

How is the serial order of a visual sequence represented? Insights from transposition latencies

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Abstract

A central goal of research on short-term memory (STM) over the past two decades has been to identify the mechanisms that underpin the representation of serial order, and to establish whether these mechanisms are the same across different modalities and domains (e.g., verbal, visual, spatial). A fruitful approach to addressing this question has involved comparing the transposition error latency predictions of models built from different candidate mechanisms for representing serial order. Experiments involving the output-timed serial recall of sequences of verbal (Farrell & Lewandowsky, 2004) and spatial (Hurlstone & Hitch, 2015) items have revealed an error latency profile uniquely predicted by a competitive queuing mechanism within which serial order is represented via a primacy gradient of activations over items, associations between items and position markers, with suppression of items following recall. In this paper, we extend this chronometric analysis of recall errors to the serial recall of sequences of visual, non-spatial, items and find across three experiments an error latency profile broadly consistent with the prediction of the same representational mechanism. The findings suggest that common mechanisms and principles contribute to the representation of serial order across the verbal, visual, and spatial STM domains. The implications of these findings for theories of short-term and working memory are considered.

Keywords: competitive queuing, serial order, short-term memory, visual, transposition latencies

How is the serial order of a visual sequence represented? Insights from transposition latencies

A critical feature of short-term memory (STM) is its capacity to encode temporal relations between events (Marshuetz, 2005)—it is often important to remember not only the specific events that we experienced, but also the order in which we experienced them. This is true of imitative behaviors (Agam, Bullock, & Sekuler, 2005; Agam, Galperin, Gold, & Sekuler, 2007) as well as linguistic behaviors, such as vocabulary acquisition (Baddeley, Gathercole, & Papagno, 1998; Page & Norris, 2009) where the ordering of sub-elements is important.

The study of how people recall serial order information from STM is one of the oldest topics in experimental psychology (cf. Ebbinghaus, 1886). A popular account of how people accomplish this serial recall task is based on a working memory model (Baddeley & Hitch, 1974) comprising a phonological loop—dedicated to the retention of verbal sequences—and a visuospatial sketchpad—dedicated to the retention of visuospatial sequences. The latter system is hypothesized to contain two separate components: a “visual cache”—dedicated to the retention of visual sequences—and an “inner scribe”—dedicated to the retention of spatial sequences (Logie, 1995). Although this model has been hugely influential and offers a qualitative account of the effects of a number of key variables on serial recall performance, a widely acknowledged criticism is that it fails to offer a mechanistic account of how people actually accomplish the serial recall task (e.g., Burgess & Hitch, 1992; Hurlstone & Hitch, 2015; Hurlstone, Hitch, & Baddeley, 2014).

This shortcoming highlights the need for more quantitative theoretical accounts of serial recall (Henson & Page, 1999; Page, 2005) and in recent years several computational theories of verbal STM have been advanced that specify explicit mechanisms for representing serial order (Brown, Neath, & Chater, 2007; Brown, Preece, & Hulme, 2000; Botvinick & Plaut, 2006; Burgess & Hitch, 1999; Farrell, 2012; Farrell & Lewandowsky, 2002; Grossberg & Pearson, 2008; Hartley, Hurlstone, & Hitch, 2016; Henson, 1998; Lewandowsky & Farrell, 2008; Page & Norris, 1998). Based on numerous recent diagnostic results (reviewed in Hurlstone et al., 2014; Lewandowsky & Farrell, 2008), several mechanisms and principles of serial order that feature in different models have been identified that must be instantiated in any adequate theoretical account of serial order in verbal STM. We discuss these shortly, but first we note that in contrast

to the theoretical developments in understanding verbal STM for serial order, progress in understanding spatial and visual STM for serial order has been much slower. This is because—perhaps out of experimental convenience (*viz.* it is harder to test memory for serial order with spatial and visual materials)—the lion’s share of research has employed verbal materials (e.g., letters, digits, words) as stimuli. Nevertheless, as we shall see next, a burgeoning body of evidence indicates that the processing of serial order across different STM domains is functionally similar, suggesting that mechanisms and principles of serial order in verbal STM may extend to visual and spatial STM.

Evidence of Functional Similarities

A long line of studies have now revealed that spatial and visual STM exhibit various phenomena of serial order previously thought to be unique properties of verbal STM. One behavioral phenomenon that has received much scrutiny is the serial position curve, which plots recall accuracy or latency by the serial position of items. When plotting recall accuracy, the serial position curve exhibits a bowed form, such that error rates are smallest for the first several items in the sequence (the primacy effect) and the last few items (the recency effect). When plotting recall latency—*viz.* inter-response times—the serial position curve follows an inverted U shape trend, and additionally exhibits a long initial recall latency for the first item (Anderson, Bothell, Lebiere, & Matessa, 1998; Farrell & Lewandowsky, 2004; Maybery, Parmentier, & Jones, 2002; Parmentier & Maybery, 2008; Thomas, Milner, & Haberlandt, 2003). These characteristic features of serial position curves are not unique to verbal STM. Accuracy serial position curves exhibiting primacy and recency effects have been witnessed in studies of spatial STM in which participants recalled sequences of seen spatial locations (Avons, 2007; Farrand, Parmentier, & Jones, 2001; Guérard & Tremblay, 2008; Jones, Farrand, Stuart, & Morris, 1995; Tremblay, Guérard, Parmentier, Nicholls, & Jones, 2006), and in studies of visual STM in which participants recalled sequences of novel visual patterns (Avons, 1998; Avons & Mason, 1999) or unfamiliar faces (Smyth, Hay, Hitch, & Horton, 2005; Ward, Avons, & Melling, 2005) presented in the same spatial location. Similarly, latency serial position curves resembling those witnessed with verbal stimuli have been observed with spatial materials (Hurlstone & Hitch, 2015; Parmentier, Andrés, Elford, & Jones, 2006; Parmentier, Elford, & Maybery, 2005).

Another behavioral phenomenon that has been the subject of a great deal of comparisons across domains is the vulnerability of serial recall to transposition errors. Such order errors occur when an item is

recalled in the wrong serial position. Transpositions can be classified according to their displacement—the numerical difference between an item’s presentation and recall positions. Anticipation errors are transpositions with negative displacement values and occur when an item is recalled before its correct position; conversely, postponement errors are transpositions with positive displacement values and occur when an item is recalled after its correct position. Transposition gradients plot the probability of transpositions according to their displacement value and exhibit three empirical regularities (Farrell & Lewandowsky, 2004; see Figure 3b): (a) the gradients peak at displacement 0 (most responses are correct); (b) the probability of a transposition decreases as the absolute displacement increases—the *locality constraint* (Henson, 1996; Henson, Norris, Page, & Baddeley, 1996); and (c) the error gradients for anticipations and postponements are approximately symmetrical. Like the serial position curves, these three hallmarks of transpositions are also not confined to verbal memoranda—transposition gradients exhibiting these functional characteristics have also been witnessed with spatial (Hurlstone & Hitch, 2015; Jalbert, Saint-Aubin, & Tremblay, 2008; Parmentier et al., 2006; Smyth & Scholey, 1996) and visual (Avons & Mason, 1999; Smyth et al., 2005) memoranda.

Functional similarities across domains are not limited to serial position curves and transposition gradients. Visual and spatial STM exhibit several additional phenomena of serial order in common with verbal STM, including similar distributions of item and order errors (Avons & Mason, 1999; Guérard & Tremblay, 2008) and similar effects of sequence length (Smyth et al., 2005; Smyth & Scholey, 1996), item similarity (Avons & Mason, 1999; Jalbert et al., 2008; Smyth et al., 2005), and Hebb repetition learning (Couture & Tremblay, 2006; Horton, Hay, & Smyth, 2008) amongst other kindred effects (see Hurlstone et al., 2014 for a review). In the next section, we delineate mechanisms and principles of serial order in computational theories of verbal STM that have been proposed to explain serial recall phenomena such as those just reviewed.

Seriating Mechanisms and Principles

Due to a certain amount of co-evolution in their development, there has been some theoretical convergence amongst computational theories of verbal STM and several mechanisms and principles for the representation and control of serial order have been proposed that are widely employed in different models. Existing models represent serial order either: (a) by using a competitive queuing sequence planning and

control mechanism, (b) by imposing a primacy gradient of activations over items, (c) by forming associations between items and some representation of their list position—viz. position marking, (d) by incorporating response suppression, and (e) by implementing output interference, or through some union of these mechanisms and principles.

Competitive Queuing

Most models of serial recall employ a mechanism known as competitive queuing (Bullock, 2004; Bullock & Rhodes, 2003; Davelaar, 2007; Glaspool, 2005; Grossberg, 1978; Houghton, 1990) to plan, represent, and recall sequences. A schematic of such a mechanism—realized as a neural network model—can be inspected in Figure 1. The model comprises two layers of localist item nodes—a parallel planning layer and a competitive choice layer. The nodes in the planning layer represent the pool of items from which sequences are generated. Recalling a sequence is a two-stage process. In the first stage, an ordering mechanism activates in parallel a subset of the nodes in the planning layer, with the relative strength of node activations coding the relative output priority of items. In the second stage, these activations are projected to corresponding nodes in the competitive choice layer. The node activations in this layer obey recurrent-competitive-field dynamics, meaning that each item node excites itself and sends lateral inhibition to competitor nodes in the same layer. This sets up a ‘winner-takes-all’ response competition over items, 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 planning layer. This process iterates until recall of the sequence is complete.

Primacy Gradient

The main difference between different competitive queuing models concerns the nature of the activation gradient used to represent serial order in the planning layer. In the most parsimonious models (Farrell & Lewandowsky, 2004; Grossberg, 1978; Page & Norris, 1998), a single monotonically decreasing activation gradient—known as a primacy gradient—is established over items during serial order encoding, such that the earlier an item occurred in a presentation sequence, the stronger the activation it is assigned. This gradient is then held static during sequence generation and serial recall is accomplished via an iterative process of selecting the strongest item before suppressing its activation—the suppression of an

item after it has been retrieved removes it from the cohort of recall candidates at the subsequent position, allowing the next strongest item to win the output competition.

Position Marking

In more sophisticated competitive queuing models, the activation gradient established over items is not static, but instead varies dynamically over time via the output of a context signal—separate from the item representations in the planning layer—during the course of sequence generation (Brown et al., 2000; Burgess & Hitch, 1999; Hartley et al., 2016; Henson, 1998; Lewandowsky & Farrell, 2008). This introduces a positional component to the representation of serial order because the state of the context signal at any given moment confers information about the current position in the sequence. Accordingly, this dynamic process of representing serial order is known as position marking.

A specific example that serves to highlight this general approach is provided by the seriating mechanism embodied in the model of Burgess and Hitch (1999). In their model, when an item is presented as part of a to-be-remembered sequence its representation is activated in a planning layer and an association is formed—via Hebbian learning—between the item representation and the current state of a time-varying (distributed) positional context signal. The context signal has the property that neighboring states (*viz.* adjacent serial positions) are more similar to one another than states that are separated in time (*viz.* non-adjacent serial positions). Recall of the sequence is accomplished by reactivating the different states of the positional context signal in order—which produces a dynamically varying activation gradient over items in the planning layer—and recalling the most activated item at each position.

Some models incorporate an activation gradient with both static (*viz.* a primacy gradient) and dynamic (*viz.* position marking) properties—generating a hybrid ordinal-positional representation of serial order. For example, in some models, a primacy gradient is incorporated into the strength of the associations between items and the different states of the positional context signal (Brown et al., 2000; Lewandowsky & Farrell, 2008). In other models, a primacy gradient is established over items but is then modulated by the output of the positional context signal during serial recall (Burgess & Hitch, 1999).

Response Suppression

Response suppression refers to the inhibition or removal of items from memory following recall and is an assumption incorporated in almost all theories of verbal STM (e.g., Brown et al., 2000; Burgess & Hitch, 1999; Farrell & Lewandowsky, 2002; Grossberg & Pearson, 2008; Henson, 1998; Lewandowsky & Farrell, 2008; Page & Norris, 1998). In competitive queuing models, response suppression occurs as a result of the inhibitory feedback signal from the competitive choice layer to the parallel planning layer following the retrieval of an item. In other models (Farrell, 2006; Lewandowsky & Farrell, 2008), response suppression is implemented through the unlearning—viz. Hebbian anti-learning (Anderson, 1995)—of the association between the item just retrieved and its position marker. This has the effect of reducing the strength with which the item competes for recall when memory is probed with subsequent position markers.

In models that rely on a primacy gradient to represent serial order, the incorporation of response suppression is crucial for sequencing, since it serves to prevent perseveration on the same response. It is a less crucial ingredient in models that rely on position marking to represent serial order because the dynamically re-evolving context signal relieves the suppression mechanism of the burden for sequencing. Nevertheless, even models that represent serial order via position marking must incorporate response suppression to minimize the occurrence of erroneous repetitions, which occur infrequently in serial recall (Henson, 1996; Vousden & Brown, 1998).

Output Interference

Output interference refers to the assumption that the act of recalling an item from STM interferes with the representation of items that are yet to be retrieved. It is an ancillary assumption incorporated in some theories of STM to more accurately model primacy and sequence length effects in serial recall (Brown et al., 2000; Lewandowsky, Duncan, & Brown, 2004; Lewandowsky & Farrell, 2008). The key feature of output interference is that recall of early items interferes with later items in the sequence. This interference occurs irrespective of whether serial order is represented via a primacy gradient or position marking (or both) and regardless of whether or not a recalled item is subsequently suppressed.

Model Selection

Functional similarities across domains suggest that at least some of the mechanisms and principles just reviewed, might also be implicated in the representation of serial order in visual and spatial STM. Indeed, in a recent comprehensive review of the serial recall literature, Hurlstone et al. (2014) identified evidence from behavioral, electrophysiological, and modeling studies that supports the contention that all short-term memories (verbal, visual, spatial) utilize the competitive queuing mechanism to plan, represent, and recall sequences. However, whilst Hurlstone et al. (2014) identified direct evidence for the operation of a primacy gradient, position marking, response suppression, and output interference in the verbal STM competitive queuing system—viz. the phonological loop—they noted that the principles that contribute to the representation of serial order in the visual and spatial STM competitive queuing systems—viz. the visuospatial sketchpad—are not yet known because the existing data in these domains—which has focused largely on serial position curves and transposition gradients—can be handled equally well by mechanisms embodying various different combinations of the representational principles.

A specific illustration of this problem is provided in Figure 2, which shows the theoretical predictions of five models of serial order originally studied by Farrell and Lewandowsky (Farrell & Lewandowsky, 2004; Lewandowsky & Farrell, 2008; see also Hurlstone & Hitch, 2015). The models were built from different combinations of a primacy gradient, position marking, response suppression, and output interference—representative of the combinations of these principles employed in theories of serial recall; see Hurlstone et al. (2014) and Hurlstone & Hitch (2015)—and implemented within a common competitive queuing neural network architecture that permitted the generation of response probability and recall latency predictions (see Appendix A for precise details of the modeling). It is apparent from inspection of this figure that the five models generate qualitatively similar accuracy serial position curves (Figure 2A), transposition gradients (Figure 2B), and latency serial position curves (Figure 2C), which makes identification of the preferred mechanism difficult. These are not the only behavioral phenomena for which different models generate comparable predictions—most phenomena of serial order can be accommodated equally well by different mechanisms for representing serial order (Hurlstone et al., 2014; Lewandowsky & Farrell, 2008). Although several more diagnostic results have been identified and studied in the context of verbal STM that confer direct support for the operation of specific representational principles, with one noteworthy exception that we discuss shortly (Hurlstone & Hitch, 2015), these have

yet to be examined in the visual and spatial domains.

One such phenomenon is known as the *latency-displacement function* (henceforth LDF; Farrell & Lewandowsky, 2004). The LDF is the latency equivalent of the transposition gradient and plots the mean recall latency of transpositions as a function of transposition displacement. Figure 3 shows the LDFs predicted by the five models of serial order. It is clear from the figure that unlike their predicted serial position curves and transposition gradients, the models' predicted LDFs differ considerably from each other. Specifically, when serial order is represented by position marking alone (PM), the LDF exhibits a symmetric V-shaped function, whereas the addition of response suppression (PM + RS) or output interference (PM + OI) reduces the slope for postponements, producing a partially asymmetric V-shaped LDF. In stark contrast to the above models, the combination of a primacy gradient with response suppression dramatically alters the shape of the LDF rendering it monotonically negative (PG + RS), whilst the addition of position marking (PG + PM + RS) flattens the slope of the function for postponements, but without removing the overall negative latency–displacement relationship.

Across three experiments involving the output-timed recall of verbal sequences, the LDFs observed by Farrell and Lewandowsky (2004) were consistently monotonically negative and additionally exhibited a reduction in slope for postponements compared to anticipations, indicating that serial order in verbal STM is represented via a mechanism combining a primacy gradient with position marking and response suppression. More recently, Hurlstone and Hitch (2015) reported three experiments exploring the dynamics of transpositions in a spatial serial recall task involving memory for sequences of seen spatial locations in which the observed LDFs were also consistently monotonically negative overall but additionally exhibited a flattening of the slope for postponements, conferring support for the operation of the same representational mechanism in spatial STM.

Current Study

The current study sought to extend the analysis of transposition latencies to the recall of visual, non-spatial sequences in order to identify: (1) whether a combination of the four representational principles is responsible for coding serial order in visual STM, and (2) whether those principles are the same as those previously identified in verbal and spatial STM. The structure of the remainder of this article is as follows. First, we report three new experiments exploring the dynamics of transpositions in a visual serial recall task

involving memory for sequences of unfamiliar faces. To foreshadow, across manipulations of sequence length (Experiments 1 & 2), articulatory suppression (Experiment 2), and temporal grouping (Experiment 3), the observed LDFs were consistently monotonically negative and additionally exhibited a flattening of the slope for postponements compared to anticipations. Next, we report quantitative fits of the models to representative data, which confirm that they are best accommodated by a model embodying a primacy gradient, position marking, and response suppression. Combined with the results of Farrell and Lewandowsky (2004) and Hurlstone and Hitch (2015), these findings suggest that the same mechanism is responsible for representing serial order across the verbal, visual, and spatial STM domains. The implications of these findings for theories of working memory are subsequently discussed.

Before reporting our experiments, we briefly motivate our choice of visual stimuli.

Choice of Stimuli

Previous studies of serial order in visual STM have employed either novel visual matrix patterns (Avons, 1998; Avons & Mason, 1999) or unfamiliar faces (Smyth et al., 2005; Ward et al., 2005) as memoranda. A limitation of the former class of visual stimuli is that they are complex and artificial, requiring slow presentation rates, which may foster a reliance on supplementary verbal encoding strategies. Faces, by comparison, are also complex visual stimuli, but they benefit from a familiar form, which adults are extremely adept at processing. Smyth et al. (2005) have shown that serial memory phenomena—viz. serial position effects on accuracy; the sequence length effect; the locality constraint on transpositions—can be obtained with sequences of unfamiliar faces presented at fast presentation rates and are not based on verbal encoding strategies.

The latter conclusion is buttressed by the independent effects of visual similarity and articulatory suppression reported by Smyth et al. The visual similarity effect refers to the finding that sequences of visually similar items are recalled less accurately than sequences of visually dissimilar items (Avons & Mason, 1999; Logie Della Sala, Wynn, & Baddeley, 2000; Logie, Saito, Morita, Varma, & Norris, 2015; Saito, Logie, Morita, & Law, 2008), whereas the articulatory suppression effect refers to the finding that serial recall performance for verbal materials (and nonverbal materials that have been subject to verbal encoding) is depressed when participants must repeat a verbal token—or sequence of verbal tokens—out loud concurrent with the presentation of the study sequence (a secondary task which occupies the speech

output system, thus blocking verbal encoding).

At first blush, the deleterious effect of articulatory suppression suggests that verbal coding strategies contribute to serial memory for faces. However, the authors failed to observe a reliable interaction between visual similarity and articulatory suppression. If verbal coding strategies do contribute to serial memory for faces then the visual similarity effect should be stronger in magnitude in the presence, than in the absence, of articulatory suppression due to the increased demands placed by suppression on visual encoding processes. That this was not the case suggests that suppression interfered instead either with attentional resources required during the encoding of the faces (cf. Meisser & Klauer, 1999) or with the representation of their serial order (cf. Henson, Hartley, Burgess, Hitch, & Flude, 2003).

Given their sensitivity to serial memory phenomena and resistance to verbal encoding strategies, we employed unfamiliar faces as visual stimuli in the three experiments that follow.

Experiment 1

Experiment 1 examined the LDFs underpinning visual STM for sequences containing different numbers of faces. The rationale for the sequence length manipulation was manifold. First, it permitted an analysis of potential performance related variability in the LDFs, since serial recall performance for sequences of visual items is known to deteriorate with sequence length (Smyth et al., 2005; Ward et al., 2005), as it does for sequences of verbal (Anderson et al., 1998; Crannell & Parish, 1957; Maybery et al., 2002) and spatial items (Smyth, 1996; Smyth & Scholey, 1994, 1996). Second, it permitted an assessment of the LDFs under conditions that should engender changes in response latencies, since chronometric studies of the sequence length effect in verbal serial recall have shown that recall times at each serial position increase approximately linearly with sequence length (Anderson et al., 1998; Maybery et al., 2002). Third, it enabled an examination of the sensitivity of the LDFs to changes in the range of possible displacements that transpositions could span, which naturally increases with sequence length.

Methods

Participants & materials. Twenty-six undergraduate students from the Department of Psychology at the University of York took part in the experiment in exchange for course credit or payment of £10 (approximately \$15). All had normal or corrected-to-normal vision.

The stimuli were sequences of four to six faces of the same gender drawn randomly without replacement from a stimulus ensemble of 814 front profile images of unfamiliar faces, subject to the constraint that no face was presented on more than two occasions across the entire experiment. The faces were drawn from various public domain face databases, were edited to remove any background noise and maximize the size of a face, and presented in greyscale on a white background at a standard height of 1.5 inches.

Design. The experiment manipulated two within-participant factors: sequence-length with three levels (four vs. five vs. six) and serial position (with as many levels as items in the sequence). Participants undertook two approximately 70 minute experimental sessions, which were spaced at least 24 hours apart. Within each session, there were 150 experimental sequences, which were divided into three blocks of 50 sequences, one block for each sequence length. The ordering of the blocks was counterbalanced across participants. Each block began with two practice sequences and there were enforced 1-minute rest periods after every twenty-five experimental sequences.

Procedure. Participants were tested individually in a quiet room in the presence of the experimenter. They initiated each trial by selecting a “begin trial” icon situated in the central screen position using a mouse-driven pointer. A central fixation cross then appeared for 1500 ms and was replaced by a sequence of faces presented singly for 500 ms each and separated by a 500-ms blank interval. The final face was followed by a 1000-ms delay after which the set of faces reappeared simultaneously at fixed positions within a circular array centred on the middle of the screen (see Figure 4). The allocation of faces to positions around the circular array was determined at random. Participants were required to click on the faces in their presentation order using the mouse-driven pointer. Once an item was selected, it disappeared temporarily for 50 ms to indicate that the response had been registered. Participants were encouraged to guess whenever they were unsure of the correct item for a given position, otherwise they could select a question mark located in the centre of the reconstruction array to omit that item. Once a response had been registered at each output position, the contents of the screen cleared and the reconstruction time for the sequence was displayed in the central screen position for 3000-ms, before the “begin trial” icon for the next trial was displayed.

Results and discussion

The data were analyzed using a strict serial recall scoring procedure: an item was only scored as correct if its output serial position was the same as its input serial position. The results are structured into four sections: (1) accuracy serial position curves, (2) transposition gradients, (3) latency serial position curves, and (4) LDFs. Effect size estimates are provided—for focused comparisons only—using Pearson's r .

Accuracy serial position curves. The accuracy serial position curves can be inspected in Figure 5A. The curves are representative of those witnessed in typical serial recall studies, showing a clear deterioration in performance with increasing sequence-length and extended primacy and restricted recency within sequences. Statistical confirmation of the effect of sequence length was obtained via a one-way Analysis of Variance (ANOVA) performed on the mean proportion of correct responses collapsed across serial positions for the different sequence lengths. This revealed a significant main effect of sequence length, $F(2,50) = 153.52, p < .001$, with four-item sequences being recalled better than five-item sequences, $t(25) = 9.13, p < .001, r = .88$, and with five-item sequences being recalled better in turn than six-item sequences, $t(25) = 9.97, p < .001, r = .89$.

Statistical confirmation of the effects of serial position was obtained by conducting one-way ANOVAs on the mean proportion of correct responses as a function of serial position at each sequence length. There was a significant main effect of serial position for sequences of four-items, $F(3,75) = 22.82, p < .001$, five-items, $F(4,100) = 23.13, p < .001$, and six-items, $F(5,125) = 41.13, p < .001$, reflecting the apparent primacy and recency effects in the data.

Transposition gradients. Figure 5B shows the transposition gradients, which exhibit the three hallmark characteristics delineated at the outset. Specifically, the gradients peak at displacement 0; the proportion of transpositions decreases as a function of increasing displacement; and the error gradients for anticipations and postponements are approximately symmetrical. Consistent with the accuracy serial position analysis, the frequency of anticipations and postponements increased with increasing sequence length.

Latency serial position curves. The mean recall latencies for correct responses can be inspected in Figure 5C. The latency curves are similar to those witnessed for the output-timed recall of verbal (Farrell & Lewandowsky, 2004; Maybery et al., 2002) and spatial sequences (Hurlstone & Hitch, 2015; Parmentier

et al., 2006), showing an elevation in recall times at each serial position with increasing sequence length along with a markedly longer recall latency at the first output position than at subsequent output positions. However, in studies of verbal and spatial serial recall, once recall has been initiated the recall times over subsequent serial positions typically rise to a saddle point mid-sequence before accelerating thereafter, giving rise to an inverted-U shaped latency curve like those generated by the models in Figure 2C. In contrast to those data and model predictions, the latency curves associated with the recall of visual sequences in Figure 5C are monotonically decreasing showing a speed-up in recall times over serial positions.

The effect of sequence length was statistically verified by performing a one-way ANOVA with sequence length as the independent variable and mean recall latencies for correct responses collapsed across serial positions as the dependent variable. There was a significant main effect of sequence length, $F(2,50) = 18.33, p < .001$, with shorter recall times for four-item than five-item sequences, $t(25) = -4.47, p < .001, r = .67$, but the difference in recall times between five-item and six-item sequences fell marginally short of conventional significance levels, $t(25) = -1.78, p = .09, r = .34$. A comparison of performance within each serial position curve revealed a significant main effect of serial position for sequences of four-items, $F(3,75) = 155.04, p < .001$, five-items, $F(4,100) = 104.64, p < .001$, and six-items, $F(5,125) = 125.40, p < .001$, reflecting the long initial recall latency and speed-up in recall times over serial positions apparent within each serial position curve.

LDFs. Turning to the data most central to the present article, Figure 6A shows the LDFs which plot the mean recall latencies of transpositions as a function of transposition displacement. Note that the effect of output position on the LDFs—viz. the speed-up in recall times over output positions visible in Figure 5C—has been removed by subtracting from each individual recall latency the mean of all responses for that sequence length condition and serial position, for each individual participant (this procedure was also adopted in the generation of the model predictions—see Appendix A). Removal of the effect of output position is necessary because it is correlated with transposition displacement—anticipations predominantly occur at early output positions, whereas postponements predominantly occur at late output positions. This is problematic because recall times are slower at early positions, which artificially elevates the recall latencies of anticipations, whereas recall times are faster at late output positions, which artificially accelerates the recall latencies of postponements. The negative latencies at some transposition

displacements are a consequence of this filtering process. It is apparent from inspection of Figure 6A that the LDFs for the different sequence lengths are monotonically negative with a reduction in slope for postponements compared to anticipations. The only visible effect of the sequence length manipulation was that the slope of the LDF for anticipations was steeper for four-item sequences than five-item and six-item sequences.

The LDFs were analyzed using the same two-stage procedure adopted in our earlier work (Hurlstone & Hitch, 2015). In the first stage, regression analyses were performed that examined the relationship between transposition latency and transposition displacement for each individual participant, for each sequence length. One set of analyses examined the relationship between latency and displacement for anticipations (displacements $-s/l+1$ to 0; where s/l represents sequence length), whilst a second set examined the relationship between latency and displacement for postponements (displacements 0 to $s/l-1$). Thus, regression equations were computed for each participant by regressing transposition latency on displacements that were anticipations and postponements, separately. Each regression equation represents the best description—in a least squares sense—of the relationship between transposition latency and the predictor variable for a specific participant.

In the second stage, the regression parameter estimates for the slopes of the LDFs for anticipations and postponements were pooled together and subjected to one-sample t-tests to determine whether they deviated reliably from zero. The regression statistics for the slope analyses are summarized in Table 1 from which it can be seen that the mean parameter estimates for the slopes of LDFs for anticipations were strongly negative and deviated reliably from zero: $t(25) = -4.26, p < .001, r = .65$, for four-item sequences, $t(25) = -2.46, p < .05, r = .44$, for five-item sequences, and $t(25) = -3.03, p < .01, r = .52$, for six-item sequences. The mean parameter estimates for the slopes of LDFs for postponements were weakly positive by comparison, but also deviated significantly from zero: $t(25) = 3.31, p < .01, r = .55$, for four-item sequences, $t(25) = 2.98, p < .01, r = .51$, for five-item sequences, and $t(25) = 2.60, p < .05, r = .46$, for six-item sequences.

One potential limitation of Experiment 1 is that a manipulation check was not incorporated to determine if memory for sequences of faces was mediated by a verbal encoding strategy. Participants may, for example, have generated a verbal description of each face in a sequence and then rehearsed those descriptions as a sequence of verbal tokens. This means that we cannot be certain that the LDFs in

Figure 6A are not underpinned in part by a verbal component. As noted previously, Smyth et al. (2005) have shown using an experimental protocol akin to our own that a verbal encoding strategy does not contribute to serial memory for faces. This renders it unlikely that such an auxiliary strategy was brought to bear on performance in the present experiment. Nevertheless, in order to examine the robustness of the results of Experiment 1 and to ensure that such a strategy did not impact upon the shape of the LDFs shown in Figure 6A, in the next experiment we sought to replicate the current results under conditions where we could be certain that a verbal recoding strategy could not be deployed by participants.

Experiment 2

The second experiment was identical to Experiment 1 in all respects except that participants were required to engage in articulatory suppression—viz. speak the digits “1”, “2”, “3”, “4” aloud repeatedly—during the encoding of study sequences in order to block the speech output system and prevent the deployment of a verbal recoding strategy. The question of interest is whether the LDFs observed in the previous experiment will hold when the opportunity to engage in verbal recoding is obstructed and performance must necessarily be based on a visual code only. Given the unrealistically large number of trials that would have been required to have participants complete both a control and an articulatory suppression condition, only the latter condition was used and an estimate of the impact of the articulatory suppression manipulation on performance was obtained by means of a between-experiment comparison with Experiment 1.

Methods

Participants. Twenty-six undergraduate students from the Department of Psychology at the University of York took part in the experiment in exchange for course credits or an honorarium of £10 (approximately \$15). None of the participants took part in the previous experiment and all had normal or corrected-to-normal vision.

Materials, design & procedure. The materials, design, and procedure were the same as for Experiment 1, with one noteworthy exception: at the beginning of each trial, once the participant had selected the “begin trial” icon they were required to repeat the sequence of digits “1”, “2”, “3”, “4” out loud, at the rate of three digits per second until the reconstruction array appeared. The articulation rate was

demonstrated to the participant prior to the first practice sequence using a digital metronome. The experimenter remained present at all times to ensure compliance with the suppression protocols. If the participant failed to keep to the rate of three utterances per second, the rate was demonstrated again using the digital metronome and they were instructed to try harder.

Results and discussion

Accuracy serial position curves. The accuracy serial position curves for this experiment are shown in Figure 7A alongside the corresponding curves for Experiment 1 to aid interpretability. Like the curves observed in the preceding experiment, there is a clear deterioration in performance with longer sequences and extended primacy and restricted recency effects within sequences. Also apparent is that the articulatory suppression manipulation reduced performance slightly for four-item sequences, but had no effect for five-item and six-item sequences, respectively.

Statistical confirmation of the effect of articulatory suppression on performance was obtained via a between experiment comparison with Experiment 1. A 2 (suppression: no-suppression vs. suppression) \times 3 (sequence length: four vs. five vs. six) ANOVA performed on the mean proportion of correct responses collapsed across serial position revealed no significant main effect of suppression, $F(1,50) = 0.18, p = .68, r = .03$, a significant main effect of sequence length, $F(2,100) = 271.02, p < .001$, with recall accuracy decreasing with increasing sequence length, and the expected interaction between the two variables, $F(2,100) = 5.13, p < .01$.

To compare performance within each serial position curve for the present experiment only, separate one-way ANOVAs were conducted on the mean proportion of correct responses as a function of serial position for each sequence length. There was a significant main effect of serial position for sequences of four-items, $F(3,75) = 32.38, p < .001$, five-items, $F(4,100) = 32.04, p < .001$, and six-items, $F(5,125) = 60.91, p < .001$, reflecting the apparent primacy and recency effects in the data.

Transposition gradients. The transposition gradients are shown in Figure 7B. They are similar to those observed in the previous experiment (Figure 5B) and exhibit the expected hallmark characteristics.

Latency serial position curves. Mirroring the latency serial position curves observed in Experiment 1 (Figure 5C), the curves for the current experiment shown in Figure 7C exhibit a high amplitude peak at the first output position and an overall monotonically negative trend. A clear effect of

sequence length is also visible, with the recall times at each output position increasing with longer sequences. Statistical confirmation of the effect of sequence length was provided by performing a one-way ANOVA with sequence length as the independent variable and mean recall latencies for correct responses collapsed across serial positions as the dependent variable. There was a significant effect of sequence length, $F(2,50) = 47.64, p < .001$, with shorter recall times for four-item than five-item sequences, $t(25) = -8.64, p < .001, r = .87$, and with shorter recall times in turn for five-item than six-item sequences, $t(25) = -4.02, p < .001, r = .63$.

A comparison of performance within each serial position curve revealed a significant main effect of serial position for sequences of four-items, $F(3,75) = 110.15, p < .001$, five-items, $F(4,100) = 154.14, p < .001$, and six-items, $F(5,125) = 117.54, p < .001$, reflecting the long initial recall latency and acceleration in recall times over serial positions apparent within the latency curves.

LDFs. The LDFs shown in Figure 6B parallel those reported in the previous experiment. They once again exhibit an overall negative latency–displacement relationship, in addition to a flattening of the slope for postponements. As in Experiment 1, the only visible effect of the sequence length manipulation is that it reduced the slope of the LDF for anticipations. The regression statistics for the LDF slopes are shown in Table 1 and provide statistical confirmation of the pattern illustrated graphically in Figure 6B. The slopes of LDFs for anticipations were steeply negative and deviated significantly—or nearly so—from zero: $t(25) = -4.49, p < .001, r = .67$, for four-item sequences, $t(25) = -1.90, p = .06, r = .36$, for five-item sequences, $t(25) = -2.58, p < .05, r = .46$, for six-item sequences. By contrast, the slopes of LDFs for postponements were only weakly positive, but differed significantly from zero: $t(25) = 4.49, p < .001, r = .67$, for four-item sequences, $t(25) = 3.64, p < .01, r = .59$, for five-item sequences, and $t(25) = 2.78, p < .05, r = .49$, for six-item sequences.

In brief, the current experiment has shown that when the opportunity to verbally recode a sequence of unfamiliar faces is precluded—by blocking the speech output system—the observed LDFs are virtually indistinguishable from those witnessed in Experiment 1. Indeed, but for a small and unreliable negative effect on the accuracy of recall of four-item sequences, serial recall performance was unaffected by the articulatory suppression manipulation. This result suggests that verbal STM codes are unlikely to have contributed to the shape of the LDFs in Experiment 1. We note also that the small negative effect of articulatory suppression on performance for four-item sequences need not reflect the disruption of a verbal

recoding strategy. As noted previously, the results of Smyth et al. (2005) suggest that such disruption is more likely to reflect either competition for attentional resources during serial order encoding or interference with the representation of serial order.

Experiment 3

To further examine the generality of the error latency profiles witnessed in Experiments 1 and 2, we next report a third experiment, which examined the impact of a temporal grouping manipulation. This manipulation involves inserting extended temporal pauses after every few items in a study sequence in order to segregate it into sub-groups. Grouping a sequence of verbal items in this manner has been shown to exert a number of systematic effects on performance. First, grouping improves serial recall performance and alters the shape of the accuracy serial position curve—the serial position curve exhibits mini primacy and recency effects within each group (Frankish, 1985, 1989; Hitch, Burgess, Towse, & Culpin, 1996). Second, grouping alters the shape of the latency serial position curve—as well as leaving a long pause before recalling the sequence, participants leave a long pause before recalling each group (Farrell & Lewandowsky, 2004; Maybery et al., 2002; Parmentier & Maybery, 2008). Third, grouping alters the pattern of transposition errors—grouping reduces the frequency of adjacent-neighbor transpositions that straddle a group boundary (e.g., items 3 and 4 exchanging positions in the sequence 123—456; Maybery et al., 2002; Ng & Maybery, 2005; Parmentier & Maybery, 2008), but increases the frequency of transpositions between groups that preserve their within-group serial position (e.g., items 2 and 5 exchanging positions; Ng & Maybery, 2002, 2005; Ryan, 1969), a class of errors known as *interpositions* (Henson, 1996). With the exception of the increase in the frequency of interpositions, the effects of grouping with verbal stimuli just reviewed have also been documented with spatial materials (Hurlstone & Hitch, 2015; Parmentier et al., 2006).

It is widely accepted that temporal grouping effects are an empirical referent of the operation of position marking. Positional models account for such effects by assuming that order information in grouped sequences is represented using two sets of position markers, one set that encodes the position of groups (Brown et al., 2000; Hartley et al., 2016; Henson, 1998; Lewandowsky & Farrell, 2008) or items (Burgess & Hitch, 1999) in the sequence, and a second set that encodes the position of items within groups. The latter set of markers are crucial for explaining the pattern of interpositions errors observed in grouped

verbal serial recall. By contrast, the absence of interpositions in grouped spatial serial recall has been taken to confer support for a subtly different representational scheme whereby position markers encoding the position of groups in the sequence are augmented by position markers encoding the position of items in the sequence as a whole, rather than within groups (Hurlstone & Hitch, 2016).

The rationale for incorporating the grouping manipulation was two-fold. First, grouping effects have not previously been examined for serial recall of visual materials, and to the extent that such effects are observed this will provide an additional test of the role of position marking in visual STM. Of particular interest is whether grouped visual serial recall is characterized by an increase in the probability of interpositions—like grouped verbal serial recall—or whether the probability of interpositions is unaffected by grouping—like grouped spatial serial recall. Assuming that grouping does exert effects on recall, the latter result might indicate that positional information in grouped visual sequences—like grouped spatial sequences—may be represented in a subtly different manner to that of grouped verbal sequences.

Second, given the multifarious effects of grouping on other aspects of recall documented earlier, it is reasonable to ask whether grouping might also exert systematic effects on the shape of the LDF. Indeed, if positional information in grouped sequences is represented via markers coding the position of groups in the sequence complemented by markers coding the position of items within groups then the positional models—viz. PM, PM + RS, PM + OI—predict that grouping should simultaneously increase the probability of interpositions and accelerate their response latencies. However, at variance with this prediction, Farrell and Lewandowsky (2004) found that although grouping a sequence of verbal items increased the probability of interpositions, this was not mirrored by faster recall times for these errors. Similarly, Hurlstone and Hitch (2015) also found that grouping did not exert any systematic effects on the LDF for spatial sequences (although they also failed to observe an effect of grouping on interposition rates). Thus, in both studies grouping exerted discernible effects on recall in terms of accuracy and latency serial position curves (and transposition gradients in the experiments of Farrell and Lewandowsky, 2004), but had only negligible—if any—effect on the LDFs, suggesting that representations other than position marking must underpin verbal and spatial serial recall. In the current experiment, we ask whether the LDF for visual serial recall is similarly unaffected by grouping.

Methods

Participants. Forty-two undergraduate students from the School of Psychology at the University of Western Australia took part in the experiment in exchange for course credits. All had normal or corrected-to-normal vision.

Design & procedure. The experiment manipulated two independent variables: grouping (ungrouped vs. grouped) was a between-participants factor, whereas serial position (1–6) was a within-participants factor. Half the participants received the ungrouped sequences, whereas the remaining half received the grouped sequences. Grouping was manipulated between-participants in order to reduce the likelihood of individuals spontaneously grouping the ostensibly ungrouped sequences, a tendency which can increase in within-participant designs in which some participants are exposed to objectively grouped sequences prior to ungrouped sequences (e.g., Henson, 1996; Farrell & Lelièvre, 2009; Parmentier et al., 2006).

The procedure was the same as for Experiment 1 with the following exceptions: participants completed only a single experimental session; the sequence length was fixed to six-items; and in the grouped condition the temporal interval separating the third and fourth item in the sequence was extended from 500 ms to 1500 ms to segregate the sequences into two sub-groups of three items. Participants attempted 80 experimental trials, which were preceded by two practice trials. Enforced 30-second rest periods were included after every 20 experimental trials. The experiment lasted approximately 40 minutes.

Results and discussion

Accuracy serial position curves. The accuracy serial position curves are shown in Figure 8A. Consistent with previous studies of grouped verbal (Frankish, 1985, 1989; Hitch et al., 1996; Maybery et al., 2002; Ryan, 1969) and spatial (Parmentier et al., 2006; Hurlstone & Hitch, 2015) serial recall, it can be seen that grouping modified the shape of the serial curve: The curve for grouped sequences exhibits effects of primacy and recency within groups and the sequence overall, whereas the curve for ungrouped sequences exhibits these effects for the sequence as a whole only. However, whilst grouping enhanced the accuracy of recall, its beneficial effect was highly localized, being restricted only to those items straddling the group boundary—viz. Serial Positions 3 and 4. This is at variance with the effects of grouping observed with verbal and spatial memoranda, which are larger in magnitude and witnessed across most—if

not all—serial positions.

That grouping modified the shape of the accuracy serial position curve was statistically verified by a 2 (grouping: ungrouped vs. grouped) \times 6 (serial position: 1–6) ANOVA. As suspected, there was no significant main effect of grouping, $F(1,40) = .23$, $p = .63$, $r = .04$, indicating that grouping did not foster an overall improvement in performance. However, the expected main effect of serial position, $F(5,200) = 61.03$, $p < .001$, and interaction between grouping and serial position, $F(5,200) = 5.03$, $p < .001$, were both significant.

Transposition gradients. In contrast to the effects of grouping on the accuracy serial position curve, Figure 8B shows that the transposition gradients were unaffected by the grouping manipulation. If grouping had fostered an increase in interposition errors then the transposition gradient for grouped sequences should exhibit peaks at ± 3 displacements. However, the transposition gradients for grouped sequences—like those for ungrouped sequences—decrease monotonically with increasing transposition displacement, indicating that grouping did not foster an increase in these interposition errors. This result is at odds with the pattern observed in studies of grouped verbal serial recall (Ng & Maybery, 2002, 2005; Ryan, 1969), but it is consistent with the pattern observed in studies of grouped spatial serial recall (Hurlstone & Hitch, 2015; Parmentier et al., 2006) where an increase in the frequency of interpositions in grouped sequences is also notably absent.

Although grouping did not increase the frequency of interpositions, consistent with studies of grouped verbal (Maybery et al., 2002; Ng & Maybery, 2005; Parmentier & Maybery, 2008) and spatial serial recall (Hurlstone & Hitch, 2015), it did reduce the frequency of adjacent-neighbor transpositions straddling the group boundary. This was confirmed by calculating the frequency of adjacent inter-group errors and interposition errors for each individual participant from the ungrouped and grouped conditions. A 2 (grouping: ungrouped vs. grouped) \times 2 (error-type: adjacent inter-group vs. interposition) ANOVA performed on the error frequencies revealed a significant effect of grouping, $F(1,40) = 4.30$, $p < .05$, $r = .56$, with more errors for ungrouped than grouped sequences, a significant main effect of error-type, $F(1,40) = 99.33$, $p < .001$, $r = 1$, with more interposition than adjacent inter-group errors, and a significant interaction between the two variables, $F(1,40) = 6.49$, $p < .05$. The interaction arose because grouping decreased the frequency of adjacent inter-group errors (ungrouped $M = 23.33$ vs. grouped $M = 13.14$), $t(40) = 4.20$, $p < .001$, $r = .55$, but exerted no effect on the frequency of interposition errors (ungrouped M

= 35.81; grouped $M = 34.19$), $t(40) = .40$, $p = .69$, $r = .11$.

Latency serial position curves. The latency serial position curves are plotted in Figure 8C. In accordance with previous studies examining the effects of grouping on response timing in verbal (Farrell & Lewandowsky, 2004; Maybery et al., 2002) and spatial serial recall (Hurlstone & Hitch, 2015; Parmentier et al., 2006), it can be seen that grouping modified the shape of the latency curve. Whereas the ungrouped curve peaks at the first output position and then decreases monotonically, the grouped curve exhibits a second lower amplitude peak at Serial Position 4, indicating that participants left a brief pause before outputting items from the second group.

The effect of grouping on the latency serial position curve was corroborated by a 2 (grouping) \times 6 (serial position) ANOVA, which revealed no significant main effect of grouping, $F(1,40) = .24$, $p = .63$, $r = .04$, a significant main effect of serial position, $F(5,200) = 264.39$, $p < .001$, and the expected interaction between the two variables, $F(5,200) = 2.78$, $p < .05$.

LDFs. The LDFs for the present experiment are displayed graphically in Figure 6C and are in accordance with the now familiar pattern reported in the two previous experiments—the LDFs are negative overall, but with a reduction in slope for postponements compared to anticipations. That the overall shape of the LDF was unaffected by the grouping manipulation is noteworthy given that grouping engendered qualitative changes in the accuracy and latency serial position curves. However, the grouping manipulation did exert some subtle effects on the LDF; thus, although we have seen that grouping did not affect the probability of interpositions, Figure 6C shows that it did nevertheless affect their response latencies, although not quite in the manner predicted by positional models. Specifically, although grouping accelerated the recall times of -3 displacements, it decelerated—rather than accelerated—the recall times of +3 displacements. It is unclear whether these discontinuities in the LDF merely coincidentally occur at displacement distances corresponding to interpositions, or whether they reflect the impact of within-group positional codes. We explore this issue later using quantitative model comparisons.

The regression statistics for the LDF slope analyses reported in Table 1 provide statistical confirmation of the pattern shown in Figure 6C. The slopes of LDFs for anticipations were steeply negative and deviated significantly from zero: $t(20) = -2.70$, $p < .05$, $r = .52$, for ungrouped sequences, and $t(20) = -3.25$, $p < .01$, $r = .59$, for grouped sequences, whereas the slopes of LDFs for postponements were only weakly positive, but also deviated significantly from zero: $t(20) = 2.71$, $p < .05$, $r = .52$, for ungrouped

sequences, and $t(20) = 4.50$, $p < .001$, $r = .71$, for grouped sequences.

Summary of Experiments

The results of the three experiments are unambiguous—across manipulations of sequence length (Experiments 1 & 2), articulatory suppression (Experiment 2), and temporal grouping (Experiment 3), the LDFs underpinning serial recall of sequences of visual items were consistently monotonically negative, but additionally exhibited a reduction in slope for postponements compared to anticipations. This empirical pattern is consistent with the theoretical prediction of a mechanism embodying a primacy gradient, position marking, and response suppression—viz. the PG + PM + RS model; it is incompatible with the error latency predictions of the four competing models and mechanisms for representing serial order (Figure 3).

Although we have hitherto restricted our analysis to the aggregate LDFs, inspection of the LDFs for individual participants reveals a similar pattern. Figure 9A and B show, respectively, the distributions of slopes of LDFs for anticipations and postponements for each individual participant for each experiment and condition. It is apparent from inspection of Figure 9A that the majority of slopes of LDFs for anticipations are negative (75%), and a significant percentage of these slopes are steep slopes falling in the range of -100 ms to -1500 ms (47%). By contrast, it is visible from inspection of Figure 9B that a larger percentage of slopes of LDFs for postponements are positive (78%), and the majority of slopes are shallow slopes concentrated in the region of -100 ms to 100 ms (91%). Figure 9 thus confirms that the steep negative anticipation slopes and approximately flat postponement slopes of the aggregate LDFs are an accurate reflection of the individual participant LDFs from which they are constructed, and therefore represent a robust and general feature of visual STM.

Model Fitting

Although the LDFs observed across the three experiments are most compatible with the error latency prediction of the PG + PM + RS model, one limit of the initial model predictions is that they are based on a single set of model parameter values chosen somewhat arbitrarily to produce comparable levels of performance across the models. It remains possible therefore that models other than the PG + PM + RS model might be able to reproduce the observed LDF under different model parameter values. To address this question, we next report further simulations in which the models were fit to the response probability

and recall latency data for the different sequence length conditions of Experiment 2.

Another aspect of the empirical data that would benefit from further quantitative modeling is the results obtained with grouped sequences in Experiment 3. A puzzling feature of those data is that whilst grouping did not affect the probability of interpositions, it nevertheless affected their recall latencies—there was a speed up in the recall times of -3 displacements and a slow down in the recall times of +3 displacements. On the one hand, the lack of an effect of grouping on response probabilities is seemingly at variance with the standard approach to modeling grouping effects, whereby position markers representing the position of groups in sequence are combined with position markers representing the position of items within groups. These results might be consistent instead with an alternative approach advanced by Hurlstone and Hitch (2015) to explain grouping effects in spatial STM, whereby position markers representing the position of groups in the sequence are combined with position markers representing the position of items in the sequence as a whole, rather than within groups. On the other hand, however, the effects of grouping on the recall times of interpositions are most consistent with the former model. Thus, there is some uncertainty regarding how positional information is represented in grouped visual sequences, and this is therefore a situation in which model comparisons might help to adjudicate between the two competing approaches.

Accordingly, we fitted two versions of the positional models to the grouped data of Experiment 3, one in which position was coded via markers representing the position of groups and items within groups, and one in which position was coded via markers representing the position of groups and items within sequence. This yielded a total of eight models for comparison—two versions of each of the models incorporating position marking (viz. PM, PM + RS, PM + OI, and PG + PM + RS; see Appendix B for precise details of how the models were extended to grouped sequences). To distinguish between the two sets of models, we use the super-scripts pwg (denoting position within group) and pws (denoting position within sequence). For example, the acronym $PM^{pwg} + RS$, refers to the version of the PM + RS model using position within-group markers, whereas the acronym $PM^{pws} + RS$ refers to the version of the PM + RS model using position within-sequence markers.

To summarize, the aims of the modeling were: (1) to verify that models other than the PG + PM + RS model cannot account for the shape of the LDF for ungrouped sequences, and (2) to shine further light on the nature of the positional representations underlying grouped visual serial recall. To fit the target data

(viz. accuracy and latency serial position curves, transposition gradients, and LDF), a polytope optimization algorithm was used to find the best-fit parameters for each individual participant for each sequence length condition of Experiment 2 and the grouped condition of Experiment 3. A maximum likelihood objective was employed and the goodness of fits of the models were compared using Akaike Information Criterion (AIC; Akaike, 1973) and Bayesian Information Criterion (BIC; Schwarz, 1978) scores, which were converted into AIC and BIC weights (Burnham & Anderson, 2002; Wagenmakers & Farrell, 2004) to facilitate identification of the best model (see Appendix C for precise details of the model fitting procedure).

Model Selection

Ungrouped sequences. Starting with the results for ungrouped sequences, the best fitting model parameters and associated goodness of fit statistics can be inspected in Tables 2 and 3, respectively. It can be seen from inspection of the latter table that the AIC weights were largest for the PG + PM + RS model for all three conditions: $w_{AIC} = 0.84, 0.76,$ and 0.71 for four-, five-, and six-item sequences, respectively. These weights were significantly larger than expected by chance—viz. $1/N = 0.2$; where $N = 5$ is the number of models under comparison—as evaluated using one sample t-tests ($t(25) > 7, p < .001, r > .82$ for all conditions) and distinctly greater than the weights of the other four models. The next largest weights were obtained by the PG + RS model, followed by the PM + OI, PM, and PM + RS models.

The results were largely the same using the more conservative BIC, with the PG + PM + RS model once again receiving the largest weights by far for all three conditions: $w_{BIC} = 0.74, 0.66,$ and $0.63,$ for four-, five-, and six-items, respectively. One sample t-tests confirmed, once more, that these weights were significantly larger than expected by chance ($t(25) > 5, p < .001, r > .75$ for all conditions). The PG + RS model obtained the next largest weights, but in departure from the results with AIC, the PM model had larger weights than the PM + OI model. This is because the BIC imposes a more stringent penalty for model complexity than the AIC. Finally, consistent with the results for AIC, the PM + RS model had the smallest weights. In brief, the model comparisons based on AIC and BIC provide strong and unambiguous evidence in favor of the PG + PM + RS model.

Another noteworthy feature of the AIC and BIC model comparisons is that the two models incorporating a primacy gradient had much larger weights than the three models that did not. Using the

AIC and BIC weights, it is possible to calculate how much more likely it is that a model incorporating a primacy gradient is to have produced the data than a model not incorporating a primacy gradient (viz. PG + RS & PG + PM + RS vs. PM, PM + RS, & PM + OI). The rows labelled PG vs. No-PG in Table 3 show these model likelihoods for w AIC and w BIC for each condition. Averaging over conditions, a model incorporating a primacy gradient is 11 times for likely to have produced the data than a model not incorporating a primacy gradient according to AIC, and 6 times more likely according to BIC. These results identify the primacy gradient as a crucial ingredient in any model of serial order in visual STM.

Grouped sequences. Turning to the results for grouped sequences, Tables 4 and 5 show, respectively, the best fitting model parameters and associated goodness of fit quantities for the eight models under comparison. It is apparent from inspection of the latter table that the AIC weight was largest for the PG + PM^{pwg} + RS model (w AIC = .41), followed by the PG + PM^{pws} + RS model (w AIC = .32). The AIC weights for both models were significantly larger than expected by chance—viz. $1/N = 0.12$; where $N = 8$ —as evaluated using one sample t-tests ($t(20) = 4.37, p < .001, r = .70$, and $t(20) = 3.35, p < .01, r = .60$, respectively). The next largest AIC weight was obtained by the PM^{pwg} + OI model, followed by its counterpart the PM^{pws} + OI model. The PM^{pwg}, PM^{pwg}, and the PM^{pws} models had the next largest weights in that order, and finally the PM^{pws} + RS model obtained the smallest weight.

The results were similar using the more stringent BIC, with the PG + PM^{pwg} + RS model once again achieving the largest weight (w BIC = .33), followed by the PG + PM^{pws} + RS model (w BIC = .26). One-sample t-tests on the BIC weights for the two models confirmed that they were significantly larger than expected by chance ($t(20) = 3.28, p < .01, r = .59$, and $t(20) = 2.45, p < .05, r = .48$, respectively). The PM^{pwg} + OI model obtained the next largest BIC weight, but in departure from the results with AIC, the PM^{pwg} model obtained a larger weight than the PM^{pws} + OI model, and the PM^{pws} model obtained a larger weight than the PM^{pwg} + RS model (once again, this is due to the more stringent penalty for model complexity imposed by the BIC). As for AIC, the PM^{pws} + RS model had the smallest model weight. In brief, the AIC and BIC model comparisons for grouped sequences reaffirm the superiority of the PG + PM + RS model. However, of the two models, the PG + PM^{pwg} + RS model had a slight edge over the PG + PM^{pws} + RS model.

Another aspect of the AIC and BIC model comparisons which merits comment is that the models incorporating position of group and position within-group markers (PM^{pwg}, PM^{pwg} + RS, PM^{pwg} + OI, PG

+ PM^{Pwg} + RS) consistently had larger weights than their counterparts incorporating position of group and position within-sequence markers (PM^{Pws} , PM^{Pws} + RS, PM^{Pws} + OI, PG + PM^{Pws} + RS). Indeed, a model based on position of group and position within-group markers was 1.32 times more likely to have generated the data than a model based on position of group and position within-sequence markers according to the AIC, and 1.35 times more likely according to the BIC (see the row labelled PWG vs. PWS in Table 4). Note, however, that these values are small and provide only weak evidence in favor of a model utilizing within-group positional codes.

Simulation Results

Ungrouped sequences. Figure 10 shows the accuracy serial position curves, transposition gradients, and latency serial position curves predicted by the models under their best-fitting parameters (the first, second, and third row of panels show the results for four-, five-, and six-item sequences, respectively). Figures 10A, D, and G show the predicted accuracy serial position curves from which it can be seen that all models generated the effects of primacy, recency, and sequence length observed empirically (Figure 7A). Similarly, the transposition gradients predicted by the models in Figures 10B, E, and H mirror the empirical data in Figure 7B in exhibiting a sharp peak at displacement 0, approximately symmetrical error gradients for anticipations and postponements, and a locality constraint on movement errors. Figures 10C, F, and I show the predicted latency serial position curves. To accommodate preparatory processes that precede the production of the first response, a 3000-ms constant has been added to the recall time for the first output position for each model to increase graphical correspondence between the model predictions and the data illustrated in Figure 7C.¹ It is apparent from inspection of the predicted latency curves that all models captured the speeding up of recall over serial positions seen in the data. In summary, notwithstanding some minor differences between models, their predictions are qualitatively similar, rendering it difficult to adjudicate between them on the basis of these three recall measures.

¹These preparatory processes that precede the production of the sequence (and groups in grouped sequences) have variously been attributed to the priming of a low-level motor output buffer (Sternberg, Monsell, Knoll, Wright, 1978) or memory search through a hierarchical representation of the order of elements in a sequence (Anderson & Matessa, 1997; Farrell, 2012; Farrell & Lelièvre, 2012). We do not model these processes here because they do not assist in discriminating between the models—since the effects of output position on recall times are removed from the model LDFs—and because additional ancillary assumptions are necessary to accommodate them.

Turning to the simulations results of chief interest, Figure 11 shows the LDFs predicted by the models under their best-fitting parameters for sequences of four- (panel A), five- (panel B), and six-items (panel C). The model LDFs for each sequence length do not differ qualitatively from the initial predictions in Figure 3. As before, the PM model predicts V-shaped LDFs, whereas the PM + RS and PM + OI models predict partially asymmetric V-shaped LDFs in which the slope for postponements is shallower than for anticipations. The error latency predictions of these models are clearly at variance with the empirical data shown in Figure 6B. In contrast to these models, the PG + RS model predicts a monotonically negative LDF. The predictions of this model are a much better approximation of the empirical pattern shown in Figure 6B. However, the PG + RS model predicts a negative LDF slope for postponements across all sequence lengths, which is still at variance with the approximately flat postponement slopes observed empirically. Like the PG + RS model, the PG + PM + RS model predicts a monotonically negative LDF, however, consistent with the empirical data the slope of the displacement function for postponements is approximately flat.

Grouped sequences. Turning to the predictions for grouped sequences, Figure 12 shows the accuracy serial position curves, transposition gradients, and latency serial position curves for the models pairing position of group with position within-group markers (upper panels), and the models pairing position of group with position within-sequence markers (lower panels). Looking at the accuracy serial position curves, it can be seen that the former models all predict within-group primacy and recency effects (Figure 12A), consistent with the empirical data (Figure 8A), whereas the latter models struggled to reproduce these mini primacy and recency effects (Figure 12C). The models combining position of group with position within-sequence markers did, however, predict monotonically decreasing transposition gradients (Figure 12E) in accordance with the data (Figure 8B), whereas the models combining position of group with position within-group markers all predicted non-monotonic transposition gradients characterized by localized peaks at ± 3 displacements. Thus, the latter models all predicted an increase in the frequency of interpositions that was not witnessed empirically (Figure 8B). The latency serial position curves for the models coupling position of group with position within-group markers can be scrutinized in Figure 12C, whereas the corresponding curves for the models coupling position of group with position within-sequence markers can be interrogated in Figure 12F. As for the predictions for ungrouped sequences, a 3000-ms constant has been added to the recall times for the first output position but, in

addition, a 500-ms constant has also been added to the recall times for the fourth output position to once more increase graphical correspondence between the model predictions and the data in Figure 8C.

Notwithstanding these augmentations to the model predictions, it is visible from inspection of Figure 12C and Figure 12E that the latency curves predicted by both sets of models bear a close resemblance to the empirical data. In brief, as per the predictions for ungrouped sequences, it is difficult to adjudicate between the four models on the basis of these conventional serial recall measures. However, the models integrating position of group with position within-group markers had the edge over the models integrating position of group with position within-sequence markers. Although the former models predicted an increase in the frequency of interpositions—which is incompatible with the data—only these models were able to reproduce the effects of grouping on the accuracy serial position curve.

Considering now the error latencies for transpositions, the predicted LDFs for the models pairing position of group with position within-group markers can be inspected in Figure 13A, whereas the predicted LDFs for the models pairing position of group with position within-sequence markers can be inspected in Figure 13B. Irrespective of the nature of the positional representations employed, the overall shape of the LDFs predicted by the four models is similar to their corresponding predictions for ungrouped sequences—the PM^{pwg} and PM^{pws} models predict symmetric V-shaped LDFs; the $PM^{pwg} + RS$ and $PM^{pws} + RS$ models predict partially asymmetric V-shaped LDFs, as do the $PM^{pwg} + OI$ and $PM^{pws} + OI$ models; whereas the $PG + PM^{pwg} + RS$ and $PG + PM^{pws} + RS$ models predict asymmetric LDFs characterized by an overall negative latency-displacement relationship, but with a flattening of the slope for postponements. The key difference between the two sets of models is that the models combining position of group with position within-group markers predict a speed-up in the recall times for ± 3 displacements, whereas the models combining position of group with position within-sequence markers do not predict such discontinuities. Looking at the data in Figure 6C, it is apparent that the $PG + PM^{pwg} + RS$ and $PG + PM^{pws} + RS$ models provide the best account of the empirically observed LDF. However, of the two models, the $PG + PM^{pwg} + RS$ model arguably provides the better account, since it captures the speed-up in the recall time for -3 displacements; it did not, however, capture the slow down in recall times for +3 displacements, predicting instead a speed-up in the recall time for these errors. The $PG + PM^{pws} + RS$ model failed to capture either of these subtleties of the LDF for grouped sequences.

General Discussion

The results of the experiments and quantitative modeling suggest that the serial recall of a sequence of visual items is driven by a competitive queuing mechanism, within which serial order is represented via a primacy gradient of activations over items, associations between items and position markers, and with suppression of items once they have been recalled. Across manipulations of sequence length, articulatory suppression, and temporal grouping the LDFs observed in the three experiments were consistently negative overall but with a reduction in slope for postponements compared to anticipations. This empirical pattern was a robust feature of the aggregate LDFs as well as the individual participant LDFs from which they were derived, thus confirming that the three representational principles are core ingredients in any adequate model of serial order in visual STM. None of the four alternative mechanisms for the representation of serial order were able to reproduce the shape of the observed LDFs, even when model parameters were free to vary across individual participants for ungrouped sequences of varying length, and for grouped sequences. In previous work (Hurlstone & Hitch, 2015), we have also shown that a representational mechanism embodying a primacy gradient, position marking, and response suppression is the only one of the five mechanisms considered that consistently predicts the observed latency-displacement relationship across broad variations of its parameters. The data and modeling are consistent with those reported by Farrell and Lewandowsky (2004) and Hurlstone and Hitch (2015) with sequences of verbal and spatial items, respectively, and give general support for the notion that common mechanisms and principles are implicated in the representation of serial order across the verbal, visual, and spatial STM domains.

The pivotal role of a primacy gradient and response suppression

If there are two representational principles that the empirical LDFs speak to the most, it is a primacy gradient coupled with response suppression. Across the three experiments, the observed LDFs were consistently negative overall, such that the recall times for items reported too soon were markedly slower than for items reported too late. The theoretical LDF analyses clearly show that only the models incorporating a primacy gradient with response suppression—viz. PG + RS; PG + PM + RS—predict this asymmetry in the recall times of anticipations and postponements. Indeed, the same analyses show that the positional models consistently predict a symmetric or partially symmetric V-shaped LDF, thus ruling out a representational mechanism based on position marking alone. Qualified support for the role of a primacy

gradient was provided by the results of the AIC and BIC model comparisons for ungrouped sequences, which revealed that a model incorporating a primacy gradient was 11 times more likely to have produced the data than a model not incorporating a primacy gradient according to AIC, and 6 times more likely according to the more conservative BIC. This amounts to fairly strong evidence in support of a role for the simple gradient based representation of serial order in visual STM.

Nevertheless, whilst a primacy gradient and response suppression are necessary to explain the finding that anticipations are slower than postponements, it is apparent that a representational mechanism based on a primacy gradient and response suppression is not sufficient to fully account for the shape of the observed LDF. Specifically, it is necessary to augment the basic primacy gradient and response suppression mechanism with a set of position markers in order to reproduce the observed flattening of the LDF slope for postponements. Converging evidence for the operation of position marking was also provided by the results of the temporal grouping manipulation, which we consider next.

Converging evidence for positional representations

Converging evidence for the operation of position marking in visual STM was provided by the results of the temporal grouping manipulation employed in Experiment 3. Consistent with previous studies of grouped verbal (Farrell & Lewandowsky, 2004; Frankish, 1985, 1989; Hitch et al., 1996; Maybery et al., 2002; Ryan, 1969) and spatial serial recall (Hurlstone & Hitch, 2015; Parmentier et al., 2006), grouping a sequence of visual items induced a number of qualitative changes in performance including effects of primacy and recency within groups; longer recall latencies at the beginning of groups; and a reduction in adjacent-neighbor transpositions straddling group boundaries. However, the effects of grouping were smaller in magnitude than those observed with verbal and spatial stimuli—we did not observe a reliable main effect of the grouping manipulation on performance. One possible reason for this is that there is no output mechanism by which visual non-spatial stimuli can be rehearsed, whereas verbal stimuli can be rehearsed sub-vocally (Baddeley, 1986) and spatial stimuli can be rehearsed via covert shifts of spatial selection attention (Awh & Jonides, 2001) or eye-movements (Postle, Idzikowski, Della Sala, Logies, & Baddeley, 2006). That output processes contribute to the magnitude of grouping effects is supported by the finding that grouping effects with visually—but not auditorily—presented verbal stimuli increase in size as the length of the inter-group pause (and the opportunity for rehearsal) increases (Frankish, 1985), and by

the finding that grouping effects are eliminated—or nearly so—under conditions of concurrent articulatory suppression (Hitch et al., 2006).

There is one hallmark feature of grouped verbal serial recall that did not materialize with grouped visual serial recall, however; this is the increase in the frequency of interpositions—transpositions between groups maintaining their within-group serial position. The same discrepancy was also noted in our earlier work exploring effects of grouping on the serial recall of spatial sequences (Hurlstone & Hitch, 2015; see also Parmentier et al., 2006). We have previously speculated that this discrepancy might be attributable to a subtle difference in the way positional information is represented in grouped verbal and nonverbal sequences. Specifically, we postulated that position in grouped nonverbal sequences might be represented via markers coding the position of groups and the position of items within the sequence as a whole, rather than the standard approach to modeling grouping effects in the verbal domain, whereby markers coding the position of groups in the sequence are combined with markers coding position of items within groups. However, we did not provide a formal test of this hypothesis, whereas one of the aims of the quantitative modeling reported here was to pit our alternative representational scheme against the standard approach to modeling grouping effects.

The results of the model fitting of grouped sequences call into question our alternative representational scheme—at least as applied to the current data. Neither of the models implementing this approach provided a satisfactory account of the observed effects of grouping. In particular, although the models predicted some within-group serial position effects on accuracy, they were not as marked as witnessed empirically (the models combining position of group with position within-group markers fared much better, although they still generally under-predicted the magnitude of within-group primacy and recency effects). Empirically such effects arise due to improved encoding of within-group serial position, as evidenced by a reduction in transpositions between groups in grouped sequences, compared to ungrouped sequences. Under the standard approach to modeling grouping effects, the improved encoding of within-group serial position arises from two sources—both the position of group and the position within-group markers help to reduce uncertainty about an items within-group position. By contrast, under our revised approach to modeling grouping effects, the improved encoding of within-group serial position arises from a single source—the position of group markers. It follows that our revised scheme has less positional resolution than the standard approach, and it appears to be for this reason that it struggles to

accommodate within-group serial position effects.

Although the results of the model comparisons cast doubt on our alternative perspective, they do not support the standard approach either. This is because the models combining position of group with position within-group markers predicted an increase in interpositions (i.e., errors at transposition displacements -3 and +3) that was not observed empirically. Nevertheless, the models also predicted shorter recall times for these errors on the LDF, which is partially consistent with the data. Notably, reduced response latencies were observed for -3 displacements but not for +3 displacements; on the contrary, we actually observed increased response latencies to these errors. The partial mismatch between models and data regarding the effects of grouping on interposition latencies raises the question of whether the effects in the data are merely coincidental or whether they constitute evidence for the operation of within-group positional codes? In our previous work (Hurlstone Hitch, 2015) and that of Farrell and Lewandowsky (2004), discontinuities in the LDF were also observed under conditions of temporal grouping. Although these discontinuities occasionally manifested at locations corresponding to interpositions, most of the time they did not. Moreover, as we have observed here, the direction of the effects was inconsistent, such that sometimes shorter recall latencies were observed—characterized by local troughs in the LDF—whereas sometimes longer recall latencies were observed—characterized by local peaks (by comparison, the models considered here can only produce troughs—but not peaks—in the LDF). This leads us to a second related point, namely that the discontinuities observed here and in the work just alluded to arose independently of any increase or decrease in the probability of the specific errors. By contrast, in the models any change in the recall time of an error must necessarily be accompanied by a corresponding change in that error's probability. These considerations lead us to suspect that the discontinuities in the LDF are coincidental rather than emblematic of the operation of within-group positional codes. They might, for example, be symptomatic of increased motor response variance induced by the grouping manipulation.

That the effects of grouping reported here cannot be reconciled with either of the two approaches considered raises the question of how best to explain those results? One possibility is that the data may be explicable in terms of a more complex model in which positional information is coded along three rather than two dimensions—viz. a model incorporating group-position-in-sequence, item-position-within-group, and item-position-within-sequence position markers. This might represent a general approach to representing positional information in STM, and what might vary across the verbal, visual, and spatial

domains is the relative weight attached to the position within-group and position within-sequence markers. In an extra set of simulations (not reported for brevity), we applied versions of the four positional models built on this assumption to the grouped condition of Experiment 3. We found that whilst these models fared better against the data than the models pairing position of group with position within-group markers, once the models were penalized for their additional model complexity—viz. via AIC and BIC—their advantage was neutralized. Moreover, at variance with the data, the models continued to predict interpositions.

A more radical but nevertheless plausible interpretation of the results of Experiment 3 is that rather than reflecting the action of a multidimensional representation of serial order based on positional information, they simply reflect the action of a selective encoding strategy adopted by participants. To explain, it may be that the localized recall advantage witnessed for items at group boundaries arose because participants paid extra attention to these items during the encoding of the sequence. The effects of grouping on the latency serial position curve are more difficult to explain on this interpretation, but one possible account is that in this instance the additional pause left before accessing the second group is reflective of a pattern matching heuristic—viz. a temporal gap at input affords a temporal gap at output—rather than the consequence of some underlying multidimensional or hierarchical representation of the sequence. Thus, although the effects of grouping observed with visual stimuli may look like those observed with verbal and spatial stimuli, this may merely be coincidental, and they may in fact reflect fundamentally different processes altogether.

In brief, it is unclear how precisely the coding of positional information in grouped visual sequences differs from grouped verbal sequences. We have formally tested two alternative approaches to positional coding and found both to be lacking. Unfortunately, this is a question to which we are currently unable to provide a clear answer, and further work will be required to test alternative hypotheses. Before closing this section, we note briefly that caution should be exercised in generalizing the results of the modeling of grouped sequences to the nonverbal domain more generally. It does not follow, for example, that just because the position of group and position within-sequence coding scheme was ineffective in explaining grouped visual recall that it would be similarly ineffective in explaining grouped spatial serial recall. Indeed, in other as yet unpublished work (Hurlstone & Hitch, 2016), we find that such a scheme provides a plausible account of the effects of grouping with spatial sequences.

Implications for Theories of Working Memory

We next consider the broader implications of our results for theories of working memory. To frame our discussion, we begin with a reprisal of the conclusions drawn in our previous work (Hurlstone and Hitch, 2015) where—based on a similar chronometric analysis of order errors in spatial serial recall—we provided evidence for the operation of a primacy gradient, position marking, and response suppression in spatial STM. This work itself, replicated and extended the earlier work of Farrell and Lewandowsky (Farrell & Lewandowsky, 2004; Lewandowsky & Farrell, 2008) who examined the dynamics of transpositions in verbal serial recall and also found empirical support for a representational mechanism embodying these three principles.

Hurlstone and Hitch (2015) asked how the competitive queuing mechanism and the three principles for representing serial order map onto the different components of the working memory model of Baddeley and Hitch (Baddeley, 1986, 2000, 2007; Baddeley & Hitch, 1974). They presented arguments and evidence in favor of the view that the competitive queuing mechanism, along with the primacy gradient and response suppression are implemented in a modality-specific manner within the working memory slave systems; that is, the phonological loop and the spatial component of the visuospatial sketchpad—viz. the “inner scribe” (Logie, 1995)—each possess their own competitive queuing sequence planning and control mechanisms and processes for generating a primacy gradient and implementing response suppression (see Hurlstone and Hitch, 2015 for a discussion of the theoretical basis for these claims). However, in common with other serial recall theorists (Burgess & Hitch, 1999; Henson 1998; Smyth, Hay, Hitch, & Horton, 2005; Tremblay, Guérard, Parmentier, Nicholls, & Jones, 2006), they noted the possibility that positional information in the verbal and nonverbal domains might be encoded via a common domain-general mechanism. For example, Burgess and Hitch (1999) postulated that the positional context signal in their network model of the phonological loop might also be responsible for coding the position of nonverbal items. In later work (Burgess & Hitch, 2005), the same authors postulated that the locus of their context signal within the working memory framework might be the episodic buffer (Baddeley, 2000)—a component of the working memory model responsible for integrating information from the working memory slave systems and long-term memory—and that the buffer might serve as a common positional coding mechanism for items maintained in the phonological loop and the visuospatial sketchpad.

The present results build on this analysis in two ways. First, they suggest that the competitive

queuing mechanism, primacy gradient, and response suppression are also key properties of the visual component of the visuospatial sketchpad—viz. the “visual cache” (Logie, 1995). Second, by showing—as Hurlstone and Hitch (2015) did with spatial sequences—that temporal grouping exerts effects on the recall of visual sequences that are similar and dissimilar to those documented with verbal sequences, the present results place further constraints on the debate regarding the domain-general or domain-specific nature of positional coding in STM. In particular, the difference in the effects of grouping across domains—viz. the presence of interpositions in the verbal domain, but not the visual and spatial domains—seems to cast doubt on the hypothesis that a shared mechanism—perhaps mediated by the episodic buffer—is responsible for coding positional information in the two working memory sub-systems. Instead, this discrepancy seems to point to the existence of distinct positional coding mechanisms that function in a similar manner, but possess subtly different representational characteristics.

Is the notion of distinct mechanisms for representing positional information tied to different content domains controversial? We believe not. Indeed, developments in this direction are already taking place. As a case in point, recently Hartley et al. (2016) have presented a model of auditory-verbal STM for serial order that relies on a context-driven timing signal to represent the serial position of items. The timing signal is based on a population of oscillators—i.e., frequency sensitive detectors—sensitive to local changes in the amplitude envelope of incoming speech. As such, the mechanism is tailored specifically for the spoken modality. Hartley et al. (2016) show that this mechanism provides an impressive account of a data pattern currently believed to be unique to auditory-verbal STM, whereby the product of the group sizes of different temporal grouping patterns—an empirical yardstick for their degree of regularity or rhythm—is a potent predictor of recall performance on those different grouping patterns.

Conclusions

To conclude, across three experiments exploring the dynamics of transpositions in a visual serial recall task we observed a consistent pattern whereby anticipation errors are slower than postponements. Additionally, whereas the latencies of anticipations increase with displacement distance, the latencies of postponements are relatively insensitive to degree of displacement. This error latency profile is consistent with that observed in previous studies of serial recall with verbal (Farrell & Lewandowsky, 2004) and spatial (Hurlstone & Hitch, 2015) sequences, and supports the prediction of a competitive queuing

mechanism within which serial order is represented via a mechanism embodying a primacy gradient, position marking and response suppression. Taken together, these results suggest that the same mechanism is implicated in the representation of serial order across the verbal, visual, and spatial STM domains. However, the same results also point to differences across domains in the manner in which positional information is represented in grouped sequences. A challenge for future research is to elucidate how precisely the coding of positional information differs across the verbal, visual, and spatial domains, and whether the similarities and differences are best understood in terms of a domain-general mechanism or domain-specific mechanisms specialized for different content domains.

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Appendix A: Formal Description of The Generic Network Architecture Used To Model Transposition Latencies

Following Farrell and Lewandowsky (Farrell & Lewandowsky, 2004; Lewandowsky & Farrell, 2008) and our own earlier modelling (Hurlstone & Hitch, 2015), we did not utilize a fully implemented competitive queuing architecture for our simulations, but instead employed a single layer *lateral inhibition* network corresponding to the competitive choice layer in competitive queuing models. For each of the representational principles being modeled, we specified the profile of activations that would be expected initially at each output position in the parallel planning layer, before feeding that pattern of activations into the lateral inhibition network in order to generate an unambiguous response and an associated recall latency. Thus, we did not simulate the process of encoding serial order, since the selection mechanism is insensitive to the exact mechanisms generating the initial activations used to drive recall.

A common lateral inhibition response selection network

A schematic of the response selection network employed for the simulations is illustrated in Figure 14. It consists of a single competitive layer of localist item nodes corresponding to the pool of response elements from which sequences can be generated. Each node has a recurrent self-excitatory connection, plus lateral inhibitory connections to all other nodes. The excitatory and inhibitory weights are a hardwired property of the network and were set to constant values of 1.1 and -0.1, respectively. This network operates as a competitive filter that selects a single response from amongst a set of parallel activated representations. As noted above, serial order is represented in the network by setting starting activation values for the item nodes at each output position, the derivation of which is determined by the representational principles being modeled (see below). The activation of each node is determined by this initial external input, plus recurrent self-excitation, and lateral inhibition received from all other item nodes, which are jointly determined by the following equation:

$$\text{net}_j(t) = a_j(t-1)\alpha + \beta \sum_{i \neq j} a_i(t-1) + \varepsilon(0, \sigma), \quad (\text{A1})$$

Where net_j is the netinput a unit receives from within the layer, a_j represents the initial activation of unit j determined by its external input, a_i constitutes the activation of all other nodes in the layer, α and β represent the excitatory and inhibitory weight values, respectively, t corresponds to time, and ε is zero

mean Gaussian noise with standard deviation σ ($\sigma = .04$ for the initial simulations). (Note that negative activations are not allowed to spread in equation A1 otherwise a node with negative activation would excite rather than inhibit its competitors). The first term on the right hand side of equation A1 represents the recurrent self excitation, whereas the second term represents the lateral inhibition received from all other nodes in the layer. This sets up a *winner-takes-all* response competition over the item nodes, and the initially most active node—the node receiving the highest external activation—has the advantage that it will send more activation to itself than any other node and will also receive the least lateral inhibition. The node activations are iteratively updated over time using equation 1. This results in a gradual increase in the activation of the strongest node and a gradual decrease in the activations of the weaker nodes as they receive more lateral inhibition. The iterations stop when the strongest node exceeds a response threshold T (set to 1.0 for all simulations) and the number of iterations required to determine the response is taken as the network's recall latency. This process is repeated at each successive output position by defining a new set of starting activations and allowing activations to iterate towards a response. In order to bring the predicted recall times of the network within the range of the observed latencies in the experiments they were multiplied by a scaling factor S ($0 < S \leq 200$; where $S = 50$ for the initial simulations—1 iterative cycle = 50 ms).

Implementation of representational principles

The representational principles were implemented through different settings of the starting activations at each output position, which were computed as follows:

Position marking. Position marking was implemented by specifying activations for item nodes that reflected the distances between item positions. Specifically, the activation a of the item node j for the current response (output) r position was strongest, whilst the activations of item nodes from neighbouring serial positions decreased as an accelerating function of their distance from the target item:

$$a_j = \Omega \theta^{|j-r|}, \quad (\text{A2})$$

Where θ is a parameter controlling the distinctiveness of the position marking activations ($0 < \theta \leq 1$; $\theta = .65$ for the initial simulations) and Ω is a weighting parameter that determines the distance of each item's initial activation from the response threshold ($0 < \Omega \leq 1$; $\Omega = 1$ for the initial simulations). For each

output position, the activations generated by θ were rescaled to sum to 1—calculated by dividing each node’s activation by the sum of the activations of all nodes—before they were multiplied by Ω . This representational scheme produces gradients of activations akin to those generated by the positional context signals in the Burgess and Hitch (1999) and OSCAR (Brown et al., 2000) models. Figure 15A shows example starting activations for position marking for the fourth output position in a six-item sequence

Primacy gradient. The primacy gradient was implemented as a decrease in activations across input positions. The activation of each node was determined by:

$$a_j = \phi \rho^{(j-1)}, \quad (\text{A3})$$

Where ϕ is the activation of the item node corresponding to the first input position ($0 < \phi \leq 1$; $\phi = .6$ for the initial simulations) and ρ is a parameter controlling the steepness of the primacy gradient ($0 < \rho \leq 1$; $\rho = .85$ for the initial simulations). Retrieval commenced by imposing the entire primacy gradient over the item nodes at the first output position and allowing activation to accumulate towards a response. This process was then repeated for each subsequent output position by imposing the same primacy gradient over the item nodes but with suppression (see below) of those nodes corresponding to previously recalled items. Example starting activations for a primacy gradient for the first output position are shown in Figure 15B.

Primacy gradient + position marking. In line with the seriating mechanisms instantiated in several theories of serial recall (Burgess & Hitch, 1999; Brown et al., 2000; Lewandowsky & Farrell, 2008), in some simulations serial order was represented through the combination of a primacy gradient and position marking by calculating starting activations as follows:

$$a_j = (1 - \omega) \phi \rho^{(j-1)} + \omega \Omega \theta^{(|j-r|)}, \quad (\text{A4})$$

Equation A4 integrates equations A2 and A3 above and incorporates an additional weighting parameter ω ($0 < \omega \leq 1$; $\omega = .5$ for the initial simulations) that governs the relative importance of the two representations of serial order. When $\omega = .5$ the two representations of order are weighted equally. However, when $\omega < .5$ more weight is given to the primacy gradient representation of order; conversely, when $\omega > .5$ more weight is given to the positional representation of order. Figure 15C shows example starting activations for the combination of a primacy gradient and position marking for the fourth output position.

Response suppression. Response suppression was implemented by reducing an item's activation once it had been recalled. For each output position, starting activation values were first calculated based on the other representational principles being modeled. The activations of nodes corresponding to items that had already been recalled were then multiplied by $1-\tau$, where τ represents the extent of response suppression ($0 < \tau \leq 1$; $\tau = .95$ for the initial simulations). Example starting activations for a primacy gradient complemented by response suppression for the fourth output position are illustrated in Figure 15D.

Output interference. Output interference was modeled by assuming that recall of an item added noise to the activations of yet to be recalled items. Accordingly, random Gaussian noise with a standard deviation that increased as a function of output position was applied to the starting activations generated by the serial ordering principles being modeled (e.g., position marking) and was determined by $\delta \times \sigma \times r$, where δ is a parameter controlling the weighting of output interference across output positions ($0 < \delta \leq 1$; $\delta = .5$ for the initial simulations) and σ is the standard deviation of noise applied to activations during the iterative updating process (see earlier). An example of the increase in the standard deviation of Gaussian noise applied to the starting activations across output positions is shown in Figure 15E.

Five models of serial order

The response probability and recall latency predictions of five models of serial order—built from different combinations of the four principles—were compared: (1) position marking (PM); (2) position marking and response suppression (PM + RS); (3) position marking and output interference (PM + OI); (4) a primacy gradient and response suppression (PG + RS); and (5) a primacy gradient, position marking, and response suppression (PG + PM + RS). These are the same set of models as those examined by Farrell and Lewandowsky (Farrell & Lewandowsky, 2004; Lewandowsky & Farrell, 2008) and Hurlstone and Hitch (2015), and they are representative of the range of mechanisms instantiated in contemporary theories of serial recall (see Table 1 of Hurlstone & Hitch, 2015 and Table 2 of Hurlstone et al., 2014). Predictions were generated for each model using 50,000 simulation trials of six-item sequences.

Appendix B: Extension to grouped sequences

In this section, we describe how the positional models—viz. PM, PM + RS, PM + OI, PG + PM + RS—can be extended to account for the recall of grouped sequences. As noted in the main text, positional models of serial recall account for grouping effects by assuming that grouped sequences recruit two sets of position markers—one set that encodes the position of groups in the sequence, and a second set that encodes the position of items within groups. This multidimensional representation has been shown to be sufficient to account for the effects of grouping documented with verbal materials. In particular, the use of a set of position markers to represent the within-group position of items is crucial to explaining the between group interposition errors that are a hallmark feature of grouped verbal serial recall.

However, the failure to observe an increase in the frequency of interpositions in grouped visual (current Experiment 3) and spatial (Hurlstone & Hitch, 2015) serial recall raises the possibility that positional information might be represented differently in the visual and spatial domains. Specifically, Hurlstone and Hitch (2015) speculated that in the visual-spatial domain, position markers encoding the position of groups in sequence might be augmented by position markers encoding the position of items in the sequence overall, as opposed to within each group. This should in principle produce the usual effects of grouping on response probabilities, but without fostering an increase in the frequency of interpositions.

To provide a formal test of this hypothesis, we contrasted two approaches to extending the positional models to grouped sequences, one in which position makers encoding the position of groups in sequence were combined with position markers encoding the position of items within groups—viz. the standard approach to modelling grouping effects—and a second in which position makers encoding the position of groups in sequence were combined with position markers encoding the position of items in the sequence overall—viz. the revised approach proposed by Hurlstone and Hitch (2015).

In the following, we outline the equations used to calculate the starting activations for position marking for grouped sequences under the two different approaches to implementing grouped positional representations. When applying the PM, PM + RS, PM + OI, and PG + PM + RS models to grouped sequences, these equations were used in substitute for equation A2.

Position of group + position within group

In the implementation of position marking combining information about the position of groups and the position of items within groups, starting activations were chosen that directly reflected the confusability of group positions in the sequence and item positions within groups:

$$a_j = (1 - \lambda)\Omega\theta^{(g-l)} + \lambda\Omega\theta^{(i-p)}, \quad (\text{B1})$$

Where j indexes an item's input position, g indexes its group's input position, l represents the input position of the group of the target item to-be-recalled at the current response position, i indexes the within-group input position of item j , and p represents the within-group input position of the target item to-be-recalled at the current response position. To illustrate, suppose we wish to calculate the activation of the second item at the sixth response position in a six-item sequence grouped into threes. In this example, $g = 1$ (since item 2 belongs to the first group), $l = 2$ (since the target item 6 belongs to the second group), $i = 2$ (since item 2 appears in the second position in the first group), whilst $p = 3$ (since item 6 appears in the third position in the second group).

As in equation A2, the parameter θ governs the distinctiveness of the position markers ($0 < \theta \leq 1$), whilst Ω is a scaling parameter ($0 < \Omega \leq 1$). The first term in equation B1 generates gradients of activations representing the confusability of the positions of groups in the sequence, whereas the second term generates gradients of activations representing the confusability of the positions of items within-groups. The parameter λ weights the amount of attention allocated to the two positional dimensions ($0 < \omega \leq 1$). When $\omega = .5$, attention is directed equally to the two dimensions; when $\omega < .5$, more attention is allocated to the group-position-in-sequence dimension of order; when $\omega > .5$, more attention is allocated to the item-position-in-group representation of order. Example starting activations based on equation B1 for all output positions in a six-item sequence grouped into threes are shown in Figure 16.

Position of group + position within sequence

In the implementation of position marking combining information about the positions of groups and the position of items within sequence, starting activations were chosen that directly reflected the confusability of group and item positions within sequence:

$$a_j = (1 - \lambda)\Omega\theta^{(lg-l)} + \lambda\Omega\theta^{(lj-r)}, \quad (\text{B2})$$

Where r represents the current response (output) position, and g , l , and j are as before. To illustrate, using the earlier example of calculating the activation of the second item at the sixth response position in a six-item sequence grouped into threes, $g = 1$ (since item 2 belongs to the first group), $l = 2$ (since the target item 6 belongs to the second group), $j = 2$ (since this is the item whose activation is being calculated), and $r = 6$ (since this is the current response position). The first term in equation ?? is the same as in equation B1 and generates gradients of activations representing the confusability of the positions of groups in the sequence. The second term generates gradients of activations representing the confusability of the position of items in the sequence, and is identical to equation A2 used to generate starting activations for position marking for ungrouped sequences. As in equation B1 the parameter λ weights the amount of attention allocated to the two positional dimensions. Figure 17 shows example starting activations based on equation B2.

Incorporating a primacy gradient

When position marking was combined with a primacy gradient—viz. the PG + PM + RS model—equations B1 and B2 were augmented as follows:

$$a_j = (1 - \omega)(\text{Eq. B1} \mid \text{Eq. B2}) + \omega\phi\rho^{(j-1)}, \quad (\text{B3})$$

Where Eq. B1 | Eq. B2 implements equation B1 or B2, $\phi\rho^{(j-1)}$ corresponds to equation A3 used to compute the primacy gradient over the input position of items, and ω is the same weighting parameter used in equation A4 to determine the attentional weight assigned to the primacy gradient and position markers.

Appendix C: Description of Parameter Fitting Procedure

The five models were fit jointly to the accuracy and latency serial position curves, transposition gradients, and LDFs (with the effect of output position removed) of individual participants using maximum likelihood parameter estimation (assuming normally distributed data with constant variance). The observed and predicted mean latencies for latency serial position curves and LDFs were divided by $10^{3.5}$ to bring the variability in recall latencies and response probabilities within a comparable range so that they received a similar weighting during the fitting process. The modeling procedure was the same as that employed for the initial simulations except that model parameter values were varied systematically using the SIMPLEX algorithm (Nelder & Mead, 1965) in order to maximize the log-likelihood:

$$\ln L = \frac{-n}{2} \ln \left(\frac{RSS}{n} \right), \quad (C1)$$

Where \ln is the natural logarithm, RSS is the Residual Sum of Squares, and n is the number of observations entering into the log-likelihood calculation (larger values of $\ln L$ indicate a better fit). Each parameter vector explored by the search algorithm involved 10,000 model simulation trials of the sequence length and grouping condition being simulated.

The parameters that were free to vary for the PM model were the weighting (Ω) and distinctiveness (θ) of the position markers. These free parameters were augmented by the amount of response suppression (τ) in the PM + RS model and the amount of output interference (δ) in the PM + OI model. The PG + RS model took as its free parameters the starting point (ϕ) and steepness (ρ) of the primacy gradient, and the degree of response suppression (τ). Finally, the free parameters for the PG + PM + RS model were the steepness of the primacy gradient (ρ), the distinctiveness of the position markers (θ), the weighting of the primacy gradient and position markers (ω), and the degree of response suppression (τ). The two remaining parameters of this model (viz. Ω and ϕ) were frozen to values of 1—which neutralizes any influence they might have—to minimize the number of to-be-estimated parameters. In addition to the above-mentioned parameters, the iteration-to-ms scaling parameter S was included as a free parameter in all models. In summary, the number of free parameters was three for the PM model, four for the PM + RS, PM + OI, and PG + RS models, and five for the PG + PM + RS model.

The models were initially fit to the data according to the procedure described above, which yielded

for each participant and each model, a set of best fitting parameter values and an associated maximum log-likelihood estimate. However, as the models differ in their number of free parameters, it is necessary to augment this goodness-of-fit metric with a penalty term that punishes excessive model complexity. Accordingly, in order to provide a measure of the descriptive accuracy of the models that takes into consideration differences in their degree of complexity, the log-likelihood estimates were converted into Akaike and Bayesian Information Criterion scores (AIC, Akaike, 1973; BIC, Schwartz, 1978, respectively). The AIC was calculated as:

$$AIC_i = -2 \ln L_i + 2V_i, \quad (C2)$$

Where V is the number of free parameters involved in maximizing $\ln L$ and i indexes the model for which AIC is being calculated (smaller values of AIC indicate a better fit). As can be seen from equation C2, the AIC rewards a model for its goodness-of-fit via its maximized log-likelihood and punishes it as a function of its number of free parameters. Similarly, the BIC was calculated as:

$$BIC_i = -2 \ln L_i + V_i \ln(n), \quad (C3)$$

Like the AIC, the BIC rewards a model for its goodness-of-fit via its maximized log-likelihood but punishes it as a function of the number of free parameters weighted by the number of observations entering into the log-likelihood calculation (smaller values of BIC indicate a better fit). Accordingly, the BIC offers a more stringent correction for model complexity.

To aid interpretation, the raw AIC and BIC scores were converted into so-called IC weights (Burnham & Anderson, 2002; Lewandowsky & Farrell, 2011; Wagenmakers & Farrell, 2004), which express the degree of support for each model on a continuous measure of evidence. The IC weight for model i was calculated by:

$$wIC_i = \frac{\exp(-0.5 \Delta IC_i)}{\sum_{k=1}^K \exp(-0.5 \Delta IC_k)}, \quad (C4)$$

Where ΔIC_i is the difference in IC between model i relative to the best model, and each ΔIC_k is the difference in IC between a specific model k in the candidate set K and the best model. These IC weights—normalized to sum to 1—represent the probability that each model is the best given the data and

the competitor models under comparison. The support for a model is considered equivocal if its IC weight does not exceed $1/N$ —where N is the number of models under comparison. Thus, with five models, the support for a particular model is considered equivocal if its IC weight does not exceed 0.2.

Table 1

Mean regression parameter estimates for the slopes of the latency-displacement functions for anticipations and postponements in Experiments 1, 2, and 3.

Experiment	Condition	Parameter	Estimate	SE	<i>t</i>	<i>p</i>	<i>r</i>
1	Four-items	Anticipation	-333.23	78.24	-4.26	.00	.65
		Postponement	50.54	15.29	3.31	.01	.55
	Five-items	Anticipation	-187.37	76.26	-2.46	.05	.44
		Postponement	33.84	11.37	2.98	.01	.51
	Six-items	Anticipation	-142.09	46.85	-3.03	.01	.52
		Postponement	34.85	13.38	2.60	.05	.46
2	Four-items	Anticipation	-345.21	78.43	-4.49	.00	.67
		Postponement	44.34	10.07	4.49	.00	.67
	Five-items	Anticipation	-293.45	157.27	-1.90	.06	.36
		Postponement	42.67	11.96	3.64	.01	.59
	Six-items	Anticipation	-263.85	104.18	-2.58	.05	.46
		Postponement	19.34	7.09	-2.78	.05	.49
3	Ungrouped	Anticipation	-222.34	82.32	-2.70	.01	.52
		Postponement	22.85	8.45	2.71	.01	.52
	Grouped	Anticipation	-204.88	63.00	-3.25	.00	.59
		Postponement	34.35	7.63	4.50	.00	.71

Table 2

Parameter estimates for the fits of the models to the different sequence length conditions of Experiment 2 averaged across participants.

Condition	Model	Ω	θ	ϕ	ρ	ω	τ	δ	S
Four-items	PM	0.55	0.70	-	-	-	-	-	43.71
	PM + RS	0.55	0.66	-	-	-	0.95	-	49.97
	PM + OI	0.55	0.64	-	-	-	-	0.56	50.21
	PG + RS	-	-	0.61	0.90	-	0.92	-	70.19
	PG + PM + RS	-	0.66	-	0.96	0.71	0.88	-	86.30
Five-items	PM	0.51	0.69	-	-	-	-	-	50.56
	PM + RS	0.56	0.67	-	-	-	0.96	-	54.05
	PM + OI	0.51	0.64	-	-	-	-	0.55	60.64
	PG + RS	-	-	0.55	0.91	-	0.93	-	66.71
	PG + PM + RS	-	0.66	-	0.96	0.73	0.90	-	81.01
Six-items	PM	0.49	0.70	-	-	-	-	-	53.81
	PM + RS	0.56	0.67	-	-	-	0.96	-	54.05
	PM + OI	0.47	0.66	-	-	-	-	0.57	63.42
	PG + RS	-	-	0.53	0.94	-	0.93	-	72.09
	PG + PM + RS	-	0.57	-	0.97	0.73	0.91	-	85.30

Note— Ω = weighting of position markers; θ = distinctiveness of position markers; ϕ = initial value of primacy gradient; ρ = steepness of primacy gradient; ω = weighting of primacy gradient and position markers; τ = degree of response suppression; δ = amount of output interference; S = iteration-to-ms scaling.

Table 3

AIC and BIC weights with associated goodness-of-fit quantities for the fits of the models to the different sequence length conditions of Experiment 2 averaged across participants.

Condition	Model	k	ln L	AIC	Δ AIC	wAIC	BIC	Δ BIC	wBIC
Four-items	PM	3	44.66	-83.32	12.83	0.0207	-78.74	9.87	0.0606
	PM + RS	4	45.94	-83.89	12.26	0.0147	-77.78	10.82	0.0210
	PM + OI	4	46.03	-84.05	12.09	0.0186	-77.95	10.66	0.0271
	PG + RS	4	48.76	-89.52	6.62	0.1089	-83.42	5.19	0.1561
	PG + PM + RS	5	53.02	-96.05	0.09	0.8371	-88.42	0.19	0.7353
	PG vs. No-PG						17.52		8.20
Five-items	PM	3	48.90	-91.80	10.83	0.0789	-87.22	8.22	0.1226
	PM + RS	4	49.21	-90.42	12.20	0.0131	-84.32	11.11	0.0170
	PM + OI	4	50.13	-92.26	10.36	0.0287	-86.15	9.28	0.0302
	PG + RS	4	52.10	-96.19	6.43	0.1185	-90.09	5.34	0.1670
	PG + PM + RS	5	56.03	-102.05	0.57	0.7609	-94.42	1.01	0.6631
	PG vs. No-PG						7.29		4.89
Six-items	PM	3	55.99	-105.98	13.66	0.0422	-101.40	11.10	0.0795
	PM + RS	4	49.21	-90.42	29.22	0.0048	-84.32	28.19	0.0068
	PM + OI	4	58.83	-109.65	9.99	0.0786	-103.54	8.96	0.0801
	PG + RS	4	59.97	-111.93	7.71	0.1692	-105.83	6.68	0.2076
	PG + PM + RS	5	64.44	-118.87	0.77	0.7052	-111.24	1.27	0.6259
	PG vs. No-PG						6.96		5.01

Note— k = number of free model parameters; $\ln L$ = log maximum likelihood; AIC = Akaike Information Criterion; Δ AIC = difference in AIC with respect to the best fitting model; wAIC = AIC weight (with the best model's weight in bold face); BIC = Bayesian Information Criterion; Δ BIC = difference in BIC with respect to the best fitting model; wBIC = BIC weight (with the best model's weight in bold face). The row labelled PG vs. No-PG shows how much more likely a model incorporating a primacy gradient (viz. PG + RS & PG + PM + RS) is to have produced the data than a model that does not incorporate a primacy gradient (PM, PM + RS, & PM + OI) based on wAIC and wBIC.

Table 4

Parameter estimates for the fits of the models to the grouped condition of Experiment 3 averaged across participants.

Model	Ω	θ	ϕ	ρ	ω	τ	δ	S
PM ^{pwg}	0.53	0.59	-	-	-	-	-	60.06
PM ^{pwg} + RS	0.50	0.55	-	-	-	0.95	-	69.00
PM ^{pwg} + OI	0.55	0.48	-	-	-	-	0.51	74.21
PG + PM ^{pwg} + RS	-	56	-	0.95	0.47	0.90	-	85.48
PM ^{pws}	0.47	0.71	-	-	-	-	-	57.20
PM ^{pws} + RS	0.46	0.67	-	-	-	0.96	-	67.49
PM ^{pws} + OI	0.48	0.64	-	-	-	-	0.52	68.46
PG + PM ^{pws} + RS	-	0.56	-	0.97	0.57	0.88	-	89.92

Note— Ω = weighting of position markers; θ = distinctiveness of position markers; ϕ = initial value of primacy gradient; ρ = steepness of primacy gradient; ω = weighting of primacy gradient and position markers; τ = degree of response suppression; δ = amount of output interference; S = iteration-to-ms scaling.

Table 5

AIC and BIC weights with associated goodness-of-fit quantities for the fits of the models to the grouped condition of Experiment 3 averaged across participants.

Model	k	ln <i>L</i>	AIC	ΔAIC	wAIC	BIC	ΔBIC	wBIC
PM ^{pwg}	3	89.50	-173.00	9.57	0.0532	-168.42	7.06	0.1002
PM ^{pwg} + RS	4	90.22	-172.45	10.12	0.0311	-166.34	9.14	0.0394
PM ^{pwg} + OI	4	91.67	-175.34	7.23	0.0778	-169.23	6.25	0.1022
PG + PM ^{pwg} + RS	5	95.40	-180.81	1.76	0.4062	-173.18	2.31	0.3324
PM ^{pws}	3	89.33	-172.67	9.90	0.0267	-168.09	7.40	0.0644
PM ^{pws} + RS	4	90.36	-172.73	9.84	0.0195	-166.62	8.86	0.0254
PM ^{pws} + OI	4	91.48	-174.96	7.61	0.0608	-168.85	6.63	0.0763
PG + PM ^{pws} + RS	5	95.23	-180.46	2.11	0.3247	-172.83	2.65	0.2597
PWG vs. PWS					1.32			1.35

Note—*k* = number of free model parameters; ln *L* = log maximum likelihood; AIC = Akaike Information Criterion; ΔAIC = difference in AIC with respect to the best fitting model; wAIC = AIC weight (with the best model's weight in bold face); BIC = Bayesian Information Criterion; ΔBIC = difference in BIC with respect to the best fitting model; wBIC = BIC weight (with the best model's weight in bold face). The row labelled PWG vs. PWS shows how much more likely a model incorporating within-group position markers (PWG) is to have produced the data than a model incorporating within-sequence position markers (PWS) based on wAIC and wBIC.

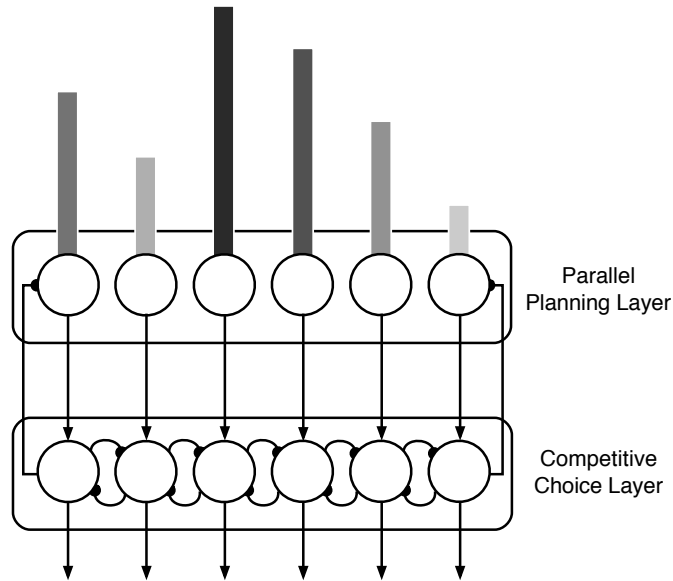


Figure 1. Schematic of a two-layer competitive queuing sequence planning and control mechanism comprising a parallel planning layer (upper field of nodes) and a competitive choice layer (lower field of nodes). Lines terminating with arrows represent excitatory connections, whereas lines terminating with 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.

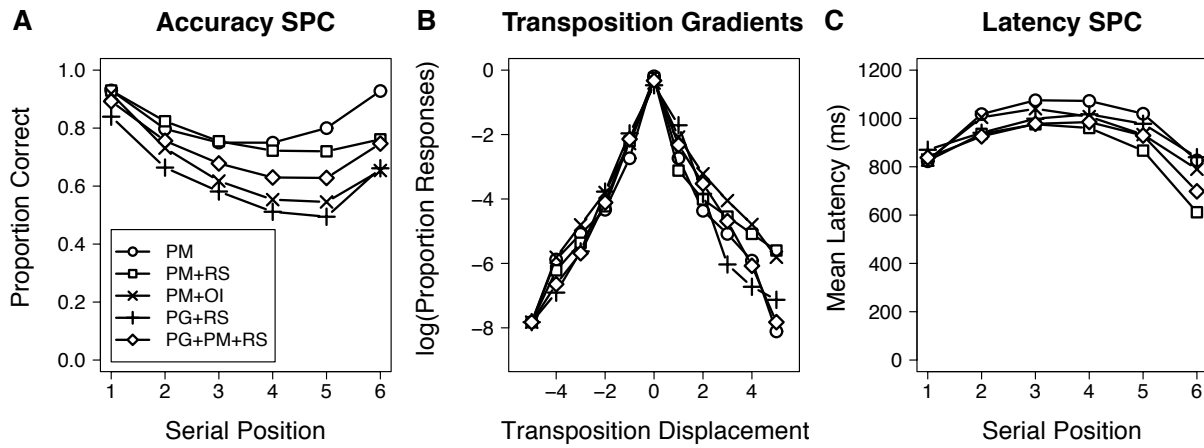


Figure 2. Predicted accuracy serial position curves (A), transposition gradients (B), and latency serial position curves (C) of five models of serial order. PM = position marking; RS = response suppression; OI = output interference; PG = primacy gradient.

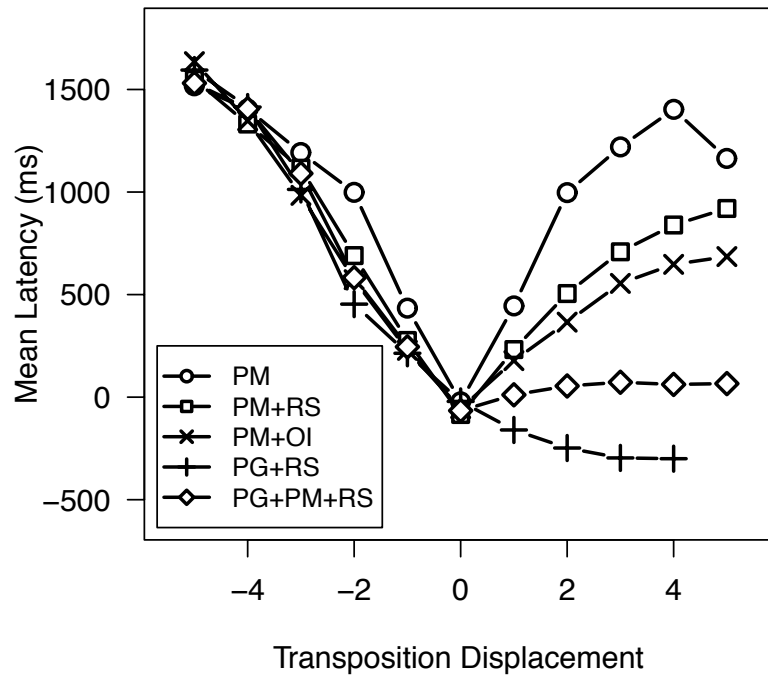


Figure 3. Predicted latency-displacement functions of five models of serial order. PM = position marking; RS = response suppression; OI = output interference; PG = primacy gradient.

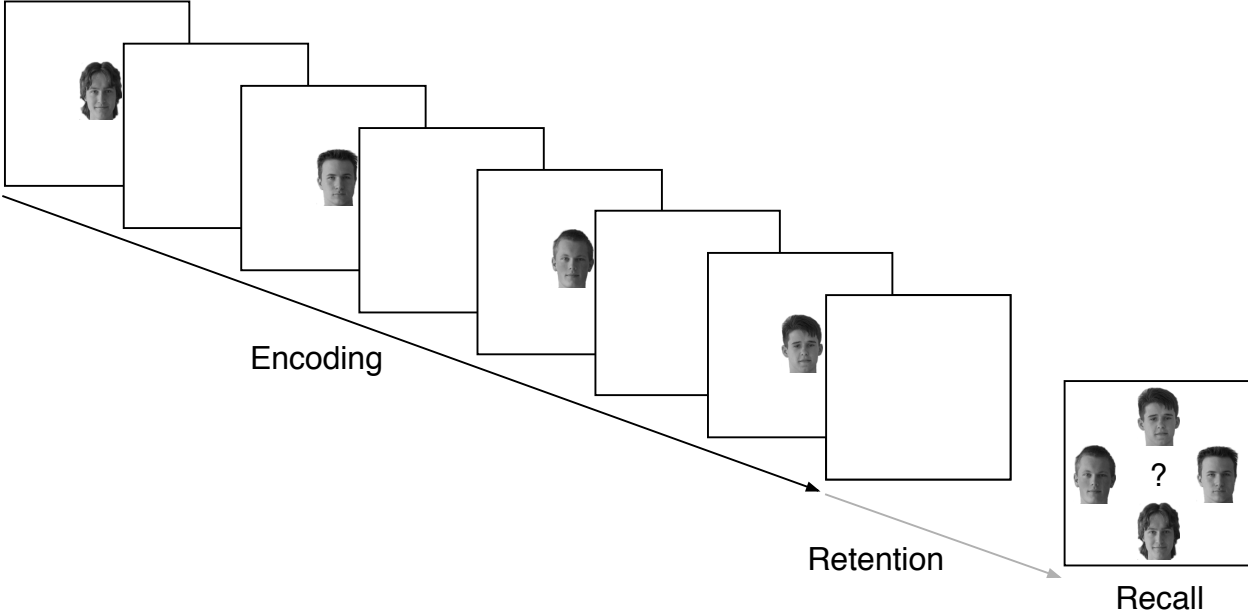


Figure 4. Schematic of the time course of events on each trial.

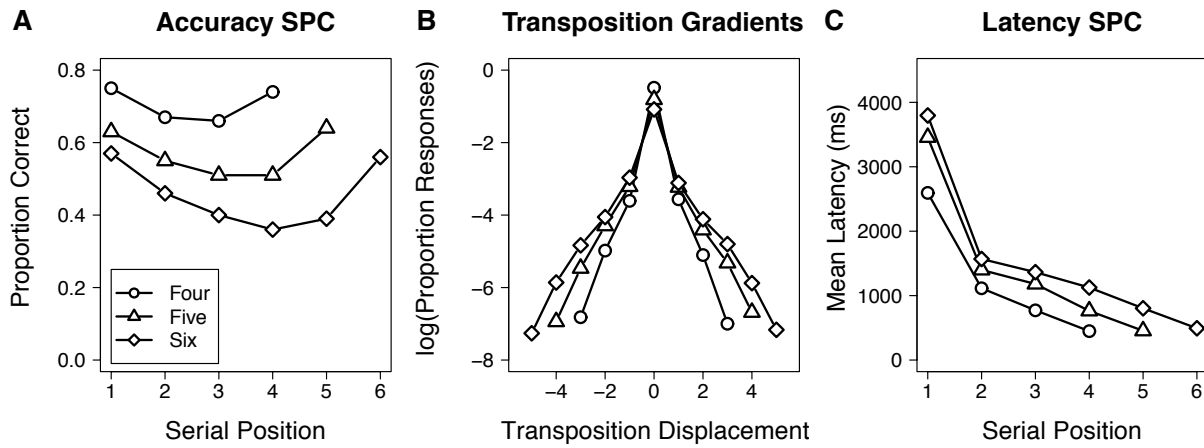


Figure 5. Accuracy serial position curves (A), transposition gradients (B), and latency serial position curves (C) for Experiment 1.

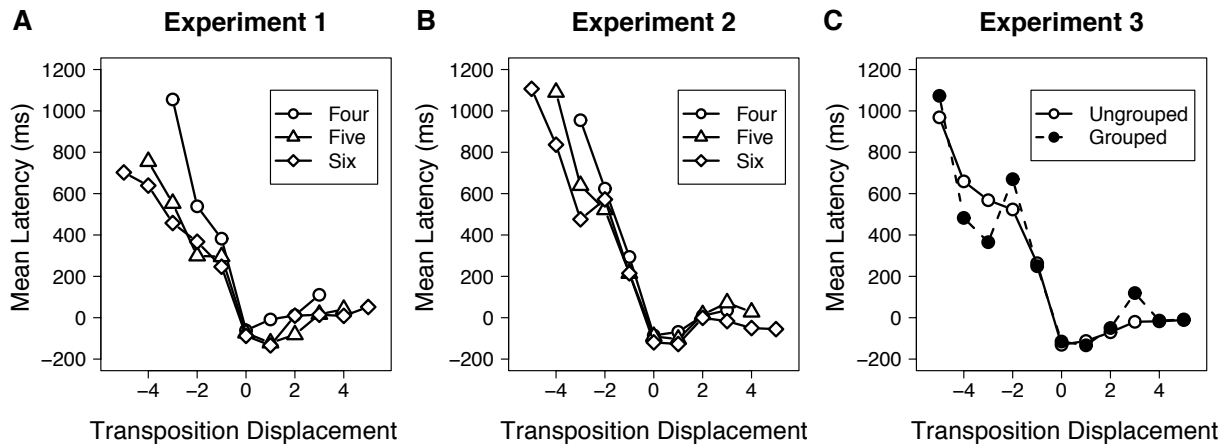


Figure 6. Latency-displacement functions for Experiment 1 (A), Experiment 2 (B), and Experiment 3 (C).

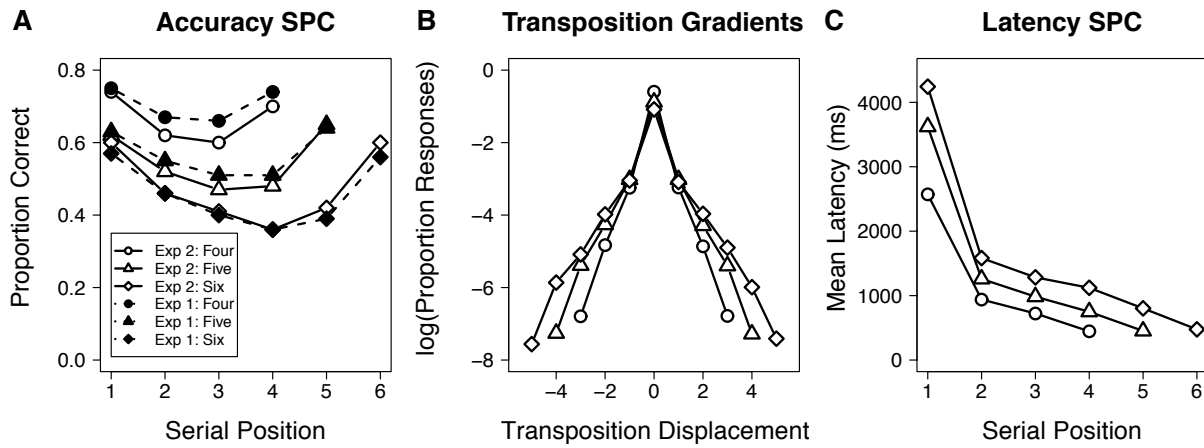


Figure 7. Accuracy serial position curves (A), transposition gradients (B), and latency serial position curves (C) for Experiment 2.

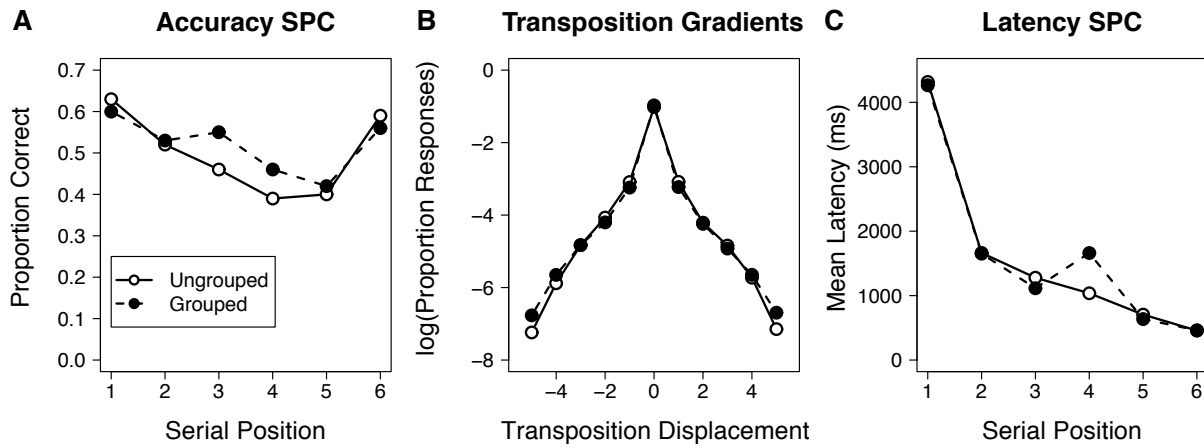


Figure 8. Accuracy serial position curves (A), transposition gradients (B), and latency serial position curves (C) for Experiment 3.

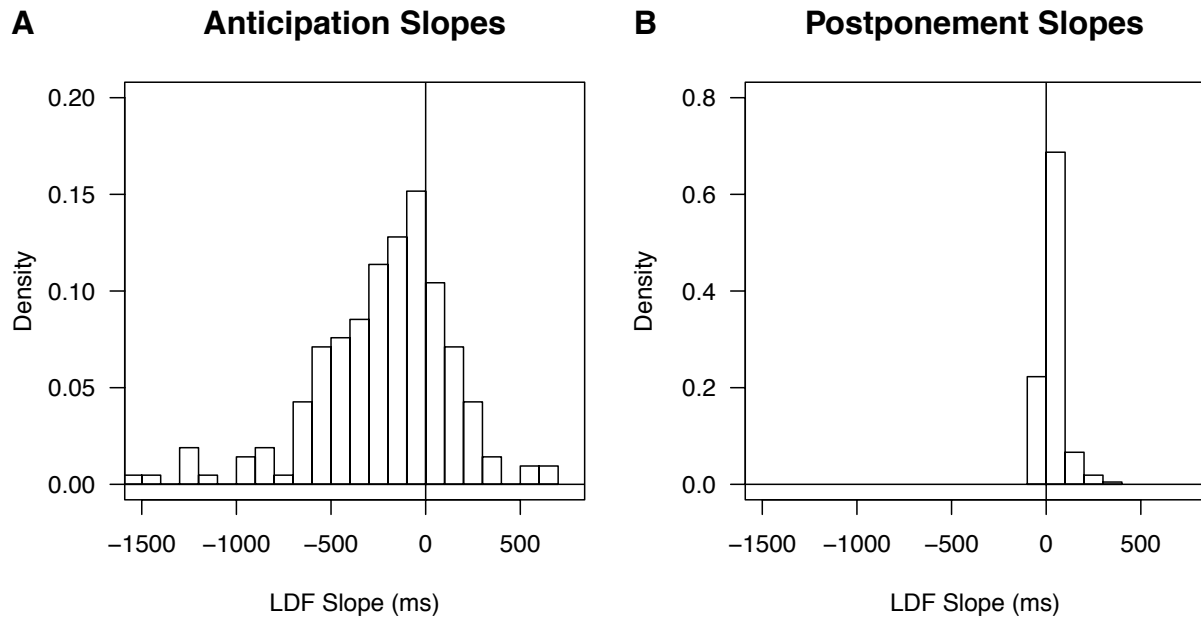


Figure 9. Distributions of slopes of latency-displacement functions (LDF) for anticipations (A) and postponements (B), across individual participants for all three experiments and conditions. The vertical line in each panel corresponds to a slope value of 0.

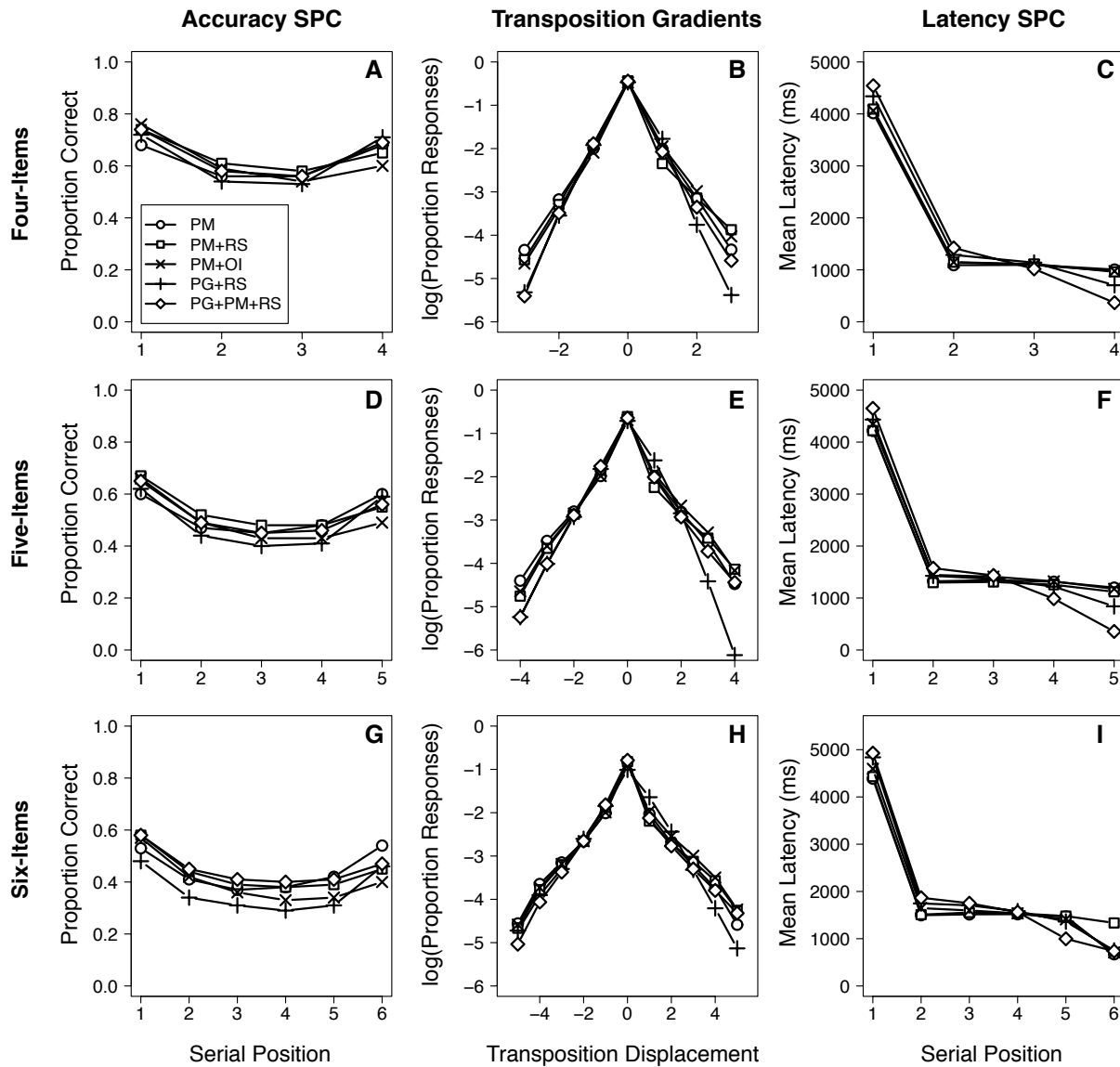


Figure 10. Fits of five models of serial order to the different sequence length conditions of Experiment 2.

Panels show accuracy serial position curves (A, D, & G), transposition gradients (B, E, & H), and latency serial position curves (C, F, & I). The upper panels show predictions for four-item sequences; middle panels show predictions for five-item sequences; whilst lower panels show predictions for six-item sequences. PM = position marking; RS = response suppression; OI = output interference; PG = primacy gradient.

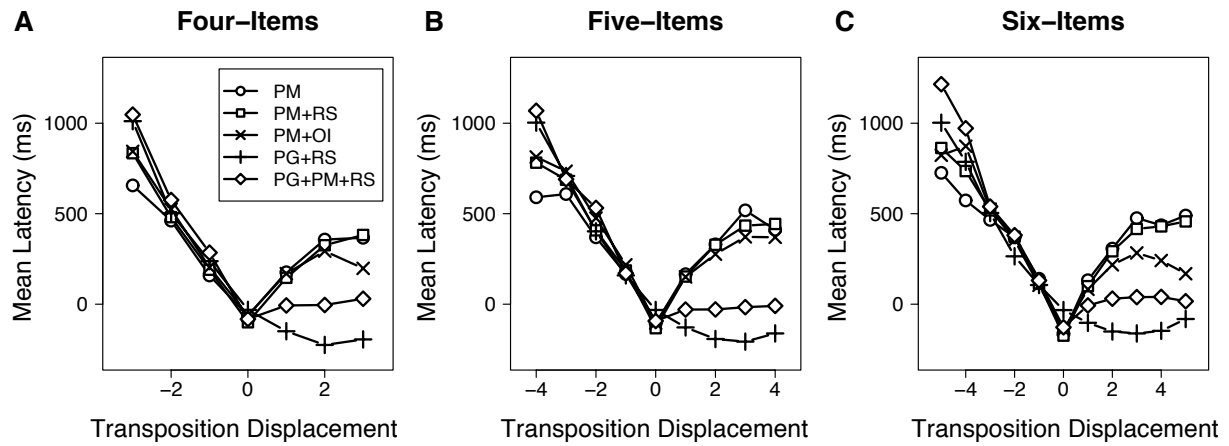


Figure 11. Fits of the five models to the latency-displacement functions of Experiment 2. Panels show predictions for four-item sequences (A), five-item sequences (B), and six-item sequences (C). PM = position marking; RS = response suppression; OI = output interference; PG = primacy gradient.

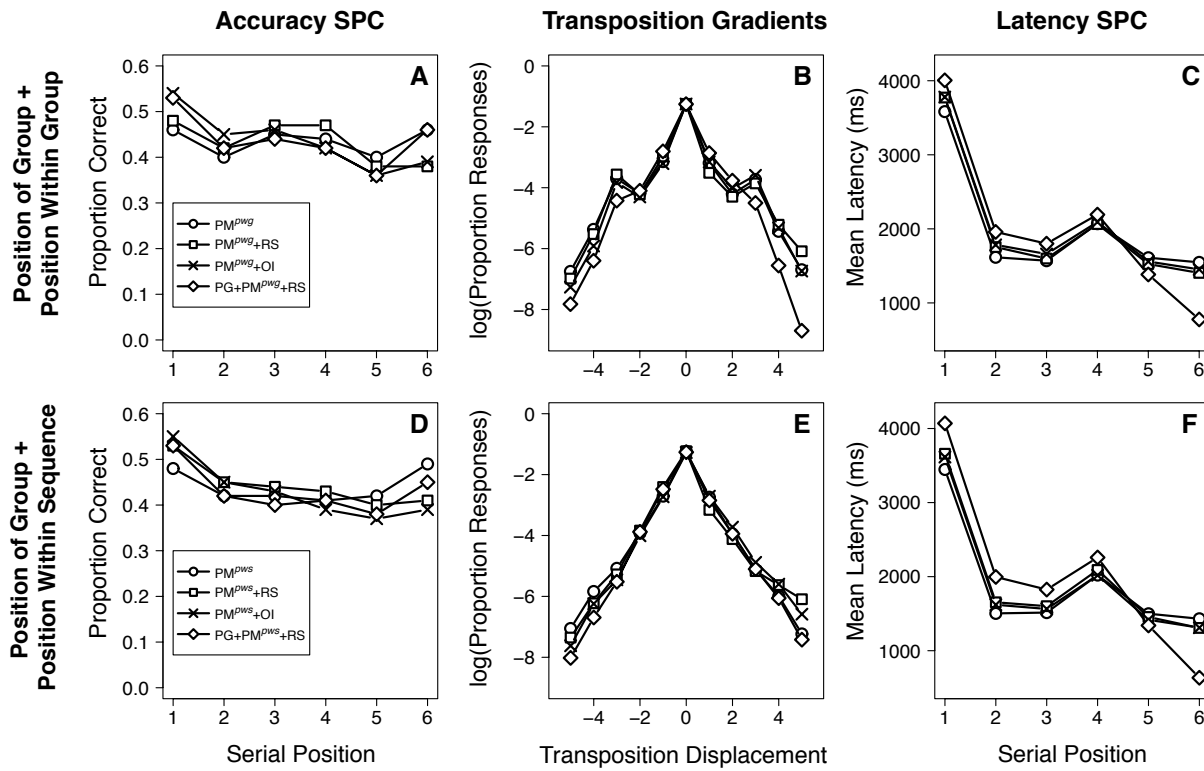


Figure 12. Fits of eight models of serial order to the grouped condition of Experiment 3. Panels show accuracy serial position curves (A & D), transposition gradients (B & E), and latency serial position curves (C & F). The upper panels show the predictions for the models pairing position of group with position within-group markers; the lower panels show the predictions of the model pairing position of group with position within-sequence markers. PM^{pwg} = position marking of groups and position within-groups; PM^{pws} = position marking of groups and position within-sequence; RS = response suppression; OI = output interference; PG = primacy gradient.

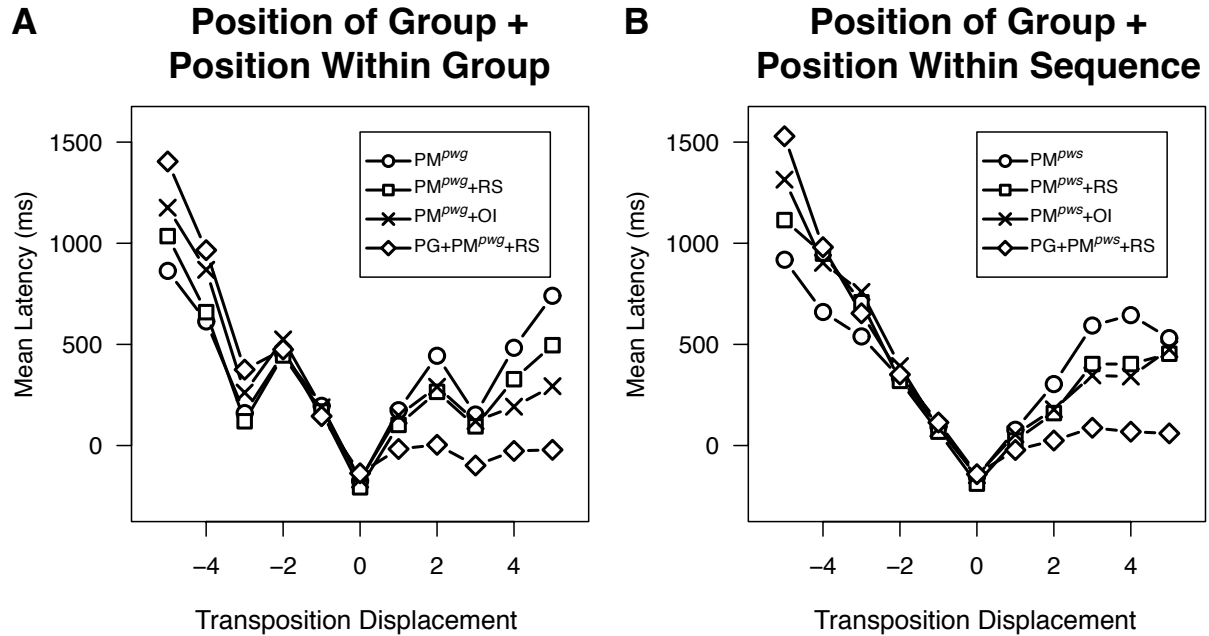


Figure 13. Fits of the eight models to the latency-displacement functions of the grouped condition of Experiment 3. Panels show predictions for the models pairing position of group with position within-group markers (A), and the models pairing position of group with position within-sequence markers (B). PM^{pwg} = position marking of groups and position within-groups; PM^{pws} = position marking of groups and position within-sequence; RS = response suppression; OI = output interference; PG = primacy gradient.

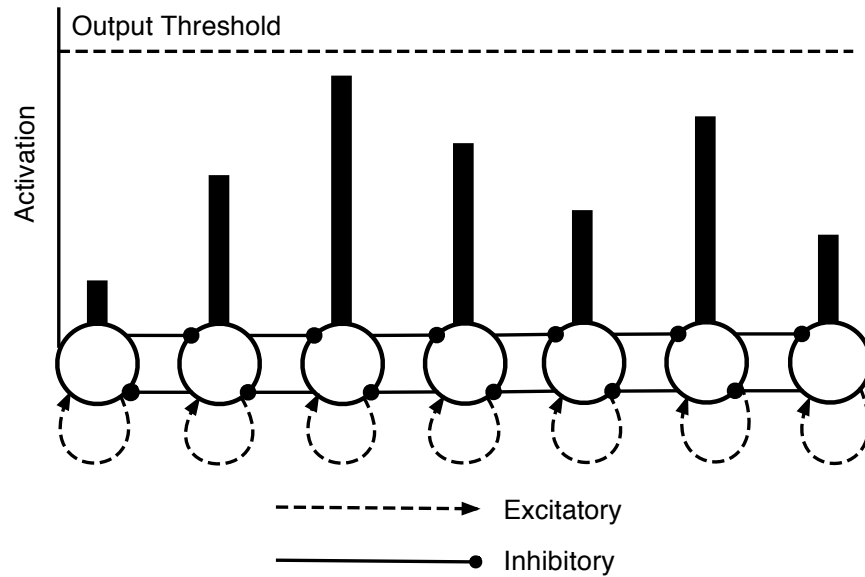


Figure 14. A schematic of the lateral inhibition neural network architecture employed for the simulations. The network is modeled on the competitive choice layer employed in competitive queuing models of serial behavior (Bullock, 2004; Rhodes & Bullock, 2003). Each localist item node possesses a single recurrent excitatory connection as well as lateral inhibitory connections to all other item nodes. Nodes are fully interconnected, but only adjacent-neighbor inhibitory connections are shown to prevent visual cluttering. The activation of a node within the layer is determined by the external input it receives from outside the layer, plus positive recurrent self-excitation, and within-layer lateral inhibition. Note—the number of nodes in the network is dependent on the sequence length being modeled.

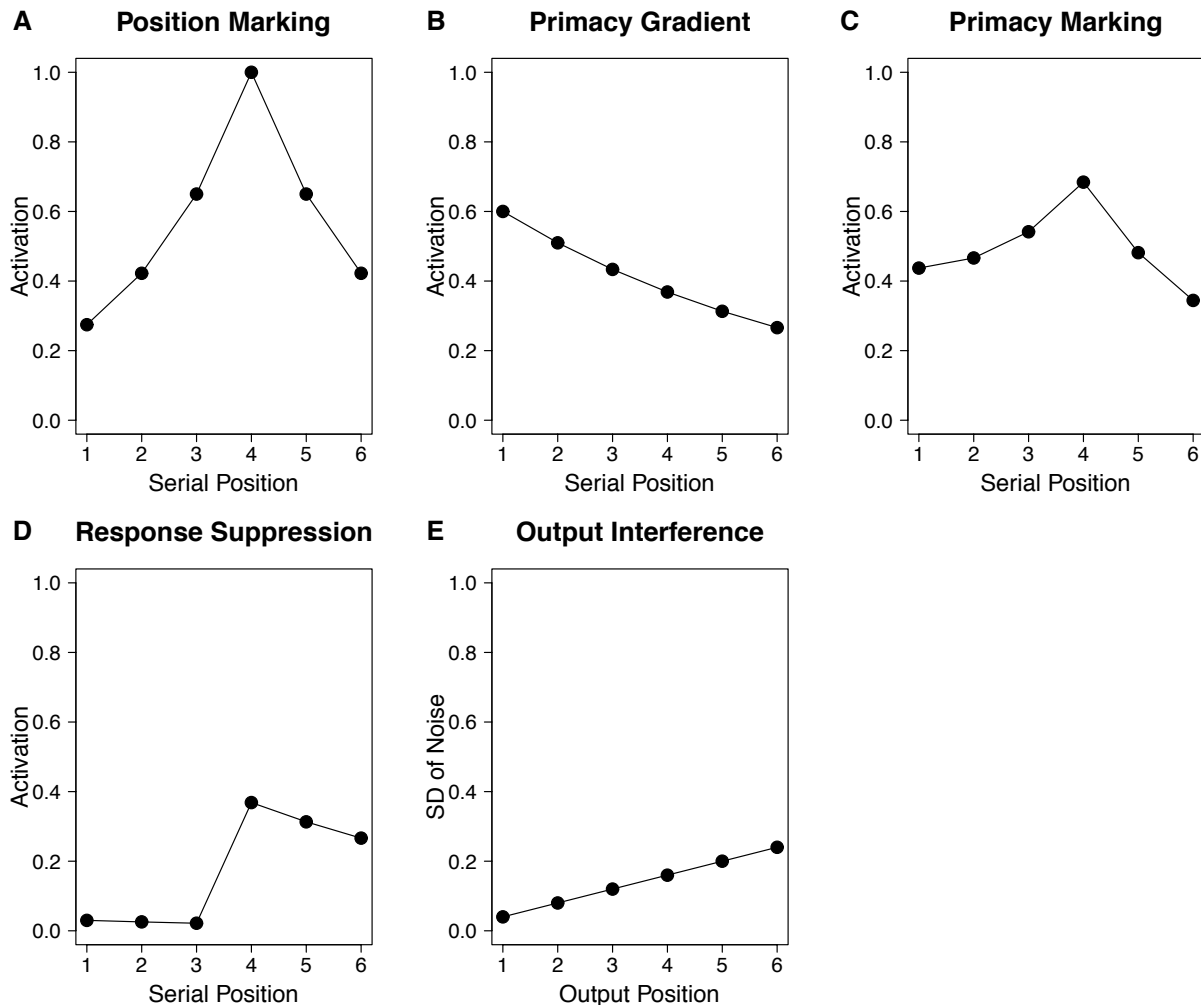


Figure 15. Example starting activations for the four representational principles—and combination of principles—for six-item sequences, based on the parameter settings employed for the initial simulations: (A) position marking (showing activations for the fourth output position), (B) a primacy gradient (showing activations for the first output position), (C) primacy gradient and position marking (showing activations for the fourth output position), (D) response suppression (showing activations for a primacy gradient with suppression of the first three recalled items), (E) output interference (showing the increase in Gaussian noise applied to the starting activations across output positions).

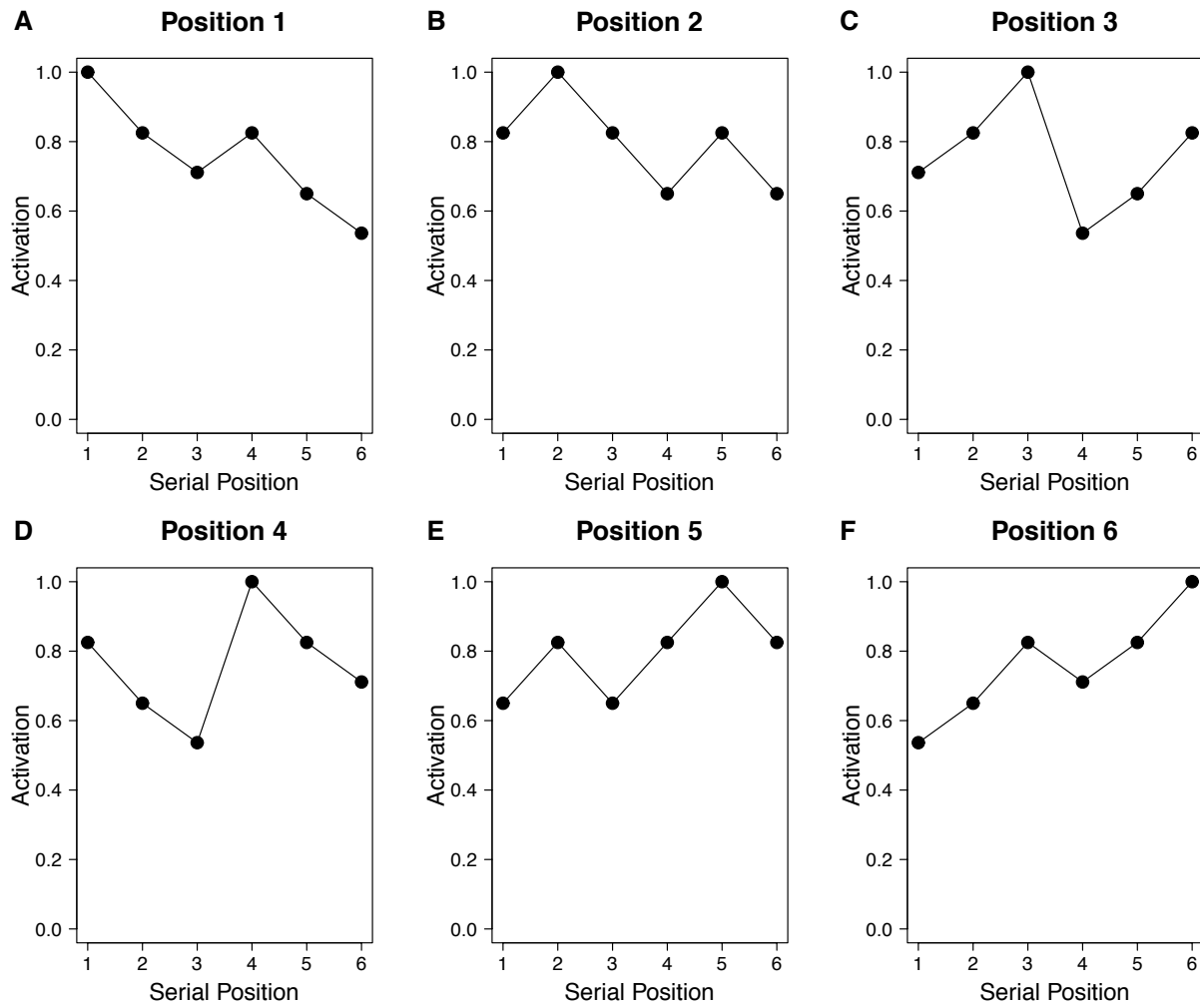


Figure 16. Example starting activations for the position-of-group and position-within-group implementation of position marking for a six-item sequence grouped into threes. Activations were generated using the following parameter values: $\Omega = 1$; $\theta = .65$; $\lambda = .5$.

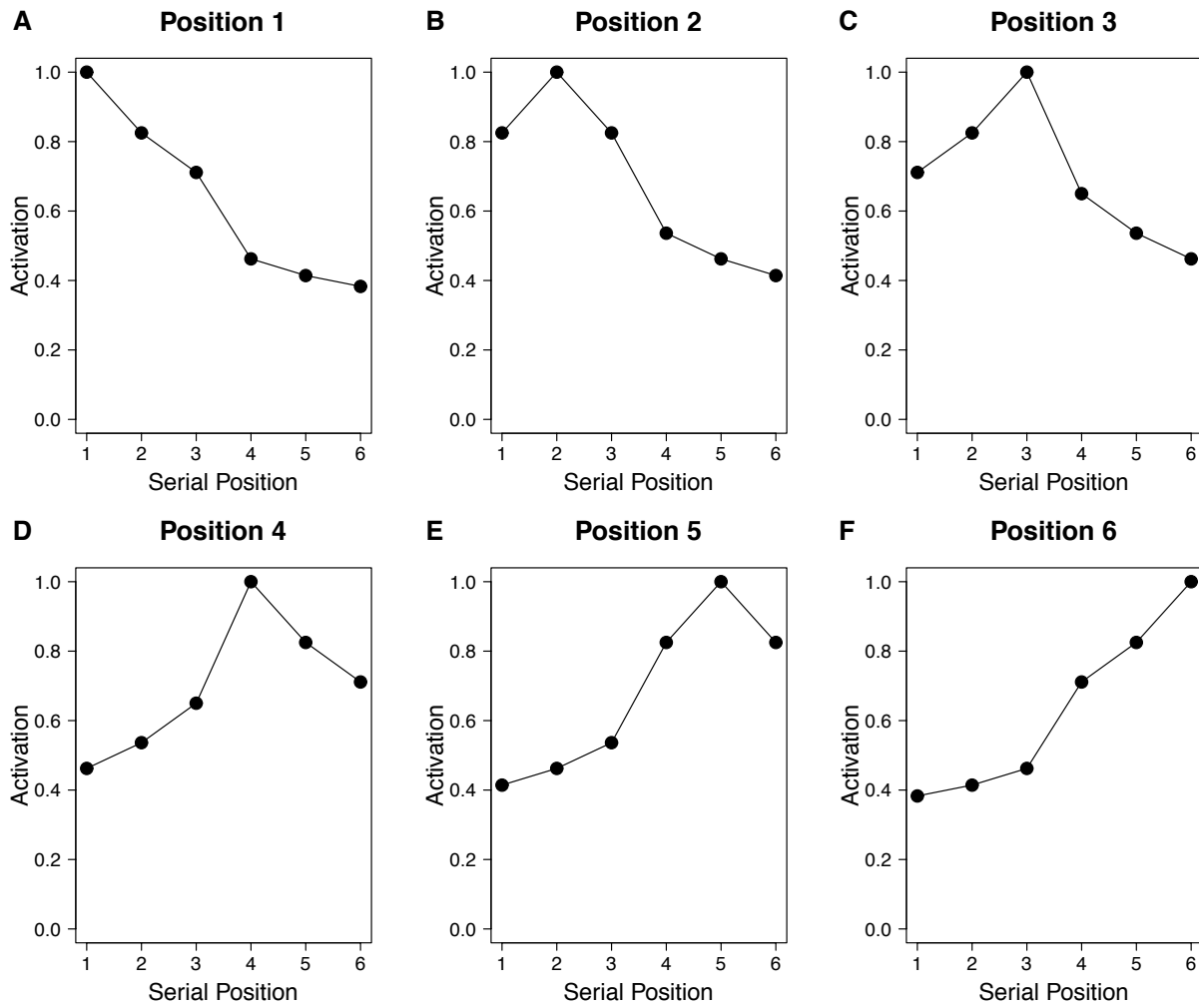


Figure 17. Example starting activations for the position-of-group and position-within-sequence implementation of position marking for a six-item sequence grouped into threes. Activations were generated using the following parameter values: $\Omega = 1$; $\theta = .65$; $\lambda = .5$.