998a) and the primacy model (Page & Norris, 1998), were unable to account for the superior recall of dissimilar items on mixed sequences. However, this empirical pattern can be explained by the C-SOB model (Farrell, 2006; Lewandowsky & Farrell, 2008a). The superior recall of dissimilar items on mixed sequences is predicted by C-SOB because its process of determining the encoding strength of each study item based on its similarity to existing information in memory—similarity-sensitive encoding—means that similar items on mixed sequences will be encoded with less strength than their dissimilar counterparts on pure dissimilar sequences. Consequently, similar items on mixed sequences will be weaker competitors during recall than dissimilar items in corresponding positions on pure dissimilar sequences. The dissimilar items on mixed sequences therefore enjoy a recall advantage relative to their twins on pure sequences. Since C-SOB appears to be the only existing theory that provides a principled, quantitative account of the mixed-sequence advantage, we conclude that in verbal short-term memory item similarity effects involve a combination of similarity-sensitive encoding and similarity-sensitive retrieval. Furthermore, because similarity-sensitive encoding also explains the genesis of a primacy gradient, we further conclude that the mixed-sequence advantage confers additional support for the role of a primacy gradient in verbal short-term memory.

The above conclusion—that item similarity effects reflect a combination of similarity-sensitive encoding and similarity-sensitive retrieval—may seem difficult to reconcile with the results of studies of the Hebb repetition effect for verbal sequences conducted by Hitch et al. (2009) that found support for a series of predictions of the Burgess and Hitch (1999) model, according to which similarity affects only retrieval of item information and not initial encoding of context-item associations. As noted earlier, Hitch et al. (2009) established a dissociation whereby phonological similarity had no effect on the rate of learning repeatedly recalled sequences, despite having a large disruptive effect on their immediate recall. In contrast, rate of learning was reduced when the temporal grouping pattern of repeated sequences was changed, consistent with the assumed effect of grouping on encoding context-item associations. If similarity affects context-item associations, as in the C-SOB model, it would have been expected to reduce rate of learning, which is not what Hitch et al. (2009) observed. However, noting that the mixed-sequence advantage for dissimilar items is empirically a small effect, it is possible that Hitch et al. (2009) may have failed to detect a small effect of similarity on rate of learning.

That the effect of similarity at encoding is small is buttressed by simulations conducted by Farrell (2006) comparing the quantitative fits of C-SOB to the results of a mixed-sequence experiment using the standard implementation of the model in which similarity-sensitive encoding was operational and a control version in which it was switched off. The two versions of the model produced comparable phonological similarity effects for pure dissimilar and similar sequences (see Figures 8 and 9 of Farrell, 2006). This result suggests that even in C-SOB, similarity actually exerts its strongest effect during the dynamic deblurring retrieval stage, otherwise switching off similarity-sensitive encoding should have significantly reduced the size of the standard phonological similarity effect with pure dissimilar and similar sequences compared to when it was operational. We

can therefore conclude from these simulations that even in C-SOB the effect of similarity at encoding is comparatively small in relation to the effect at retrieval. On balance, therefore, the present evidence suggests that similarity affects both encoding and retrieval, but that by far the bigger effect is that on retrieval.

In visual and spatial short-term memory, effects of item similarity have only been examined using pure sequences of visually similar and dissimilar items (e.g., Avons & Mason, 1999; Jalbert et al., 2008; Smyth et al., 2005). As already noted, all theories can accommodate this standard item similarity effect. Similarly, the impact of item similarity on the Hebb repetition effect in the visual and spatial domains has yet to be explored. Accordingly, it is currently unclear whether the effects of item similarity in these domains occur solely at retrieval or during encoding also.

General discussion

The ability to store and retrieve a novel sequence of items in the correct order is thought to be fundamental for various verbal and nonverbal higher-level cognitive activities, including vocabulary learning and the acquisition of many motor skills and social behaviors. The purpose of this review has been to examine the principles underlying the operation of the mechanisms responsible for generating serial order in short-term memory, and to establish whether these principles are the same in the verbal and visuospatial domains.

Consistent with Lashley's (1951) insights on serial order, our analysis suggests that verbal, visual, and spatial sequences are collectively planned and controlled by a cyclical CQ mechanism that converts parallel activated representations of items into serial output by iteratively selecting the most active item representation over time. This claim was motivated on the basis of several direct and indirect empirical and theoretical precedents which we reiterate here: First, all CQ models, irrespective of the precise manner in which

they represent serial order, can account for the major phenomena of memory for serial order witnessed in the verbal and visuospatial domains. In particular, CQ models, by virtue of their parallel sequence dynamics, provide a natural basis for explaining the high incidence of transposition errors in serial tasks and their adherence to the locality constraint. Second, there is direct evidence from electrophysiological recording data obtained from monkeys engaged in a spatial imitation task (Averbeck et al., 2002; Averbeck, Chafee, et al., 2003; Averbeck, Crowe, et al., 2003) which supports the hypothesis that the brain uses CQ to plan, represent, and recall sequences, and aspects of these data have subsequently been verified in ERP studies of spatial sequential memory in humans (Agam et al., 2010; Agam & Sekuler, 2007). Third, there is mounting evidence from the explanatory success of CQ models in other serial performance domains (see sub-section on competitive queuing for example domains and relevant citations) that CQ is a general basis for all sequence planning and control.

Our claim that serial order generation in all short-term memory domains is based on a CQ process is not unique and has been endorsed by other CQ theorists. For example, Grossberg (1978a, 1978b), who developed the CQ model, presented it as a domain-general mechanism for serial order generation in short-term memory, not one tied exclusively to the planning and control of verbal sequences. Other CQ theorists, notably Bullock and Rhodes (Bullock, 2004; Bullock & Rhodes, 2003; Rhodes & Bullock, 2002; Rhodes et al., 2004) and Glasspool and Houghton (Glasspool, 2005; Glasspool & Houghton, 2005) have, like ourselves, emphasized that the CQ mechanism may underpin most, if not all, cognitive sequential behaviors. Within the working memory framework of Baddeley and Hitch, we propose that both the phonological loop and visuospatial sketchpad are governed by a CQ mechanism and that it is this common reliance on CQ that is primarily responsible for the observed similarities between serial order across short-term memory domains. Indeed, it is noteworthy that both of the explicit computational models of the phonological loop,

namely the Burgess and Hitch (1992, 1999, 2006) model and the primacy model (Page & Norris, 1998, 2009), postulate that it operates as a CQ system. Moreover, the LIST PARSE model of Grossberg and Pearson (2008) provides what can be construed as a neurocomputational instantiation of the phonological loop and visuospatial sketchpad in which both systems share a similar neural circuit design based on CQ principles.

Although the evidence points to CQ as the preferred mechanism for sequence planning and control across short-term memory domains, there is nevertheless considerable heterogeneity in the evidence pertaining to how serial order information is represented within the different CQ systems. Table 3 lists the more diagnostic phenomena that we have considered in our review, the short-term memory domains in which they have been witnessed, and the principles of serial order and ancillary assumptions they are attributable to. It can be seen by inspection that, within the verbal short-term memory CQ system, there is robust evidence for the confluence of a panoply of principles. Specifically, evidence suggests that serial order is represented by associations between items and position markers, a primacy gradient of activations, response suppression, and cumulative matching. Evidence further indicates that the recall of items from verbal short-term memory is accompanied by output interference and that item similarity effects manifest both during serial order encoding—via a similarity-sensitive encoding process (Farrell, 2006; Lewandowsky & Farrell, 2008a)—and during retrieval.

By contrast, the principles underlying the representation of serial order within the visual and spatial short-term memory CQ systems are less well-defined, largely because the relevant studies have yet to be performed (most of the cells in Table 3 for visual and spatial short-term memory are filled with question marks). In spatial short-term memory, there is some evidence for position marking and a primacy gradient. However, the contribution (or lack thereof) of response suppression, cumulative matching, and output interference is unclear, because the empirical assays of these principles have not yet been

examined in the spatial domain. Similarly, it is uncertain whether item similarity effects in spatial short-term memory occur solely during retrieval or whether item similarity also exerts an effect during serial order encoding. In visual short-term memory, the situation is even less palpable. Here, there is no direct evidence for any of the principles of serial order and ancillary assumptions, because none of the empirical indices of these theoretical constructs have yet been examined in the visual domain.

Future directions

We now consider some directions for future research on short-term memory for serial order. We begin by considering some directions for further exploration in the visuospatial domain, before considering some directions for further exploration in the verbal domain.

Visuospatial short-term memory

That far less is known about the principles of serial order underlying the operation of the visual and spatial short-term memory CQ systems is attributable to the fact that, for the most part, the empirical phenomena listed in Table 1 that have been examined in these domains are explicable in terms of various different combinations of model principles and assumptions, making identification of the preferred combination difficult. It follows that an important objective for future research is to seek direct evidence for the different theoretical constructs by exploring in visual and spatial short-term memory the more diagnostic phenomena listed in Table 3 that can be uniquely attributed to the action of a particular theoretical construct or combination of constructs.

A second important objective is the development of computational theories of memory for serial order in the visuospatial domain. As noted at the outset, although a wealth of computational theories of serial order in verbal short-term memory have been developed, computational theories of serial order in visuospatial short-term memory are currently lacking.⁶ Such a theory must be able to accommodate the basic phenomena of

memory for serial order observed in visual and spatial short-term memory listed in Table 1, as well as the outcomes of the empirical studies we have proposed above. To these data, one must add the findings from studies highlighting how organizational principles facilitate the encoding of the serial order of sequences of seen spatial locations. Until recently, little consideration had been given to the question of how organizational factors influence memory for spatial sequences. Indeed, a tacit assumption of most researchers has been that characteristics of the spatio-temporal path formed by a sequence of spatial locations are relatively unimportant, and that the limiting factor on recall accuracy is the length of the spatial sequence to be recalled. However, recent studies, which have parametrically varied the stimulus characteristics in spatial serial memory tasks, have identified a number of key effects associated with the encoding of visual-spatial sequences that illuminate the pivotal role of organizational processes in shaping recall performance.

One such effect is the *spatial-clustering effect*, which refers to the finding that when a sequence of locations is divided into clusters based on their spatial proximity to one another, recall accuracy is higher when the sequence path involves navigating through each spatial cluster in turn than when the sequence path involves alternating between different spatial clusters (De Lillo, 2004; De Lillo & Lesk, 2010). This outcome suggests that when the spatial and serial organization of sequence elements coincides, grouping by spatial proximity is an important organizational principle in spatial short-term memory. Studies have shown that other perceptual grouping principles also influence memory for spatial sequences. For example, sequences which follow smooth and continuous trajectories—and hence conform to the Gestalt principle of good continuation—are better recalled than sequences that follow discontinuous trajectories (Kemps, 2001), whilst sequences containing one sub-component that is a symmetrical analogue of another sub-component—and hence adhere to the Gestalt principle of symmetry—are better recalled than asymmetrical sequences (Kemps, 2001; Rossi-Arnaud, Pieroni, & Baddeley,

2006).

Another key effect underlying the recall of spatial sequences is the *path-length effect*, which refers to the finding that sequences containing locations separated by long distances are recalled less effectively than sequences of locations separated by short distances (Guérard, Tremblay, & Saint-Aubin, 2009; Parmentier, Andrés et al., 2006). One interpretation of the path-length effect is that sequences with long paths are more likely than sequences with short paths to violate grouping on the basis of spatial proximity. That is, the locations in sequences with short paths can be unitized into sub-groups based on their spatial proximity to one another—thereby reducing the cognitive demand imposed by the sequence—whereas locations in sequences with long paths will tend to be encoded individually, which imposes a greater burden on memory.

Path-length is not the only property of the sequence path that influences the accuracy of recall of spatial sequences. Studies have additionally shown that spatial sequences containing crosses in the path formed by successive locations are recalled less effectively than sequences that do not contain such crossings (Parmentier & Andrés, 2006; Parmentier et al., 2005). Like the path-length effect, it is possible that this so-called *path-crossing effect* is attributable to the violation of perceptual grouping principles operating during the encoding of spatial sequences. To elaborate, sequences that are devoid of path-crossings tend to follow predictable linear constraints and therefore adhere strongly to the Gestalt principle of good continuation. By contrast, sequences containing crosses in the sequence path follow trajectories that are discontinuous and unpredictable, thereby violating the principle of good continuation.

The effects delineated above underscore the important role played by organizational principles in supporting the encoding of serial order information in spatial sequences. Simple sequences that are high in internal redundancy and well-described by perceptual grouping principles are recalled better than complex sequences. Accordingly, an important

target for any adequate model of visuospatial short-term memory is to explain the process(es) by which the elements in a spatial sequence are parsed and unitized into perceptual groups, and how these groupings support and interact with more elementary mechanisms of serial order.

Verbal short-term memory

We now consider some directions for future research in the verbal domain. Specifically, we suggest that an important future step is to evaluate the extent to which contemporary theories of serial recall and their core principles of operation can be extended to account for performance in kindred memory tasks, such as complex span and free recall. We further suggest that augmenting these models with mechanisms for accounting for serial ordering at the sub-lexical and supra-lexical levels of representation is important if they are to be able to deal with more realistic linguistic inputs.

Extending models of serial recall to complex span. One paradigm that offers a natural test bed for extending theories of serial recall is the complex span task. In this task, participants are presented with a sequence of items (typically words, letters, or digits) for serial recall, but interspersed between the presentations of each item they must engage in some processing activity. Naturally, this processing activity renders the complex span task more difficult than its serial recall counterpart. There are many different versions of complex span which differ in terms of the nature of the processing task that must be performed. For example, in reading span, people read sentences (Daneman & Carpenter, 1980), in counting span (Case, Kurland, & Goldberg, 1982), people count the number of dots in spatial arrays, whilst in operation span (Turner & Engle, 1989), people verify simple arithmetic operations.

There has been an explosion of interest in the complex span task in recent years, largely owing to studies demonstrating that performance on this task correlates strongly

with a wide range of abilities including general intelligence, whereas immediate serial recall is a poorer predictor (Conway, Kane, & Engle, 2003; Oberauer, Süß, Wilhelm, & Sander, 2007). Accordingly, there is a conviction that a better understanding of the principles and mechanisms underpinning performance in the complex span setting may ultimately pave the way to a greater understanding of cognition more generally.

Computational models of serial recall are well positioned to contribute to a comprehensive theory of performance in the complex span task, since they already possess the mechanisms required to perform the serial recall component of the task. Recently, Oberauer and colleagues (Oberauer & Lewandowsky, 2011; Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2013) have begun to explore how theories and principles of short-term memory can be extended to account for performance in the complex span setting. Oberauer and Lewandowsky (2011) have developed a model, dubbed TBRS*, which is a computational implementation of a successful verbal-conceptual model of complex span, known as the Time-Based Resource Sharing (TBRS) theory (Barrouillet et al., 2004), whilst Oberauer et al. (2013) have developed a computational model, known as SOB-CS (where CS stands for complex span), that shows how the C-SOB theory of serial recall can be generalized to account for performance in the complex span task.

The two theories share some common assumptions. For example, both assume that serial order is encoded by associating items to position markers and that items are removed from memory after they have been recalled using response suppression. However, the theories make different assumptions about the cognitive consequences of the processing component in complex span. In keeping with its verbal-conceptual counterpart, TBRS* assumes that items in memory inexorably decay with the passage of time and that to counteract this decay, during the pauses in between items, their representations are revived using a compensatory process of attentional refreshing. It is assumed that the processing component in complex span reduces the time available to engage in attentional

refreshing during these pauses, since a bottleneck prevents refreshing and processing from being performed in parallel. This causes the memory representations of items to fade, with negative repercussions for subsequent recall accuracy. In contrast, SOB-CS appeals neither to decay nor rehearsal to account for performance in complex span. Instead, in SOB-CS it is assumed that the representations of distracters in the processing task are added to the same position marker as the to-be-remembered item that preceded the processing activity. As in previous instantiations of the SOB theory, SOB-CS employs similarity-sensitive encoding to determine the encoding strength of incoming items. Importantly, the model employs the same encoding process to determine the encoding strength of incoming distracters. Accordingly, distracters in the processing task that are similar to existing information in memory are encoded only weakly onto the position markers, whereas distracters that are dissimilar to existing information in memory are encoded strongly, by virtue of their novelty. The addition of distracter representations on to the position markers renders these markers less effective cues at retrieval, increasing the likelihood that the wrong item will be cued at a given position. To offset the interfering action of the processing task, SOB-CS assumes that during any free-time in which the processing task is not being completed a process of distracter removal is engaged whereby interfering material encoded into memory is partially removed.

Both TBRs* and SOB-CS account for a number of benchmark findings from the complex span paradigm. Although detailed quantitative comparisons of the models are yet to be performed, a study by Lewandowsky, Geiger, and Oberauer (2008) has already provided empirical support for a core prediction of SOB-CS, specifically that distracters in the processing task are encoded into memory, thereby causing interference and promoting forgetting. Crucially, the extent of this forgetting is governed by the similarity of each incoming distracter to previously encoded distracters, as predicted by similarity-sensitive encoding. However, we note that boundary conditions for interference have yet to be

defined as memory for distracting material can have a positive effect on performance when it is related to the span items (Schroeder, Copeland, & Bies-Hernandez, 2012; Towse, Hitch, Horton, & Harvey, 2010).

The work of Oberauer and colleagues represents an important theoretical development and highlights how models and principles of short-term memory, when augmented with additional assumptions, are extensible to the complex span setting. With the establishment of two competing computational accounts of complex span, an important avenue for future research will be to conduct precise quantitative comparisons of the models and test some of their novel architectural features, such as the distracter removal mechanism employed in SOB-CS. To date, the two models have only been applied to verbal instantiations of the complex span paradigm (although see simulation 5 of Oberauer et al., 2013). Therefore evaluating the extent to which the principles and assumptions of these theories can account for performance in visuospatial versions of the complex span task (e.g., Shah & Miyake, 1996) will also prove valuable.

Extending models of serial recall to free recall. In the free recall task, participants are presented with sequences of items that they must subsequently recall either immediately or after a brief delay. The sequence length is typically longer than in serial recall (e.g., 10 items or more) and people can recall the items in any output order they choose. Like the serial recall task, the free recall task has generated a wealth of data (for a review, see Kahana, 2012) and this has culminated in the development of numerous computational theories that account for major phenomena using well-defined principles and assumptions (e.g., Davelaar, Goshen-Gottstein, Ashkenazi, Haarmann, & Usher, 2005; Howard & Kahana, 2002; Laming, 2010; Polyn, Norman, & Kahana, 2009; Raaijmakers & Shiffrin, 1981).

Historically, serial and free recall have been considered as fundamentally different memory tasks that tap different mechanisms of memory. Accordingly, until recently there

has been little attempt at a theoretical integration of the two tasks. Principal amongst the reasons for believing that serial and free recall rely on different memory mechanisms is that the two tasks generate functionally distinct serial position curves: Serial position curves in immediate free recall exhibit extensive recency accompanied by limited primacy, a pattern at odds with the primacy-dominant serial position curves witnessed in serial recall. Furthermore, recency continues to be observed in immediate free recall when a secondary task involving immediate serial recall for digits is performed during list presentation (e.g. Baddeley & Hitch, 1977). These findings, together with extensive evidence for long-term recency effects in a wide range of different free recall tasks, added weight to the idea of recency as a general phenomenon not restricted to short-term memory and immediate serial recall (see e.g. Baddeley & Hitch, 1993).

However, recent work by Ward and colleagues has shown that immediate serial recall and immediate free recall share a number of functional similarities. For example, both tasks exhibit similar patterns of rehearsal, and both are similarly affected by manipulations of word length and articulatory suppression (variables traditionally associated with serial recall) and manipulations of presentation rate (a variable traditionally associated with free recall) (Bhatarah et al., 2009). Moreover, people exhibit a considerable propensity to engage in serial recall when performing free recall, despite the fact that output order is unconstrained (Bhatarah et al., 2009; Bhatarah et al., 2006, 2008; Grenfell-Essam & Ward, 2012; Ward et al., 2010; see also Howard & Kahana, 1999; Kahana, 1996). Indeed, this tendency toward serial recall is also witnessed in other tasks where output order is uncontrolled (e.g., Lewandowsky, Nimmo, & Brown, 2008; Tan & Ward, 2007), suggesting that forward ordered recall may be a general principle of memory. One key variable that mediates the differences in the serial position curves observed in serial and free recall is the sequence length. Ward et al. (2010) and Grenfell-Essam and Ward (2012) have shown that at short sequence lengths, people initiate both serial and

free recall with the first item in the sequence, after which recall proceeds in forward order. However, at longer sequence lengths, people are more likely to initiate free recall, and to some extent serial recall, with one of the last several items. Critically, the initial item recalled determines the shape of the serial position curve: If the first item is output initially then primacy-dominant serial position curves resembling serial recall are observed, whereas if one of the last several items is output initially then recency-dominant serial position curves resembling free recall are witnessed. Nevertheless, irrespective of the sequence length, people exhibit a considerable propensity in free recall to engage in serial recall.

The findings of Ward and colleagues set a precedent for attempts towards an integration between theories of serial and free recall. To date though, no model of free recall has been extended to account for serial recall. However, a number of theories of serial recall have been developed that also account for free recall (e.g., Brown et al., 2007; Farrell, 2012; Grossberg & Pearson, 2008). Of these theories, arguably the recent model of Farrell (2012) provides the most promising attempt at a theoretical unification of the two tasks. Farrell's model is noteworthy since it incorporates a combination of principles of short-term memory including position marking, a primacy gradient, response suppression, and output interference and is capable of simulating an impressive set of benchmark findings from serial and free recall, as well as the recent data of Ward and colleagues. In Farrell's model, it is assumed that people spontaneously parse continuous sequences into episodic clusters. Items within a cluster are associated both with a group level representation of temporal context and with a representation of temporal context that codes their position within the cluster itself. During recall, a cluster must first be accessed before its contents can be retrieved. An important assumption of the model is that the group level context used to retrieve a cluster is not "given for free", but must instead be actively retrieved from memory. A key exception to this rule is the group context for the

last episodic cluster encoded which is automatically carried over into the recall phase and used to probe that cluster's contents. The position-within-group context cues associated with that cluster are then sequentially reinstated in forward order, each time probing memory for an item. For long sequences, which contain several episodic clusters, this means that recall will commence with one of the last several items and then proceed in forward order until the final item is recalled. Recall then continues via an iterative process of retrieving an episodic cluster using its group context cue before recalling its contents in forward order via the sequential reinstatement of its associated position-within-group context cues. In contrast, with short sequences, items can be subsumed under a single episodic cluster, so recall will naturally start with the first item in the sequence and then proceed in forward serial order.

Farrell's model serves as a "proof of principle" that a theoretical integration of serial and free recall is possible and that principles of short-term memory for order—which feature prominently in the model—may be core ingredients to such a theoretical linkage. It will be interesting in future research to test some of the model's novel explanatory assumptions, such as the idea that sequences are organized into episodic clusters, that recall of items within a cluster proceeds in forward order, and that the group context for the final cluster is automatically carried over into the recall phase. As noted by Ward and colleagues (Grenfell-Essam & Ward, 2012; Ward et al., 2010), further theoretical developments in this area might be facilitated by extending other theories of serial recall to account for free recall and, conversely, by extending theories of free recall to account for serial recall. However, despite the apparent promise of recent attempts towards an integration of the two tasks, it is important to emphasize that free recall involves additional phenomena that are not reducible to serial recall, such as subjective organization (Tulving, 1962), semantic clustering (Bousfield, 1953; Bousfield, Sedgewick, & Cohen, 1954), and source clustering (Murdock & Walker, 1969). Accordingly, it remains

an open question how far theoretical progress will be enhanced by extending models of serial recall to free recall (and vice versa).

Modeling serial order at multiple levels. One major criticism of existing theories of verbal short-term memory is that they only handle serial ordering at the lexical level. If these models are to be able to deal with more realistic verbal material then they will need to be elaborated to deal with serial ordering at the syntactic, semantic, and phonological levels. The importance of modeling serial order at the supra-lexical level is perhaps best revealed by the *sentence-superiority effect*: Memory span for words in sentences is more than twice that for sequences of words in random order (e.g., Baddeley et al., 2009; Jefferies, Lambon Ralph, & Baddeley, 2004), indicating that, in natural language settings, syntactic and semantic constraints play a major role in supporting verbal short-term memory for serial order. It is noteworthy that a number of models of sentence production that deal with serial order at the syntactic level have been developed based on CQ-compatible principles (Chang, Dell, & Bock, 2006; Dell, 1986; Dell et al., 1997; Ward, 1994). The mechanisms employed in these models may provide a useful starting point for modeling serial ordering at the syntactic level within CQ models of memory for serial order.

The importance of modeling serial order at the sub-lexical level is reflected by the need for a short-term memory system that is capable of learning nonwords, since this is one of the major functions ascribed by Baddeley (Baddeley et al., 1998) to the phonological loop. Extending models of verbal short-term memory to the learning of nonwords requires augmenting these models with a mechanism for retaining the serial order of sequences of phonemes. Hartley and Houghton (1996) have presented a CQ model capable of encoding and recalling nonwords, which uses a positional context signal similar to that employed by Burgess and Hitch (1999), combined with a top-down syllable template that biases the assignment of phonemes to positions within a syllable. This

syllable template offers a promising mechanism for extending CQ models of verbal short-term memory to the learning of nonwords. However, as noted elsewhere (Burgess & Hitch, 2006), such a mechanism would need to be augmented with a cumulative matching process like that employed in the model of Burgess and Hitch (2006) if it is to be capable of learning and recognizing multiple sequences of phonemes.

Conclusions

The problem of serial order is one of the most complex and far-reaching problems in psychology (Lashley, 1951). This article focused on one aspect of this general problem: How people store and retrieve a novel sequence of items in the correct order. Specifically, we sought to identify some fundamental principles of serial order in short-term memory and to establish whether these principles are the same in the verbal and visuospatial domains.

Our review of phenomena of serial order identified a number of commonalities between short-term memory for verbal, visual, and spatial information, and these similarities point to the existence of some domain-general serial ordering principles. Notably, there is evidence to support the notion that all three short-term memory systems rely on a CQ sequence planning and control mechanism in which items are simultaneously active in parallel and the most active item is output. Within the verbal short-term memory CQ system, evidence suggests that serial order is represented using a primacy gradient, position marking, response suppression, and cumulative matching. Additional evidence suggests that output interference contributes to recall and that item similarity effects manifest during both retrieval and serial order encoding. These results specify the required architecture of a model of verbal short-term memory quite precisely. One model that instantiates most of the above principles and assumptions is the CQ model of Burgess and Hitch (2006). The Burgess and Hitch model is arguably the strongest of the

current field of competitor models of verbal short-term memory. It accounts for an impressive amount of serial recall data and is the only current model that can handle the detailed pattern of findings underlying the Hebb repetition effect. This explanatory success notwithstanding, there is scope for future development of the model. One of the model's strengths is its ability to account for the effects of temporal grouping on immediate recall and sequence learning via its multidimensional context signal. However, one major limitation of the context signal in this model—and indeed all current models—is that to simulate the effects of temporal grouping, the structure of the context signal must be specified *a priori* by the modeler to reflect the grouping structure of the input sequence. It would represent a formidable theoretical advancement if a bottom-up implementation of the context signal could be developed that is capable of representing the grouping structure “on the fly” based on the temporal properties of the input sequence. Another limitation of the model—again shared with other contemporary models—is that it only deals with serial ordering at the lexical level. If the model is to be able to deal with more realistic linguistic inputs then it must be extended to account for serial ordering at the semantic, syntactic, and phonological levels. Such an extension could provide the opportunity for a theoretical linkage between short-term memory, vocabulary acquisition, and language production.

The principles of serial order underlying the operation of the visual and spatial short-term memory CQ systems are less transparent, largely because the phenomena that provide direct support for the different principles have not yet been examined in these domains. In spatial short-term memory, there is some direct evidence for the operation of a primacy gradient and position marking, whereas in visual short-term memory there is no direct evidence for any of the principles of serial order. Accordingly, further empirical research is required in order to narrow down the preferred combination of principles and assumptions that should feature within a theory of serial order in visuospatial short-term

memory. The functional similarities across domains reviewed here suggest it is likely that these principles will be similar to—if not the same as—those required for the accurate modeling of verbal short-term memory.

Finally, we have noted recent developments that suggest it is timely to consider whether a broader theoretical integration can be achieved by extending the principles of models of serial order in immediate serial recall to other memory tasks that involve serial output, such as complex span and free recall.

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Author Note

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Footnotes

¹It is well-known that the magnitude of the recency effect associated with the forward recall of verbal sequences is stronger when the presentation modality of items is auditory than when it is visual (Conrad & Hull, 1968; Crowder & Morton, 1969; Penney, 1989)—a result dubbed the *modality effect*. The modality effect is not confined to the use of verbal memoranda: Tremblay et al. (2006) have shown that the recency effect associated with the forward recall of sequences of auditory-spatial locations is stronger than for sequences of visual-spatial locations.

We do not consider the modality effect here as it arguably falls outside the scope of the current article, our view being that it seems most likely to reflect the action of a modality-specific input store (e.g., Crowder & Morton, 1969) a line of reasoning that has proved popular in modeling the modality effect in some contemporary computational theories of short-term memory for serial order (e.g., Grossberg & Pearson, 2008; Page & Norris, 1998; although see Henson, 1998a for an account of the modality effect based on the superior coding of positional information in the auditory modality). Note, however, that the features of memory for serial order described in this article are generally common to both the auditory and visual modalities.

²When the forward and backward serial recall of verbal stimuli are compared using a memory span procedure, backward recall is typically harder than forward recall (e.g., Gardner, 1981). However, when the sequence length is fixed—as in the studies of backward recall cited here—the typical finding is that overall levels of recall accuracy for forward and backward recall do not differ reliably from one another (although see Farrand & Jones, 1996, Experiments 2 and 3, for exceptions).

³Recently, Solway, Kahana, and Murdock (2012) have reported an analysis of four serial recall data sets in which the converse pattern was found, whereby infill errors actually outweighed fill-in errors. However, the experiments upon which these new

analyses are based are not representative of the serial recall task as it is typically conducted. Specifically, the experiments examined by Solway and colleagues employed a long sequence length of 19-items and the recall protocols emphasized that participants need only report items in their correct relative order of presentation. This contrasts with typical studies of serial recall which employ a much shorter sequence length of around 6-items (with 9-items considered as the upper-bound) where the recall protocols emphasize that participants must recall items in their correct absolute serial position of presentation. In response to the analyses of Solway et al. (2012), Farrell et al. (2013) have recently performed an analysis of sequential error dependencies in 21 representative published serial recall experiments. The results of this new analysis are unambiguous: Fill-in errors consistently outweigh infill errors, consistent with the original analyses of these errors (Henson, 1996; Page & Norris, 1998; Surprenant et al., 2005) and at odds with the new analyses presented by Solway et al. (2012).

⁴This context cue is similar to that employed in models that use position marking to represent serial order (e.g., Burgess and Hitch, 1999). The key difference is that in positional models, each item in the sequence is associated with its own context cue and during recall these context cues must each be reinstated, in turn, to produce a dynamically changing activation gradient over items. By contrast, in the primacy model, the single context cue is sufficient to retrieve the primacy gradient of activations after which ordered recall can proceed without the need to reinstate any additional context cues.

⁵Note that the predictions displayed in Figure 8 are not taken directly from Farrell and Lewandowsky (Farrell & Lewandowsky, 2004; Lewandowsky & Farrell, 2008a) but were instead generated by implementing the dynamic recall architecture and models employed by these authors. The predictions shown in this figure are comparable to those illustrated in Figures 2 and 3 of Farrell and Lewandowsky (2004) and Figure 1 of Lewandowsky and Farrell (2008a) but note that the different predictions were not

necessarily generated using all the same model parameter values.

⁶One exception to this rule is the LIST PARSE model of Grossberg and Pearson (2008), mentioned above, which provides a neurocomputational instantiation of the brain substrates of verbal and spatial short-term memory. However, it is important to acknowledge that Grossberg and Pearson did not apply their model to any human data on spatial short-term memory, but instead restricted application of their model to data obtained from verbal short-term memory studies. Moreover, there is currently insufficient empirical evidence available to determine whether the model's core principles of a primacy gradient complemented by response suppression are sufficient to account for memory for serial order in the visuospatial domain or whether further theoretical constructs will be necessary.

Table 1

Phenomena of serial order and the short-term memory (STM) domains in which they have been demonstrated. See main text for further details. Note: SPC = Serial Position Curve.

Phenomenon	STM domain		
	Verbal	Spatial	Visual
1. Forward SPC			
<i>Accuracy</i>			
Primacy	✓	✓	✓
Recency	✓	✓	✓
<i>Latency</i>			
Long initial latency	✓	✓	?
Inverted U shape	✓	✓	?
2. Backward SPC			
<i>Accuracy</i>			
Reduced primacy	✓	✓	?
Enhanced recency	✓	✓	?
<i>Latency</i>			
Long initial latency	✓	?	?
Inverted U shape	✓	?	?
Slower than forward recall	✓	?	?
3. Sequence length effect	✓	✓	✓
4. Error patterns			
Transposition gradients	✓	✓	✓
Transposition latencies	✓	?	?

Table 1

(Continued)

Phenomenon	STM domain		
	Verbal	Spatial	Visual
Fill-in: infill ratio	✓	✓	?
Intrusions	✓	✓	✓
Protrusions	✓	?	?
Omissions	✓	✓	?
Repetitions	✓	?	?
More order than item errors	✓	✓	✓
5. Temporal grouping effects			
Grouping advantage	✓	✓	?
Accuracy SPC	✓	✓	?
Interpositions	✓	✗	?
Latency SPC	✓	✓	?
6. Item similarity effects			
Pure sequences	✓	✓	✓
Mixed sequences	✓	?	?
7. Ranschburg effect	✓	?	?
8. Hebb repetition effect			
Basic effect	✓	✓	✓
Sensitive to sequence start	✓	?	?
Sensitive to grouping pattern	✓	?	?
Insensitive to item similarity	✓	?	?

Table 2

Contemporary models of verbal short-term memory and the principles of serial order and ancillary assumptions they instantiate.

Model	Serial Order Principles					
	Competitive	Position	Primacy	Response	Cumulative	
	Queuing	Marking	Gradient	Suppression	Matching	
<i>SRN</i> (Botvinick & Plaut, 2006)	✓	✗	✗	✗	✗	✗
<i>SIMPLE</i> (Brown et al., 2007)	✗	✓	✗	✗	✗	✗
<i>OSCAR</i> (Brown et al., 2000)	✓	✓	✓	✓	✗	✗
Burgess & Hitch (1992)	✓	✓	✗	✓	✗	✗
Burgess & Hitch (1999)	✓	✓	✓	✓	✗	✗
Burgess & Hitch (2006)	✓	✓	✓	✓	✓	✓
Farrell (2012)	✓	✓	✓	✓	✗	✗
<i>SEM</i> (Henson, 1998a)	✓	✓	✓	✓	✗	✗
<i>SOB</i> (Farrell & Lewandowsky, 2002)	✗	✗	✓	✓	✗	✗
<i>C-SOB</i> (Lewandowsky & Farrell, 2008a)	✗	✓	✓	✓	✗	✗
<i>LIST PARSE</i> (Grossberg & Pearson, 2008)	✓	✗	✓	✓	✗	✗
<i>Feature model</i> (Nairne, 1990; Neath, 2000)	✗	✓	✗	✓	✗	✗
<i>Primacy model</i> (Page & Norris, 1998)	✓	✗	✓	✓	✗	✗
<i>Primacy model</i> (Page & Norris, 2009)	✓	✗	✓	✓	✓	✓

Table 2

(Continued)

Model	Ancillary Assumptions	
	Output	Locus of Similarity Effects
<i>SRN</i> (Botvinick & Plaut, 2006)	✗	Encoding+Retrieval
<i>SIMPLE</i> (Brown et al., 2007)	✓	Encoding+Retrieval
<i>OSCAR</i> (Brown et al., 2000)	✓	✗
Burgess & Hitch (1992)	✗	Retrieval
Burgess & Hitch (1999)	✗	Retrieval
Burgess & Hitch (2006)	✗	Retrieval
Farrell (2012)	✓	✗
<i>SEM</i> (Henson, 1998a)	✗	Retrieval
<i>SOB</i> (Farrell & Lewandowsky, 2002)	✗	✗
<i>C-SOB</i> (Lewandowsky & Farrell, 2008a)	✓	Encoding+Retrieval
<i>LIST PARSE</i> (Grossberg & Pearson, 2008)	✗	✗
<i>Feature model</i> (Nairne, 1990; Neath, 1999)	✗	Encoding+Retrieval
<i>Primacy model</i> (Page & Norris, 1998)	✗	Retrieval
<i>Primacy model</i> (Page & Norris, 2009)	✗	Retrieval

Table 3

Phenomena of serial order, the short-term memory (STM) domains in which they have been demonstrated, and the theoretical constructs they can be attributed to based on the preceding analysis. Note: PM = Position Marking; PG = Primacy Gradient; RS = Response Suppression; CM = Cumulative Matching; OI = Output Interference; SE = Similarity-At-Encoding; SR = Similarity-At-Retrieval.

Phenomenon	Representative Study	STM domain			Inferred Constructs
		Verbal	Spatial	Visual	
Forward SPC					
Primacy (input position)	Oberauer (2003)	✓	?	?	PG
Primacy (output position)	Oberauer (2003)	✓	?	?	OI
Conditional recency	Farrell & Lewandowsky (2012)	✓	?	?	RS
Error patterns					
Transposition latencies	Farrell & Lewandowsky (2004)	✓	?	?	PG+PM+RS
Fill-in: infill ratio	Surprenant et al. (2005)	✓	✓	?	PG+RS
Protrusions	Henson (1999)	✓	?	?	PM
Repetitions	Duncan & Lewandowsky (2005)	✓	?	?	RS
Temporal grouping effects					
Grouping advantage	Hitch et al. (1996)	✓	✓	?	PM
Accuracy SPC	Hitch et al. (1996)	✓	✓	?	PM

Table 3

(Continued)

Phenomenon	Representative Study	STM domain			Inferred Constructs
		Verbal	Visual	Spatial	
Interpositions	Ryan (1969a)	✓	✗	?	PM
Latency SPC	Farrell & Lewandowsky (2004)	✓	✓	?	PM
Item similarity effects					
Mixed-sequence advantage	Farrell & Lewandowsky (2003)	✓	?	?	PG+SE
Ranschburg effect	Henson (1998b)	✓	?	?	RS
Hebb repetition effect					
Sensitive to sequence start	Schwartz & Bryden (1971)	✓	?	?	CM
Sensitive to grouping pattern	Hitch et al. (2009)	✓	?	?	CM+PM
Insensitive to item similarity	Hitch et al. (2009)	✓	?	?	SR
Absence of item-position transfer	Cumming et al. (2003)	✓	?	?	CM

Figure Captions

Figure 1. Serial position curves for forward and backward recall of verbal sequences. Panels show data for recall accuracy (A), and inter-response latency (B). Serial position is represented as input (presentation) position. In forward recall, input and output (retrieval) position are perfectly positively correlated, whereas in backward recall they are perfectly negatively correlated: Input position 6 corresponds to output position 1, input position 5 corresponds to output position 2, input position 4 corresponds to output position 3, and so forth. Accuracy data from Guérard and Saint-Aubin (2012; Experiment 1a); latency data from Haberlandt et al. (2005).

Figure 2. Transposition error gradients (A), and transposition latencies (B) for forward recall of 6-item verbal sequences. Data from Farrell and Lewandowsky (2004).

Figure 3. Temporal grouping effects in forward recall of verbal sequences. Panels show accuracy serial position curves (A), transposition gradients (B), and inter-response latency serial position curves (C) for 9-item sequences temporally grouped into threes and ungrouped sequences. Data from Hurlstone (2010; Experiment 7).

Figure 4. Accuracy serial position curves for alternating sequences of phonologically similar (S) and dissimilar (D) items—with similar items at odd positions (SDSDSDS) or even positions (DSDSDSD)—and purely phonologically dissimilar sequences (DDDDDDD). Data from Henson et al. (1996; Experiment 2).

Figure 5. Schematic of a two-layer competitive queuing sequence planning and control mechanism comprising a parallel planning layer (upper field of nodes) and a competitive choice layer (lower field of nodes). The columns in the parallel planning layer represent the activation levels of the various nodes representing items in the to be recalled sequence. Lines terminating with arrows represent excitatory connections, whereas lines terminating

with semi-circles represent inhibitory connections. Note that each node in the lower competitive choice layer has an inhibitory connection to every other node in the same layer, but for simplicity only adjacent-neighbor inhibitory connections are shown. Similarly, each node in the competitive choice layer has an inhibitory connection to its corresponding node in the parallel planning layer, but to avoid visual clutter only feedback connections for the leftmost and rightmost nodes are illustrated. See main text for further details.

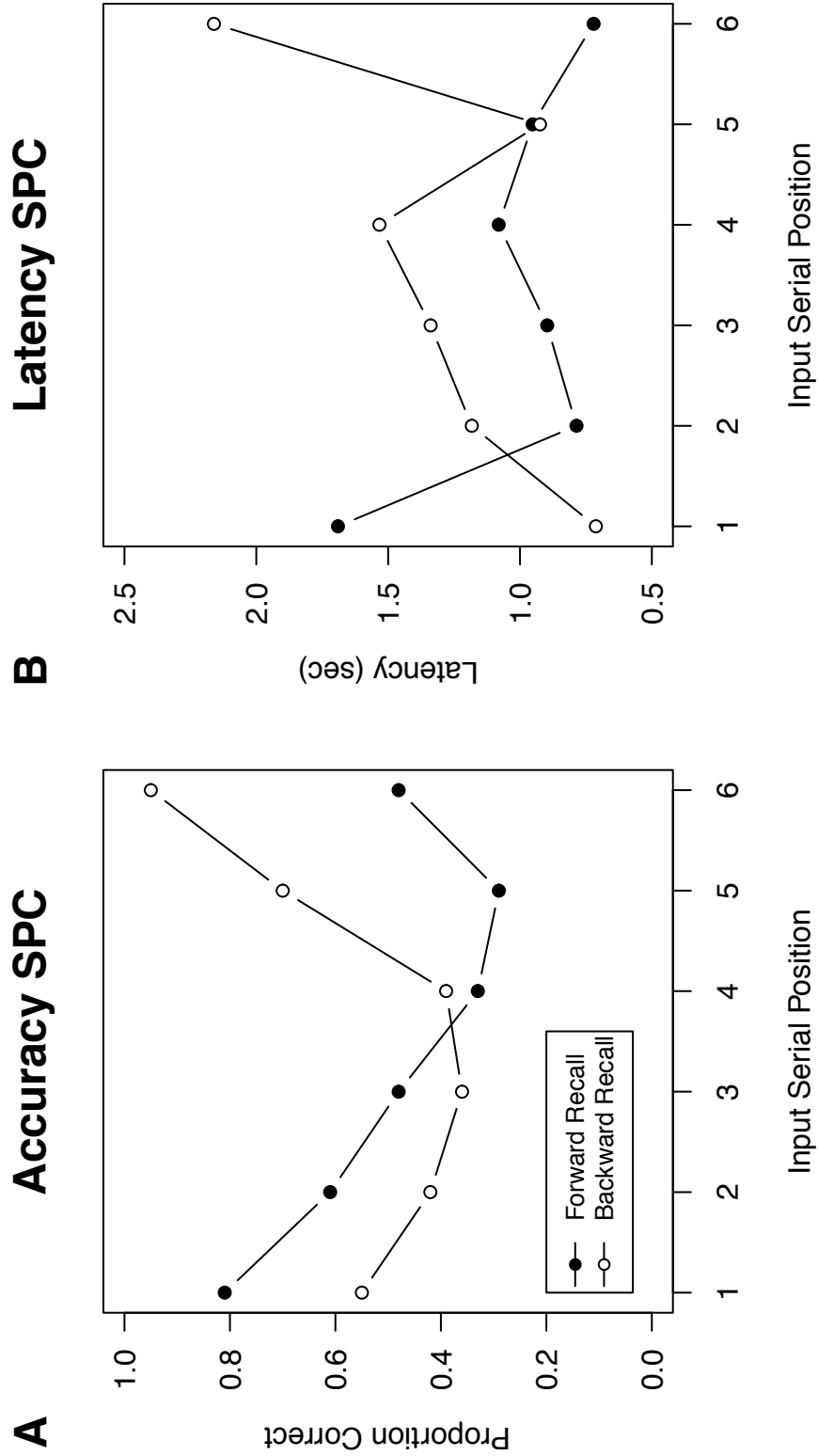
Figure 6. Varieties of positional representations of serial order: (A) a temporal representation of position based on the endogenous clock envisaged in OSCAR (Brown et al., 2000); (B) an absolute representation of position based on the moving window of activation scheme employed by Burgess and Hitch (1992); and (C) a relative representation of position based on the start and end markers in Henson's (1998a) SEM. Note that the numbers in each graphic refer to the order of item presentations. Figure adapted from Henson (1999b).

Figure 7. Initial state of a primacy gradient (A), followed by suppression of the first two emitted items (B).

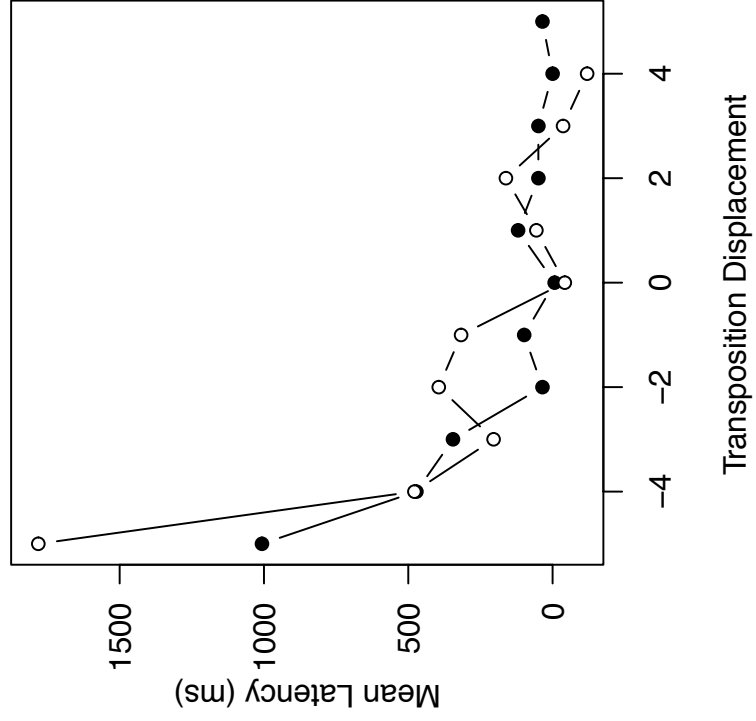
Figure 8. Predicted accuracy serial position curves (A), transposition gradients (B), latency serial position curves (C), and transposition latencies (D) of five models of serial recall built from different combinations of principles for representing serial order. PM = Position Marking; PG = Primacy Gradient; RS = Response Suppression; OI = Output Interference. The models were implemented in a common neural network architecture resembling the competitive choice layer in competitive queuing models of serial behavior.

Figure 9. Accuracy serial position curves for alternating sequences of phonologically similar (S) and dissimilar (D) items—with similar items at odd positions (SDSDSD) or

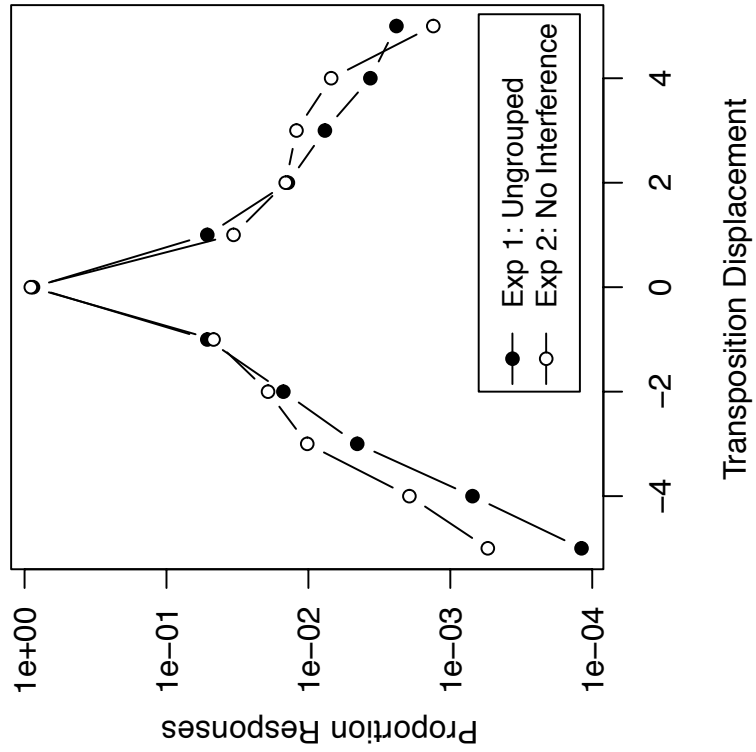
even positions (DSDSDS)—and purely phonologically dissimilar sequences (DDDDDD). Contrary to the analogous data depicted in Figure 4, these data show a mixed-sequence advantage: Dissimilar items in mixed sequences are recalled more accurately than their counterparts in pure dissimilar sequences. Data from Lewandowsky and Farrell (2008b; Experiment 2).



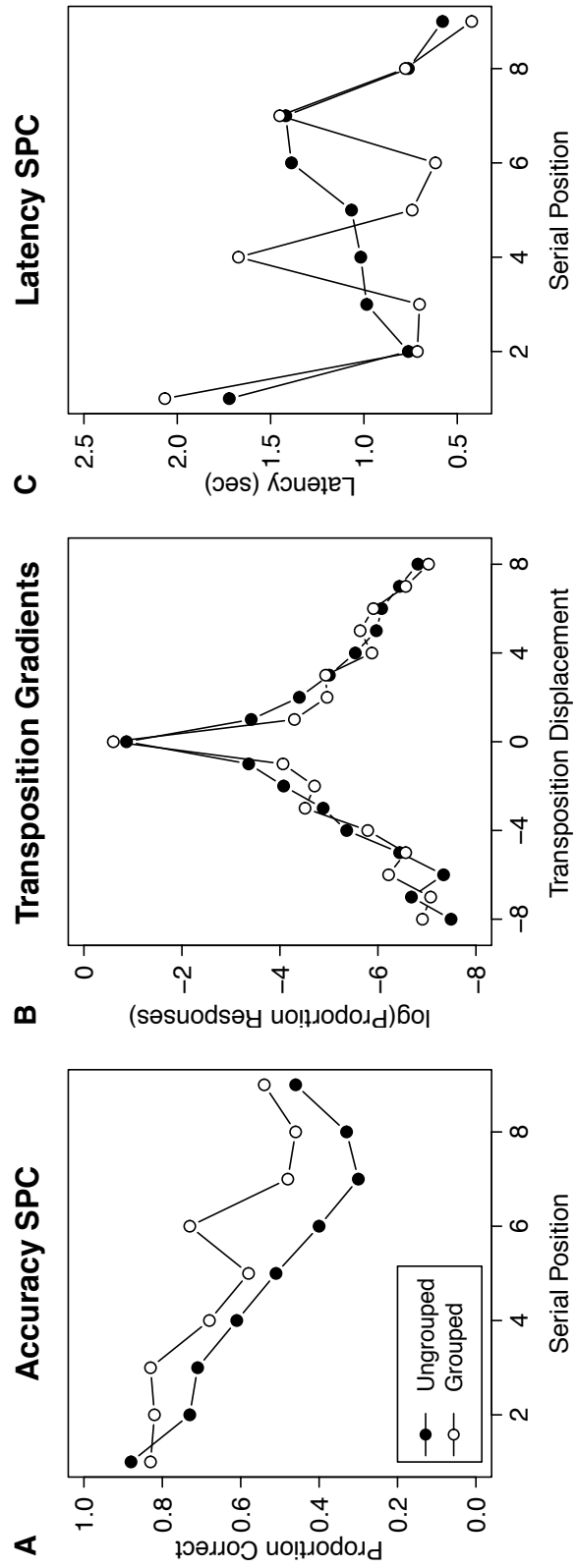
B Transposition Latencies



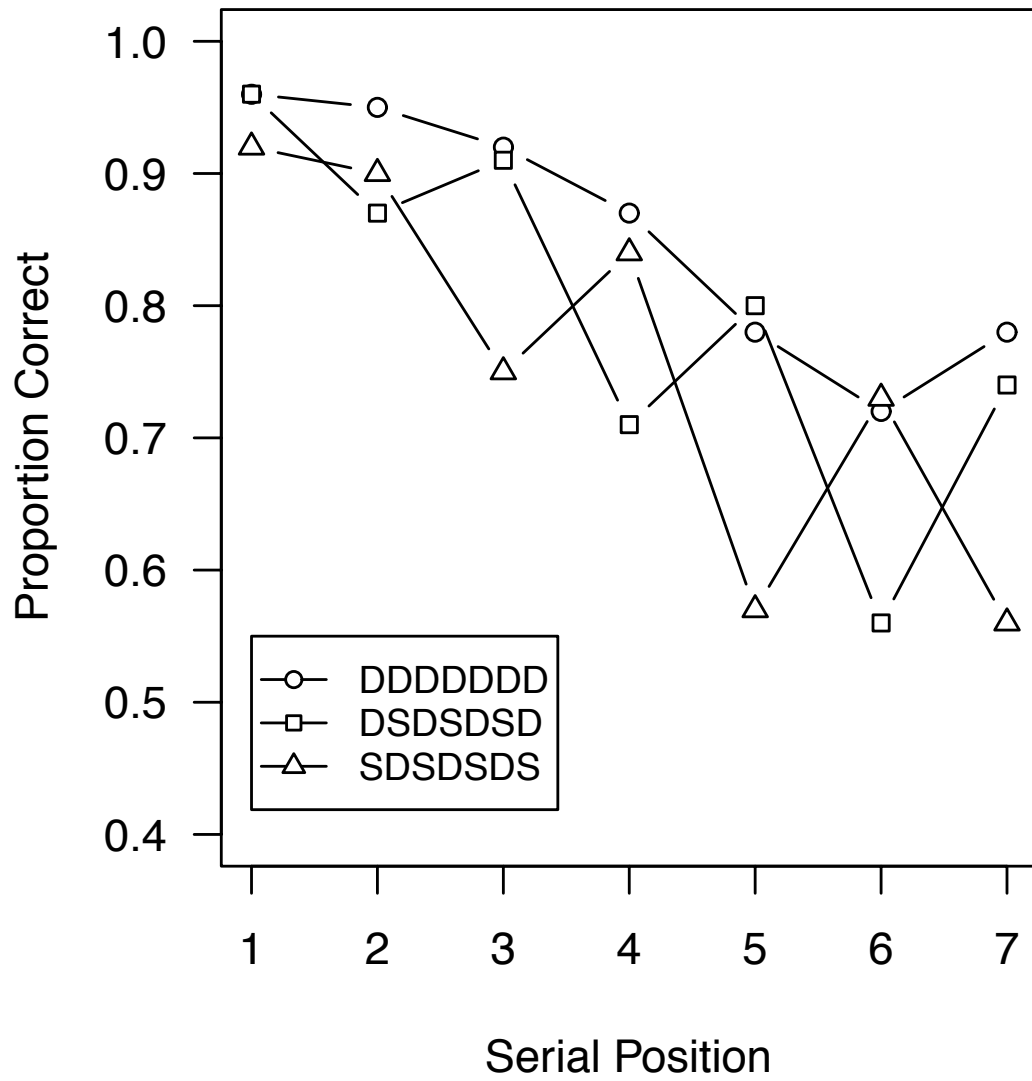
A Transposition Gradients



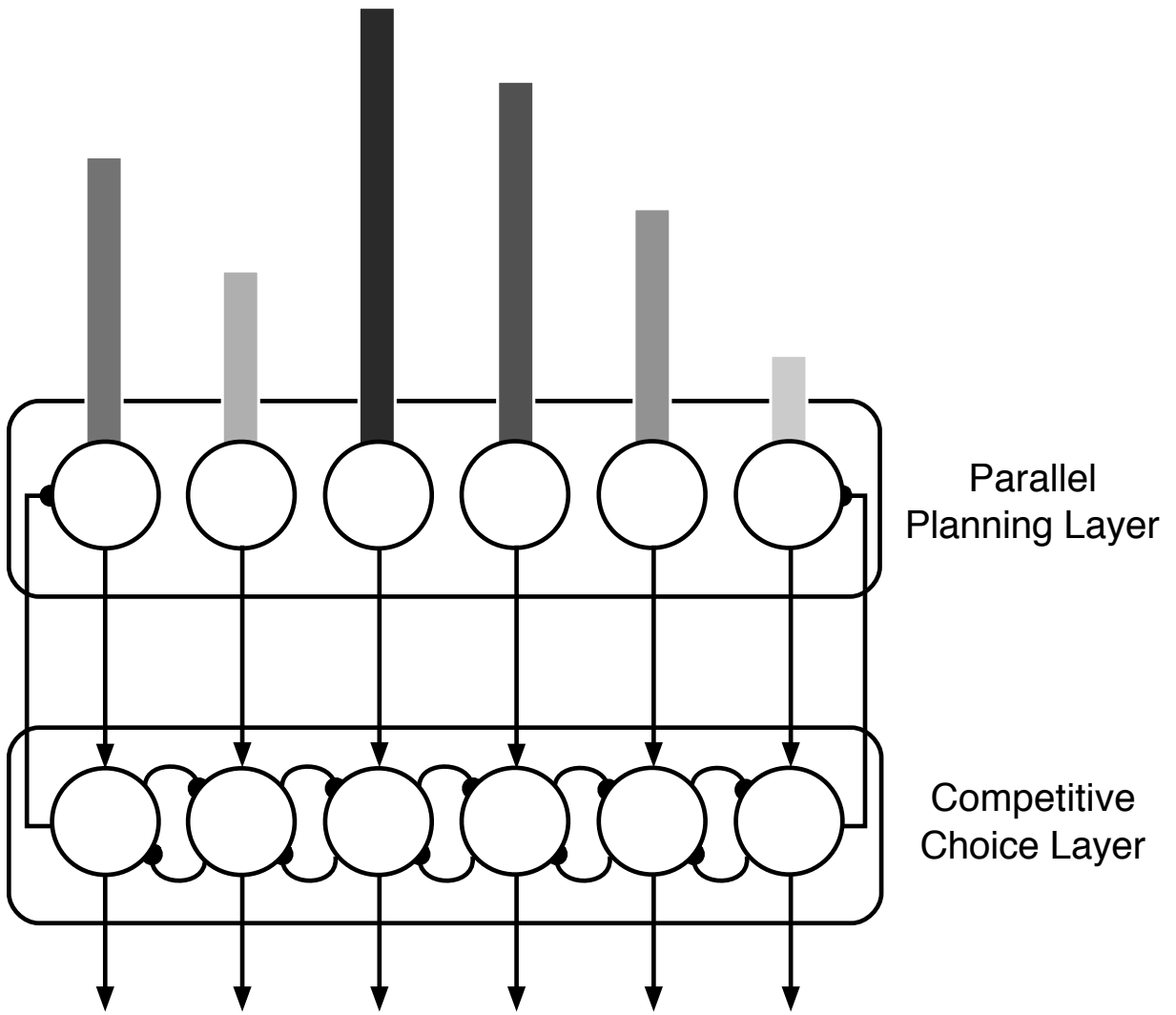
Memory for serial order, Figure 3

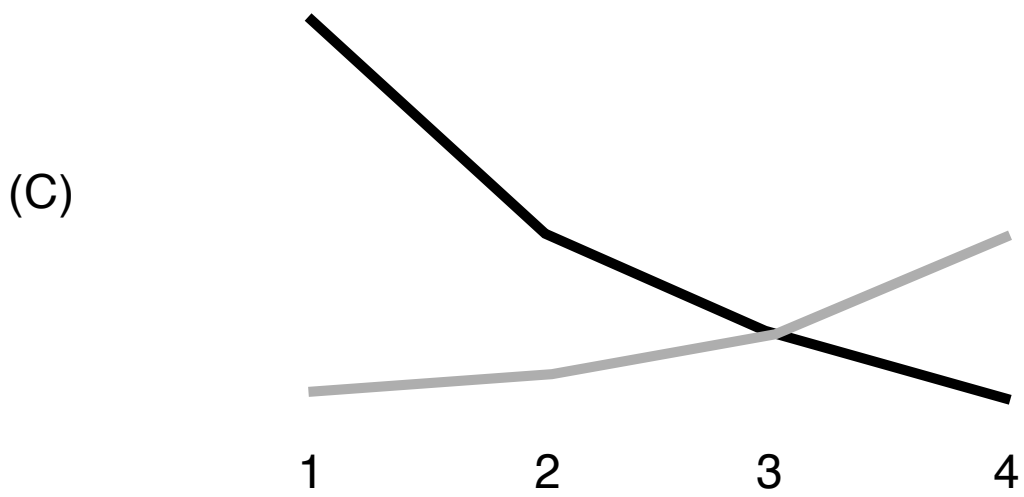
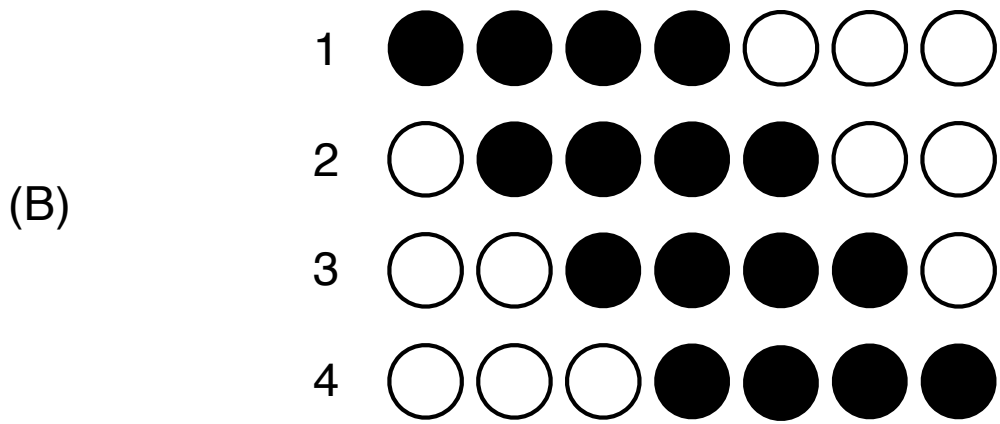
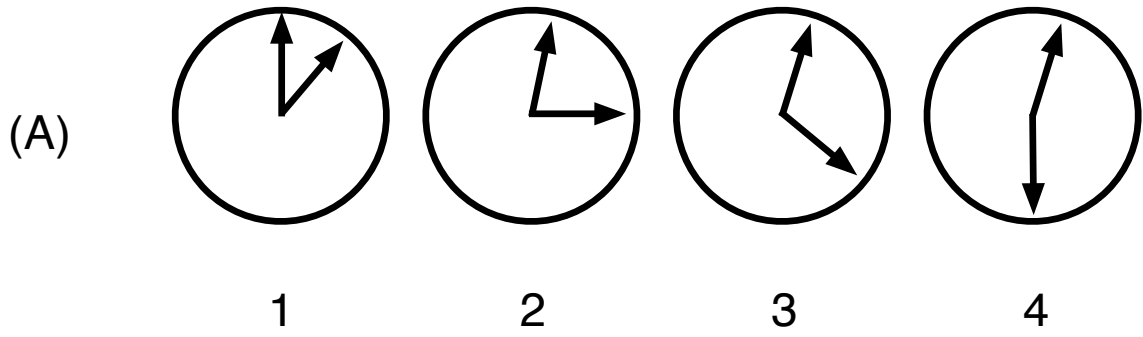


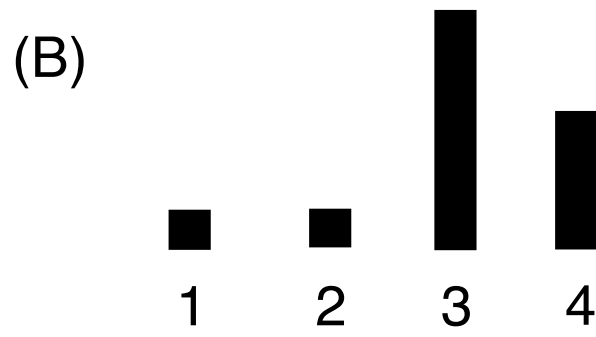
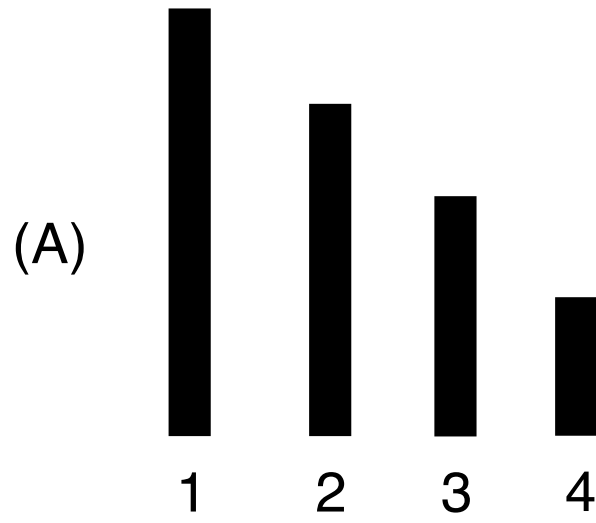
Memory for serial order, Figure 4



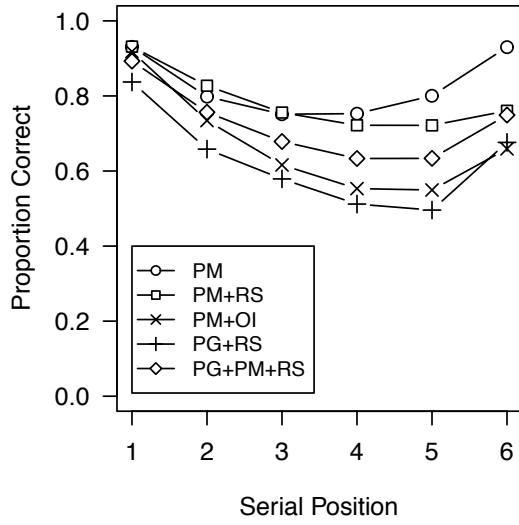
Memory for serial order, Figure 5



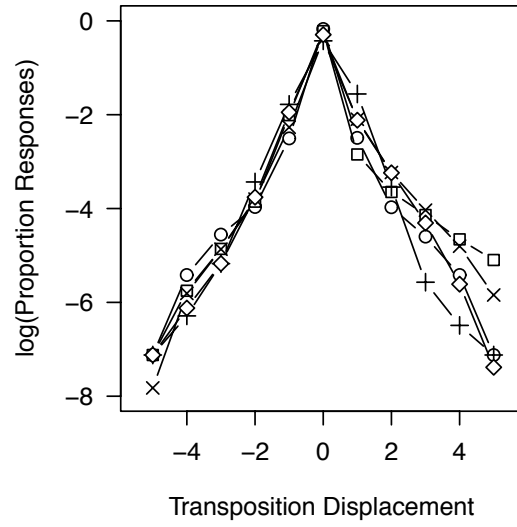




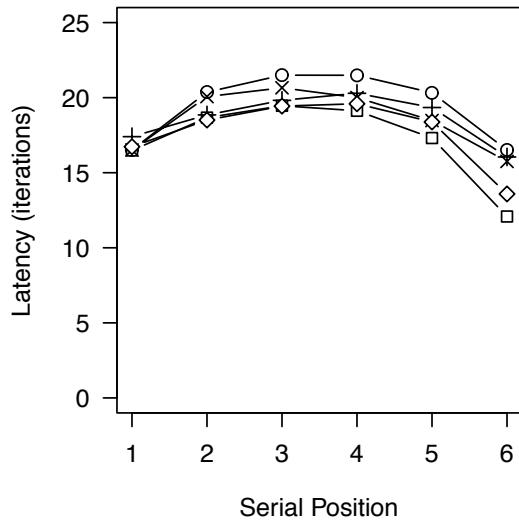
A Accuracy SPC



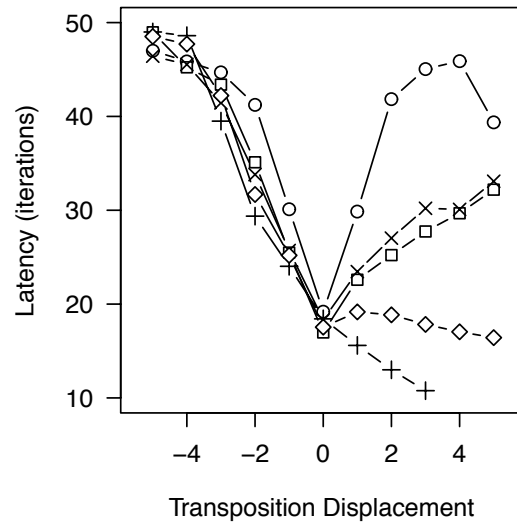
B Transposition Gradients



C Latency SPC



D Transposition Latencies



Memory for serial order, Figure 9

