Neural processes for learning and monitoring sequential regularities in changeable environments.

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Abstract

Neural processes for learning and monitoring sequential regularities in changeable environments.

A dissertation presented to the Faculty of the Graduate School of Arts and Sciences of Brandeis University, Waltham, Massachusetts

by Abigail LaBombard Noyce

The world is largely stable and predictable. Humans and other organisms are sensitive to that stability, and use it to support cognitive processes. This work consists of a series of studies that explore how humans learn about such stability, use that information to generate predictions about forthcoming sensory input, and detect when such predictions are inadequate. First, I present a modeling study that quantified the distributions of errors that people make on a complex, visuomotor sequence learning task, and examine the serial position dynamics of several parameters describing short-term visual memory. Both precision and capacity for these sequences increases with familiarity, and the worst-represented items show the largest increases. Next, I present an experiment that used the same task to understand the effects of deviant items within familiar sequences. By measuring ERPs to new, familiar, and deviant items, I dissociate the neural activity associated with detecting a deviant from that associated with encoding task-relevant stimulus characteristics. Finally, I present an experiment investigating the role of prediction in a task that is stochastic, rather than sequential, and in which deviant events occurred among the distractors rather than among the task-relevant stimuli. Unexpected events among the distractors seem to obligatorily attract attention, enhancing or impairing performance. Further, I show that the individual differences in the neural response to such unexpected events is predicted by temperament. Together, these studies illuminate how the brain learns about predictability in a range of settings, and leverages such predictability to facilitate cognition.
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Chapter 1

Introduction

The nervous systems of humans (and many other organisms) are exquisitely tuned to patterns and structure in sensory inputs. This tuning is generally adaptive, as the world contains a great deal of sequential regularity—cases where one sensory event reliably predicts a following event. These regularities extend from simple, predictable inputs, such as background noise or the sensation produced by a surface on which one is sitting, all the way to elaborately structured regularities such as the syntax of language, or the key of a piece of music.

The brain uses these regularities to increase the efficiency and efficacy of perceptual and cognitive processes. Reports of visual stimuli held in short-term memory are biased towards the average or most-common stimulus characteristics (Dube & Sekuler, 2012; Huang & Sekuler, 2010a, 2010b; Payne, Guillery, & Sekuler, 2013). Such bias occurs even when the characteristics of a currently-visible stimulus must be reported (Chalk, Seitz, & Seriès, 2010). In tasks involving natural scenes, perception is biased towards stimuli that are consistent with the surrounding context, as seen by facilitated speed and accuracy of identifying such stimuli (e.g. Bar, 2004; Biederman, Mezzanotte, & Rabinowitz, 1982; Kersten, Mamassian, & Yuille, 2004; Gronau, Neta, & Bar, 2008; Mandler, 1980), and in tasks involving faces and attributes, people are faster and more accurate when
the physical features of the face are congruent with the trait being described (Cassidy, Zebrowitz, & Gutchess, 2012). Cross-modally, visual input can impair or enhance speech perception, as in the McGurk effect, or when auditory input is embedded in noise (Guttman, Gilroy, & Blake, 2005; Zion Golumbic, Cogan, Schroeder, & Poeppel, 2013). Perception is also facilitated by occurring at a predictable time. The brain appears to modulate the signal-to-noise gain of the visual system when the timing of upcoming stimuli is known (Cravo, Rohenkohl, Wyart, & Nobre, 2013).

Regularities are also able to guide attention. It is well documented that attentional cueing can facilitate detection and processing of cued stimuli (e.g Posner, 1980; Posner, Snyder, & Davidson, 1980; Huang & Sekuler, 2010a, 2010b). Such cueing depends on the expectation that cues are predictive, which allows the subject to allocate attention appropriately (C. Summerfield & Egner, 2009). However, such attentional shifting does not require explicit cues. Structured scenes enable the allocation of attention to appropriate objects (J. J. Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006), and even when temporal structure is irrelevant, it triggers spatial and featural attentional capture (Le Pelley, Vadillo, & Luque, 2013; Zhao, Al-Aidroos, & Turk-Browne, 2013).

Anticipation and predictions derived from such regularities also manifest in anticipatory eye movements (Barnes, 2008; Burke & Barnes, 2007; Elsner, Falck-Ytter, & Gredebäck, 2012; Kowler, 1989; Maryott, Noyce, & Sekuler, 2011; Rotman, Troje, Johansson, & Flanagan, 2006) and motor control schema (Cohn, DiZio, & Lackner, 2000; Hu, 2010; Pigeon, Bortolami, DiZio, & Lackner, 2003). The studies that I report in this dissertation improve our understanding of the neural mechanisms that underly anticipatory and predictive effects on cognition.

1.1 Sequences in short-term memory

Cognitive skills ranging from language and navigation to visually guided manipulation of tools and devices depend upon an ability to represent the sequential order of events. In particular, humans
frequently need to maintain a sequence of events in short-term memory for subsequent analysis or reproduction. Previous work with serial recall tasks has demonstrated that sequences held in memory are susceptible to strong primacy and recency effects (e.g. Agam, Bullock, & Sekuler, 2005; Kahana & Jacobs, 2000; Lashley, 1951; Maryott et al., 2011), and may depend on chunking adjacent items within a sequence (Farrell, Hurlstone, & Lewandowsky, 2013; Hitch, Fastame, & Flude, 2005; Maryott & Sekuler, 2009). Although much of the classic work on learning and short-term memory for sequences has used lists of verbal stimuli (e.g. Ebbinghaus, 1913; Hebb, 1961; Hitch et al., 2005; Howard & Kahana, 1999; Kahana & Jacobs, 2000), studying short-term memory for visual stimuli has some pronounced advantages. Verbal (and verbalizable) stimuli can be tightly compressed in short-term memory; further, subjects can actively rehearse a verbal representation, refreshing it over the course of retention with very little loss of fidelity (Ricker & Cowan, 2010).

The graded fidelity with which subjects can reproduce previously-seen visual stimuli is ideal for testing the relationships between precision and capacity limits in short-term memory for sequences of visual stimuli. The study presented in Chapter 2 investigates how familiarity changes the precision and effective capacity of short-term memory. To do this, I quantified the distributions of errors that people make on a visuomotor sequence learning task.

1.2 Dissociating new and deviant events in a dynamic environment

As described above, humans use sequential regularities in the environment to support a wide range of cognitive processes. These effects depend upon the brain’s ability to work in a predictive, anticipatory way, using context, prior knowledge, and previous experiences to build expectations
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about forthcoming sensory inputs. However, to navigate and manage a dynamic environment, people cannot blindly follow those expectations. Otherwise, we may step onto a non-existent stair, or walk into a previously-safe location only to be attacked by an unexpected foe. Monitoring mechanisms are required to detect events that deviate from the previously established regularities, allowing people to change planned behaviors and learn about the new state of the world.

Monitoring processes are evident in tasks with an explicitly sequential structure, such as the serial reaction time task (Nissen & Bullemer, 1987). In this task, various stimuli on the screen cue subjects to press a particular key, and the sequence of stimuli (and thus key presses) repeats throughout the course of the experiment. When a stimulus that is not part of the usual sequence occurs, people are slower and less accurate to respond to it (Ferdinand, Mecklinger, & Kray, 2008; Gobel, Sanchez, & Reber, 2011; Rüsseler & Rösler, 2000). These tasks do not require explicit memory and encoding for the sequence of stimuli, and moreover, the sequence remains stable over the course of a relatively-long experimental block.

When a subject’s expectation is specifically about a reward value, the relationship between expectation and actual reward is coded by dopaminergic cells in the ventral tegmental area (Schultz, 2006; Schultz, Dayan, & Montague, 1997). Rewards that are lower than the predicted reward lead to a decrease in dopamine release; rewards that are greater than the predicted reward lead to an increase (Schultz et al., 1997). This dopaminergic signal is generally thought to be a key driver of learning from outcomes that are better or worse than expected (e.g. Schoenbaum, Esber, & Iordanova, 2013; Takahashi et al., 2009, 2011), but it’s not known whether it is appropriate to extrapolate such mechanisms to predictions that are not explicitly about reward. (See Kakade and Dayan (2002) for an argument that novelty is intrinsically rewarding, leading to dopaminergic spiking, and Laurent (2008) for a counter.)

One area involved in prediction monitoring regardless of the presence of reward is the anterior cingulate cortex (Botvinick, Cohen, & Carter, 2004; Kennerley, Behrens, & Wallis, 2011). The
anterior cingulate has strong links to frontal and prefrontal cortical areas, to sensory cortices, and to the limbic system (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Its activation to new information in the environment is accompanied by the P3 ERP component, a positive-going deflection over central electrodes from 300–500 ms after such information is presented (Crottaz-Herbette & Menon, 2006; Linden, 2005). ACC activation (and the P3) have been observed in a wide range of cognitive contexts, and are theorized to reflect a cognitive control process that is responsible for developing and adjusting the working memory representation of the context, task set or forthcoming actions (Goldstein, Spencer, & Donchin, 2002; Crottaz-Herbette & Menon, 2006; Nieuwenhuis, Aston-Jones, & Cohen, 2005; Ridderinkhof et al., 2004). A similar theory is proposed by Holroyd and Yeung (2012), who assert that the ACC’s primary role is to hold and monitor the options available for behavior. The P3 has at least two subcomponents: the Novelty P3, elicited by stimuli that violate expectations, and the P300, elicited by task-relevant stimuli (Goldstein et al., 2002; Linden, 2005; Nieuwenhuis et al., 2005; Polich, 2007).

Prediction monitoring processes’ main role may be to guide learning (Maier & Steinhauser, 2013). Pearce and Hall (1980) argue that classical conditioning depends on the unconditioned stimulus being unpredictable, while Wills, Lavric, Croft, and Hodgson (2007) demonstrate that associative learning occurs most rapidly for cues that remain predictive, but whose outcome changes and Ouden, Friston, Daw, McIntosh, and Stephan (2009) show that when auditory distractors predict visual distractors, the neural response to such predicted events decreases across trials. Similarly, in motor control tasks, subjects learn from the mismatch between the expected motor output and the movement that actually occurs (Cohn et al., 2000; Lackner & DiZio, 2005), but not from explicit knowledge about the state of the world (Hu, 2010).

The experiment reported in Chapter 3 investigates the neural processes that support (i) explicit sequential encoding and (ii) monitoring such sequences for deviant events. Using the visuomotor sequence learning task described in Chapter 2, I measured ERPs to new, familiar, and deviant
sequence items. By comparing ERPs to new and to deviant items, I dissociated the neural activity related to triggering a prediction-monitoring mechanism from that related to encoding a new stimulus exemplar. I hypothesized that both new and deviant items would enhance a P3 ERP, but that new items would elicit only an enhanced P300, while deviant items would also elicit a Novelty P3. These results show that the theoretical structure surrounding P3 generation is also applicable to dynamic environments where governing regularities are frequently changing.

1.3 Neural and behavioral effects of implicit prediction monitoring

While the task in Chapters 2 and 3 has sequential structure that subjects are explicitly aware of, predictive and monitoring processes occur even when subjects are not attending to the governing regularity. In Chapter 4, I looked for behavioral and neural evidence that people are sensitive to regularities in peripheral stimuli that they are actively attempting to ignore.

Previous work in associative-learning contexts demonstrated that unexpected outcomes trigger the allocation of attention (Wills et al., 2007). Further, deviant events in a stream of unattended auditory stimuli capture attention, leading to poorer detection of targets in a simultaneously-presented stimulus stream (Schröger, 1996), and deviant tones (Escera, Alho, Winkler, & Näätänen, 1998; Nöstl, Marsh, & Sörqvist, 2012; Parmentier, Elford, Escera, Andrés, & San Miguel, 2008) and vibro-tactile stimuli (Parmentier, Ljungberg, Elsley, & Lindkvist, 2011; Ljungberg & Parmentier, 2012) preceding a visual target delay target detection.

The mismatch negativity (MMN) is a negative-going deflection in the ERP elicited by a stimulus that violates some governing regularity. While it is historically studied in the auditory domain, the existence of a visual mismatch negativity (vMMN) has recently been established (Czigler, 2007;
CHAPTER 1. INTRODUCTION

Kimura, Schröger, & Czigler, 2011; Stefanics, Kimura, & Czigler, 2011). The MMN is believed to be generated by interactions between a predictive signal from higher-order (likely prefrontal) areas and the bottom-up input reaching sensory cortex (Garrido, Kilner, Stephan, & Friston, 2009; Wacongne, Changeux, & Dehaene, 2012; Wacongne et al., 2011; Winkler, 2007).

To investigate the potential attentional capture of deviant events in a task that requires stimulus discrimination rather than mere target detection, I drew upon the Eriksen flanker task, an experimental paradigm that was designed to elicit interactions between multiple, conflicting sources of visual information (Eriksen & Eriksen, 1974). A single target, which can generally be in one of two states, is accompanied by flanking distractors, which can match or differ from the target. The congruency between the distractors and the target influences the accuracy and reaction time with which subjects can report the state of the target (e.g Eriksen & Eriksen, 1974; Ridderinkhof, Band, & Logan, 1999).

The experiment presented in Chapter 4 examined how predictability of distractors influenced cognitive processing in the flanker task, and the relationship between such influences and the ERPs elicited by onset of standard and deviant distractors.
Chapter 2

Dynamic reallocation of VSTM resources

2.1 Introduction

Holding visual information in short-term memory is critical in many daily tasks. As researchers have attempted to characterize the structure of visual short-term memory (VSTM), it has become necessary to understand how resources are allocated among multiple items that are held simultaneously in memory. Here, I investigate how such allocation changes as people gain experience with the items. Real-life use of visual short-term memory almost always interacts with learning and long-term memory.

Recent work attempting to quantify the allocation of VSTM resources among items has drawn on signal-detection approaches to understanding cognition. This approach assumes that the representations of items in memory are noisy, or otherwise imperfect, and attempts to characterize that imperfection. The most common method has been to ask subjects to reproduce from memory some characteristic of an item, measure the degree to which their reproduction differs from the initial stimulus, and use the resulting distribution of errors as a proxy for the noise of the memory representation (e.g. Wilken & Ma, 2004; Zhang & Luck, 2008).
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A family of related models has been proposed to characterize such error distributions. The earliest had two parameters: one describing the probability that subjects responded randomly, presumably due to guessing, rather than by reporting the probed item; the other describing the spread of responses around the true value (Zhang & Luck, 2008, 2009, 2011). Another group extended this basic model to include the possibility that subjects report the identity of a non-probed item from the memory set, leading to a third parameter: the probability of a non-target report (Bays, Catalao, & Husain, 2009; Bays, Gorgoraptis, Wee, Marshall, & Husain, 2011; Bays, Wu, & Husain, 2011; Gorgoraptis, Catalao, Bays, & Husain, 2011; Zokaei, Gorgoraptis, Bahrami, Bays, & Husain, 2011). Finally, recent work has moved towards fitting the error distributions with a model in which the amount of resources allocated to each object may vary from trial to trial (van den Berg, Shin, Chou, George, & Ma, 2012; Fougnie, Suchow, & Alvarez, 2012).

While the majority of these experiments have used “snapshot” displays, in which an array of items are briefly presented and then one item is probed, a handful of notable exceptions have controlled for the possibility that this approach may confound encoding bottlenecks, such as perceptual crowding, with limits on VSTM capacity (Bays et al., 2009). For example, Emrich and Ferber (2012) and Gorgoraptis et al. (2011) both showed that inter-item confusion (i.e. non-target reports) increases when items are shown in succession, but precision and the rate of random responses remain constant. However, both of these studies used arrays of static stimuli and compared a “snapshot” display to a series of two or three displays each containing a subset of the items. The static nature of their stimuli leave open questions about VSTM structure for dynamic stimuli.

Further, none of the previous work with this family of models has investigated the effects of learning on VSTM representations of information. It is well-established that memory accuracy improves as items become more familiar (e.g. Ebbinghaus, 1913; Hebb, 1961; Howard & Kahana, 1999; Maryott et al., 2011), presumably due to increased support from long-term memory. However, it is unknown how such support changes the distribution of errors, or the probability that a non-target
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is reported.

Sekuler, Siddiqui, Goyal, and Rajan (2003) and Agam et al. (2005) established a VSTM memory task with the dynamic properties that have been lacking in the previous modeling work. In their task, subjects observed and reproduced motion trajectories enacted by a disk on a computer screen. The stimuli themselves comprised position changes over time, and each segment of a motion trajectory was linked with its successor. Agam et al. put forth a single, scalar measure of reproduction accuracy that has thus far been used to describe memory performance in this task. Several following papers have used that measure to characterize the effects of learning on such performance (Agam, Galperin, Gold, & Sekuler, 2007; Agam, Huang, & Sekuler, 2010; Maryott et al., 2011). However, the body of VSTM modeling work described above has made it clear that memory errors may arise from multiple sources: An item may be successfully retrieved from memory, but with added noise; an item may fail to be encoded into memory, or fail to be retrieved; or an item may be mis-bound with its location in the stimulus set, leading to non-target reports. The measure used in these previous studies does not distinguish between these sources of recall errors.

Here, I characterize familiarity-induced changes in VSTM representations by fitting four related VSTM models to responses generated on the visuomotor sequence learning task introduced by Agam et al. (2005). I fit each model to errors generated at each level of increasing familiarity in order to assess how model parameters changed as subjects learned a sequence. Using the resulting serial position dynamics, I then characterized the effects of learning on VSTM characteristics such as precision and number of items stored. The results presented in this chapter show that VSTM has a remarkable ability to reallocate memory resources over the course of learning.
2.2 Methods

To investigate the effects of learning on visual short-term memory, I fit several models to data from a motion trajectory learning task. These data were previously collected by myself and others to characterize the effects of learning on memory for non-verbal sequences, using a single measure of accuracy (mean absolute error; Agam et al., 2005), and to investigate neural correlates of such learning (see Agam et al., 2007; Maryott et al., 2011; Noyce & Sekuler, in revisions). All subjects (N = 64) were young adults recruited from the Brandeis University community. Re-analyzing this data with multiple parameters, as I have done here, leads to new insights into the effects of learning on memory for these sequences.

2.2.1 Experimental task and accuracy measures

The data were collected from a task in which subjects observed and reproduced psuedo-random motion trajectories. Each trajectory was presented multiple times in succession, and each subject saw approximately 75 such trajectories. The details of the task varied slightly between experiments; Table 2.1 summarizes the relevant details for each dataset.

Figure 2.1 illustrates the sequence of events within one presentation of a trajectory. On each presentation, a small disk traversed a path comprising either five or six connected linear motion segments. After each segment, the disk paused briefly before resuming its motion in a changed direction. The disk then disappeared from view. After a retention interval, a second disk appeared at a random point within the central portion of the display, cueing the subject to move a handheld stylus over the surface of a graphics tablet in order to reproduce from memory the sequence of disk motions that had just been seen. During the reproduction, the disk’s motion was yoked to the movement of the stylus’ tip on the graphics tablet. No other feedback was provided. Note that neither the stimulus nor the reproduction disk left a visible trail while moving across the computer.
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Figure 2.1: One presentation of a motion sequence stimulus. At the start of each presentation, a disk appeared at the center of the display before beginning to move in a series of either five or six connected linear segments without leaving any visible trail. After enacting the movements, the disk disappeared from view. After a retention interval, a second disk appeared, signaling the subject to begin reproducing from memory the path that had been traveled by the first disk. Each trial consisted of either four or five such presentations.

display. To obtain a complete representation of the disk’s path, subjects would have to extract it from the disk’s motions, and maintain it in short-term memory until reproduction was required (Geisler, Albrecht, Crane, & Stern, 2001; Jancke, 2000).

Each trial’s quasi-random sequence of motion segments was generated by the algorithm described by Agam et al. (2005). The direction of a sequence’s initial motion was chosen randomly, and the magnitude of the direction change at each “corner” of the trajectory was between $30^\circ$ and $150^\circ$. Changes in direction could be clockwise or counter-clockwise, with equal probability. The motions comprising a sequence were constrained by several additional rules: Motion segments were not permitted to intersect, could not come within one-half a segment’s length of intersecting, nor could they extend beyond the boundaries of the visible display area.

The fidelity of each reproduction was quantified offline by means of an algorithm that used the subject’s pauses and direction changes to divide the reproduction into segments (Agam et al., 2005; Maryott & Sekuler, 2009; Maryott et al., 2011). After segmentation, the algorithm estimated the direction of each such segment by fitting a line to its beginning and end points. Reproduction accuracy was then quantified by directional error: the angular difference between the direction of a
Table 2.1: Details and sources of the datasets included in these analyses.

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Trials</th>
<th>Published in</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 segments and 4 presentations</td>
<td>12</td>
<td>76 Agam et al. (2007)</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>88 Noyce and Sekuler (in revisions); presented in Chapter 3</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>88 Noyce and Sekuler (unpublished)</td>
</tr>
<tr>
<td>6 segments and 5 presentations</td>
<td>12</td>
<td>76 Agam et al. (2007)</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>72 Maryott et al. (2011)</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>72 Maryott et al. (2011)</td>
</tr>
</tbody>
</table>

motion segment in the reproduction and the direction of the corresponding segment in the stimulus model. (See Agam et al. (2005) for a comparison of scalar measures for accuracy on this task.)

On every trial, a unique trajectory was presented either four or five times (see Table 2.1), with subjects reproducing the sequence after each such presentation. This allowed me to measure familiarity-induced changes in the quality of the reproduction.

### 2.2.2 Datasets

Table 2.1 identifies the sources and details of the behavioral data used to fit a family of four related models. Four of the datasets were previously published using mean absolute direction error to characterize learning. Each dataset is from an experiment with between 8 and 12 subjects and approximately 75 trials per subject. Three datasets are from experiments using five-segment motion trajectories with each trajectory repeated four times; three are from experiments using six-segment trajectories with each trajectory repeated five times.

The precise size and timing of stimuli varied somewhat across the six studies. Each segment of a trajectory took 500-525 ms; pauses at the corners of segments lasted 225-450 ms. Stimuli were thus 3400-5400 ms in length. During one experiment, subjects were instructed to track the
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stimulus disc with their eyes (Maryott et al., 2011, Experiment 1), in two others they were instructed to maintain fixation at the center of the screen (Noyce & Sekuler, in revisions; Noyce & Sekuler, unpublished), and in the remaining three they were given no instructions about eye movements (Agam et al., 2007, Experiments 1 and 2; Maryott et al., 2011, Experiment 2). Depending on the eye movement instructions, the size of the stimulus varied, such that each segment traversed $4.5^\circ$ (tracking), $1^\circ$ (fixation), or $1.5^\circ$ (free eye movements) visual angle.

2.2.3 Models

I fit four members of a family of VSTM models to data collected from a visual sequence-learning task, and assessed the ways that the models’ parameters varied with serial position and repeated presentation.

Model 0: Slots Mixture Model

The simplest class of models I considered was based on the one described by Wilken and Ma (2004) and Zhang and Luck (2008). Here, the probability that subjects make a response error $x$ is given by:

$$P(x) = (1 - g) \times M_{(0, \text{SD})}(x) + g \times U(x)$$

responses from memory  
guess responses

where $M_{(\mu, \sigma)}(x)$ is the probability density function of the von Mises distribution with mean $\mu$ and standard deviation $\sigma$, as evaluated at $x$ and $U(x)$ is the probability density function of a uniform distribution, evaluated at $x$.

This model predicts a distribution of response errors that comprises the sum of a von Mises (circular Gaussian) distribution with standard deviation $\text{SD}$ and mean zero, and a uniform distribution. $g$ specifies the proportion of the distribution that is from the uniform component; the
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remainder is from the von Mises component. In other words, SD relates to the precision of an item’s representation in working memory, and g relates to the probability that the item is in memory at all.

Model 0 required each of these parameters to be fixed across serial positions, to allow testing of the hypothesis that VSTM for items does not vary with their serial position. Zhang and Luck (2008, 2009, 2011)’s conceptualization of VSTM as a set of two to four slots specifies that memory resources are allocated in fixed quanta, and cannot accommodate effects of serial position on memory accuracy.

Model 1: Standard Mixture Model

Model 1 allows both SD and g to vary across serial positions. The probability of a response error x is given by the same equation as in Model 0, except that this distribution is computed independently for each serial position on each repeated presentation. Previous analyses of these data have shown strong serial-position effects on accuracy, and so this and all subsequent models allow parameters to vary with serial position.

Model 2: Standard Mixture Model With Swaps

The third model in the family was described by Bays et al. (2009). This model extends the Standard Mixture Model to account for the possibility that subjects report non-target items from a stimulus display, rather than making random errors. Remember that “random” here means that subjects selected a response without being affected by the item they’re supposed to be reproducing, nor by any other items in the stimulus set. In Model 2, the probability that subjects make a response error
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\[ P(x) = (1 - g - B) \times M_{(0, SD)}(x) + g \times U(x) + \sum_{i=1}^{D} \left( \frac{B}{D} \times M_{(d, sd)}(x) \right) \]

responses from memory  \hspace{2cm} \text{guess responses}  \hspace{2cm} \text{inter-item confusion responses}

with distribution terms as above; \( d_i \) refers to the \( i \)th other segment in the trajectory, of \( D \) total other segments. (These are equivalent to “distractors” in the snapshot displays.)

This model incorporates information about the other segments in the trajectory, and produces a distribution of response errors that comprises the sum of a uniform distribution with several Gaussian distributions. With probability \( B \), responses are drawn from a von Mises distribution centered on one of the other segments in the display (each other segment is equiprobable); with probability \( g \), responses are drawn from the uniform distribution; with probability \( (1 - g - B) \), responses are drawn from the von Mises distribution centered on the target.

Note that my implementation of this model does not restrict to “true swaps” among items. That is, I don’t restrict to cases where item A is reported as item B and item B is reported as item A. The swaps are estimated for each serial position independently. This allows the possibility that subjects report one item at more than one serial position.

Model 3: Variable Precision Model

The final of my family of models is based on those described by Fougnie et al. (2012) and van den Berg et al. (2012). Instead of fixing a precision parameter, this model allows it to vary across trials. It is plausible that the allocation of memory resources among items, and even the amount of memory resources available to encode the set, may vary across trials. Thus, the probability of a
response error \( x \) on the \( i \)th trial is given by:

\[
P(x) = (1 - g) \times M_{(0, sd_i)}(x) + g \times U(x)
\]

where \( sd_i \) is drawn from the Gamma distribution with scale:

\[
\theta = \frac{2sdSD^2}{\text{modeSD} + \sqrt{\text{modeSD}^2 + 4sdSD^2}}
\]

and shape:

\[
k = 1 + \text{modeSD} + \frac{1}{\theta}
\]

The parameters that are fitted here are \( g \), the probability that responses are from the uniform distribution, and \text{modeSD} and \text{sdSD} which characterize the Gamma distribution from which precision values are drawn on any given trial. High \text{modeSD} values characterize a distribution “centered” around less-precise representations, while high \text{sdSD} values characterize a distribution with a lot of variability in precision values.

This model produces a distribution of responses that comprises the sum of a uniform distribution and many von Mises distributions with mean 0 and varying SDs. The resulting distribution is “peakier” than that of the Standard Mixture Model.

### 2.2.4 Model fitting

Models were specified and fitted using the MemToolbox (Suchow, Brady, Fougnie, & Alvarez, 2013) for Matlab (The MathWorks, In., Natick, MA). Within each dataset, I fitted each model to the distribution of responses produced at each serial position on each repeated presentation. For example, for the five-segment datasets, I fit each model independently to five segment serial positions on each of four repeated presentations. The model fitting protocol used an iterative
maximum likelihood procedure, which started three searches at different locations within the parameter space, adjusted the parameters until a local maximum was reached, and ran until the three searches converged. Further, I took advantage of MemToolbox’s hierarchical fitting abilities, which constrain the parameters by requiring that each fitted parameter be normally distributed across the subjects in each dataset. This helps keep the fitting procedure from converging on extremely unlikely values, a trait that was particularly important because of the noisiness of these data, and because of the correlations among model parameters.

### 2.2.5 Measures

After fitted model parameters were calculated, I used two measures to summarize familiarity’s influence on the representation of items in VSTM. First, to characterize the overall trend in each parameter, I took its mean fitted value across serial positions, on each repeated presentation. Second, to characterize the magnitude of serial position effects, I took the standard deviation of the parameter’s values at each serial position.

To test the significance of these summary measures’ changes across presentations, I used a permutation test. On each of 10,000 iterations, each subject’s fitted parameter values were randomly allocated among segments and presentations. The two summary measures described above were calculated subjectwise for each simulated presentation. The slope of the best-fitting line over serial positions was calculated, giving a distribution of 10,000 such slopes for each measure and parameter. Familiarity-induced changes in parameter values were then tested against these distributions.

I used two measures to compare models. First, the Akaike information criterion (AIC), given by

\[
AIC = 2k - 2 \ln(L)
\]

where \(k\) is the number of parameters in the model, and \(L\) is the likelihood of the fitted model.
Because the models were fitted using maximum likelihood estimation, AIC is maximized in the fitting process. I therefore also compared models using a statistic that will behave somewhat differently, the Kuiper statistic (Kuiper, 1960). Unlike measures such as likelihood and root mean squared error, the Kuiper statistic is intended for comparing continuous, rather than discrete, distributions. It is related to the better-known Kolmogorov-Smirnov (K-S) measure, but is more sensitive at the tails of the distribution and is cyclicly invariant (and so better suited for assessing probability distributions in circular space). The Kuiper statistic consists of the empirically-obtained cumulative distribution function’s maximum distance above the model cumulative distribution function, added to the empirical cumulative distribution function’s maximum distance below the model cumulative distribution function.

\[
\text{Kuiper} = \max(\text{cdf}_{\text{model}} - \text{cdf}_{\text{data}}) + \max(\text{cdf}_{\text{data}} - \text{cdf}_{\text{model}})
\]

For each pairwise comparison between models, I bootstrapped a distribution of mean difference in Kuiper statistics and mean difference in AIC. For each subject, I averaged the probability density functions of the two models being compared, and used the resulting distribution to generate two samples of trials. I calculated the Kuiper statistic and AIC for each sample, took the differences, and averaged those differences across my 64 subjects. I thus derived a distribution of 500 such differences that arose when the null hypothesis was true and the samples were drawn from the same distribution. Comparing my empirically-obtained Kuiper statistics and AIC differences to this distribution allowed me to obtain \(p\)-values.
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Table 2.2: Results of repeated-measures ANOVAs on mean absolute directional error, with factors presentation and serial position.

<table>
<thead>
<tr>
<th>parameter</th>
<th>source</th>
<th>df1, df2</th>
<th>five-segment data</th>
<th>six-segment data</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>F</td>
<td>partial \eta^2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>F</td>
<td>partial \eta^2</td>
</tr>
<tr>
<td>presentation</td>
<td></td>
<td>3, 96</td>
<td>77.435***</td>
<td>.708</td>
</tr>
<tr>
<td>serial position</td>
<td></td>
<td>4, 128</td>
<td>44.036***</td>
<td>.579</td>
</tr>
<tr>
<td>pres. × serial pos.</td>
<td></td>
<td>12, 384</td>
<td>5.655***</td>
<td>.150</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4, 120</td>
<td>156.237***</td>
<td>.839</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5, 150</td>
<td>57.457***</td>
<td>.657</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20, 600</td>
<td>15.708***</td>
<td>.344</td>
</tr>
</tbody>
</table>

\^p < .1. *p < .05. **p < .01. ***p < .001.

2.3 Results

In this section, I first present the actual accuracy data, then fitted parameters from each model, and finally comparisons between the four models I tested.

2.3.1 Accuracy

Figures 2.2 and 2.3 show the distributions of errors that subjects make while performing this task, for the five-segment and six-segment data. Subjects’ mean absolute directional error on each segment was $21.66^\circ$ (SD = $6.46^\circ$).

Separate two-way repeated-measures ANOVAs on the five-segment and six-segment data confirmed a significant main effect of presentation ($p < .001$), a significant main effect of serial position ($p < .001$), and a significant interaction between the two ($p < .001$). The full results are shown in Table 2.2.
Figure 2.2: Histograms showing the distributions of errors generated by 33 subjects on the five-segment task. Each row corresponds to a presentation; each column corresponds to a serial position. Distributions generated on early presentations are short, squat, and kurtotic, especially at the penultimate serial position; distributions generated on late presentations are tall and narrow.
Figure 2.3: Histograms showing the distributions of errors generated by 31 subjects on the six-segment task. Each row corresponds to a presentation; each column corresponds to a serial position. Distributions generated on early presentations on short, squat, and kurtotic, especially at the penultimate serial position; distributions generated on later presentations are tall and narrow.
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Figure 2.4: Model 0: Standard Mixture Model with no serial position variability. Fitted SD (top) and g (bottom) values from the standard mixture model, by segment serial position and repeated presentation. Note that the fitted g values for 5-segment sequences are nearly identical on presentations three and four, making the plotted lines overlap to the point where presentation four appears to be missing. Error bars are repeated-measures standard error (Loftus & Masson, 1994; Cousineau, 2005; Morey, 2008).
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Figure 2.5: Model 0: Error distributions and fitted model predictions for a representative subject. Panels are arranged in rows by presentation and in columns by serial position.

2.3.2 Model 0: Standard Mixture Model with no serial position variability

Figure 2.4 shows the fitted SD and g values from Model 0 (Standard Mixture Model with no serial position variability), across segment serial position and repeated presentation. In each panel, five-segment sequences are shown on the left and six-segment sequences are shown on the right. Note that for both parameters and both sequence lengths, the fitted values are higher (reflecting worse memory performance) on the first presentation than on subsequent presentations.

Figure 2.5 shows the error distributions generated by a representative subject who was perform-
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Table 2.3: Results of repeated-measures ANOVAs on each parameter of Model 0, with factor presentation.

<table>
<thead>
<tr>
<th>parameter</th>
<th>source</th>
<th>five-segment data</th>
<th></th>
<th></th>
<th>six-segment data</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>SD</td>
<td>presentation</td>
<td>3, 96</td>
<td>10.270***</td>
<td>.243</td>
<td>4, 120</td>
<td>12.684***</td>
<td>.297</td>
</tr>
<tr>
<td>g</td>
<td>presentation</td>
<td>3, 96</td>
<td>5.132**</td>
<td>.138</td>
<td>4, 120</td>
<td>15.395***</td>
<td>.339</td>
</tr>
</tbody>
</table>

*p < .05. **p < .01. ***p < .001.

ing the five-segment version of the task. Overlain on the histograms are the distributions predicted by this subject’s fitted Model 0 parameters.

Separate one-way repeated-measures ANOVAs on the five-segment and six-segment data confirmed a significant main effect of presentation (p < .003 for both SD and g). The full results are shown in Table 2.3.

Figure 2.6 summarizes the change in each parameter across repeated presentations. On average, SD decreases across presentation (p < .001), suggesting that subjects represent each item more precisely as items become more familiar. Similarly, on average, g decreases across presentations (p < .001), suggesting that increased familiarity supports subjects in successfully forming a representation of each item.

2.3.3 Model 1: Standard Mixture Model

Figure 2.7 shows the fitted SD and g values from Model 1 (Standard Mixture Model), across segment serial position and repeated presentation. In each panel, five-segment sequences are shown on the left and six-segment sequences are shown on the right. Note that for both parameters and both sequence lengths, fitted values are higher (reflecting worse memory performance) on the first presentation than on subsequent presentations. Further, the shapes of the first presentation curves
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Figure 2.6: Effects of repeated presentations on the fitted parameters of Model 0 (Standard Mixture Model with no serial position variability). (top) Mean SD significantly decreases over repeated presentations for 5-segment (blue) and 6-segment (green) stimuli ($p < .001$). (bottom) Mean g significantly decreases over repeated presentations ($p < .001$).

for SD differ substantially from the those for g, with SD showing a strong primacy effect through the penultimate item, while g shows only a 1-item primacy effect.

Figure 2.8 shows the error distributions generated by a representative subject who was performing the five-segment version of the task. Overlaid on the histograms are the distributions predicted by this subject’s fitted Model 1 parameters.

Separate two-way repeated measures ANOVAs on the five-segment and six-segment data separately confirmed a significant main effect of presentation ($p < .001$) and a significant main effect of serial position ($p < .001$) for both parameters, and a significant presentation by serial
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Figure 2.7: Model 1: Standard Mixture Model. Fitted SD (top) and g (bottom) values from the standard mixture model, by segment serial position and repeated presentation.

position interaction for SD (p < .01). The full results are shown in Table 2.4.

Figure 2.9 summarizes the change in each parameter across repeated presentations. On average, SD decreases across presentations (p < .001), suggesting that subjects represent each item more precisely as items become more familiar. Further, the inter-item variation in SD also decreases as items become more familiar (p < .001), suggesting that the learning process enables subjects to more evenly allocate resources among items in a sequence. Similarly, on average, g decreases across
Figure 2.8: Model 1: Error distributions and fitted model predictions for a representative subject. Panels are arranged in rows by presentation and in columns by serial position.
Table 2.4: Results of repeated-measures ANOVAs on each parameter of Model 1, with factors presentation and serial position.

<table>
<thead>
<tr>
<th>parameter</th>
<th>source</th>
<th>df₁, df₂</th>
<th>F</th>
<th>partial $\eta^2$</th>
<th>df₁, df₂</th>
<th>F</th>
<th>partial $\eta^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SD</td>
<td>presentation</td>
<td>3, 96</td>
<td>38.131***</td>
<td>.544</td>
<td>4, 120</td>
<td>64.438***</td>
<td>.682</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>21.169***</td>
<td>.398</td>
<td>5, 150</td>
<td>24.223***</td>
<td>.447</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>2.833**</td>
<td>.081</td>
<td>20, 600</td>
<td>6.456***</td>
<td>.177</td>
</tr>
<tr>
<td>g</td>
<td>presentation</td>
<td>3, 96</td>
<td>27.084***</td>
<td>.458</td>
<td>4, 120</td>
<td>44.223***</td>
<td>.600</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>15.484***</td>
<td>.587</td>
<td>5, 150</td>
<td>13.946***</td>
<td>.317</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>1.457</td>
<td>.044</td>
<td>20, 600</td>
<td>2.475**</td>
<td>.076</td>
</tr>
</tbody>
</table>

~p < .1. *p < .05. **p < .01. ***p < .001.

presentations ($p < .001$), suggesting that increased familiarity supports subjects in successfully forming a representation of each item, and the inter-item variation in $g$ also decreases ($p < .001$), further supporting the hypothesis that learning enables subjects to allocate resources more evenly.

2.3.4 Model 2: Standard Mixture Model With Swaps

Figure 2.10 shows the fitted SD, g, and B values from Model 2 (the model with inter-item swaps), across segment serial position and repeated presentation. Five-segment sequences are shown on the left of each panel; six-segment sequences are shown on the right. The fitted values of SD and g are higher (reflecting worse memory performance) on the first presentation than on subsequent presentations, and the curves for these parameters are extremely similar to those from Model 1. B (probability of inter-item confusions) accounts for less than 1% of all responses, and shows no consistent patterns across serial position or repeated presentation.

Figure 2.11 shows the error distributions generated by a representative subject who was performing the five-segment version of the task. Overlaid on the histograms are the distributions predicted
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![Graphs showing serial position effects on SD and g](image)

Figure 2.9: Effects of repeated presentations on the fitted parameters of Model 1 (Standard Mixture Model). (A) Mean SD decreases over repeated presentations for 5-segment (blue) and 6-segment (green) stimuli. (B) Variability in SD across serial positions decreases over repeated presentations. (C) Mean g decreases over repeated presentations. (D) Variability in g across serial positions decreases over repeated presentations.

by this subject’s fitted Model 2 parameters. These distributions appear virtually identical to those predicted by Model 1 because the contribution of B is very small.

Separate two-way repeated measures ANOVAs on the five-segment and six-segment data confirmed a significant main effect of presentation \((p < .001)\) and a significant main effect of serial position \((p < .001)\) for both SD and g, and a significant presentation by serial position interaction for SD \((p < .001)\). Neither main effect, nor the interaction, was significant for B. The full results
Figure 2.10: Model 2: Fitted SD (top), g (middle), and B (bottom) values from the model with inter-item confusions, by segment serial position and repeated presentation.
Figure 2.11: Model 2: Error distributions and fitted model predictions for a representative subject. Panels are arranged in rows by presentation and in columns by serial position.
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Table 2.5: Results of repeated-measures ANOVAs on each parameter of Model 2, with factors serial position and presentation.

<table>
<thead>
<tr>
<th>parameter</th>
<th>source</th>
<th>five-segment data</th>
<th>six-segment data</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>df₁, df₂</td>
<td>F</td>
</tr>
<tr>
<td>SD</td>
<td>presentation</td>
<td>3, 96</td>
<td>37.866***</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>21.869***</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>2.948***</td>
</tr>
<tr>
<td>g</td>
<td>presentation</td>
<td>3, 96</td>
<td>26.498***</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>16.169***</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>1.349</td>
</tr>
<tr>
<td>B</td>
<td>presentation</td>
<td>3, 96</td>
<td>.104</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>1.498</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>1.198</td>
</tr>
</tbody>
</table>

~p < .1. *p < .05. **p < .01. ***p < .001.

are shown in Table 2.4.

Figure 2.12 shows the change in each parameter across repeated presentations. SD and g show essentially the same patterns as in Model 1 (means and variability decrease across presentations, all ps < .001); B does not reliably change with presentation, nor does its serial position variability (all ps > .1).

2.3.5 Model 3: Variable Precision Model

Figure 2.13 shows the fitted modeSD, sdSD, and g values from Model 3 (variable precision model with guessing). Five-segment sequences are shown on the left of each panel, six-segment sequences are shown on the right. The fitted values of modeSD, sdSD, and g are all higher (reflecting worse memory performance) on the first presentation than on subsequent presentations.
Figure 2.12: Effects of repeated presentations on the fitted parameters of Model 2 (model with inter-item confusions). (A, C) Mean SD and g decrease over repeated presentations for 5-segment (blue) and 6-segment (green) stimuli. (B, D) Variability in SD and g across serial positions decreases over repeated presentations. (E) B does not vary over repeated presentations. (F) Variability in B across serial positions does not vary with repeated presentations.
Figure 2.13: Model 3: Fitted modeSD (top), sdSD (middle), and g (bottom) values from the variable-precision model with guessing, by segment serial position and repeated presentation.
Figure 2.14: Model 3: Error distributions and fitted model predictions for a representative subject. Panels are arranged in rows by presentation and in columns by serial position.
Table 2.6: Results of repeated-measures ANOVAs on each parameter of Model 3, with factors presentation and serial position.

<table>
<thead>
<tr>
<th>parameter</th>
<th>source</th>
<th>five-segment data</th>
<th>six-segment data</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df1, df2</td>
<td>F</td>
<td>partial η²</td>
</tr>
<tr>
<td><strong>modeSD</strong></td>
<td>presentation</td>
<td>3, 96</td>
<td>6.615***</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>6.645***</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>0.936</td>
</tr>
<tr>
<td><strong>sdSD</strong></td>
<td>presentation</td>
<td>3, 96</td>
<td>5.414**</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>3.021*</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>0.941</td>
</tr>
<tr>
<td><strong>g</strong></td>
<td>presentation</td>
<td>3, 96</td>
<td>19.409***</td>
</tr>
<tr>
<td></td>
<td>serial position</td>
<td>4, 128</td>
<td>11.425***</td>
</tr>
<tr>
<td></td>
<td>pres. × serial pos.</td>
<td>12, 384</td>
<td>1.583</td>
</tr>
</tbody>
</table>

* p < .05. ** p < .01. *** p < .001.

Figure 2.14 shows the error distributions generated by a representative subject who was performing the five-segment version of the task. Overlaid on the histograms are the distributions predicted by this subject’s fitted Model 2 parameters. The markedly-different shapes of these distributions is caused by the combination of multiple von Mises distributions, due to the assumption of variable precision across trials.

Separate two-way repeated measures ANOVAs on the five-segment and six-segment data separately confirmed a significant main effect of presentation (p < .001) and a significant main effect of serial position (p < .001) for both modeSD and g, and a significant presentation by serial position interaction for both parameters on the six-segment data (p < .05). Neither main effect, nor the interaction, was significant for sdSD. The full results are shown in Table 2.6.

Figure 2.15 summarizes the change in each parameter across repeated presentations. On average, modeSD decreases across presentations (p < .001 for both 5-segment and 6-segment stimuli),
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Figure 2.15: Effects of repeated presentations on the fitted parameters of Model 3 (the variable-precision model with guessing). (A) Mean modeSD decreases over repeated presentations for 5-segment (blue) and 6-segment (green) stimuli. (B) Variability in modeSD across serial positions decreases over repeated presentations. (C) Mean sdSD does not reliably change over repeated presentations. (D) Variability in sdSD across serial positions does not reliably change over repeated presentations. (E) Mean g decreases over repeated presentations. (F) Variability in g across serial positions decreases over repeated presentations.
implying that subjects are drawing from a range of precisions centered around increasingly precise representations. The inter-item variability in \texttt{modeSD} also decreases with repeated presentations. However, while both the mean values of \texttt{sdSD} and the serial position effects on \texttt{sdSD} had negative slopes, their decrease was less reliable ($0.020 < p < 0.071$). Finally, as in Models 1 and 2 both the average fitted values of $g$ and the serial position variability of $g$ decrease with repeated presentations ($p < 0.001$), similarly to the behavior of $g$ in Models 1 and 2.

One point which is not evident from any of the stats displayed here is that a majority of subject-segment-presentation combinations converge at the minimum \texttt{sdSD} value, making them effectively equivalent to the Model 1 (standard mixture model) fits. On average, 90.5\% of fits to the five-segment data and 87.0\% of fits to the six-segment data converged on the minimum \texttt{sdSD} value. To test whether such convergence depended on the presentation and segment serial position, I ran two-way repeated-measures ANOVAs on the five-segment and six-segment data separately. There was no significant effect of presentation, serial position, or the interaction between them (all $ps > 0.09$). This high rate of convergence to the minimum \texttt{sdSD} value makes me somewhat skeptical of Model 3’s apparent improvements.

### 2.3.6 Assessing model fits

I used the Akaike information criterion (AIC) and Kuiper statistic to assess the fit of each model. After computing the difference in these measures between pairs of models, I bootstrapped a distribution of differences that occurred when data were drawn from the same generative model. This allowed me to compute $p$-values for measures whose distributions are not known a priori, such as AIC and Kuiper.

Table 2.7 shows the pairwise differences in mean Akaike information criterion (AIC) between each of the models, and the associated $p$-values. As expected, the models with increasing complexity
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Table 2.7: Pairwise AIC comparison between models. Positive numbers imply a better fit (lower AIC) for the model in column B; negative numbers would imply a better fit for the model in column A.

<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>difference</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 0</td>
<td>Model 1</td>
<td>5.102</td>
<td>.500</td>
</tr>
<tr>
<td>Model 0</td>
<td>Model 2</td>
<td>9.217</td>
<td>.224</td>
</tr>
<tr>
<td>Model 0</td>
<td>Model 3</td>
<td>19.005</td>
<td>.032</td>
</tr>
<tr>
<td>Model 1</td>
<td>Model 2</td>
<td>3.779</td>
<td>.596</td>
</tr>
<tr>
<td>Model 1</td>
<td>Model 3</td>
<td>17.531</td>
<td>.024</td>
</tr>
<tr>
<td>Model 2</td>
<td>Model 3</td>
<td>13.752</td>
<td>.076</td>
</tr>
</tbody>
</table>

Table 2.8: Pairwise Kuiper statistic comparison between models. Positive numbers imply a better fit (lower Kuiper statistic) for the model in column B; negative numbers imply a better fit for the model in column A.

<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>difference</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 0</td>
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<td>−0.008</td>
<td>.524</td>
</tr>
<tr>
<td>Model 0</td>
<td>Model 2</td>
<td>−0.006</td>
<td>.596</td>
</tr>
<tr>
<td>Model 0</td>
<td>Model 3</td>
<td>0.006</td>
<td>.636</td>
</tr>
<tr>
<td>Model 1</td>
<td>Model 2</td>
<td>0.002</td>
<td>.776</td>
</tr>
<tr>
<td>Model 1</td>
<td>Model 3</td>
<td>0.014</td>
<td>.036</td>
</tr>
<tr>
<td>Model 2</td>
<td>Model 3</td>
<td>0.013</td>
<td>.232</td>
</tr>
</tbody>
</table>
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do show an AIC benefit, although the only significant differences are between Model 3, the variable precision model, and Models 0 and 1 (mean AIC is 19.005 lower in Model 3 than Model 0, \( p = .032 \); AIC is 17.531 lower in Model 3 than Model 1, \( p = .024 \)). Table 2.8 shows the pairwise differences in mean Kuiper statistic between each of these models. Effects here are almost entirely non-significant, with Model 0 outperforming Models 1 and 2 (although with \( p > .52 \)), and Models 2 and 3 outperforming Model 1. However, the only significant effect is between Model 3, the Variable Precision Model, and Model 1, the Standard Mixture Model (mean Kuiper statistic is 0.014 lower in Model 3, \( p = .036 \)).

2.4 Discussion

I investigated the effects of learning on visual short-term memory by using data collected from a visuomotor sequence-learning task. Subjects viewed and reproduced sequences of motion segments several successive times, and the accuracy with which they did so was recorded. I then fit four related models to the distributions of response errors, and assessed how the models’ parameters changed with increased familiarity with each sequence. Unlike previous work on the role of learning in this task (Agam et al., 2007, 2010; Maryott et al., 2011), my model-fitting can specify the degree to which different kinds of memory failures contribute to subjects’ performance.

I found that no matter which model I fit, the value of the parameter or parameters describing the spread of subjects’ responses decreased over repeated presentations, suggesting that the learning process utilizes long-term memory to increase the precision of representation in memory. Further, this decrease was not linear; rather, the decrease from the first presentation to the second was larger than any of the following changes. Familiarity produced a noticeable increase in VSTM precision after only a single exposure. The magnitude of the serial position effect on this parameter also decreased across repetitions, again with large decreases from the first to second presentation,
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followed by smaller changes thereafter.

Similarly, when models included a parameter describing the probability that subjects responded randomly rather than giving a response based on the item being probed, that parameter’s value decreased over repeated presentations. This suggests that long-term memory resources not only enable subjects to reproduce items more precisely, but also enable them to maintain more items in memory. Again, the magnitude of the serial position effect decreased across repeated presentations, and, again, both of these decreases were largest from the first to second presentation, with smaller changes thereafter.

Previous work on this task assessed the likelihood of transpositions, operationalizing them as cases where swapping two segments in the reproduction led to lower absolute error on both (Agam et al., 2005). Here, I am using a very different approach to assess the frequency of swaps. Simulations suggest that, even if each memory representation is centered on the correct segment, the imperfections of such representations can lead to cases where swapping segments would reduce absolute error. The analysis here only counts swaps that occur above the levels that are attributable to imperfect representations. Unlike Agam et al. (2005)’s result, my Model 2 found very low levels of inter-item confusions, with no systematic effects of serial position and presentations. Apparent transpositions can result from noisy representations alone.

My results make clear that the learning induced by repeated encounters with each trajectory changes two separate aspects of the VSTM representation of the segments in that trajectory. The representation of each segment becomes more precise, and the probability that each segment is successfully stored and retrieved increases. In short, familiarity is not just inducing a tradeoff between parameters, but actually increasing the amount of information that subjects are able to hold in VSTM and retrieve on demand. Further, these simultaneous changes are seen after even one prior presentation – the mechanism underlying this increased capacity is capable of one-shot learning. I should note that I am assuming that long-term memory supports increased retention
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ability, but it is also possible that the support is occurring instead (or as well) at encoding or at retrieval. These studies do not allow me to determine at which memory stage the improvements are occurring. This is counter to other results that propose a trade-off between precision and capacity in VSTM (Roggeman, Klingberg, Feenstra, Compte, & Almeida, 2013). However, those authors did not look at the effects of learning or familiarity; their subjects only saw each display one time.

One possible neural mechanism by which long-term memory processes are able to support VSTM after previous exposures to a stimulus is chunking, in which subjects group segments into larger items (Miller, 1956; Agam & Sekuler, 2008; Gobet & Simon, 1998). When an item is composed of a few chunks rather than of many segments, each chunk can have more memory resources allocated to it, possibly leading to improved precision and capacity. Maryott and Sekuler (2009) showed that young adults perform better on trajectories whose segments are easily grouped than they do on those whose segments are not, suggesting that a grouping or chunking process may underly performance on this task.

Another possible mechanism underlying these changes with familiarity is that as the brain learns about a given stimulus, it develops a sparser representation of the elements of that sequence (Barlow, 1961; Agam et al., 2010; Karlsson & Frank, 2008). That is, the number of neurons required to represent each element is decreased, likely through changes in neuronal tuning. As the representation becomes sparser, there may be less overlap among the representations of the elements of a given trajectory, so that it is easier for the brain to maintain separate representations. This could allow both more precise representations of a direction of motion, and the maintenance of a greater number of such representations simultaneously.

Note that familiarity-induced changes in both precision and guess rate converge on a flat serial position curve. On successive presentations of the same stimulus sequence, the VSTM system is reallocating memory resources such that errors are distributed more evenly among items. In other words, the presentation-over-presentation changes in precision and guess rate are larger for items
that had high amounts of error on the first presentation, and lower (or even zero) for those that had low amounts of error. Such dynamic reallocation suggests a strong preference within the system for representing all items imperfectly, rather than trading off high precision on one item for poor precision on another.

It also demonstrates that the VSTM system has access to a great deal of metacognitive information about the quality of the representations in long-term memory. This information may be directly accessible from long-term memory, or it may be accessed more indirectly. For example, the system may attempt to predict the direction of the disk on the subsequent presentation, and use the degree of error on each segment as a cue to allocate more memory resources to that segment. Future work should attempt to distinguish between these possibilities.

Further, my results are inconsistent with a slots conceptualization of VSTM resource allocation (as proposed by Zhang & Luck, 2008, 2009, 2011), in which short-term memory resources are allocated in quanta of fixed size. Such a model is insufficient to account for the variation in precision and guess rate that I see in my fitted model parameters. The effects of segment serial position and of repeated presentation, along with the model-fitting comparison’s support for the variable-precision model, implies greater flexibility in the system, and integration with long-term memory processes, than has previously been demonstrated. In particular, the reliable familiarity-induced decrease in guessing cannot be accounted for by a slot model. VSTM resources must be flexibly allocated to produce the results presented in this chapter.
Chapter 3

P300 to violations of newly learned predictions

3.1 Introduction

The human brain frequently operates in feedforward mode, exploiting previously-experienced regularities to build expectations for future events. This proactive operation facilitates perceptual processing (Bar, 2009) and makes it possible for appropriate behaviors to be prepared and executed in a timely fashion (e.g. Kowler, 1989; Maryott et al., 2011). Among the richest regularities available to the brain are ones entailed not in single isolated events, but in event sequences. In fact, the brain constructs and continuously updates its representation of such sequential regularities in an obligatory and effortless manner (Johnson & Donchin, 1982; Kimura, Kondo, Ohira, & Schröger, 2011; Sternberg & McClelland, 2012).

In order to benefit fully from the advantages of feedforward operation, the brain must have a mechanism to detect events that violate its expectations, and to thereby trigger an appropriate response (Winkler, 2007). Such responses might include heightening attention to the unexpected
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event, modifying or delaying a prepared behavior, or updating the brain’s representation of the
regularity at hand.

Event-related brain potentials (ERPs) provide a direct measure of neural activity that is time-
locked to specific events (Luck, 2005). Their temporal precision makes ERPs a useful tool for
studying the neural reaction to individual events within a sequential structure. The P3 is one ERP
component that has been hypothesized to reflect the brain’s response to a novel or surprising stimulus
(Linden, 2005; Polich, 2007; K. C. Squires, Wickens, Squires, & Donchin, 1976). While the P3
has historically been studied in oddball paradigms (e.g Courchesne, Hillyard, & Galambos, 1975;
N. K. Squires, Squires, & Hillyard, 1975; Zuijen, Simoens, Paavilainen, Näätänen, & Tervaniemi,
2006), where a stream of stimuli contains both frequent and infrequent stimulus exemplars, it has
also been studied in sequence-learning tasks. Stimuli that deviate from an established sequential
structure elicit a larger P3 response than stimuli that conform to the sequential structure (Ferdinand et
al., 2008; Rüsseler & Rösler, 2000; Rüsseler, Hennighausen, Münte, & Rösler, 2003; Schlaghecken,
Stürmer, & Eimer, 2000). However, the studies demonstrating this P3 enhancement have required
subjects to learn only a single sequence per block of trials, allowing them to encode and maintain
one sequential regularity that remained valid for an extended period of time.

I wanted to investigate the neural mechanisms underlying sequence learning and prediction
monitoring in a more ecologically valid setting, where the governing regularities were short-lived.
To do so, I adopted the task used by Maryott et al. (2011) to investigate the behavioral response to
deviant events embedded in complex sequential structures that frequently changed. In that study,
subjects had to remember and reproduce short sequences of movements, each approximately five
seconds long. Each sequence was seen and reproduced several times, but occasionally a deviant,
unexpected item was inserted into a well-learned sequence. Subjects successfully incorporated the
deviant items into their representation of the sequence, and even showed a slight benefit for deviant
items. Note that Maryott et al.’s task differs from traditional sequence-learning paradigms such as
the serial reaction time task (Nissen & Bullemer, 1987) in that it required that the brain frequently update its representation of the governing sequential structure, as a new sequence began every 60-90 seconds.

To investigate whether this dynamic, changing context would alter the brain’s response to a deviant sequence item, I recorded EEG signals from subjects who were performing a variant of the task used by Maryott et al., and measured ERPs to new, familiar, and deviant sequence items. I hypothesized that I would find a P3-like component in response to both new and deviant sequence items, but that the timing and distribution would vary somewhat between the two conditions, capturing the distinctions that have previously been found between the Novelty P3 and the task-relevance P300 (Polich, 2007; Goldstein et al., 2002; Linden, 2005).

Here, I show that both new and deviant sequence items evoke a larger P3 than do familiar sequence items. Deviant sequence items elicit both a P300 and a Novelty P3 relative to familiar items, while new sequence items elicit only a P300 (and that of slightly lower amplitude). My results show that the neural response to deviant sequence elements in a frequently updated environment confirms that to deviant items in more stable settings.

### 3.2 Methods

#### 3.2.1 Subjects

Twelve young adults (seven female, ages 19–28) participated in this experiment. All were naïve to the task; all were right-handed.
3.2.2 Experimental task

To induce and measure sequence learning, I asked participants to observe and reproduce pseudo-random motion trajectories. Each trajectory was presented four successive times, and each participant saw 128 different trajectories.

On each presentation of a trajectory, a small disk traversed a path comprising five connected linear motion segments. Figure 2.1 illustrates the sequence of events within one such presentation. Each segment of the trajectory was 1 cm (approximately 1° visual angle) in length, and the disk moved at a constant speed of 2 cm per second, taking 500 ms to travel the length of each segment. After each segment, the disk paused for 400 ms before resuming its motion in a changed direction. The yellow disk then disappeared from view. After a retention interval of 3750 ms, a second disk appeared, cueing the subject to move a handheld stylus over the surface of a graphics tablet (31 × 24 cm; Intuos 3, Wacom, Vancouver, WA) in order to reproduce from memory the sequence of disk motions that had just been seen. During the reproduction, the disk’s motion was yoked to the movement of the stylus’ tip on the graphics tablet. No other feedback was provided. Note that neither the stimulus nor the reproduction disk left a visible trail while moving across the computer display. Subjects viewed the stimuli from a distance of approximately 57 cm, and were instructed to maintain fixation on a central cross, and refrain from blinking, while the stimulus disk was on the screen.

Each trial’s quasi-random sequence of five motion segments was generated by the algorithm described by Agam et al. (2005). The direction of a sequence’s initial motion was chosen randomly, and the direction change at each corner of the trajectory was between 30° and 150°. These changes in direction could be clockwise or counter-clockwise, with equal probability. The motions comprising any sequence were constrained by several additional rules: Motion segments were not permitted to intersect, could not come within one-half a segment’s length of intersecting, nor could they extend
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beyond the boundaries of the display area.

3.2.3 Design and procedure

On every trial, that trial’s unique trajectory was presented four times, with participants reproducing the sequence after each such presentation. Each set of four presentations constituted either a Congruent trial, in which all four presentations of a sequence were identical to one another, or a Flip trial, in which one motion segment changed direction on the sequence’s fourth (and final) presentation. On the last (fourth) presentation of a Flip trial, the established trajectory’s final segment was replaced by a segment in which the disk’s motion was $180^\circ$ opposite. Figure 3.1 illustrates these two conditions.

I operationalized three types of events: new, familiar, and deviant. New events were motion segments on their first presentation; familiar events were segments on their fourth presentation; deviant events were the “flipped” final segment of the final presentation on Flip trials. See Section 3.2.6 (page 52) for further descriptions of these operationalizations. Note that new events are congruent with the task context, and thus very similar to other events within the experiment.

Each subject completed four 45-minute experimental sessions, in which he or she observed and reproduced 32 different trajectories four times each. In each session, the first two trials were Congruent trials, followed by 20 Congruent and 10 Flip trials, block-randomized so that Flip trials were more evenly distributed. Forty trials (approximately 31%) were Flip trials; the remainder (88 trials) were Congruent trials. This approximates the ratio of Flip to Congruent trials used by Maryott et al. (2011), in which subjects did not anticipate the flips (as demonstrated by subjects’ anticipatory eye movements). Subjects were never informed that some trials would be Flip trials.
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Figure 3.1: The sequence of presentations that made up a Congruent trial or Flip trial. In my analyses I consider the first presentation of a stimulus to be new, the fourth presentation of a Congruent trial to be familiar, and the “flipped” segment at the end of a Flip trial to be deviant.

3.2.4 Behavioral data analysis

The fidelity of each reproduction was quantified offline by means of a two-step algorithm (Agam et al., 2005; Maryott et al., 2011) that used pauses and direction changes to divide the reproduction into segments. The algorithm then estimated the direction of each such segment by fitting a line to its beginning and end points. Reproduction accuracy was quantified by directional error: the absolute angular difference between the direction of a motion segment in the reproduction and the direction of the corresponding segment in the stimulus model.

Note that this segmentation algorithm fails if it divides a reproduced trajectory into a number of segments that differs from the number in the model trajectory. To increase the likelihood that reproductions would be successfully divided into five motion segments, I instructed subjects to try to produce the same number of segments that had been in the stimulus (five) and to, insofar as possible, draw straight lines with corners between them. These instructions allowed the segmentation algorithm to successfully divide over 90% of trials.
3.2.5 Electrophysiological recording

A high-density EEG system (Electrical Geodesics, Inc., Eugene, OR) with 129 electrodes sampled scalp electroencephalographic signals at 250 Hz using a high-impedance amplifier. Signals were recorded for later, off-line analysis. All channels were adjusted for scalp impedance below 50 kΩ; after 12 trials, channels were again adjusted for impedance below 50 kΩ scalp impedance before the subject completed the final 20 trials of the session.

3.2.6 EEG analysis

EEG data were cleaned and analyzed in the EEGLAB (Delorme & Makeig, 2004) and FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) toolboxes for Matlab (The Mathworks, Inc., Natick, MA). Data were re-referenced to the average voltage, bandpass filtered to between 0.25 and 75 Hz, and divided into epochs for each segment and each presentation. Every such epoch extended from 200 ms before that segment’s disk motion onset to 600 ms after. Data were visually inspected for muscle artifacts, eye movements, and bad channels; epochs containing such artifacts were rejected. Independent components analysis was used to isolate eye blink activity, which was subtracted from the data. Finally, data were again visually inspected for artifacts not corrected by the previous two processes. After cleaning, data were averaged across trials and sessions to create a subject average ERP for each combination of condition (Congruent or Flip), segment (one, two, three, four, or five), and presentation (one, two, three, or four.).

For each of the following investigations, I used a data-driven, non-parametric clustering approach (Maris & Oostenveld, 2007) to select time windows and electrodes for analysis. The FieldTrip toolbox includes software implementing this approach. It first calculates Student’s $t$ for each electrode and time point, and identifies clusters of time- and/or space-adjacent electrodes with $|t| > t_{critical}$. Critical $t$-values were selected by the experimenters according to several criteria,
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including the degrees of freedom of the comparison, the magnitude of the difference between the conditions, and the degree of spatial and temporal specificity desired.

For each cluster, the $t$-scores of the member electrodes and time-points were summed, giving a cluster score that reflected both the extent of the cluster (in space and time) and the magnitude of the difference between the conditions. A reference distribution of test statistics was generated by randomly permuting the data across the two conditions being compared, computing such scores for each resulting cluster, and taking the largest such cluster score on each of 1,000 permutations. Where cluster-wise $p$-values are reported, they are derived by comparing the empirically-obtained cluster score to such a reference distribution.

To confirm that experimenter selection of $t_{\text{critical}}$ is appropriate, I compared the clusters generated by the algorithm at three different values of $t_{\text{critical}}$. Results are shown in Figure 3.2. In each panel, blue circles denote the electrodes that are included in a statistically-significant (cluster-wise $p < .05$) positive cluster; red circles denote electrodes included in a statistically significant negative cluster. Below each electrode map is a timeline with a gray box showing the time window over which the cluster is significant. With the least-stringent value, $t_{\text{critical}} = 2.093$, the algorithm identifies a positive central cluster composed of 42 electrodes over a time window from 384–526 ms after disk motion onset (Figure 3.2, upper left panel). At a moderate value, $t_{\text{critical}} = 2.861$, the algorithm identifies a positive central cluster composed of 18 electrodes over a time window from 396–448 ms after disk motion onset (Figure 3.2, upper right panel). Finally, at $t_{\text{critical}} = 3.883$, the algorithm identifies a positive central cluster composed of 5 electrodes over a time window of 404–412 ms after disk motion onset (Figure 3.2, lower left panel). Adjusting the value of $t_{\text{critical}}$ expands or contracts the electrodes and time windows included in a cluster without dramatically distorting the cluster’s position or timing.

Grand average ERPs for each comparison of interest were created by averaging across subjects and across the electrodes identified as part of the cluster. I did three such comparisons.
Figure 3.2: The electrodes identified by my clustering algorithm at three different values of $t_{\text{critical}}$. In each panel, blue circles denote the electrodes that are included in a statistically-significant ($p < .05$) positive cluster, while red circles denote electrodes included in a statistically-significant negative cluster. The gray boxes on each timeline show the time window of each cluster. As cluster size decreases with higher criterion values, the position of the cluster is stable in both space and time.
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First, to assess the changes in neural responses as a new sequence item becomes increasingly familiar, I collapsed across segments two, three, four, and five\(^1\) of Congruent trials and computed subject-average ERPs for each presentation. I will refer to these four presentations as pres1, pres2, pres3, and pres4. Because the clustering approach requires pairwise comparisons, I used the difference between pres1 and pres2 to identify the electrodes and time window for this comparison. As seen in Chapter 2, the encoding and maintenance of repeated presentations of a given sequence item are supported by long-term memory. Therefore, the neural response to pres1 should reflect the increased demands of encoding an item that has not been previously seen and thus cannot draw on such long-term memory support.

Next, to measure the differences between neural responses to deviant sequence items and those to familiar sequence items, I calculated ERPs to segment five of presentation four on Congruent and Flip trials. Note that this is the segment and presentation on which the “flip” occurs on Flip trials. I will use Con_p4s5 and Flip_p4s5 to denote these two segments. Here, the response to Flip_p4s5 segments should reflect both the increased encoding demands also seen in pres1 and the prediction-monitoring processes that trigger such new encoding.

Finally, because both the comparison between new and familiar sequence items and the comparison between deviant and familiar sequence items incorporate an increased encoding load for one condition (new and deviant), and a reliance on expectation for the other (familiar), I directly compared the neural responses to new and deviant sequence items to allow me to dissociate the ERP correlates of unexpectedness from those of mere novelty. I computed ERPs to segment five of Flip trials on both presentation one and presentation four. I will refer to these two segments as Flip_p1s5 and Flip_p4s5. On presentation one, subjects cannot predict the segment’s direction of motion, nor do they expect to be able to predict it, while on presentation four, subjects do have

\(^{1}\)The sudden onset of disk motion at the start of the first segment evokes a neural response that is very different from that to the other segments (Agam & Sekuler, 2007).
predictions about the disk’s motion, which are violated by the deviant stimulus.

3.3 Results

3.3.1 Behavioral accuracy

Figure 3.3A shows subjects’ reproduction accuracy on Congruent trials. I ran a 5×4 repeated-measures ANOVA with factors segment (one, two, three, four, or five) and presentation (one, two, three, or four). There was a main effect of segment \( F(4,44) = 8.955, p = .003, \text{partial } \eta^2 = .449 \), and a segment by presentation interaction \( F(12,132) = 6.310, p = .048, \text{partial } \eta^2 = .364 \). There was also a main effect of presentation \( F(3,33) = 38.866, p < .001, \text{partial } \eta^2 = .779 \).

Follow-up analyses showed that the improvement in reproduction accuracy from presentation one to presentation two was significant \( F(1,11) = 62.654, p < .001, \text{partial } \eta^2 = .850 \), but the changes from presentation two to three and from three to four were not.

I also compared mean directional error on Flip and Congruent trials on presentation four (that is, the presentation on which these two trial types differed). I found no significant main effect of condition (Flip vs. Congruent, \( F(1,11) = 2.554, p = .138, \text{partial } \eta^2 = .189 \)), as shown in Figure 3.3B. These results replicate a central finding of Maryott et al. (2011) and confirm that subjects can successfully incorporate unexpected events into their planning and execution of a reproduced motion sequence.

3.3.2 ERPs

Figure 3.4 illustrates the changes in neural activity that accompany learning, as a stimulus goes from being new to being familiar over the course of four successive presentations. A data-driven clustering and permutation algorithm identified the cluster of electrodes that best captured \( p = .098 \)
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Figure 3.3: A: Mean directional error on Congruent trials across the five segments in a motion sequence. Data are displayed separately for each of the four presentations of a sequence. Subjects’ accuracy improved over repeated presentations. B: Mean directional error on Flip and Congruent trials for the fourth (final) presentation. The two conditions do not differ significantly. Error bars are repeated-measures standard error (Morey, 2008).

the change in scalp voltage topographies between pres1 and pres2. This cluster was derived using \( t_{\text{critical}} = 2.201 \), the critical \( t \)-value at \( \alpha = .05 \), \( df = 11 \). The cluster consisted of nine electrodes that were more positive-going on pres1 than pres2 during an interval from 200–280 ms after disk motion onset. The inset in Figure 3.4 depicts the distribution of \( t \)-scores between ERPs to the two presentations during that time window and the locations of the electrodes comprising this cluster;
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Figure 3.4: ERPs, collapsed across segments two through five, to **pres1**, **pres2**, **pres3**, and **pres4** on Congruent trials, at a cluster of central electrodes. The inset topographical plot shows the locations of the nine electrodes making up the significant cluster, and the distribution across the scalp of $t$ values at 200–280 ms after disk motion onset. The traces show ERPs at the cluster, timelocked to disk motion onset of each segment. Error ribbons are within-subject standard error (Morey, 2008), and thus do not reflect the process or results of the permutation significance test.
Figure 3.5: ERPs to \texttt{Con\_p4s5} (familiar) and \texttt{Flip\_p4s5} (deviant) at a cluster of central electrodes. The inset topographical plot shows the locations of the 18 electrodes making up the significant cluster, and the distribution across the scalp of \( t \) values at 396–448 ms after disk motion onset. The traces show ERPs at the cluster, timelocked to disk motion onset of each segment.

The traces in the main body of the figure show ERPs at this cluster, timelocked to each segment’s disk motion onset, for \texttt{pres1}, \texttt{pres2}, \texttt{pres3}, and \texttt{pres4}.

Figure 3.5 illustrates the differences between neural activity that accompanies familiar sequence item and that accompanying deviant items. I used the same approach as above to identify the cluster of electrodes that best captures \( p < .001 \) the difference between \texttt{Flip\_p4s5} and \texttt{Con\_p4s5} \( (i.e., \) deviant and familiar sequence items). This cluster was derived using \( t_{\text{critical}} = 3.106 \), the critical \( t \)-value at \( \alpha = .01 \), \( df = 11 \). The resulting cluster consisted of 18 electrodes that were more positive-going to the deviant item than to the familiar item from 396–448 ms after disk motion onset. The inset in Figure 3.5 depicts the distribution of \( t \)-scores between ERPs to \texttt{Flip\_p4s5} and to
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Con_p4s5 segments during that time window and the locations of the electrodes comprising this cluster; the traces in the main body of the figure depict ERPs at the cluster, timelocked to disk motion onset of segment five, for Flip_p4s5 (deviant) and Con_p4s5 (familiar).

Figure 3.6 highlights the differences between neural response to new and to deviant sequence items. Using the clustering algorithm described above, I identified two clusters of electrodes that captured differences between a new item, Flip_p1s5, and a deviant item in the same sequential position, Flip_p4s5. These clusters were derived using \( t_{\text{critical}} = 2.201 \), the critical \( t \)-value at \( \alpha = .05 \), \( df = 11 \). Figure 3.6A depicts the first (by time) resulting cluster \( (p = .025) \), which consisted of 16 electrodes that were more negative-going to the deviant sequence item than to the new item from 244–344 ms after disk motion onset for the segment. The inset of Figure 3.6A shows the distribution of \( t \)-scores between ERPs to the two segments during that time window (negative values imply Flip_p1s5 is more positive) and the locations of the electrodes comprising this cluster; the traces in the main body of Figure 3.6A depict ERPs at that cluster, time locked to disk motion onset. I included traces of the ERP to the equivalent familiar segment, Con_p4s5, for comparison. The second cluster \( (p = .002) \) consisted of 26 electrodes that were more positive-going to deviant items than to new items from 376–468 ms after disk motion onset for the segment. The inset of Figure 3.6B depicts the distribution of \( t \)-scores between the two conditions during this time window and the locations of the electrodes comprising this cluster. The traces in the main body of Figure 3.6B show ERPs at the cluster, time locked to disk motion onset.

Note that the two clusters depicted in Figure 3.6 likely capture two different ERP sub-components. The enhanced positive-going response to new motion segments (Flip_p1s5) relative to familiar motion segments (Con_p4s5) is only evident at the centro-parietal electrodes of the cluster shown in Figure 3.6A. Further, it onsets earlier than the response to deviant segments (Flip_p4s5), although the response to deviant segments peaks substantially higher than that to new segments. In contrast, the enhanced positive-going response to deviant segments is evident at both clusters. Over fronto-
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Figure 3.6: ERPs to Flip_p1s5 (new), Flip_p4s5 (deviant), and Con_p4s5 (familiar) at two clusters. The inset in each panel shows the locations of the electrodes making up each cluster and its distribution of t-scores; the traces show ERPs at the cluster to each segment. A: A slightly right-lateralized centro-parietal cluster composed of 16 electrodes that were more negative-going on Flip_p4s5 (deviant) than on Flip_p1s5 (new) from 244–344 ms after disk motion onset for the segment. B: A fronto-central cluster composed of 26 electrodes that were more positive-going on Flip_p4s5 (deviant) than on Flip_p1s5 (new) from 376–468 ms after disk motion onset.
central electrodes (Figure 3.6B), its amplitude is substantially larger than that of the ERP to new or familiar items, although it onsets at the same time.

### 3.4 Discussion

I recorded high-density scalp EEG while subjects performed a visuomotor sequence-learning task, with occasional deviant elements inserted into familiar sequences. Subjects successfully reproduced the sequences, including the deviant items. Because the sequence changed every 60-90 seconds, subjects had to dynamically update their representation of the relevant sequential structure. In order to characterize the neural mechanisms that respond to unpredictability within newly-learned sequences, I measured ERPs to novel, familiar, and deviant sequence items. As compared to familiar, well-predicted sequence items, both new and deviant items evoked an enhanced centralized P3, as identified by a data-driven, bottom-up analysis approach. For new elements, this P3 was consistently timed and over fronto-central electrodes, while the deviant elements evoked a P3 over fronto-central electrodes as well as a slightly later positivity over centro-parietal electrodes.

These results fill an important gap in the previous work on the neural response to sequence deviants, most of which has been done using a serial reaction time task (SRTT). In the SRTT, subjects make key presses to a stream of letters or other stimuli (Nissen & Bullemer, 1987). When a repeating sequence of letters is embedded within the stream, subjects respond more quickly to those items, and some subjects develop explicit knowledge of the sequence’s presence and structure. Subjects who have such explicit knowledge show an enhanced P3 to letters that violate the established sequence, but subjects without such knowledge do not (Ferdinand et al., 2008; Schlaghecken et al., 2000). Similarly, subjects who are instructed that an underlying sequence exists show an enhanced P3 (Rüsseler et al., 2003).

Rüsseler and Rösler (2000) created an SRTT variant in which multiple stimuli mapped onto each
response key, so that they could separate the neural response to perceptual deviants (wrong letter but same response) from that to perceptual + motor deviants (wrong letter AND different keypress). They found an enhanced P3 only to the latter category of sequence deviants, and concluded that the P3 effect reflects the need to change or update a response rather than the mere detection of an unexpected stimulus. In my task, participants are explicitly aware of the sequential structure, as their task is to memorize and reproduce it. Thus, deviant sequence items in my study require participants to change a planned motor output as well as to encode information about the new event. My findings of P3 enhancement to deviant sequence items is consistent with Rüsseler and Rösler’s hypothesis. Interestingly, de Bruijn, Schubotz, and Ullsperger (2007) showed participants slideshows of everyday actions, with or without execution errors, and found an enhanced P300 for observed errors relative to correct executions. In that task, subjects are presumably drawing on their previous knowledge about the sequential structure of the familiar, everyday actions; observed errors deviate from this structure but do not require a response from the participant.

Two distinct subcomponents with very similar timing have been identified in the P300 literature (Polich, 2007; Linden, 2005; Goldstein et al., 2002; Spencer, Dien, & Donchin, 2001; N. K. Squires et al., 1975). The slightly earlier subcomponent, the Novelty P3, is centered over fronto-central electrodes, and is described as elicited by deviant stimuli that are salient, low-probability, and do not require a response (Goldstein et al., 2002). The second subcomponent, the P300, is more posterior, centered over centro-parietal electrodes. The P300 is elicited by task-relevant stimuli such as targets. Deviant sequence elements in the SRTT enhance the P300 (also sometimes called P3b) subcomponent (Ferdinand et al., 2008; Rüsseler et al., 2003; Schlaghecken et al., 2000).

My results support the presence of separable P3 subcomponents using a clustering approach to separate ERPs to novel from deviant items. One, a centro-parietal ERP peaking around 400 ms after disk motion onset, is enhanced by new and deviant items in comparison to familiar ones. This response appears to be parallel to the P300, as both new and deviant sequence items are task-relevant.
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This activity most likely reflects the perception and encoding of a task-relevant stimulus (which subjects must do for both new and deviant items). The second subcomponent is a fronto-central ERP, also peaking about 400 ms after disk motion onset. At these electrodes, the ERP to novel and familiar sequence items are indistinguishable, but the P3-like peak to deviant sequence items is substantially enhanced. This response likely parallels the P3a or Novelty P3 subcomponent and suggests that “novel” may be better characterized as “expectation-violating” (Vossel, Weidner, Thiel, & Fink, 2009; Yu & Dayan, 2005). This ERP may specifically reflect inhibition or rejection of a perceptual representation and motor plan that are actively stored in working memory.

Differences between the neural responses to new and deviant stimuli highlight the importance of prediction-monitoring in cognition. On the surface, new and deviant items are quite similar: both require the subject to perceive and encode a direction of motion that has not previously been observed, in order to reproduce it from memory. The difference is in the context: When viewing a deviant sequence item, participants have strong predictions about the disk’s direction of motion; when viewing a new item, they have no such predictions. The differences in neural response between these two conditions therefore reflects the effects of these predictions on perceiving and encoding the element.

Although my results contribute to the understanding of the relationship between sequential structure, unpredictability, and the P3, the present study has two important limitations. First, because participants were explicitly aware of both the sequential structure of the task and the points at which new trials (and thus new sequences) began, these findings cannot be extended to explain the mechanisms by which people come to identify sequential structure in continuous streams of sensory input, nor to explain the processes by which people identify changes in that structure. Second, because the deviant items in this paradigm always differed from the familiar items by 180°, I cannot say anything about the effect of the magnitude of prediction violations. Both of these questions will need to be investigated before the relationship between expected unpredictability, unexpected
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unpredictability, and the subcomponents of the P3 can be fully described.

In summary, I have shown that, when learning motion sequences, people show distinct neural responses to new stimuli, familiar stimuli, and stimuli that deviate from the governing sequence. The neural responses to a deviant sequence item are different than those to a new sequence item, further supporting the hypothesis that identifying prediction errors is a cognitive process. Finally, my results extend previous work on monitoring sequential regularities and show that the neural mechanisms involved are similar when the sequential structure is dynamic and when it is stable over time.
Chapter 4

Leaky ignoring in the flanker task

4.1 Introduction

The human brain is sensitive to events that violate its explicit and implicit predictions about forthcoming sensory inputs (Ferdinand et al., 2008; Nassar et al., 2012; Ouden et al., 2009; Schultz et al., 1997). As I showed in Chapter 3, humans detect such prediction-violating events and incorporate them into working memory representations in a task that requires explicit reproduction of visuomotor sequences. In this chapter, I directly investigate the effect of such events on attention. In associative learning or other explicitly predictive tasks, prediction-violating events trigger the allocation of attention (Wills et al., 2007). Further, as is familiar from everyday experience, when an unattended stimulus stream contains an event that is unexpected, that event becomes distracting, impairing performance on the attended task (e.g. Escera et al., 1998; Parmentier et al., 2008; Schröger, 1996).

The Eriksen flanker task is frequently used to investigate the cognitive processes involved in response conflict and spatial attention (Eriksen & Eriksen, 1974; Ridderinkhof et al., 1999). In this paradigm, a central target is surrounded by flanking distractors which may be congruent with
(i.e., match) the target or be incongruent with it. The classic finding from this task is that, despite subjects’ attempts to ignore the flanking distractors, flankers that are incongruent with the central target interfere with processing, leading to reduced speed and accuracy on those trials.

I modified the flanker task to incorporate unexpected events among the unattended flankers. I hypothesized that the behavioral effect of the flankers should be magnified on trials with those unexpected flanker events, due to unexpected events’ obligatory attraction of attentional resources.

To characterize the effects of unexpected flankers, I compared ERPs to the onset of stimuli containing expected and unexpected flankers. The visual mismatch negativity (vMMN) is an early, negative-going deflection in the ERP that occurs in response to occasional deviant elements within a sequence of visual stimuli that obey some regularity (Czigler, 2007; Pazo-Alvarez, Cadaveira, & Amenedo, 2003). It is parallel to the well-established auditory MMN, which is theorized to be generated in auditory cortex when a predictive signal from prefrontal areas is disconfirmed by incoming sensory information (Garrido et al., 2009; Wacongne et al., 2011, 2012). The auditory and visual MMNs do not depend on attention, and arise even when subjects are attending to other stimulus streams, such as a listening task in one ear with a sequence of tones in the other, or a visuomotor task with irrelevant stimuli in the periphery (Näätänen, Paavilainen, Titinen, Jiang, & Alho, 1993; Stefanics et al., 2011; Winkler, Teder-Sälejärvi, Horváth, Näätänen, & Sussman, 2003).

There is some evidence that the MMN reflects characteristics of stimulus processing (Kimura, Kondo, et al., 2011; Näätänen, Paavilainen, Rinne, & Alho, 2007; Tales, Troscianko, Wilcock, Newton, & Butler, 2002). I measured the vMMN elicited by unexpected flankers in the Eriksen flanker task, and tested its relationship to behavioral evidence of oddball flanker interference.

I also measured individual differences in task performance and neural activity. The processes involved in this task are likely influenced by individual differences in emotional, motor, and attentional reactivity (Rothbart, 2007). I hypothesized that individual differences in temperament—particularly the factors relating to perceptual sensitivity and attentional control—would predict
individual susceptibility to unexpected flankers.

Finally, I investigated the mechanisms linking the neural response to a prediction error with changes in behavior. Error-induced behavior changes are theorized to rely on the low-level motivational systems that drive organisms to avoid aversive experiences (Hajcak & Foti, 2008; Holroyd & Coles, 2002; Ridderinkhof, Ramaur, & Wijnen, 2009), and responses to prediction errors may be similarly organized. A recent study found that the human startle response is slightly potentiated after an incorrect response (Hajcak & Foti, 2008). I thus attempted to replicate their finding, and investigated whether similar startle potentiation accompanies unexpected flanker events.

4.2 Methods

4.2.1 Subjects

Twenty members of the Brandeis University community (15 female, age range 18-21) participated in this study. All were right-handed (mean score on the revised Edinburgh Handedness Inventory 89.49, SD = 12.85). Two other subjects completed one experimental session but did not return for the second; their data are not reported here.

4.2.2 Experimental task

I designed a modified Eriksen flankers task using chevron stimuli (Eriksen & Eriksen, 1974; Ridderinkhof et al., 1999). The basic trial structure is shown schematically in Figure 4.1. On each trial, subjects were presented with an array of five chevrons that were displayed for 50 ms and were not masked upon offset. They were instructed to report whether the central chevron was pointing to the left or to the right. I will refer to this central chevron as the target, and the two chevrons on each side of it as the flankers. The four flankers were always consistently oriented, and the central
CHAPTER 4. LEAKY IGNORING IN THE FLANKER TASK

Figure 4.1: The sequence of events within a trial with no startle probe. After fixation, the flanker stimulus appeared for 50 ms, after which participants had two seconds to report the direction of the center chevron.

the chevron’s orientation was equiprobably congruent or incongruent with its flankers. After a subject’s response, a fixation cross was displayed for an inter-trial interval of 1000 ms before the next trial display appeared.

Subjects viewed the display from a difference of approximately 57 cm. Each chevron subtended approximately 1.40° visual angle, and the full array extended to an eccentricity of 4.67°.

In order to maintain more-consistent error levels across subjects and conditions, subjects received feedback about their performance after every thirty trials (after Hajcak & Foti, 2008). If the subject had responded correctly on between 75% and 90% of those trials, the feedback was “You’re doing great!” If their accuracy was lower than 75%, the feedback instructed them to increase their accuracy; if it was above 90%, the feedback instructed them to respond more quickly.

Trial types were distributed among four conditions in a two-by-two design, as shown in Figure 4.2. The first factor governed the direction of the four flanker chevrons. On ninety percent of trials, the flanker chevrons pointed in one direction (the Standard direction) and on ten percent of trials they pointed the other (the Oddball direction). The second factor governed the relationship between
**CHAPTER 4. LEAKY IGNORING IN THE FLANKER TASK**

**Figure 4.2:** Diagram of the two-by-two trial design. One factor, **flanker direction**, governed the direction of the four flanker chevrons; the second, **congruency**, governed the relationship between the central target and its flankers. Whether the **Standard** flanker direction was left or right was counterbalanced within subjects. 90% of trials incorporated the **Standard** flankers (45% **Congruent** and 45% **Incongruent**); 10% of trials incorporated the **Oddball** flankers (5% **Congruent** and 5% **Incongruent**).

the central target and the flankers. On half of trials, the target was **Congruent** with the flankers, and on half it was **Incongruent**. Note that left-facing and right-facing target were equally frequent, and the directions comprising **Standard** and **Oddball** flankers were counterbalanced within subjects.

### 4.2.3 Startle probes

In order to elicit startle responses, occasional trials included a 105 dB burst of white noise lasting 50 ms (Blumenthal et al., 2005; Hajcak & Foti, 2008). These startle probes were presented through a single speaker resting on the display monitor. As one aim of this study was to compare response-induced to stimulus-induced startle priming, participants completed four blocks of trials. Two of these blocks included **stimulus-aligned** startle probes; the other two included **response-aligned**
Figure 4.3: **A:** The sequence of events within one trial with a stimulus-aligned startle probe. The 50 ms noise burst played 350 ms after stimulus onset. See page 71 for a description of the rules governing whether startle probes occurred. **B:** The sequence of events within one trial with a response-aligned startle probe. Subjects had to respond within two seconds of stimulus onset; the noise burst played 300 ms after their response.
startle probes. Block order was counter-balanced across participants using all possible orders.

In the stimulus-aligned condition, startle probes occurred 350 ms after stimulus onset and were contingent on the flanker direction of the stimulus displayed on that trial (Figure 4.3A). In these blocks, startle probes occurred on 50% of Oddball trials, 50% of Standard trials immediately following an Oddball trial, and 4% of all other Standard trials. No explicit constraint on was placed on startle probes on successive trials. The two separate rules for Standard trials control for the predictability of the Oddball-contingent startle probes. On average, blocks with stimulus-aligned startle probes featured 64 probes per 510-trial block.

In the response-aligned condition, startle probes occurred 300 ms after the subject’s response, and were contingent on whether the subject responded correctly (Figure 4.3B). In these blocks, startle probes occurred on 50% of error trials, on 50% of correct trials following an error trial, and on 4% of all other correct trials. On average, blocks with response-aligned startle probes featured 73 probes per 510-trial block.

To assess whether unexpected stimuli and unexpected responses similarly recruit defensive alerting mechanisms, I measured the eye blink response to startle probes following Oddball and Standard stimuli, and the response to probes following Error and Correct responses. The magnitude of subjects’ eye-blink responses was measured via electromyography (EMG), using a subset of the electrodes on the EEG cap. Page 74 describes details of the recording and analysis.

### 4.2.4 Procedures and analyses

Each recording block comprised 510 trials, with the first thirty discarded as practice. Each subject completed two blocks with stimulus-aligned startle probes (one with left-facing flankers as the Standard direction, the other with right-facing flankers) and two blocks with response-aligned startle probes. These four blocks were completed in two separate recording sessions; the order of
blocks was counterbalanced across subjects using all possible orders. By the end of the experiment, each subject had completed 2040 trials, 1920 of which were included for analysis.

Subjects filled out an anonymous questionnaire after each recording session, confirming that they got reasonable amounts of sleep, were not under the influence of any psychoactive substances, and had no medical history, such as a head injury or neurological diagnosis, that should lead me to exclude their data.

**Behavioral measures**

Subjects’ reaction times and responses were recorded from each trial and analyzed. I computed accuracy for each of Congruent Standard, Incongruent Standard, Congruent Oddball, and Incongruent Oddball conditions. I also computed decile reaction times and accuracy for all four conditions, computed ex-Gaussian fits to reaction time distributions (Balota, Yap, Cortese, & Watson, 2008), and measured post-error slowing—the difference in reaction time between the trial following an error and the trial preceding an error (Dutilh et al., 2012).

After the end of their final experimental session, subjects completed the Adult Temperament Questionnaire Short Form (ATQ). This instrument has 77 items which form several self-report scales describing temperament factors (Evans & Rothbart, 2007). I selected two factors a priori for testing: Attentional Control and Orienting Sensitivity. Attentional Control refers to the capacity to focus attention, and to shift attention as desired. “It’s often hard for me to alternate between two different tasks,” is an example of a reverse-scored Attentional Control item. Orienting Sensitivity refers to awareness of low-intensity environmental and self-generated stimuli and experiences. “I often notice visual details in the environment,” is an example of an Orienting Sensitivity item. I hypothesized that the Attentional Control would account for some variability in people’s task performance, while Orienting Sensitivity would account for variability in startle responses.
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EEG recording and measures

A high-density EEG system (Electrical Geodesics, Inc., Eugene, OR) with 129 electrodes sampled scalp electroencephalographic signals at 250 Hz using a high-impedance amplifier. Signals were recorded for later, off-line analysis. All channels were adjusted for scalp impedance below 50 kΩ impedance; after one experimental block, channels were returned to at most 50 kΩ scalp impedance before the subject completed the session.

After recording, EEG data were preprocessed using the EEGLAB Matlab toolbox (Delorme & Makeig, 2004). Continuous EEG signals were bandpass filtered to between 0.25 and 100 Hz using a first-order Butterworth filter. A 60 Hz notch filter was also applied to the continuous data, to reduce line electrical noise. Then, data were broken into epochs time-locked to stimulus onset and subject responses. Stimulus-locked epochs comprised a window from 200 ms preceding stimulus onset to 500 ms after; response-locked epochs comprised 200 ms preceding keypress responses to 500 ms after. Finally, data were cleaned using the process described in Section 3.2.6 (page 51).

Using the clustering analysis described in Section 3.2.6 (page 52), I ran two comparisons. First, I identified time windows and electrodes that captured the differences between Standard and Oddball stimuli, and computed the ERPs to stimulus onset at those electrodes. The mean difference between the two ERPs during the significant time window was my measure of vMMN magnitude.

To verify that the clustering algorithm identifies valid ERP components, I also compared the ERPs elicited by Correct and Incorrect responses. The error response negativity (ERN) is a negative-going deflection in the ERP that occurs very shortly after incorrect responses. I identified time windows and electrodes that captured the differences between Correct and Error responses, and computed ERPs to subject responses at those electrodes. The mean difference between the two ERPs during the significant time window was my measure of ERN magnitude.
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EMG recording and measures

EMG data were recorded simultaneously with the EEG data, using electrodes 14, 21, 126, and 127 of the sensor net. These electrodes are positioned directly above and below the eyes, and are designed to capture the vertical/blink component of eye-movement EMG. Using a 4th-order Butterworth filter, the data were bandpass filtered to 28–100 Hz and broken into epochs from 200 ms preceding each startle probe to 350 ms after its onset. Epoched data were rectified, low-pass filtered at 50 Hz and visually inspected for non-blink artifacts (Blumenthal et al., 2005; Hajcak & Foti, 2008). Artifact-contaminated epochs were removed from the processing stream. Cleaned data were baseline-corrected using the 200 ms immediately preceding each startle probe, and blink magnitude was operationalized as the maximum voltage within a time window from 20–150 ms after a startle probe.

4.3 Results

4.3.1 Behavioral measures

Figure 4.4 shows the effects of congruency and expectedness on subjects’ speed and accuracy in the flankers task. On trials in which the flankers were in the Standard condition (presented in blue in Figure 4.4), subjects were faster and more accurate on Congruent trials (proportion correct 0.93, SD = 0.04; median correct reaction time 356 ms, SD = 33) than on Incongruent trials (proportion correct 0.86, SD = 0.05; median correct reaction time 378 ms, SD = 37), with the largest accuracy differences occurring on trials where subjects responded quickly. This effect was exaggerated when the flankers were in the Oddball condition (presented in green in Figure 4.4). On Oddball Congruent trials, subjects were faster and more accurate (proportion correct 0.95, SD = 0.04; median correct reaction time 343 ms, SD = 31) than on Standard Congruent trials, and on
Figure 4.4: (A) Reaction time and proportion correct for each decile of Standard (blue) and Oddball (green) trials, when the flankers are Congruent (solid lines) and Incongruent (dashed lines). (B) Proportion correct (left) and median reaction times (right) for each condition, summarizing the above. Error bars are repeated-measures standard error.
CHAPTER 4. LEAKY IGNORING IN THE FLANKER TASK

Table 4.1: ANOVA results for ex-Gaussian fits to RT distributions.

<table>
<thead>
<tr>
<th>parameter</th>
<th>source</th>
<th>df₁, df₂</th>
<th>F</th>
<th>partial $\eta^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu$</td>
<td>Flanker</td>
<td>1,19</td>
<td>10.976**</td>
<td>.366</td>
</tr>
<tr>
<td></td>
<td>Congruency</td>
<td>1,19</td>
<td>0.015</td>
<td>.015</td>
</tr>
<tr>
<td></td>
<td>Flanker $\times$ Congruency</td>
<td>1,19</td>
<td>2.202</td>
<td>.104</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Flanker</td>
<td>1,19</td>
<td>0.848</td>
<td>.043</td>
</tr>
<tr>
<td></td>
<td>Congruency</td>
<td>1,19</td>
<td>25.323***</td>
<td>.571</td>
</tr>
<tr>
<td></td>
<td>Flanker $\times$ Congruency</td>
<td>1,19</td>
<td>3.343</td>
<td>.150</td>
</tr>
<tr>
<td>$\tau$</td>
<td>Flanker</td>
<td>1,19</td>
<td>11.425**</td>
<td>.376</td>
</tr>
<tr>
<td></td>
<td>Congruency</td>
<td>1,19</td>
<td>0.094</td>
<td>.005</td>
</tr>
<tr>
<td></td>
<td>Flanker $\times$ Congruency</td>
<td>1,19</td>
<td>0.004</td>
<td>.000</td>
</tr>
</tbody>
</table>

*p < .05. **p < .01. ***p < .001.

**Oddball Incongruent** trials, subjects were slowest and least accurate (proportion correct 0.59, SD = 0.16; median correct reaction time 427 ms, SD = 47).

These results were confirmed by two-way repeated measures ANOVAs with factors congruency and flanker direction. There was a main effect of congruency on proportion correct ($F(1,19) = 94.211, p < .001$), a main effect of flanker direction on proportion correct ($F(1,19) = 80.019, p < .001$), and a congruency $\times$ flanker direction interaction ($F(1,19) = 101.809, p < .001$). There was a significant main effect of congruency on median correct reaction time ($F(1,19) = 92.244, p < .001$), no main effect of flanker direction on median correct reaction time ($F(1,19) = 0.026, p = .875$), but a significant congruency $\times$ flanker direction interaction ($F(1,19) = 30.917, p < .001$).

To further characterize the reaction times, I fit ex-Gaussian curves to the reaction time distribution generated by each subject on each condition. These curves have three parameters: $\tau$, which characterizes the positive tail of the distribution (the exponential component); $\mu$, the mean of the
Figure 4.5: Ex-Gaussian fits to reaction time distributions for each stimulus condition. A: **Oddball** flanker directions increased $\mu$ relative to *Standard*. B: **Incongruent** trials had higher $\sigma$ than **Congruent** trials. C: *Standard* flanker directions increased $\tau$ relative to **Oddball** trials.
Gaussian component, and $\sigma$, the standard deviation of the Gaussian component. Figure 4.5 shows the results. Two-way repeated-measures ANOVAs on each parameter confirmed the effects. There was a main effect of **flanker** on $\mu$ ($p = .037$), with unexpected flanker directions shifting the entire reaction time distribution slower relative to expected flanker directions, and on $\tau$, with unexpected flanker directions actually decreasing the skewness of the RT distribution. (While this effect seems paradoxical at first, it is due to the two-second timeout for subjects’ responses. With such a limit, as the distribution shifts right, it must become less skewed.) There was a main effect of **congruency** on $\sigma$, suggesting that incongruent stimuli increased the variability of subjects’ reaction times relative to congruent stimuli. Complete ANOVA results are shown in Table 4.1.

There was substantial post-error slowing in this experiment. On average, subjects responded 30 ms more slowly (SD = 24 ms) on the trial following an error than on the trial preceding one. I ran a three-way repeated-measures ANOVA on this post-error slowing with factors **congruency**, **flanker direction**, and **startle probe timing**. There was a marginal main effect of **startle probe timing**, with subjects exhibiting less post-error slowing on blocks with stimulus-contingent startle (26 ms, SD = 18 ms) than on blocks with response-contingent-startle (42 ms, SD = 38 ms; $F(1,19) = 4.031, p = .059$). There was no main effect of **congruency** or **flanker direction** ($p > .5$) and no significant interactions (all $ps > .08$).

On average, subjects scored near the center of the temperament self-report range from the ATQ. The mean Perceptual Sensitivity score was 5.00 (SD = 0.86), and the mean Attentional Control score was 4.03 (SD = 0.91). There was a non-significant negative correlation between Attentional Control and proportion correct ($r = -0.291, p = .213$),
Figure 4.6: ERPs to **Standard** and **Oddball** flanker directions at a cluster of posterior electrodes. A: Topographical plot showing the locations of the 16 electrodes making up the cluster, and the distribution across the scalp of $t$-values at 180–320 ms after stimulus onset. B: Traces show ERPs time locked to stimulus onset for **Standard** (shown in blue) and **Oddball** (green) flankers, at the cluster of electrodes shown in panel A. C: Trace depicts the difference between the two traces shown in panel B. Negative values occurred when ERPs to **Oddball** flankers were more negative-going than those to **Standard** flankers. Error ribbons are within-subject standard error, and thus do not reflect the process or the results of the permutation significance test.
CHAPTER 4. LEAKY IGNORING IN THE FLANKER TASK

4.3.2 ERPs

Standard vs. Oddball

Figure 4.6 illustrates the neural activity that accompanied the presentation of Standard and Oddball flanker directions. A data-driven clustering and permutation analysis (Maris & Oostenveld, 2007; see page 52) identified the cluster of electrodes that best captured \( p < .001 \) the difference in scalp voltage topographies between Standard and Oddball flankers. This cluster was derived with \( t_{\text{critical}} = 3.883 \), the critical \( t \)-value at \( \alpha = .001 \) and \( df = 19 \). The cluster was composed of 16 posterior electrodes that were more negative-going on Oddball than on Standard trials during an interval from 180–320 ms after stimulus onset. Figure 4.6A depicts the locations of the electrodes making up the cluster and the distribution of \( t \)-scores between ERPs to the two flanker directions during that time window. The traces in Figure 4.6B show ERPs at the cluster, time locked to stimulus onset, to Standard (blue) and Oddball (green) flankers. Figure 4.6C shows the difference between the two traces in Figure 4.6B. Negative values reflect Oddball-evoked ERPs that were more negative-going than Standard-evoked ERPs.

I tested whether vMMN magnitude reflected subjects’ susceptibility to interference from unexpected flanker directions. To account for differences in neural function and anatomy that are unrelated to such susceptibility, I partialled out each subjects’ N2 magnitude to Standard flankers. N2 magnitude was operationalized as each subject’s mean amplitude of the ERP from 180–220 ms after stimulus onset on Standard trials. The residual vMMN values were marginally correlated with Attentional Control score \( (r = -0.439, p = .053) \), suggesting that subjects who scored higher on Attentional Control tended to have larger (negative) MMNs. They were also correlated with Orienting Sensitivity score \( (r = 0.464, p = .039) \), such that subjects who scored higher on Orienting Sensitivity tended to have smaller vMMNs. Figure 4.7 illustrates the relationship between these three measures. Combining Attentional Control and Orienting Sensitivity in a multiple linear
Figure 4.7: A multiple linear regression on Attentional Control and Orienting Sensitivity scores predicts inter-individual differences in N2-corrected vMMN magnitude. Data points are plotted according to Orienting Sensitivity score and vMMN magnitude; note that because vMMN is negative, lower values here correspond to larger vMMNs. The two fit lines show the relationship between Orienting Sensitivity and vMMN magnitude at different ranges on the Attentional Control factor.

Regression significantly predicted N2-corrected vMMN magnitude ($R^2 = 0.35, p = .026$).

Residual MMN values were also correlated with proportion correct on Oddball Congruent trials ($r = -0.448, p = .048$), such that those subjects who were most accurate on these trials had larger (negative) MMNs. However, residual MMN magnitude did not correlate significantly with proportion correct on Oddball Incongruent trials ($r = 0.194, p = .412$), nor did it correlate with any reaction time measures (all $p$s > .08).

Correct vs. Error

Figure 4.8 depicts the neural activity that occurs following Correct and Error responses. The same approach as above was used to identify the cluster of electrodes that best captured ($p < .001$) the difference in scalp voltage topographies following Correct and Error responses. The cluster was
Figure 4.8: ERPs to Correct and Error responses at a cluster of central electrodes. A: Topographical plot showing the locations of the 33 electrodes making up the cluster, and the distribution across the scalp of $t$-values from 100 ms before subject responses to 80 ms after. B: Traces show ERPs time locked to responses for Correct (shown in yellow) and Error (red) responses, at the cluster of electrodes shown in panel A. C: Trace depicts the difference between the two traces shown in panel B. Negative values occurred when ERPs to Error responses were more negative-going than those to Correct responses.
Figure 4.9: Magnitude of the blink EMG response to startle probes following **Standard** (blue) and **Oddball** (green) flankers, and to startle probes following **Correct** (yellow) and **Error** (red) responses.

Derived using $t_{\text{critical}} = 5.949$, the critical $t$-value at $\alpha = .00001$ and $df = 19$. This cluster was composed of 33 central electrodes that were more negative-going on **Error** than on **Correct** trials, during a window from 100 ms before participants’ responses to 80 ms after. Figure 4.8A illustrates the distribution of $t$-scores between ERPs to **Correct** and **Error** responses during that time window, and the locations of the electrodes making up this cluster. The traces in Figure 4.8B show ERPs at the cluster, time locked to subjects’ responses, for **Correct** (yellow) and **Error** (red) trials. Figure 4.8C shows the difference between the two traces in Figure 4.8B. Negative values reflect **Error** ERPs that are more negative-going than **Correct** ERPs.

### 4.3.3 Startle blink

On average, subjects’ mean startle blink magnitude was $7.676 \mu V$ ($SD = 6.556$). Figure 4.9 shows blink magnitudes for each startle probe condition. Because there was no significant difference between the two **Standard** conditions, nor between the two **Correct** conditions ($p > .06$), I collapsed across **Standard Unpredictable** and **Predictable**, and across **Correct Unpredictable**
and Predictable. Startle blinks were of almost identical magnitude following Oddball flankers (7.19 µV, SD = 6.84) than following Standard flankers (7.19 µV, SD = 6.80). This difference was not significant (paired $t(19) = 0.010$, $p = .993$). Startle blinks following Error responses (7.95 µV, SD = 7.47) were very slightly smaller than those following Correct responses (8.26 µV, SD = 6.32). This difference was not significant (paired $t(19) = 0.496$, $p = .626$).

As I hypothesized, average startle blink magnitude was significantly positively correlated with subjects’ Orienting Sensitivity score on the ATQ ($r = 0.539$, $p = .010$). However, startle blink magnitude and startle priming were not correlated with any of the ERP measures (all $p$s > .1). Interestingly, subjects’ Orienting Sensitivity scores were also significantly correlated with the effects of Oddball flankers on exGaussian fits to reaction times. There was a significant positive correlation between Orienting Sensitivity score and the flanker direction × congruency interaction on $\mu$ (the mean of the Gaussian component; $r = 0.482$, $p = .031$) and a significant negative correlation between Orienting Sensitivity score and the interaction on $\tau$ (the exponent component; $r = -0.491$, $p = .028$). This suggests that Orienting Sensitivity captures subjects susceptibility to the Oddball flankers, as well as their overall sensitivity to the startle probes.

4.4 Discussion

I modified the Eriksen flanker task by manipulating flanker frequency to create Standard and Oddball flanker directions. As expected, I replicated the usual flanker congruency effect: subjects were faster and more accurate when flankers were congruent with the target than when the flankers were incongruent. This effect was markedly larger for Oddball flankers than for Standard flankers. On trials with Oddball flankers that were congruent with the target, subjects were fastest and most accurate, while on trials with Oddball flankers that were incongruent with the target, subjects were worst.
CHAPTER 4. LEAKY IGNORING IN THE FLANKER TASK

Several groups of researchers have proposed competing models of the interference between flankers and targets. Yu, Dayan, and Cohen (2009) proposed a Bayesian account where subjects’ priors incorporated a bias for congruency among spatially proximate regions. White et al. (2011, 2012) proposed a diffusion model in which the spotlight of spatial attention changes size over time. The sudden onset of the stimulus requires attention to be spread across the entire display; over time, it contracts to encompass only the target. Neither of these models is capable of describing the differences in my data between Standard and Oddball flankers without adding a parameter describing subjects’ expectations about flanker directions. Such expectations facilitate suppression of incongruent flankers when they are as predicted, but not when they are deviant. The behavioral evidence from this experiment thus supports the hypothesis that unexpected events obligatorily capture attention (Parmentier, Elsley, Andrés, & Barceló, 2011; Schröger, 1996), enhancing the flanker congruency effect.

This same hypothesis was further supported by the visual mismatch negativity (vMMN) elicited by the Oddball flankers. This ERP component is thought to reflect a potentiation of the neural response to stimuli that do not match a predictive feedback signal sent from higher cortical areas to the sensory cortices (Garrido et al., 2009; Wacongne et al., 2012, 2011). The presence of a vMMN to the Oddball flankers confirm that subjects’ brains are sensitive to the regularity governing flanker direction, despite the fact that most subjects did not express awareness of that regularity.

I assessed whether subjects’ self-reported temperament factors could predict the effects of Oddball flankers. Two factors of temperament—Attentional Control and Orienting Sensitivity—together predicted about a third of the variance in vMMN magnitude. It appears that high Attentional Control ability facilitates predictive coding, leading to larger differences between Standards and Oddballs. Similarly, high Orienting Sensitivity impairs ignoring of the Standards, reducing such differences.

Future work should explore whether temperament predicts the relative strength of bottom-up
and top-down neural processes in other settings. Another area for future work is to identify traits that predict individual differences in behavior in response to the Oddball flanker directions, as my results only predict the magnitude of the neural responses. Finally, future work should investigate the role that alpha-band EEG oscillations play in performing this modified flanker task. Such oscillations are thought to gate incoming sensory information, reducing interference from incoming sensory signals (Jones et al., 2010; Payne et al., 2013; Romei, Gross, & Thut, 2010).

My attempts to demonstrate startle potentiation to errors and to Oddball flankers did not result in any measurable effect. It is possible that my strategy of measuring EMG using the oculomotor channels of the EEG cap resulted in electrode placement that was not reliably precise, or that the high-impedance amplifier was not able to capture subtle EMG effects. Further, the effect I was attempting to replicate is quite small (Hajcak & Foti, 2008), and it may be too small to be reliably identified.

In summary, my novel modification of the Eriksen flanker task has produced a very strong behavioral effect, showing that Oddball flankers have an exaggerated effect on subjects responses. I also demonstrated that the vMMN produced by such flankers varies across subjects, and that about a third of such variation can be explained by individual differences in temperament. The human brain is sensitive to stochastic as well as sequentially-structured regularities, and can use them to facilitate ignoring of incongruent distractors.
Chapter 5

Conclusion

The studies presented and discussed in the preceding chapters expand our understanding of how humans learn to represent sequences and structure, how they use those representations to support cognition, and how they monitor whether those representations actually predict sensory input.

In Chapter 2 I used cognitive modeling to fit the error distributions that subjects generated on a visuomotor sequence learning task. The best-fitting parameters make it clear that subjects’ improved performance on familiar sequences is due to increases in both the precision with which items are represented and the probability that all items have actually entered short-term memory, as seen in Figures 2.7, 2.10, and 2.13. I also found that serial position curves flatten as sequences become familiar, suggesting that items that are poorly-represented on the first presentation are allocated more VSTM resources when the sequence is presented a subsequent time (Figures 2.9, 2.12, and 2.15).

In Chapter 3 I measured neural responses to new, familiar, and deviant sequence items, and found that the neural responses to both new and deviant items differ from those to familiar items (Figures 3.4 and 3.5). Further, one P3 subcomponent is enhanced for both new and deviant items, while another is enhanced only for deviant items (Figure 3.6), dissociating the processes of identifying
CHAPTER 5. CONCLUSION

and encoding task-relevant information from the processes detecting deviance.

Chapter 4 showed that unexpected events interspersed within a stream of actively-ignored stimuli interfere with attention and action planning (Figure 4.4), and that individual differences in the neural responses to such events are related to temperament (Figure 4.7).

5.1 Further evidence for human sensitivity to environmental structure and predictability

Regardless of task or setting, sequences, predictions, and prediction monitoring are greatly important to human cognition. For example, it appears that contextual cueing for items occurs even if the items themselves are not present. When contexts are predictive of their accompanying items, re-presentation of the context without the items strengthens subjects’ recollection of the items on a later memory test (Smith, Hasinski, & Sederberg, 2013). This finding extends previous work on the role of context in item processing and recognition (Biederman et al., 1982; Kersten et al., 2004; Gronau et al., 2008; Mandler, 1980), and shows that context alone is capable of activating an object representation to such a degree that memory is facilitated. Note that this only occurs when contexts are reliably predictive, showing that the system has access to information about which cues should be attended to and which should not.

Even more interesting are cases where people fail to use prediction information to facilitate some task. For example, in a series of studies where people could choose how to allocate time spent studying, a substantial portion of subjects made suboptimal decisions, even with information available about their level of mastery and what would be tested (Ariel, 2013). Further, people’s belief about the causal structure of the world influences their predictions within a series of events. Subjects who believe they caused an outcome assume non-temporally-dependent structure, and make
optimal predictions; subjects who believe outcomes are computer-generated search for patterns, and probability-match (Green, Benson, Kersten, & Schrater, 2010). Subjects also assume positive recency effects for short runs of events, and negative recency effects for long runs—the classic Gambler’s Fallacy (Scheibehenne & Studer, 2013). Finally, despite Green et al. (2010)’s results suggesting that people seek sequential patterns and structures, non-verbalizable sequences that are periodic are quite difficult for subjects to learn (Kalish, 2013).

5.2 Future work

Several future lines of research could extend the projects presented in the preceding pages.

5.2.1 Modeling projects

Multi-parameter models for describing distributions are a rich and valuable tool. Both the VSTM mixture models described in Chapter 2 and the exGaussian models described in Chapter 4 enrich our understanding of exactly how task manipulations influence people’s processing and performance. Future work with the VSTM mixture models should explicitly test the dynamic reallocation hypotheses by fitting parameters to errors that are produced when a segment is poorly-represented on the first presentation and to those that are produced when a segment is well-represented. The hypothesis predicts smaller presentation-over-presentation changes on the remaining segments of the display when one segment is poorly represented, due to memory resources being allocated to that segment.

Another possible line of investigation is to follow up on the apparent encoding-limited nature of this VSTM task. Repeated presentations lead to improved performance, suggesting that more information is encoded each time. This contradicts the claims of Vogel, Woodman, and Luck (2006),
CHAPTER 5. CONCLUSION

who found that visual short-term memory is equally effective whether subjects are exposed to a stimulus for 200 ms or 500 ms. They argue that this shows that VSTM cannot be encoding-limited at moderate display lengths, which my task has. Vogel et al. (2006) did not, however, test the effect of multiple short presentations. Future work could compare memory performance for single short displays, single long displays, and multiple short displays, and determine whether there is a benefit of repeated exposure.

5.2.2 Types of predictions

Chapters 3 and 4 test two very different paradigms within the space of predictive cognition. In Chapter 3, the predictions involved are explicitly known, are derived from a fixed sequence, and the task is to represent the sequence itself. In Chapter 4, the predictions are not explicitly known (by most subjects), they are stochastic rather than sequential, and they are incidental to the actual task subjects are performing. This dissertation does not speak to the great range of situations that are in the middle. People have varying degrees of access to information about regularities in the world; those regularities can perfectly sequential, somewhat sequential, or entirely stochastic; and the predictability can be central or incidental to the task people are trying to perform. One can conceptualize a three-dimensional space defined by strictness of temporal regularity on one axis, relevance of that regularity on a second axis, and people’s access to information about the regularity on a third. An area of rich further exploration would be to develop a task and a set of regularities which can be used to systematically explore the space from sequential to stochastic regularities, applying to elements which are task-relevant, irrelevant, or distractors.

Other work has been done that measures the influence of predictability at different spaces in this domain. The serial reaction time task (SRTT; Nissen & Bullemer, 1987) measures the accuracy and reaction time with which subjects can make keypress responses. Various stimuli on
CHAPTER 5. CONCLUSION

the screen cue subjects to press particular keys, and the sequence of stimuli (and thus keypresses) repeats throughout an experimental block. Here, the prediction is sequential, not stochastic, and central to the task. Subjects develop varying degrees of awareness of the sequential structure; such awareness does not affect the facilitation of performance for trials that obey the sequence, but does predict neural responses to trials that deviate from it (Ferdinand et al., 2008; Rüsseler et al., 2003; Rüsseler & Rössler, 2000; Schlaghecken et al., 2000). In short, these results are in the same area of this three-dimensional conceptual space as my results from Chapter 3.

In a very different domain, Vo and Wolfe (2012) measured ERPs to stimuli that violated scene context rules, which is in between the explicitly sequential and the completely stochastic structures that I created for Chapters 3 and 4. The predictability was central to the task (identifying objects in naturalistic scenes), and subjects were generally aware when the context rules were violated. Their ERP results are very different from mine, but due to the differences in the tasks and stimuli, those differences are hard to interpret. One possible explanation is that predictions derived from temporal regularities are qualitatively different from predictions derived from scene structure and co-occurrence rules, and that a different system is involved in monitoring in this case. Further work should more carefully follow up on this question.

5.2.3 Neuroimaging

My work has focused on the neural processes that are easily measured by scalp EEG: the anterior cingulate and frontal areas, as measured by the P3, and sensory cortices, as measured by the MMN. Other brain areas are of course involved in detecting and responding to deviant events. In particular, the hippocampus has been implicated in binding events to their spatial and temporal contexts, and in detecting associative novelty when an event occurs outside its usual context (Kumaran & Maguire, 2006, 2007; Manns, Howard, & Eichenbaum, 2007). Investigating hippocampal contributions
will require the use of fMRI or MEG, as those imaging methods are more capable of measuring
the activity of subcortical structures. A question of particular interest is whether and how the
hippocampus and the anterior cingulate cortex are connected. It is not known whether hippocampal
detection of associative novelty lead to anterior cingulate activation, or vice versa.

In summary, this dissertation describes three projects that further our understanding of the pro-
cesses by which people learn sequences and regularities, use predictions based on such regularities
to support cognition, and monitor when the predictions are validated by actual events.
References


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