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Memory for order in monkeys *(Macaca mulatta)*

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Memory for order in rhesus monkeys *(Macaca mulatta)*

By

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M.A. Emory University, 2009

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Advisor: Robert Hampton, PhD.

An abstract of a dissertation submitted to the Faculty
of the James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy in Psychology

2014

Abstract

Memory for order in rhesus monkeys *(Macaca mulatta)*

By Victoria L. Templer

One important aspect of episodic memory is the ability to remember the unique order of events that comprise personal experience. For example, remembering that you first went snorkeling, then visited a volcano, and finally went sailing, is essential to accurately retelling your vacation story. Mnemonic representation of order is also necessary when actions are taken in routinized habit sequences, such as executing a favorite cooking recipe. The distinction between episodic and habit memory is fundamental to theories of human memory, but it is difficult to test in nonhuman animals. Cognitive tests suitable for nonverbal species have been developed that model the temporal order aspect of consecutively experienced unique events and the order of routinized responses in a serial order task. This dissertation includes four papers that explain attempts to characterize memory for order of events and order of responses in rhesus monkeys (*Macaca mulatta).* Paper 1 is a review article about the study of episodic memory in nonhuman animals. Paper 2 presents evidence that monkeys use a temporal order mechanism, rather than knowledge of ordinal position, or relative recency, to remember the order in which trial-unique images were seen and touched. Monkeys better encoded order when intervening images occurred, but not when unfilled intervals of equivalent duration occurred, indicating that the occurrence of intervening events may serve to mark the passage of time, thereby increasing the subjective separation of events. Paper 3 provides evidence that when fixed orders are repeatedly executed in a serial order task, knowledge of ordinal position, rather than image-image associations, maintains mental representation of order. Errors during list execution were consistently prospective, indicating use of a prospective rather than retrospective code to update position in the list. Paper 4 reviews evidence that suggests the study of order memory along analogous cognitive behavioral manipulations across paradigms is a promising avenue for understanding the types of memory systems existing in monkeys. Together, these studies provide rich characterizations of the specific features of cognitive representations underlying memory for ordered stimuli. Ultimately these findings help make small steps towards answering questions about whether the types of memory systems nonhuman primates possess overlap with those that define common human memory taxonomies.

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1. General Introduction

We engage constantly in a world full of order. More than a half a century ago Karl Lashley argued that one of the most important problems in psychology is the "problem of serial order in behavior" (Lashley, 1951). From verbal behaviors such as speech perception and generation to nonverbal organized behaviors such as executing a series of responses in goal-directed behavior, the ability to process ordinal information is necessary in most behaviors (Lashley, 1951). Even before Lashley, Ebbinghaus (1885/ 1964) was invested in determining what is learned and mentally represented when a list or order is remembered.

One example of when memory for order is critical is when naturally occurring unique events are linked through experiential time and then subsequently remembered in the correct temporal order, such as those that comprise a day on a vacation when you first went snorkeling, visited a volcano, and then went sailing (Figure 1; top left). However, the mnemonic representation that allows for consecutively experienced events to be remembered in the correct temporal order is not yet a well-developed model. For example, the extent to which time or the unfolding of unique events contributes to subjective experience of what occurred earlier and what occurred more recently is not well-known.

In addition to the natural order of stimuli we perceive, orders are also inherit to actions we take. Often, the series of actions or responses we take are fixed and sometimes become habitual. For example, to create a favorite recipe a defined sequence of actions is followed, and overtime this fixed order of responses becomes routinized (Figure 1; top right). Researchers of serial learning have investigated the question of what is the content of memory for order of responses by asking whether subjects learn associations between successive items (Ebbinghaus 1885/1964), as the chaining theorists would argue (Skinner, 1934), or by knowledge of item-position information, as ordinal position theorists would argue (S. Chen, K. B. Swartz, & H. S.

Terrace, 1997; Ebenholtz, 1963). While most researchers now agree that chaining of stimulus-response units cannot explain behavior in most cases of serial learning (Scarf & Colombo, 2011; H.S. Terrace, Son, & Brannon, 2003), an unequivocal answer to the question of how ordinal information is mentally represented has yet to be provided. However, when mental representation of both order of events and memory for order of responses are analyzed for standard psychological properties the nature of the ordinal representation maintained for specific mnemonic demands becomes more transparent.

The goal of this dissertation was to determine the cognitive mechanisms underlying memory for different types of order to inform the structure of basic memory representations in a nonverbal species. The temporal order of events is a critical feature of episodic memory, as explained in the vacation example. However, memory for order of events, and for memory for responses, as well as other similar ordinal tasks, are also used as a model of other cognitive systems such as working memory (Amiez & Petrides, 2007; Destrebecqz & Cleeremans, 2001; Destrebecqz et al., 2005; Heuer & Bachevalier, 2013). Here, the aim is to identify and directly compare psychological properties of memory for unique and routinized orders by determining the cognitive mechanisms required for each ordinal task, that have been adapted for monkeys, outlined in Figure 1.

The overarching aim is to characterize the memory processes of two types of cognitive representations and make small steps towards answering questions about whether the types of memory systems monkeys possess overlap with those that define common human memory taxonomies. Capturing cognitive mechanisms uncontaminated by linguistic factors will inform basic scientific understanding of the structure of memory processes and organization of monkey memory systems. Ultimately, with continued studies, these efforts may lead to translational understandings of human memory systems, especially when neurobiological manipulations are applied to paradigms and techniques described here.

1.1. Episodic memory

Episodic memory is critical for independent function and for our knowledge of the autobiographical events that give us each a sense of self. It is the most fragile type of memory: it develops latest in childhood, deteriorates first in old age, and is most susceptible to neurodegenerative disease (Fouquet, Tobin, & Rondi-Reig, 2010). Episodic memories, like those of one's vacation to Hawaii, include information about the order in which events occurred. For example, you may have snorkeled, visited a volcano, and then went sailing (Figure 1; top left). The way we encode and explicitly remember the order of unique events is likely similar in many ways, but also critically different, from how we encode and remember the order of responses we take to execute a cooking recipe (Figure 1; top right). Nonhuman animal models of both of these types of memories exist (Figure 1; bottom) but systematic comparisons of the cognitive representations required for them have not been conducted.

Severe episodic memory deficits occur with aging and following brain injury or neuropsychiatric disease (Hoff & Mobbs, 2009). Animal models are required because they allow rigorous behavioral studies with a degree of anatomical, pharmacological, genetic, and molecular precision not available in human studies (Dere, Kart-Teke, Huston, & Silva, 2006). One tractable approach for developing necessary animal models is to study individual components of episodic memory, like memory for the order in which unique events occur (Fortin, Agster, & Eichenbaum, 2002; Templer & Hampton, 2013).

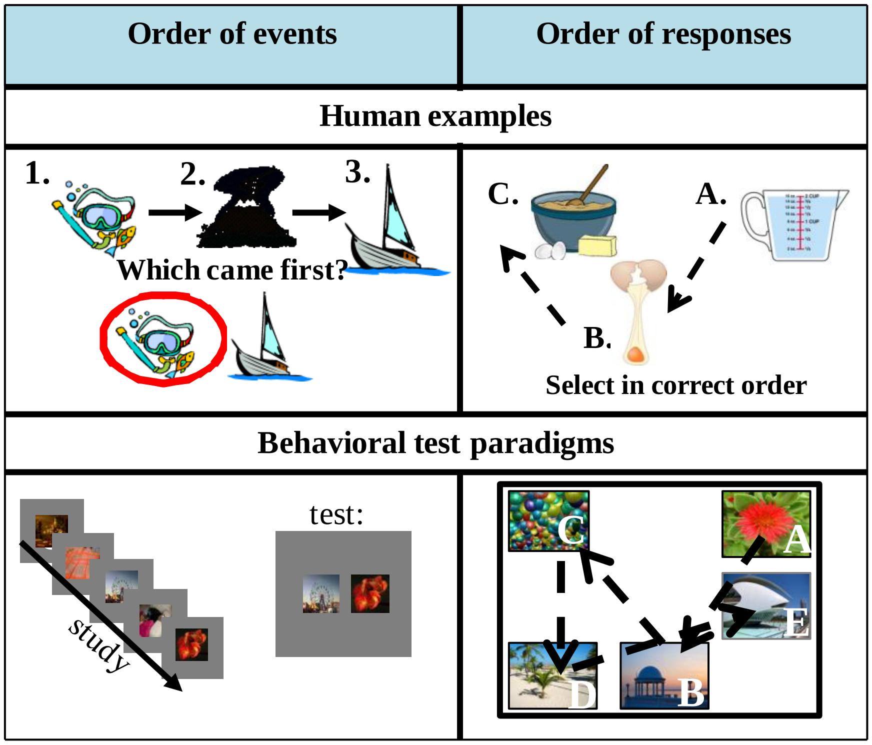

Figure 1. Human examples (top) and behavioral models (bottom) of two order tasks. **Memory for order of events** *(top left):* the earlier of two items in a behavioral episode, like one's vacation, can be identified. *Bottom left:* 5 items appear in sequence and subjects are rewarded for choosing the earlier item in the Temporal Order (TO) paradigm (Templer & Hampton, 2012, modeled after Fortin et al., 2002). **Memory for order of responses** *(top right):* multiple actions, like those taken to execute a cooking recipe, are completed in the correct order. *Bottom right:* 5 images appear together, and must be selected in the correct order (after Terrace, 2005) in the Simultaneous Chaining (SC) task.

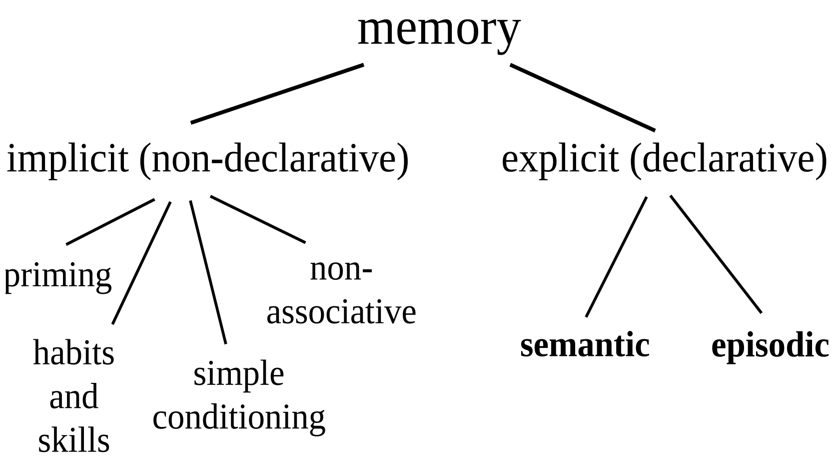

Figure 2. Common human long-term memory taxonomy. Explicit (or declarative memory) is divided into two systems, semantic and episodic memory. (Squire & Zola-Morgan, 1991).

An essential feature that distinguishes between explicit memories, as in the Hawaii vacation example, is that one can access the contents of explicit memory to retell particular stories from one's vacation. Using semantic memory, another type of explicit memory (Figure 2), one can access one's memory for general facts or knowledge about the world and report that Rome is the capital of Italy, for example. Episodic memories are thought to be supported by the hippocampus (Eichenbaum, 2006). In contrast, implicit memories, like those that let us ride a bike or perform other well-established skills or habits, cannot be accessed and require the striatum and do not rely on the hippocampus (Yin & Knowlton, 2006). These classic implicit/explicit and episodic/semantic distinctions have not been applied to order of events (Figure 1; bottom left) and order of responses (Figure 1; bottom right) in monkeys, but exploring the possibility of these distinctions may provide important insights into the memory systems underlying performance on these tasks. While it is possible that identifying the cognitive properties of these two types of memories may help with the development of such distinctions in a nonhuman primate, the tasks developed here will nonetheless improve the utility of these paradigms for advancing understanding monkey memory systems.

1.2. Aims

While the background of this dissertation is motivated through an episodic memory orientation, it should be reiterated that the goal of these studies was not to model episodic memory in its entirety. My objective in this dissertation was to directly compare two types of memories for order by examining the cognitive properties in each task. Neurological diseases and normal aging impair memory for order of events and memory for order of responses. Animal models that will permit identification of brain structures supporting memory for order may help in the development of future treatments for memory loss. Developing strong cognitive behavioral models is the first step in establishing such a model system and appropriate task paradigms.

Representative ordinal tasks (Figure 1; bottom) that capture important aspects of explicit memory are therefore useful as they may lead to improved understandings of specific cognitive mechanisms and neural structures supporting these abilities. Such memory system characterizations may eventually help the development of treatments for memory impairments in human clinical populations. Rhesus monkeys were used to capture the richness of human memory because they share many neuroanatomical and cognitive features with humans (Dehaene, 2005). We aimed to determine the extent to which memory for order of unique events and memory for order of routinized responses are distinct in terms of the properties of the cognitive representations underlying them.

While it is an important limitation that we cannot assess whether episodic processing is accompanied by conscious experience in nonverbal species, this hurdle also creates a crucial advantage in nonhuman animal studies. Behaviorally-based approaches distance us from epiphenomenal self-reflective verbal reports. The fact that we know humans have episodic memory from examples like one’s anecdotal description of their vacation does not necessarily mean that the current scientific methods used to test it are ideal (Dere et al., 2006). As a result of clever paradigms and methodological advances designed to suit nonverbal species, research on nonhumans has flourished in the last several decades (Eichenbaum & Cohen, 2001; Shettleworth, 2010). One benefit to studying cognition in animals is that otherwise seemingly complex human abilities can be isolated and simplified (Hampton, 2005). Evaluating the psychological features of memory for order or other cognitive behaviors in animals even without invasive procedures or lesions is therefore fruitful in itself (Marshuetz, 2005; W. A. Roberts, Medin, D.L., Davis, R.T, 1976). Moreover, the definition of phenomena like episodic memory and metacognition, or thinking about thinking, might be improved as focus is drawn to cognitive mechanisms and their specific functions rather than reported phenomenology initially used to characterize these abilities (Hampton, 2005).

Memory for order of events; explored in Paper 2 (Temporal Order: TO Task). While some research has shown that the prefrontal cortex (PFC) is necessary for the ability to remember order of events; (e.g. Amiez & Petrides, 2007; DeVito & Eichenbaum, 2011; Petrides, 1995) Fortin et al. (2002; see also Kesner et al., 2002) have shown that in other tasks that more closely resemble elements of episodic memory, the hippocampus also mediates the ability to remember order (Eichenbaum, 2013). Fortin et al. (2002) rewarded rats for choosing the odor that appeared earlier from amongst two odors that were presented in a five-item sequence. Following hippocampal lesions, rats performed significantly worse than controls on these ordinal tests but performed comparably on recognition tests in which rats chose between an odor presented in the list (unrewarded) and one that was not in the list (rewarded). This elegant study in rats illustrates how lesions can dissociate two neurobiological mechanisms (Fortin et al., 2002; Kesner et al. 2002), but the specific cognitive representations rats used to correctly order stimuli were not characterized.

Determining the extent to which the TO test simulates the temporal order aspect of episodic memory requires characterizing the mechanism used to select the earlier item in the list. Extending this study to monkeys allowed us to conduct the extensive behavioral testing necessary to identify the cognitive features of memory for order of events and develop an animal model system more directly applicable to the human brain (Dehaene, 2005). To address the need to properly characterize the cognitive features of memory for order of events we developed a test that examines memory for order of unique visual events in monkeys. In this task monkeys saw and touched five trial-unique images and after a short delay, were rewarded by selecting the image that occurred earlier in the sequence from amongst any two images seen during study.

Memory for order of responses (Simultaneous Chaining: SC Task); explored in Paper 3. Terrace's group approached memory for order from a different perspective by evaluating monkeys' ability to learn serial order (e.g. S. Chen et al., 1997; H.S. Terrace et al., 2003). Monkeys were presented with highly familiar stimuli and required to touch them in a particular order (e.g. List 1: $A_1 \rightarrow B_1 \rightarrow C_1 \rightarrow D_1 \rightarrow E_1$; numbers indicate list and letters indicate different items within a list; Figure 1, bottom right; Terrace, 2005). The spatial arrangements of the items varied randomly in each trial such that responses must have been guided by memory for the position of each image in a mental list, rather than by execution of a spatially-guided motor program. We examined several candidate mechanisms to probe the contents of memory that underlies the ability to remember fixed orders in during list execution in SC.

1.3. Approach

Here we develop a cognitive behavioral model by directly comparing two representative tasks which differ along several dimensions but share the property that they require memory for order. The TO task requires memory for trial-unique order of events, (Figure 1; bottom left) and is modeled after a study done in rats (Fortin et al., 2002). The SC task requires memory for routinized order of responses (Figure 1; bottom right H. S. Terrace, 2005).

The following four papers report recent findings about memory for ordinal stimuli and synthesize research on aspects of episodic memory and memory for order in nonhumans. Paper 1 is a review paper that introduces the topic of the study of episodic memory in nonhuman animals, which includes memory for order of events. This paper serves an extended general introduction and provides a useful framework for Paper 2, an empirical paper that examines how rhesus monkeys *(Macaca mulatta)* remember the order in which trial-unique stimuli are experienced in the TO paradigm. Paper 3 is another empirical paper that also tests memory for order, in the SC paradigm, where the to-be-remembered information is the order of responses to stimuli in fixed lists that becomes routinized list after continued experience with list execution. Finally, Paper 4 serves as a general discussion as it describes the results presented in Paper 2 and Paper 3 by contrasting the nature of mental representations for order in cases when stimuli are trial-unique and when stimuli are repeating. The dissertation closes with the final section, conclusions and future directions.

2. Introduction to Paper 1

Paper 1 was chosen as the introduction to this dissertation because it provides a background to the study of episodic memory in nonhumans which serves as useful foundation with which to lead into Paper 2, an empirical paper that examines the temporal aspect of episodic memory. Reviews of the study of nonhuman animal memory exist but many summarize work done in the behavioral domain by comparative cognition researchers, or work done in the neurobiological domain by neuroscientists, rather integrating those subfields. Here, we aimed to review both types of studies, give examples of researchers who are making great strides in combining cognitive and neuroscientific techniques, and identify areas for improvement.

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3. Paper 1

Minireview

Episodic Memory in Nonhuman Animals

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3.1. Abstract

Episodic memories differ from other types of memory because they represent aspects of the past not present in other memories, such as the time, place, or social context in which the memories were formed. Focus on phenomenal experience in human memory, such as the sense of ‘having been there’, has resulted in conceptualizations of episodic memory that are difficult or impossible to apply to nonhuman species. It is therefore a significant challenge for investigators to agree on objective behavioral criteria that can be applied in nonhuman animals and still capture features of memory thought to be critical in humans. Some investigators have attempted to use neurobiological parallels to bridge this gap; however, defining memory types on the basis of the brain structures involved rather than on identified cognitive mechanisms risks missing crucial functional aspects of episodic memory, which are ultimately behavioral. The most productive way forward is likely a combination of neurobiology and sophisticated cognitive testing that identifies the mental representations present in episodic memory. Investigators that have refined their approach from asking the naïve question “do nonhuman animals have episodic memory” to instead asking “what aspects of episodic memory are shared by humans and nonhumans” are making progress.

3.2. Introduction

Memory is not a single thing: our apparently seamless experiences of remembering result from the combined action of cognitively and neurobiologically distinguishable systems in the brain. These distinct systems have evolved because they each serve specialized functions that have promoted survival and reproduction (Sherry & Schacter, 1987). One type of memory is episodic memory, which enables use of contextual information about distinct episodes from one's personal past to guide behavior. For example, you might remember loading ripe tomatoes and watermelon for a barbecue on the supermarket checkout belt while reading about the anti-cancer properties of a plant in a tabloid headline. In this case, contextual information about where and when you formed a memory is useful in discriminating facts learned reading tabloids from facts learned during a trip to the botanical gardens. By contrast, semantic memories lack contextual details: you may know that monkeys have tails, but probably do not remember the occasion on which you learned this fact. The distinction between episodic and semantic memory in humans is central in cognitive neuroscience and has been well-established by the combination of behavioral studies, neuroimaging studies, and studies of patients with brain damage (Gardiner, Brandt, Baddeley, Vargha-Khadem, & Mishkin, 2008). The extent to which these specific memory systems exist in nonhumans is debated. Some cognitive scientists argue that episodic memory may be uniquely human, at least in part because episodic memory is often defined using criteria based in human conscious experience that are difficult or impossible to apply in nonhumans (Suddendorf, 2013; Tulving, 2005).

Comparative psychologists and neurobiologists who study the evolutionary and mechanistic relations among memory systems across species generally define episodic memory in terms that can be operationalized in objective studies with nonverbal species. Studies of memory in nonhuman animals have resulted in a rich set of methodologies, findings and perspectives. Mapping specific performances in nonhumans to human episodic memory remains controversial, but there is no doubt that our understanding of memory in humans and nonhumans is advancing. Here, we shall highlight some of the problems inherent in studying episodic memory in nonhumans and use selected examples to illustrate distinct perspectives and demonstrate progress. Central to our review is acceptance of the idea that episodic memories have distinct functional properties not found in other memory systems.

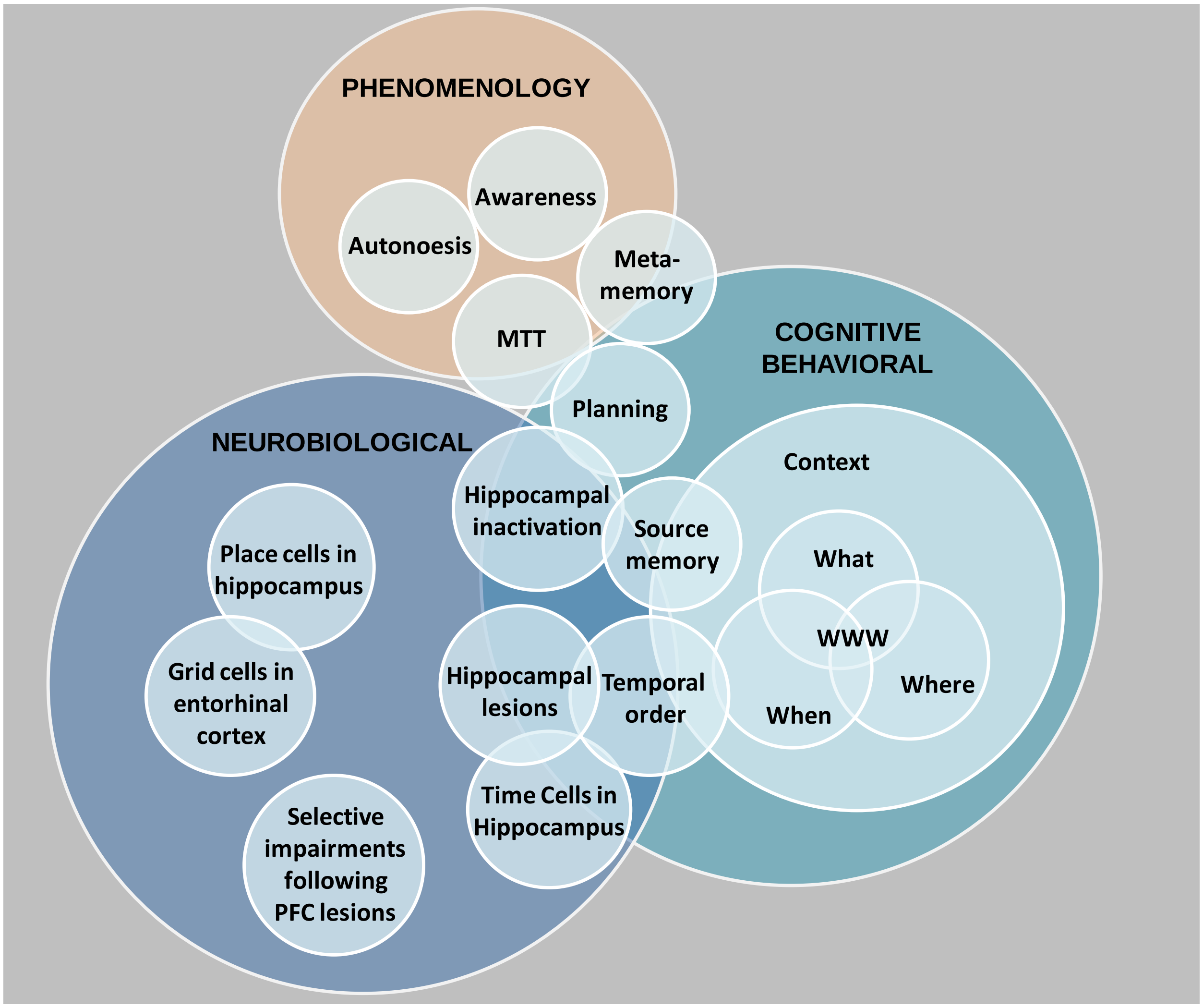

Figure 1. Constellation of Mnemonic Features of Episodic Memory. Mnemonic features are grouped within the phenomenological, neurobiological, and cognitive behavioral approaches. Some areas of potential overlap are indicated. These are meant to be representative examples; there exist more mnemonic features, and more approaches, than could be depicted here. Future research might be directed at creating more overlap in the research domains indicated by the bubbles.

It is possible to dissociate episodic memories from other types of memory based on the particular features of events that are mentally represented and the neurobiological systems that instantiate these representations (Easton, Webster, & Eacott, 2012; Shettleworth, 2010). These dissociations become possible when we design experiments based in the question, “what can an animal with episodic memory do that one without it cannot do?”

3.3. Moving beyond anthropocentrism and phenomenology

The term ‘episodic memory’ was coined by Endel Tulving in 1972 to describe a type of human memory, and was elaborated to apply to memory of autobiographical events resulting from ‘mental time travel’ associated with self-awareness or ‘autonoesis’ (Tulving, 2005). The first efforts to search for episodic memory in nonhuman species were therefore necessarily anthropocentric and faced the potentially insurmountable problem of mapping the objective performance of nonhuman animals in memory tests to human reports of the phenomenology of remembering. Debate continues about whether nonhuman animals ‘mentally travel in time’ and experience autonoesis (W. A. Roberts, 2012; Suddendorf, 2013), and these debates can shift attention away from the well-designed objective studies of nonhuman memory that yield progress (Figure 1). However, to the extent that these and similar phenomenology-rich conceptualizations of memory can be objectively operationalized, they will stimulate progress by challenging experimentalists to design better studies.

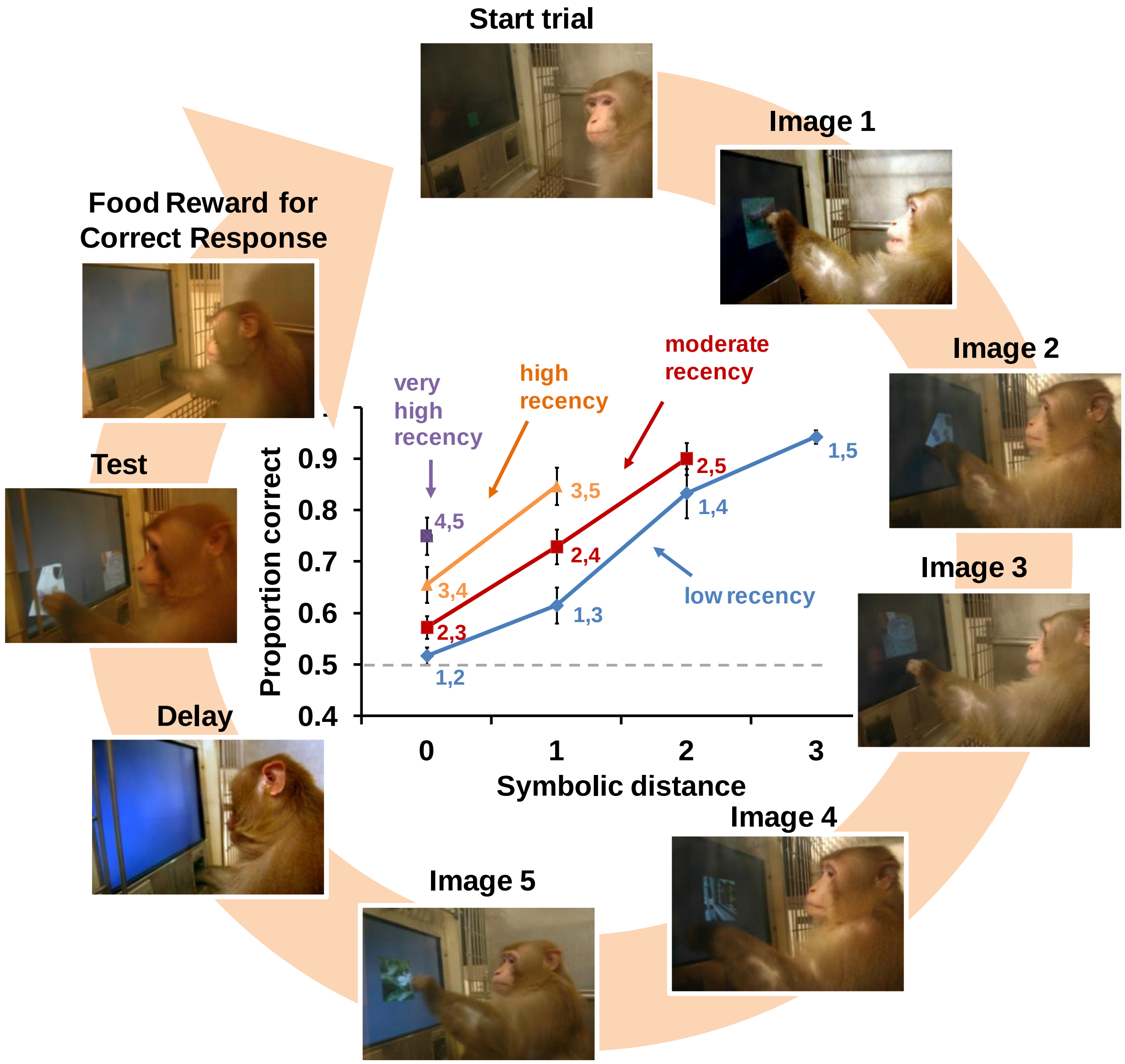

Figure 2. Temporal order memory test for monkeys (Templer & Hampton, 2013, modeled after Fortin et al. 2002). The images around the perimeter depict the stages in this behavioral test; the graph in the middle depicts typical results from averaging thousands of test trials. Trials began when the monkey touched the green square. The monkey then touched five trial-unique images presented one after the other. After a short delay, the monkey chose between a randomly selected pair of images from the list (here images 2 and 3; a “2, 3” test). Selecting the image that had appeared earlier in the study list was rewarded with a positive sound and a food pellet in the reward trough. The graph in center shows accuracy in tests with pairs of images from each combination of study list positions. Accuracy was higher for tests consisting of pairs that were widely separated in the study list (symbolic distance) and for images that were near the end of the list (recency). The dashed line indicates the accuracy expected if the monkey were guessing. Monkeys remembered the order in which images appeared, demonstrating an important property of EM.

Natural selection has resulted in different memory systems because of the distinct functional roles these systems play in the service of overt behavior, not because of differences in the way these memories are phenomenally experienced. Nonetheless, some students of nonhuman memory continue to struggle with definitions of memory systems that emphasize phenomenology and private experience, arguing that “the main ingredient missing [in studies of episodic memory in nonhumans] is autonoetic consciousness” (Suddendorf, 2013). This problem was famously sidestepped with the term ‘episodic-like’ to describe some memory in nonhumans (N.S. Clayton & Dickinson, 1998). Whatever terminology is used, progress will be most rapid when we define memory systems in entirely functional terms that can be objectively operationalized in behavioral experiments with a variety of species. As Bertrand Russell is believed to have stated: “The greatest challenge to any thinker is stating the problem in a way that will allow a solution.”

3.4. Neurobiological approaches

Neurobiological manipulations can establish correspondences between specific memory capacities and specific neurobiological systems. Episodic memories in humans are particularly dependent on the integrity of the hippocampus and related structures, while other kinds of memory are not (Eichenbaum, Yonelinas, & Ranganath, 2007). Because human episodic memory is known to be dependent on the hippocampus, determining which nonhuman memories are dependent on the hippocampus is one approach taken to episodic memory in nonhumans. After encountering a list of five odors in sequence, rats with hippocampal lesions were unable to report which odor occurred earlier in the list. By contrast, these rats could still correctly recognize whether an odor was familiar from having been presented during study and could discriminate one odor from another (Fortin et al., 2002). This dissociation of memory for order from the ability to recognize items parallels findings from humans, where hippocampal dependent episodic memory is dissociated from other types of memory (Mayes et al., 2001). Similarly, monkeys with fornix transections, which disrupt one of two major afferent-efferent pathways of the hippocampus, were unable to make accurate recency judgments (Charles, Gaffan, & Buckley, 2004). Subsequent lesion studies (Farovik, Dupont, & Eichenbaum, 2010) and pharmacological inactivation studies suggest that, in the hippocampus, area CA3 and the dentate gyrus (DG) rapidly encode spatial separation, whereas area CA1 encodes temporal order (for example (e.g. Barbosa, Pontes, Ribeiro, Ribeiro, & Silva, 2012)).

Determining the extent to which similar kinds of neural processing, representing similar aspects of memory, occur across species is a powerful method for establishing correspondences in memory systems. Whereas removal and inactivation of brain systems provide strong causal evidence regarding the locations of brain functions, electrophysiological recordings provide information about how processing in specific areas might be carried out. The representation of the spatio-temporal structure of sequences of events in hippocampal neural ensembles may be conserved across species (for review see [15]). During an odor-order test based on the one described above, the magnitude of changes in patterns of rat hippocampal ensembles predicted memory performance (Manns, Howard, & Eichenbaum, 2007).

Specific ensembles have been shown to encode specific memories and likely the passage of time (Pastalkova, Itskov, Amarasingham, & Buzsaki, 2008). The lateral prefrontal cortex (PFC) in monkeys (Ninokura, Mushiake, & Tanji, 2004) and medial PFC in rats (DeVito & Eichenbaum, 2011) also encode temporal order. Neural ensembles in the hippocampus have been found to ‘replay’ events encountered during spatial navigation tasks, with place cells firing in the same order during rest and sleep as they had when rats traveled a particular route. Similarly, the same neurons in the human hippocampus fire when subjects watch movie scenes and later recall them (Gelbard-Sagiv, Mukamel, Harel, Malach, & Fried, 2008). Disruption of this neural replay in rats impaired performance in a delayed alternation test, suggesting that reactivation of neural ensembles underlies memory for places recently visited (Jadhav, Kemere, German, & Frank, 2012). Evidence that hippocampal cells in rodents encode time is accumulating (Farovik et al., 2010; Suh, Rivest, Nakashiba, Tominaga, & Tonegawa, 2011), but it is still a challenge to establish direct parallels with humans, from whom relevant electrophysiological data are rarely collected. Less direct parallels are seen in human functional magnetic resonance imaging (fMRI) studies in which tests of temporal order result in activation of the hippocampus (Tubridy & Davachi, 2011). To the extent that discriminating the temporal order and locations in which events occurred are functional properties of episodic memory, these studies provide strong evidence for a homologous episodic memory function of the hippocampus among humans, monkeys, and rodents.

3.5. Cognitive behavioral approaches

Neurobiological studies of memory focus on identifying the brain areas and neural processes responsible for memory. Cognitive studies complement this work by establishing in more detail which aspects of events are represented, or stored, in the brain and how this information controls behavior (Figure 1). Episodic memory was described as memory for what happened, where and when (WWW memory) in food-caching scrub-jays (*Aphelocoma coerulescens*), birds that remember what foods they hid in which locations at which points in time (N.S. Clayton & Dickinson, 1998). Comparative researchers have developed analogous paradigms in other food-hoarding species (for example (e.g. Feeney, Roberts, & Sherry, 2011b)), in rodents (Babb & Crystal, 2006), and in primates (Martin-Ordas, Haun, Colmenares, & Call, 2010). Other behavioral paradigms for modeling aspects of episodic memory in nonverbal species include memory for temporal order (Fortin et al., 2002), memory for the source of memories (Crystal, Alford, Zhou, & Hohmann, 2013), and planning (Crystal, 2013; W. A. Roberts, 2012).

The many tests of whether particular species ‘show’ WWW memory equate to asking, “does species X have episodic memory?” This approach can be problematic for several reasons. Humans have many semantic memories that include what happened, where it happened and when it happened, such as knowledge of historical facts. We also have many episodic memories that do not include all three elements (T.R. Zentall, Clement, Bhatt, & Allen, 2001). Surprisingly, when tests similar to the WWW tests designed to model episodic memory in nonhumans are conducted with humans, performance may not always depend on episodic memory (Easton et al., 2012). A more nuanced approach tests the extent to which various species manifest different aspects of episodic memory, and has many advantages. First, we should expect memory to have evolved differently in different species so as to match their cognitive capacities to species-specific ecological demands, making a single conception of episodic memory overly restrictive. Focus on a single specific set of criteria can make it difficult to identify interesting and informative species-specific specializations in memory. Second, rather than simply rejecting behavioral paradigms as ‘failures’ to demonstrate fully-developed episodic memory if they do not meet a narrow definition, studying different aspects of episodic memory across species promotes new interesting areas of research to flourish. Third, considering episodic memory as a constellation of mnemonic functions, rather than a single entity, may allow us to make best use of studies of nonhumans to illuminate the organization of memory more generally by identifying commonalities and differences among memory systems and across species. Studies of episodic memory in nonhumans may allow reevaluation of the type of memory we call episodic in humans and may better establish commonalities among evolutionarily conserved memory systems.

3.6. What is mentally represented in episodic memory?

The example of WWW memory shows how memories can be encoded in a variety of ways. ‘When’ could consist of different kinds of temporal information, from the time of day at which an event occurred, how long ago an event occurred, how strong a given memory is, to which events preceded and which followed a particular event (Figure 3). When monkeys *(Macaca mulatta)* were presented with trial-unique sequences of images, it was the number of intervening items, rather than passage of time *per se*, that most strongly determined memory for the order of occurrence (Templer & Hampton, 2012a; Figure 2)). Honeybees used circadian timing in a WWW memory test, perhaps because they are obligate nectar feeders and nectar availability follows a robust circadian pattern (Pahl, Zhu, Pix, Tautz, & Zhang, 2007). Foraging decisions in rats often depend on elapsed time, consistent with the finding that the performance of rats in a WWW task was not controlled by circadian time (Babb & Crystal, 2006), and in a separate test depended on elapsed time (William A. Roberts et al., 2008). More recently, however, Zhou and Crystal (Zhou & Crystal, 2009) designed a WWW experiment that prevented rats from using elapsed time to guide behavior and found that under these conditions the behavior of rats was controlled by time of day. Not surprisingly, different species under different conditions encode time in different ways, some showing stronger parallels to human episodic memory than others.

3.7. Memory is for the future

Episodic memory, like other types of memory, evolved not for idle reminiscence about the past but because it promotes adaptive action in the present and future ((Shettleworth, 2010, p. 250)). In accord with this view, mental simulations of future events in humans rely on the same neural systems responsible for episodic memory (Schacter et al., 2012). Interest in the extent to which nonhumans plan and otherwise anticipate the future has grown with the development of studies of episodic memory. Black-capped chickadees (Feeney, Roberts, & Sherry, 2011a) and western scrub jays (Correia, Dickinson, & Clayton, 2007) selectively chose which foods to cache so as to have access to foods that will address anticipated motivational states, even when currently satiated on that particular food. In a related task, squirrel monkeys (*Samiri scireus)* altered behavior in anticipation of future thirst (Naqshbandi & Roberts, 2006). Researchers have begun to develop prospective memory tests to study planning because prospective memory is proposed to require encoding, retention, and retrieval of an intended future action, as when we remember to buy milk on the way home (Beran, Perdue, Bramlett, Menzel, & Evans, 2012; Wilson & Crystal, 2012).

3.8. Recall and recognition

Humans with episodic memory deficits are dramatically impaired in tests of free recall, in which they are required to recollect and produce, rather than simply recognize, remembered material (Gardiner et al., 2008). Nearly all memory tests used with nonhumans are recognition tests but comparative psychologists have begun to develop recall tests, and measures of recollection, for nonhumans. Several hours after observing food being hidden in an outdoor enclosure, a lexigram-trained chimpanzee *(Pan troglodytes)* spontaneously requested to go outside, indicated which food she wanted to locate by pointing to a lexigram keyboard, and successfully directed a human to the location of the food (Menzel, 1999). In a study paralleling the human ability to recall and reproduce images from memory, rhesus monkeys reproduced simple shapes from memory on a touchscreen (Basile & Hampton, 2011). Analysis of error patterns in rhesus monkeys indicated the presence of both recollective and familiarity-based memory processes in recognition memory tests (Basile & Hampton, in press). Recollective processes are associated with episodic memory in humans (Gelbard-Sagiv et al., 2008).

3.9. Convergence of cognition and neurobiology

The most informative and exciting studies of episodic memory combine sophisticated behavioral paradigms that identify what information is mentally represented with neurobiological manipulations or measures that identify the neural bases of performance (Figure 1). The rodent studies of memory for order described earlier are good examples of such studies (DeVito & Eichenbaum, 2011; Fortin et al., 2002). Episodic memories are often encoded incidentally and remembered when unexpectedly needed (T.R. Zentall et al., 2001). Rats reported correctly whether or not they had recently found food, even under conditions in which they should not have expected a test of memory. Availability of this apparently incidental memory was abolished by inactivation of the hippocampus (Zhou, Hohmann, & Crystal, 2012). As described in the introduction, episodic memory encodes the context, or source, of memories. Rats with temporary inactivation of the hippocampus could no longer remember whether they recently entered the arm of a maze on their own or had been placed there by an experimenter (Crystal et al., 2013). We have not mentioned many other excellent studies combining important cognitive and functional properties of episodic memory with neurobiology, but have rather used these examples to foreshadow the exciting studies we see ahead.

3.10. Gaps and future studies

Few cognitive studies of episodic memory in nonhumans have sought to dissociate episodic memory from other types of memory, although it is known that hippocampal lesions dissociate memory for order from familiarity (Fortin et al., 2002). In particular the distinction between semantic and episodic memory has not been extensively developed in nonhumans. Performance in memory tests requires at least two kinds of knowledge. The first is reference memory of the ‘rules of the game’, such as that food can be found at the end of the arms of a maze or that food can be earned by selecting the image seen most recently. The second is often called ‘working memory’ and is memory for what has happened recently, such as which maze arms have been visited or which image was seen at the beginning of the current trial ((Shettleworth, 2010, p. 216)). Reference memory has properties of human semantic memory, but the relations between human and nonhuman semantic memory have not been the focus of anything like the effort devoted to the study of episodic memory. It is well-known in humans that no memories, even episodic memories, are simple records of the past. Instead, memories result from reconstructive processes, including interactions between semantic and episodic memory (Friedman, 2005; Loftus, 2003). We often infer when our episodic memories were formed by reference to semantic knowledge, for example by reasoning that we must have conversed with our colleague two days ago rather than yesterday because we were out of town yesterday. To our knowledge, no studies of episodic memory in nonhumans have directly addressed the extent to which nonhumans process episodic memories as embedded in structured sequences of events analogous to human’s use of calendars and routines.

Some of the most comprehensive and exciting behavioral data on episodic memory has come from studies of birds (N.S. Clayton & Dickinson, 1998; Feeney et al., 2011b) but there are no studies to our knowledge that directly assess the neurobiology of episodic memory in birds using lesion studies, physiological mapping, or neurophysiology. This gap may be due in part to the difficulty inherent in evaluating the role of the hippocampus in WWW memory, given the well-established role for this structure in spatial memory in primates (Hampton, Hampstead, & Murray, 2004), rodents (Clark, Broadbent, & Squire, 2005), and birds (White, Strasser, &

Bingman, 2002). It is difficult to distinguish a deficit in episodic memory from one in spatial memory in any behavioral design with a spatial component. This difficulty highlights the need to avoid circular reasoning based on neurobiology alone, for instance concluding that because a particular behavioral performance is dependent on the hippocampus, it necessarily involves episodic memory. Instead, it is critical to determine the cognitive representations that control behavior in a given test, and which components of this represented information are lacking following hippocampal removal, for example.

Comparative and evolutionary studies should focus on differences among species at least as much as similarities, yet within comparative psychology and neurobiology it is common to emphasize similarities. Identifying differences, or specializations, in episodic memory between species can allow testing of hypotheses about the evolution of memory. For example, highly social species may have evolved episodic memory that is especially sensitive to the precise social context in which memories were formed, enabling sophisticated social behavior. By contrast, food-storing birds that cache and recover perishable foods may be especially sensitive to the temporal context in which memories were formed. Only comparative studies, conducted with a broad conception of what episodic memory is, can identify such differences if they exist.

Most modern taxonomies of human memory make a fundamental distinction between memories about which we are aware (declarative or explicit memories) and memories that are unconscious (non-declarative or implicit; Squire & Zola-Morgan, 1991)). Human episodic memories are explicit. Studies of metamemory in nonhumans, in which subjects show that they ‘know when they know’, suggest that at least some memories in nonhumans are also explicit. For example, monkeys and apes chose to take memory tests in which they were likely to answer correctly but declined memory tests they were likely to fail. Some nonhumans also selectively seek information only as needed before completing memory tests (For review Hampton, 2009)).

Metamemory tests have not yet been combined with studies of episodic memory in nonhumans, but such approaches might be useful.

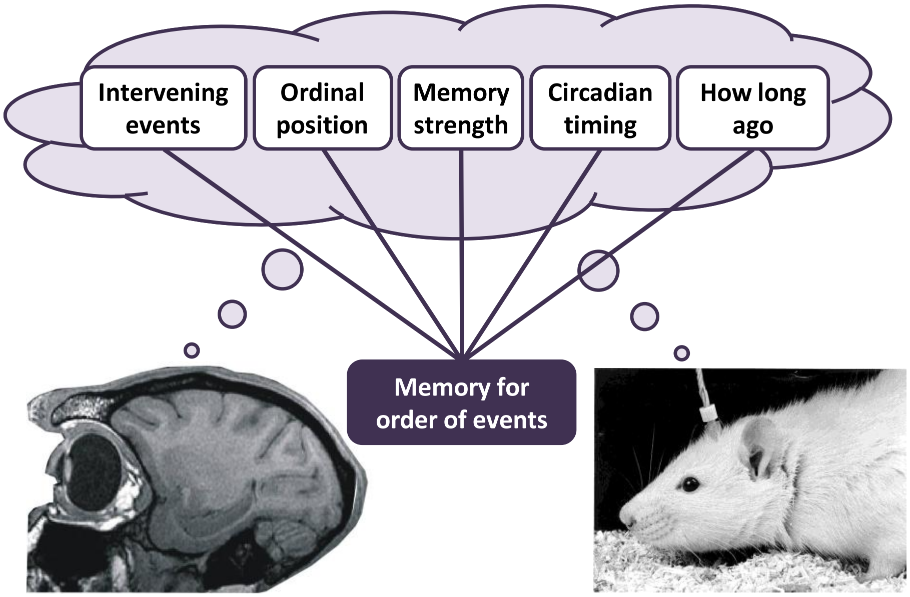

Figure 3. Brain manipulations do not directly identify cognitive mechanisms. The lower panel depicts the fact that manipulation of the brain, such as inactivation of the hippocampus, may impair performance in a given test, such as memory for the order of events. The upper panel indicates that this impairment might be caused by any of a variety of changes in the mental representations responsible for performance. The combination of brain manipulations and sophisticated cognitive testing is required to identify the relationships between brain mechanisms and cognitive representations. As described in the text, different species may encode temporal order differently, making independent tests in different species necessary.

3.11. Conclusions

Advances in our understanding of episodic memory depend on establishing robust dissociations between memory systems based on the neurobiological systems serving memory, the aspects of events mentally represented, and in the kinds of transformations represented information undergoes in the generation of behavior. As these characterizations develop, we will be better able to compare and contrast these systems across species, and to describe the way these systems have likely evolved. By better understanding functional differences in memory among species we will better know what episodic memory is. This knowledge serves the basic science goal of understanding the autobiographical memories that constitute our sense of self, and the more practical need to appreciate which animal models best capture which aspects of episodic memory for biomedical research. We likely will never have satisfactory answers to questions about the phenomenology of memory in nonhumans, but we are making great strides in understanding what features of events are represented, where in the brain, now.

4. Introduction to Paper 2

This paper arose from the goal of developing a non-human primate model of memory for temporal order analogous to the one developed in rats in which rats, as explained in the general introduction (Fortin et al., 2002; R.P. Kesner, Gilbert, & Barua, 2002). We were initially motivated to develop a more comprehensive cognitive account of the temporal aspect of memory, which is fundamental to episodic memory. The term temporal order memory is used frequently, but many researchers do not actually define what “temporal order” means or specifically define how use of such a mechanism informs the structure of the representation itself. For example, does experiencing events consecutively contribute to the representation of memory for order or does the passage of time alone create perceived distinction between two experienced events? Does memory for unique images model the continuous stream of events humans experience in normal life and then remember sequentially? If so, memory for each image should have a temporally defined “tag” unconstrained to the list in which that image was experienced; if not images should have a tag constrained to the discrete sets of images. We also determined whether monkeys have knowledge of ordinal position and know that image one came first, image two came second, etc. These are the questions we answered about the cognitive mechanism for memory for unique order of events in Paper 2.

A supplemental video of how engaging in this task (with a set-size of 20) appears to a monkey please see: http://www.psychology.emory.edu/lcpc/demos.html.

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5. Paper 2

Cognitive mechanisms of memory for order in rhesus monkeys *(Macaca mulatta)*

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5.1. Abstract

One important aspect of episodic memory is the ability to remember the order in which events occurred. Memory for sequences in rats and has been shown to rely on the hippocampus and medial prefrontal cortex (DeVito & Eichenbaum, J Neuro 2011; 31: 3169-3175; Fortin et al., Nat Neuro 2002; 5:458-462). Rats with hippocampal lesions were impaired in selecting the odor that had appeared earlier in a sequence of five odors but were not impaired in recognition of previously sampled odors (Fortin et al., 2002; R.P. Kesner et al., Behav Neuro 2002; 116:286-290). These results suggest that order is not represented by relative familiarity or memory strength. However, the cognitive mechanisms underlying memory for order have not been determined. We presented monkeys with lists of five images drawn randomly from a pool of 6,000 images. At test, two images were presented and monkeys were rewarded for selecting the image that had appeared earlier in the studied list. Monkeys learned to discriminate the order of the images, even those that were consecutive in the studied list. In subsequent experiments we found that discrimination of order was not controlled by list position or relative memory strength. Instead, monkeys used temporal order, a mechanism that appears to encode order of occurrence relative to other events, rather than in absolute time. We found that number of intervening images, rather than passage of time per se, most strongly determined the discriminability of order of occurrence. Better specifying the cognitive mechanisms nonhuman primates use to remember the order of events enhances this animal model of episodic memory, and may further inform our understanding of the functions of the hippocampus.

5.2. Introduction

Imagine that you hear a noise coming from under the hood of your car. Before making an appointment with the mechanic, you struggle to remember whether you first noticed it before or after you had the car in for a tune up recently. Memory for the order of these events would help you decide whether to suggest that the mechanic may have caused the problem during the tune-up. Humans often remember the order in which events occurred (Eichenbaum, 2005; Tulving, 2005), probably using multiple cognitive mechanisms (e.g. Friedman, 2005; McColgan & McCormack, 2008).

A significant hurdle in the study of nonhuman memory is the fact that nonhuman animals cannot verbally report the rich details of private experience that often demonstrates human memory of personal events (e.g. Dere et al., 2006; Templer & Hampton, 2012b). One successful approach has been to test for specific aspects of episodic memory in nonhumans, rather than attempting to capture all the properties of episodic memory with a single paradigm (e.g. N.S. Clayton, Griffiths, Emery, & Dickinson, 2001; N. S. Clayton & Russell, 2009; Dere et al., 2006; Fortin et al., 2002; Hampton & Schwartz, 2004; W.A. Roberts & Roberts, 2002). The study of memory for the order of unique events appears to capture some aspects of episodic memory (Fortin et al., 2002; Kesner et al. 2002). In these studies, rats encountered five odors in sequence. Two odors from this list were then presented at test, and rats were rewarded for choosing the odor that appeared earlier in the list. Rats with hippocampal lesions were significantly impaired in reporting the order of odors but performed comparably to controls on recognition tests that required subjects to choose between an odor from the list and one that was not in the list. These results suggest that memory for order is dependent on the hippocampus and relies on cognitive mechanisms different from those responsible for recognition performance.

Fortin’s and Kesner’s experiments elegantly dissociate memory for order from recognition performance, but they do not unambiguously identify the cognitive mechanism by which order is remembered. Multiple memory processes, including relative familiarity and memory strength, may contribute to performance in both recognition tests (Charles et al., 2004; Tu, Hampton, & Murray, 2011) and tests of memory for order. Because memory fades over time, memory strength tends to correlate with order of presentation, with items presented earlier weakly represented compared to more recent items. Studies of memory for order conducted to date “do not provide definitive evidence that animals solve these tasks using a direct representation of the order of events (DeVito & Eichenbaum, 2011 , pp. 3169).” This significant issue in memory representation necessitates closer examination of the cognitive mechanisms that underlie the ability to remember sequences. By directly manipulating multiple sources of information that might support memory for order, including memory strength, list position, intervening events, and temporal spacing, we evaluated several possible mechanisms for memory of the order of trial-unique sequences.

5.3. Materials and Methods

Subjects

Six four-year-old male rhesus monkeys *(Macaca mulatta*) were used. Monkeys were pair-housed and kept on a 12:12 light:dark cycle with light onset at 7:00 am. Four of the monkeys were fed a full ration of food at the end of testing each day and the other two were fed half of their food ration in the morning before testing and the other half of food after testing each day. Water was available *ad libitum*.

Apparatus

Subjects were tested on computerized touch-screen systems in their home cages. Each system consisted of a 15-inch LCD color monitor (3M, St. Paul, MN) running at a resolution of 1024 X 768 pixels, generic stereo speakers, two automated food dispensers (Med Associates Inc., St. Albans, VT), and two food cups located below the screen.

General procedure

Each monkey had access to his cage-mate at all times except during testing and during feeding at the end of the day. Immediately before testing, monkeys were separated by insertion of plastic dividers between cage-mates that allowed limited visual and physical contact, but prevented access to the cage-mate’s testing equipment. Testing systems were locked to the front of each monkey’s cage. Cage doors were then raised, giving subjects full access to the screen during testing. Food rewards were nutritionally balanced banana flavored pellets (Bio-Serv, Frenchtown, NJ). One to five test sessions were conducted daily between 10 am and 5 pm, six days per week.

Six-thousand color photographs collected from public online digital image databases were used as memoranda. Images of humans were not used. Images were resized to 300 x 300 pixels.

Data analysis

Proportions were arcsine transformed before statistical analysis to better approximate the normality assumption underlying parametric statistics (Keppel & Wickens, 2004, p. 155). All t-tests were two-tailed.

5.4. Experiment 1

To prepare monkeys for a series of experiments designed to identify the cognitive mechanisms for memory for order, we trained them to identify which of two images from trial-unique sequences of five images had been presented first (Fortin, et al., 2002; Kesner, et al., 2002). Based on previous findings from monkeys (Petrides, 1991a, 1991b, 1995), and rats (Fortin, et al., 2002; Kesner, et al., 2002), we hypothesized that monkeys would learn to select the earlier image.

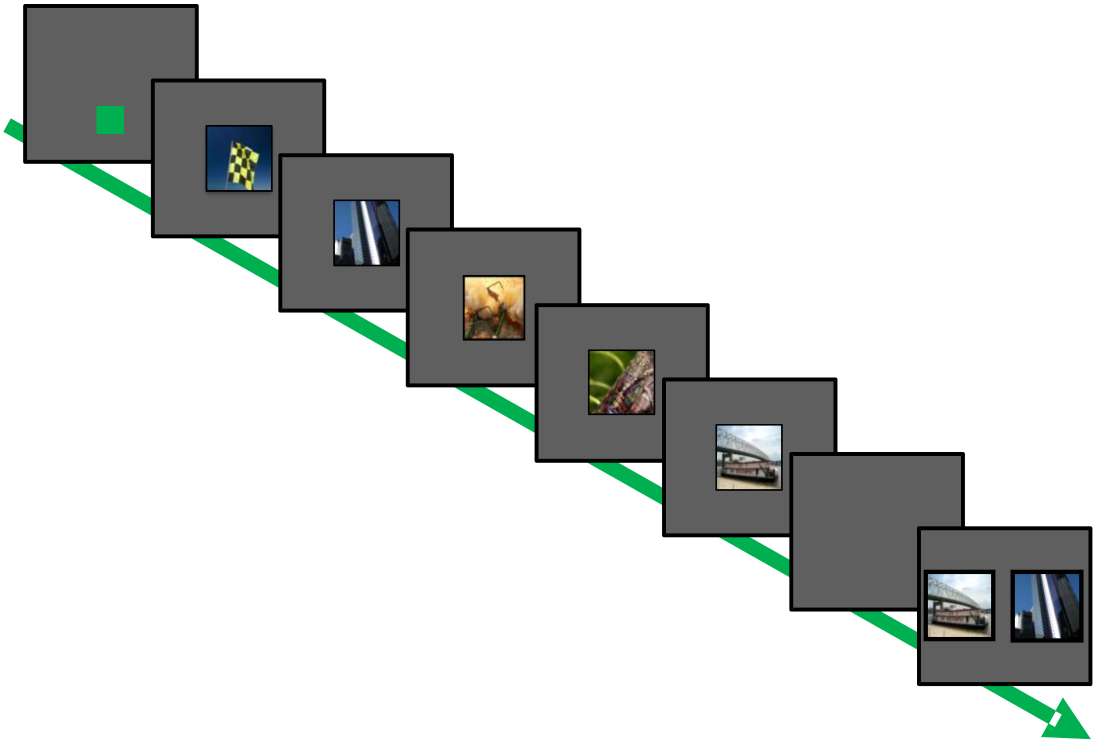

Figure 1. Trial progression in Experiment 1. Monkeys initiated the study phase of each trial by touching the green ready box. They then saw and touched five images in sequence, separated by a 500 millisecond ISI. After a 500 millisecond delay after the fifth image, monkeys were rewarded for choosing the image that had occurred earlier in the sequence at test. In this example, the second and fifth images are presented at test and the image of the skyscrapers would have been correct.

Phase 1: Training on non-adjacent images

A green box appeared at the bottom of the screen and remained until the monkey touched it (FR2) to start a trial (Figure 1). A photograph then appeared in the center of the screen on a gray background. The image was only sensitive to touch (FR 2) after a required minimum study period of 250 milliseconds. After the image was touched, it disappeared, a 500 millisecond inter-stimulus interval (ISI) occurred during which the screen was gray, and a second randomly selected image appeared in the same place as the first. This process repeated until five sample images were presented and touched. Following touches to the fifth image and a 500 millisecond retention interval, two test images from the list appeared to the left and right of the center of the screen separated by 400 pixels. Selection of the image that had occurred earlier in the sequence was rewarded with a positive auditory stimulus and a pellet food reward 100% of the time. Selection of the image that had occurred later in the sequence was followed by a negative auditory stimulus and a 10 second time-out during which the screen was black. The position of the correct and incorrect test images was pseudo-randomized such that the correct image did not appear on the same side of the screen on more than four consecutive trials. After errors, the entire trial was repeated. If the subject erred again, a one second time out was followed by appearance of only the choice images. This last phase of the trial, with the same images, was repeated as many times as needed until the subject selected the correct image. Trials were separated by a 500 millisecond inter-trial interval (ITI) during which the screen was black. Six-hundred images were randomly drawn from the entire set of 6,000 for use in each session. Tests consisted of images from each of the six possible non-adjacent list positions. Each type of test was presented 20 times in a session, resulting in sessions of 120 trials (Table 1).

Monkeys progressed to Phase 2 after achieving 80% correct in each of three consecutive sessions.

Table 1. Trial types using all combinations of the five samples
Experiment 1 consisted of all normal non-adjacent trials. Experiment 2 consisted of both non-adjacent and adjacent trials. + indicates that, if selected, positive reinforcement followed; - indicates that, if selected, negative auditory reinforcement and a time-out followed. Experiment 5 consisted of normal non-adjacent trials and probe novel trials, on which monkeys received positive auditory reinforcement for either selection.

Normal non-adjacent trials	Normal adjacent trials	Novel trials
1+ versus 3-	1+ versus 2-	1 versus novel
1+ versus 4-	2+ versus 3-	2 versus novel
1+ versus 5-	3+ versus 4-	3 versus novel
2+ versus 4-	4+ versus 5-	4 versus novel
2+ versus 5-		5 versus novel
3+ versus 5-		

Phase 2: Transfer to adjacent images

All procedures were identical to Phase 1, except that all possible pairs of images were tested, including adjacent images, as shown in Table 1. The 10 test types were randomly intermixed in sessions of 120 trials, resulting in 12 tests of each type per session. Monkeys completed 10 sessions, and then progressed to Experiment 2.

Results and discussion

Monkeys took between 16 and 163 sessions to reach criterion in Phase 1 (mean: 76). Results from the 10 sessions of Phase 2 are shown in Figure 2. Symbolic distance refers to the number of images that intervened between test images in the study list. For example, a test using the first and second image from the study list had a symbolic distance of 0, whereas a test contrasting the first and fifth image had a symbolic distance of 3. Recency reflects the amount of time that passed since presentation of the earliest of the tested images. A test involving images 1 and 5 is labeled low recency because 1 is the least recent image, whereas a test involving images 4 and 5 is high recency because image 4 occurred comparatively recently (Figure 2).

Subjects were more accurate the greater the symbolic distance (Figure 2, repeated measures ANOVAs and paired sample t-test: low recency (blue line): $F_{3,15}$ =7.23, *p*=.003; moderate recency (red line): $F_{2,10}$=53.1, *p*<.001; high recency (orange line): t_5= 9.09, *p*<.001). The symbolic distance effect suggests that discrimination of order resulted from a continuous representation of relative order rather than from image-image associations (e.g. Shettleworth, 2010). An image-image associative mechanism predicts the opposite pattern: subjects would perform better on test images that were closer together in the list because direct image-image associations would exist between adjacent pairs but do not between widely separated images (e.g. 2 vs. 3 would be an easier than 2 vs. 5).

Recent images were better discriminated than images that occurred earlier in the list (Figure 2, stacking lines, repeated measures ANOVAs: symbolic distance 0: $F_{3,12}$ =39.29, *p*<.001; symbolic distance 1: $F_{2,10}$ =33.50, *p*<.001). Performances at a symbolic distance of 2 (1, 4; 2, 5 tests), however, did not differ significantly (paired sample t-test: t_1 =-2.32, *p*=.068). The fact that images were better discriminated when they had occurred later in the list indicates that memory for order decays with time. Similar recency effects are seen in human serial recall (Howard & Kahana, 2002; Oberauer & Lewandowsky, 2008).

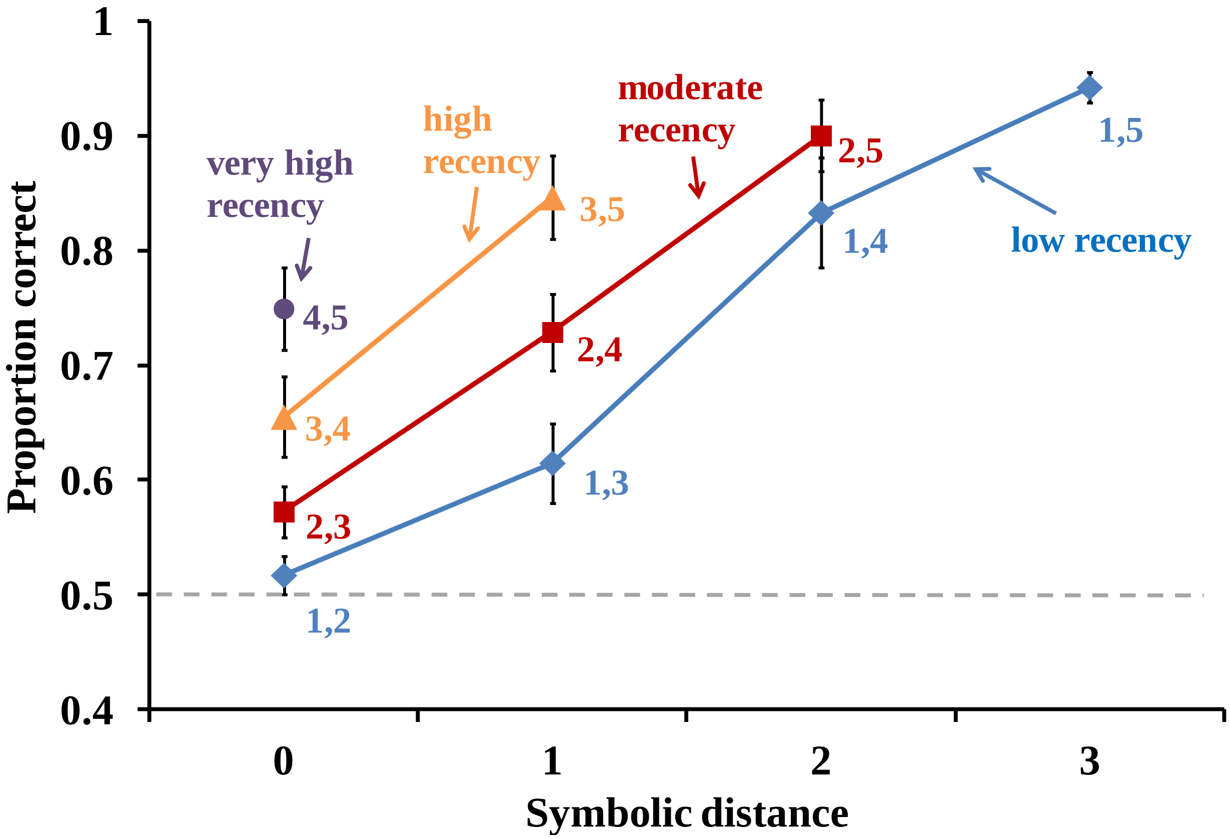

Figure 2. Proportion correct for all non-adjacent and adjacent test pairs in Experiment 1. The symbolic distance effect is evident in the upward trend of each colored line. A recency effect is shown by the fact that each of the colored lines stacks one above another. Error bars are standard errors of the mean. The dashed line indicates the chance rate of 50%.

While the symbolic distance effect we observed indicates that image-image associations are not the cognitive mechanism supporting memory for order, the presence of this effect does not discriminate among a variety of other candidate memory mechanisms. We conducted a series of tests that evaluate several different possible cognitive mechanisms. Each putative mechanism is described and operationalized in the introduction to the relevant experiment.

5.5. Experiment 2. Evaluating the influence of memory strength

In Experiment 1, monkeys remembered the order in which unique lists of images appeared. The pronounced symbolic distance effect observed indicates that the cognitive representation underlying performance is not an associative one. The symbolic distance effect is consistent with discrimination of order based on memory strength. Because memory decays with time, earlier images in a sequence will have weaker memory strengths, and monkeys may learn to choose the image with the weakest memory strength at test. In Experiment 2 we directly manipulated memory strength to determine the extent to which monkeys chose based on differences in memory strength. Images that had not been seen before and therefore had memory strength of zero were paired with one of the five images from the studied list in probe tests. If monkeys selected the image with the weakest memory strength in normal tests, they should choose the novel image significantly more often than any image from the studied list in these probe tests.

In order to prepare subjects for probe tests with no reinforcement, intermittent primary reinforcement was instituted. All correct trials were followed by positive auditory reinforcement but only 70% were also followed by food reward. After 10 adaptation sessions with all non-adjacent test pairs, monkeys received five 116-trial sessions with 20 randomly intermixed probe tests in which a novel image was drawn from a set of 100 never before seen images and presented at test with one of the images from the study list (Table 1). All responses on probe tests were reinforced with the positive auditory reinforcement but no food reward.

All other testing procedures were the same as in Experiment 1, except for image randomization. Study lists were generated using the same list of 6,000 images as before but images were selected by randomization without replacement. This ensured that monkeys saw all 6,000 images without repetition before the entire set of 6,000 images was reshuffled and used again. Monkeys worked at different rates, but it took on average about a week to use all 6,000 images, at which time they were re-randomized.

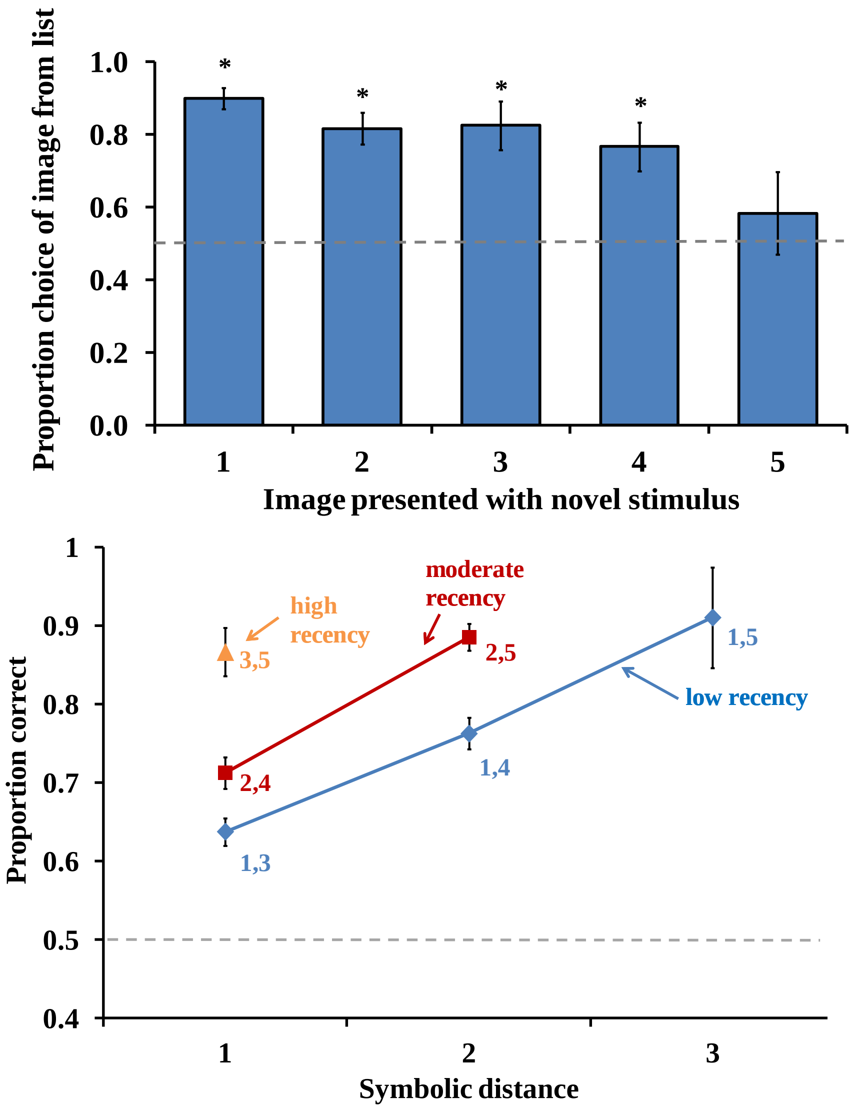

Figure 3a) Performance on novel image probe tests in Experiment 2. Figure 3a displays the proportion of trials on which monkeys chose the image from the list rather than the novel image for each test pair type (image 1 versus a novel image, image 2 versus a novel image, and so on). Averages significantly above chance (50%, indicated by dashed line; p<.05, one sample t-tests) are indicated by "*." **3b) Performance on control tests in Experiment 2.** Figure 3b displays the proportion correct for all control test-pairs, which included all non-adjacent items (symbolic distance 0 items were not tested in Experiment 2; compare to Figure 2). Error bars are standard errors of the mean.

Results and discussion

Monkeys did not select the image with the lower memory strength. On novel image probe tests subjects chose the image from the list significantly more often than expected by chance, except in tests in which the novel image was paired with the fifth image from the list (Figure 3;

one-sample t-tests: 1 vs. novel: t_5=7.51, *p*=.001; 2 vs. novel: t_5=6.15, *p*=.002; 3 vs. novel: t_5=3.90, *p*=.011; 4 vs. novel: t_5=3.79, *p*=.013; 5 vs. novel: t_5=0.76, *p*=.483). If monkeys had learned to select the image with the weakest memory strength they would have selected the novel image significantly above chance because the novel image has never been seen before and has memory strength of zero. Because we observed the opposite pattern, we conclude that choice of earlier images was not controlled by memory strength. It is likely that subjects did not choose image five significantly more often than expected by chance because the last image in the sequence was never correct and monkeys had learned to avoid selecting images that appeared in this position. Faced with a test involving two incorrect choices, one image that was not in the study list and the last image from the list, monkeys chose indiscriminately. Even in this case, monkeys did not select the novel image more than the image from the studied list. It is unlikely that monkeys' strategy changed between Experiment 1 and 2 because we observed the same pattern of performance in Experiment 1 and in normal trials that were administered concurrently with the probe trials in Experiment 2 (Figure 3b). Furthermore, probes were infrequent, making it unlikely that monkeys switched strategies depending on test type, especially because during study, it was not known which test would appear. The average amount of reinforcement, across both trial types was approximately 70%, the same as before normal and probe trials were intermixed.

A possible alternative explanation of the finding that subjects did not choose the novel item is that they treated it as the "sixth" and last image in the list, which should never be selected. This is unlikely because subjects had extensive history seeing and touching sample images in one particular location, and after a delay, touching one of two test items, in two different locations. They do not appear to have ever treated the test items as additions to the list. In fact, if subjects treated the novel test image as an additional list image to study they should have touched it, because this is what they have to do with all list images during study. Finally, if monkeys had treated the novel image as the sixth image in the list, performance on 5 vs. novel tests should have shown the recency effect and would have been significantly higher, more like normal tests of image 4 versus image 5, but in fact performance was close to chance (Figure 3).

5.6. Experiment 3. Evaluating the influence of list position

Results from Experiment 2 indicate that memory strength does not determine image choice in tests of memory for order. Previous research with humans (Henson, 1998; D. J. Merritt & Terrace, 2011) and animals (Scarf & Colombo, 2011; H. S. Terrace, 2005) shows that, in some tests of memory for order, the underlying cognitive representation codes list position. For example, with extensive training monkeys learn to touch a set of five simultaneously presented and randomly arranged images in a pre-defined order. Performance in such simultaneous chaining paradigms transfers to so-called derived lists, consisting of pairs of images taken from separate previously learned sets. Thus, when presented with image B from one list and image D from a different list, monkeys reliably touch B first and D second, even though these two images were never seen together before (H. S. Terrace, 2005). Such performance indicates that monkeys represent the list positions of images in each learned list using a common code that applies across lists. We tested whether monkeys encode the list positions of images in the present task by presenting subjects with between-list probe tests, consisting of one image from the most recently studied list and one image from the previously studied list. Some of these cross-list tests were arranged such that the image with the lower list position occurred later in time. In these tests, list position and temporal order predict different choices, allowing us to determine which controls behavior.

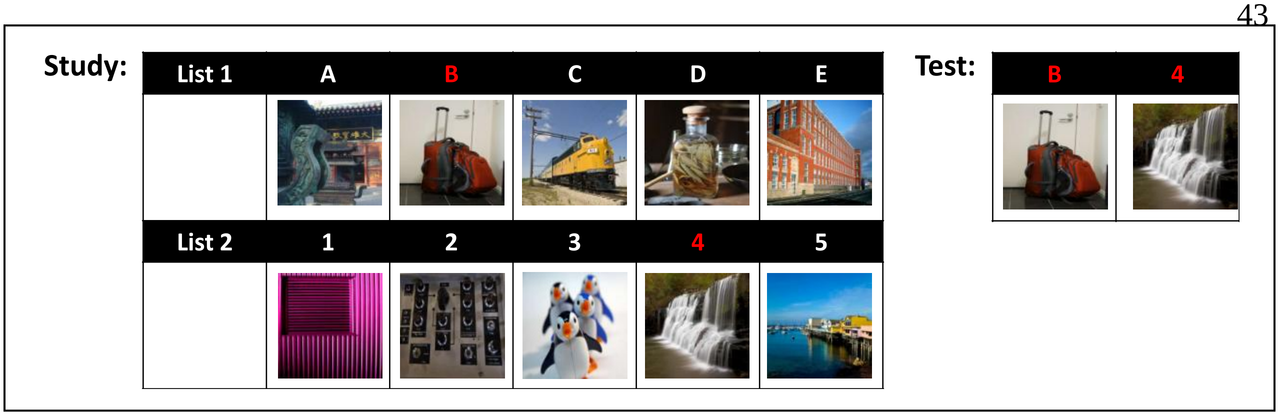

Figure 4. Example of study and test phases of a between list probe test in Experiment 3. In this example, image B from the earlier list appeared with image 4 from the most recent list. Different pairs of images were used in other probe tests. Sometimes ordinal position was congruent with temporal order, sometimes neutral with respect temporal order, and sometimes incongruent with temporal order.

We presented between-list probe tests in which one test image was from the previous list, A,B,C,D,E, and the other was from the current list, 1,2,3,4,5 (Figure 4). Sessions consisted of 120 trials: 96 normal trials, including all nonadjacent pairs, and 24 probe tests. Two blocks of 10 probe sessions were conducted. In the first block, half of the probe tests consisted of image E, the last image from the previous list and image 1, the first image from the current list; on the other half of the probe tests, image C, the third image in the previous list was presented with image 3’ the third image in the current list. In the second block of sessions, monkeys chose between B, the second image in the previous list, and 4, the forth image in current list on half of probe trials. In the other half of probe trials monkeys chose between D, the forth image in previous list, and 2, the second image in current list (Table 2). All choices in probe trials were non-differentially reinforced to prevent new learning. E vs. 1 and C vs. 3 probes were unreinforced, no matter which item was chosen; B vs. 4 and D vs. 2 probes were all reinforced with food and auditory feedback, no matter which item was chosen.

Table 2. Experiment 3 probe tests.
Between-list probe types are shown on the far left. Temporal order and list position mechanisms predict selection of particular test items which are indicated in the second and third columns. Probe tests were either rewarded with positive auditory reinforcement and food reward or no reward. The distance or number of intervening test items between the two test items is displayed in the far right column.

Probe test	Temporal order	List position	Reinforcement	Distance
B versus 4	B	B	reinforced	6
C versus 3	C	-	unreinforced	4
D versus 2	D	2	reinforced	2
E versus 1	E	1	unreinforced	0

Because one entire list occurred before the other, choice of any image from the earlier of the two lists would be consistent with control of choice by temporal order. Each image also occupied a list position within its respective list, and this list position could either be congruent, neutral, or incongruent with respect to temporal order. In B vs. 4 tests, selection of B would be consistent with both temporal order and list position. B occurred in the earlier list and in a lower list position within that list. In C vs. 3 tests, C occurred before 3, but both images share the same list position within their lists. In D vs. 2 tests, selection of D would be consistent with temporal order but not list position, because image D has a higher list position in its list than does 2. Finally, selecting E in E vs. 1 tests would be consistent with temporal order, but inconsistent with list position. If choices were controlled by list position, monkeys should select the image with the lower list position in each test (e.g. 1 over E). See Table 2 for predictions based on list position and temporal order.

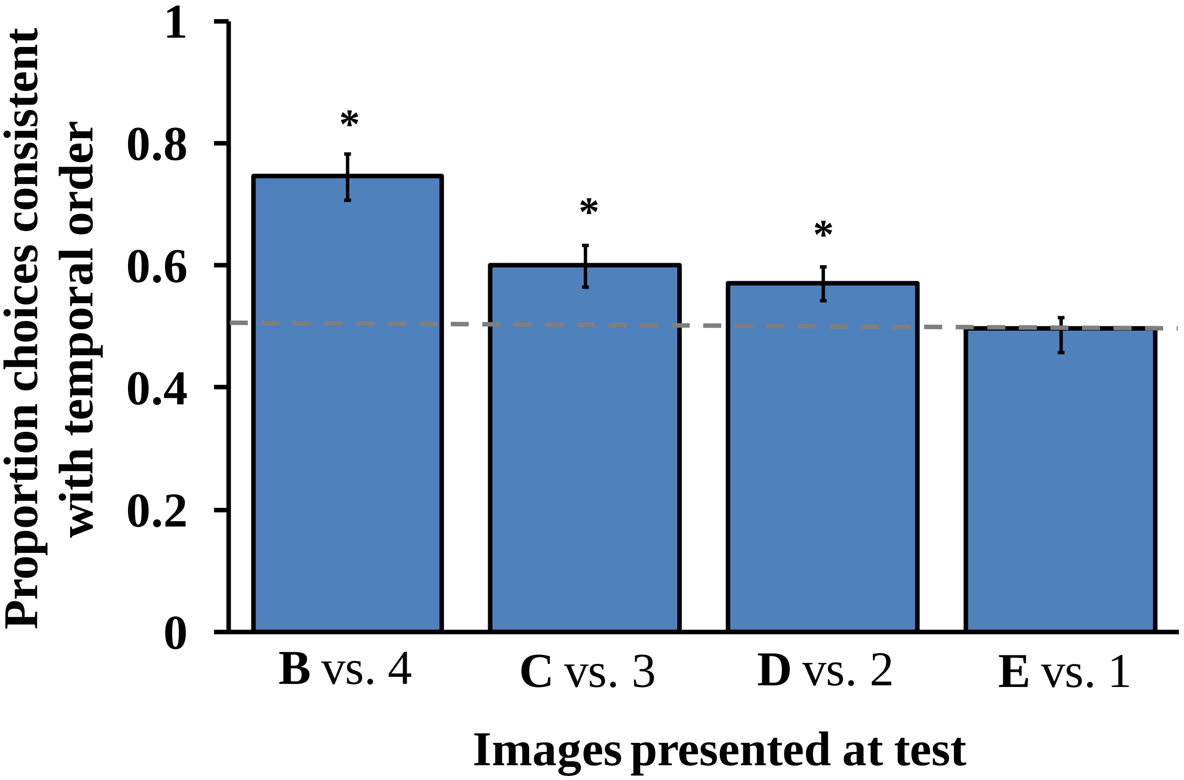

Figure 5. Performance on between list probe tests in Experiment 3. Images from two adjacent lists were tested (list one consisted of images, A, B, C, D, and E; list two of images 1, 2, 3, 4, 5). The temporal order hypothesis predicts that subjects would choose the image from the earlier list, because it occurred earlier in time: B over 4, C over 3, D over 2, and E over 1. The list position hypothesis predicts the opposite. Monkeys should choose the image with the lowest list position within its respective list, regardless of whether that list came first or second (see Table 2). Bars with "*" indicate averages significantly above chance (50%, dashed line; p<.05; one sample t-test).

Results and discussion

Results of tests with images from two adjacent lists were consistent with control of choice by temporal order. Subjects predominantly chose the image from the earlier list, and the size of this effect varied along with temporal distance (Figure 5; one-sample t-tests: B vs. 4: t_5=5.85, *p*=.002; C vs. 3: t_5=-2.89, *p*=.034; D vs. 2: t_5=2.59, *p*=.049; E vs. 1: t_5=-0.19, *p*=.856). Monkeys may not have chosen E significantly more than 1 because a temporal distance of 0 was not sufficiently salient. The chance-level performance on these tests is clearly inconsistent with list position because 1 occupies the lowest list position and E occupies the highest list position in their respective lists. If choice at test was controlled by list position, this test pair should have created the largest difference in favor of list position. It is possible that B was so strongly selected over 4 because of the congruence of temporal order and list position (Figure 5; *far left bar*), however, this test pair also manifests the largest temporal separation (Table 2). Together, these results clearly favor control of choice by temporal order rather than list position.

5.7. Experiment 4. Temporal order: intervening images and intervening time

Experiment 1 revealed that memory for order is most accurate with largest symbolic distances or temporal separations. Experiment 3 showed a similar pattern: earlier images were selected most reliably when the temporal separation between probe test images was greatest. The evidence presented so far suggests that choice is controlled by temporal order, not by list position or memory strength. However, temporal order itself can be characterized in different ways. At least two things change with temporal order in these experiments. First, temporal order can be characterized, as done in Figure 2, by the number of images intervening between to-be-discriminated test images. Second, larger differences in temporal order mean that the images are separated by longer intervals of time. To distinguish between these alternatives and to further characterize the control of choice in this task, we compared the effects of temporal spacing with those of intervening images on the accuracy of order discrimination in Experiment 4.

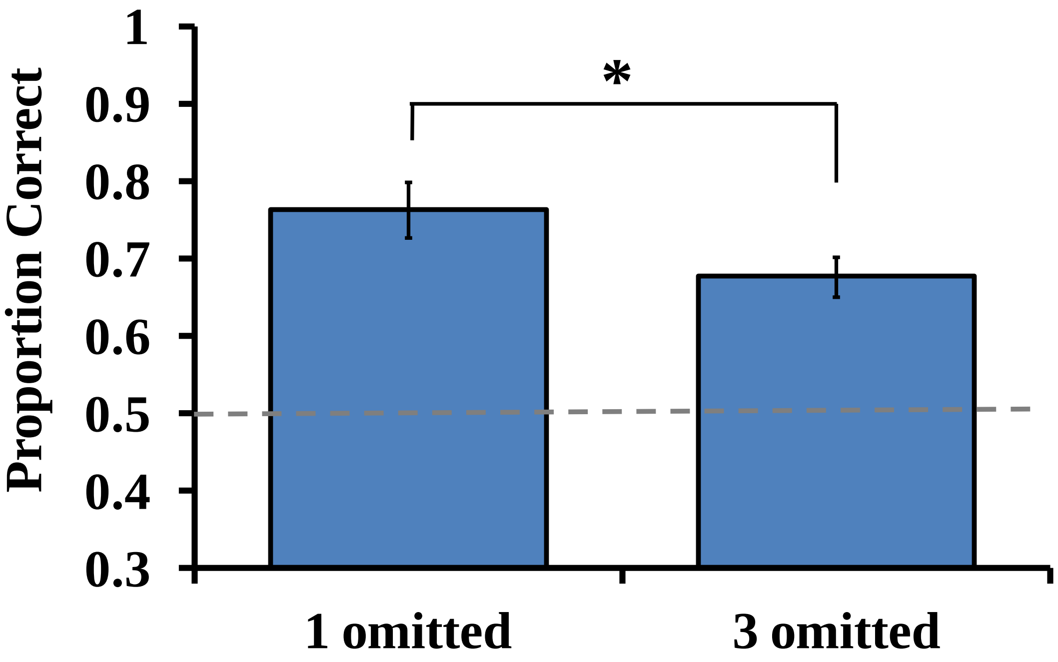

Figure 6. Performance on 2,4 probe tests in Experiment 4.1. In probe tests, either image 1 or image 3 was omitted, and a test of images 2 and 4 always occurred. Both types of probes involved 4 image study lists, and the temporal spacing of the images was held constant despite the omission of an image. Error bars represent standard errors of the mean. The "*" indicates that the two conditions differ significantly from each other (p<.05; paired t-test). Chance is indicated by the dashed line.

Experiment 4.1.

We maintained temporal spacing while manipulating the number of images intervening between to-be-discriminated images by dropping either image 1 or image 3 from the study list on probe trials and inserting an unfilled temporal gap. Twenty probe trials were randomly scheduled among the 120 trials in a session. On half of the probe trials image 3 was omitted, yielding the list: 1, 2, _, 4, 5, where "_" denotes an omitted image. The other half of the probe trials controlled for list length by omitting image 1 from this study list (_, 2, 3, 4, 5), thus shortening the list to four images while maintaining the temporal spacing and placement of images in the remainder of the list. In place of the omitted images in both types of probes a 550 millisecond unfilled interval was inserted during which the screen was black. This duration is the average latency for touching images in the studied lists. The test phase of all probe trials consisted of a choice between images 2 and 4 from the studied list. Subjects were reinforced with 100% food and auditory feedback following correct responses. Negative auditory feedback and a time-out followed incorrect responses. The remaining normal test trials included all adjacent and nonadjacent images, and all other testing parameters remained the same. If accuracy of the order discrimination was controlled by the absolute amount of time intervening between images, there should be no difference in accuracy between the two probe types because the test images were separated by the same temporal interval in the study list. By contrast, if performance was controlled by the number of intervening study images, performance would decrease when image 3 was omitted in the study list. Monkeys received 10 sessions resulting in 100 probe trials of each type.

Results and discussion

Monkeys were significantly less accurate on 2 vs.4 probe tests when image 3 was omitted than they were when image 1 was omitted (Figure 6; paired-sample t-test: t_5=3.76, *p*=.013). This result indicates that the number of intervening images has a stronger effect on accuracy than does the duration of the interval separating study images. However, one possible concern is that poorer performance represents a generalization decrement caused by the novelty of this trial type. We attempted to control for this by comparing performance to control probe trials on which image 1 was omitted, but it is possible that omitting image 3 is more surprising than omitting image 1. In the next experiment we controlled for this potential confound by more directly comparing the effect of increasing the time interval between study images with the effect of increasing the number of images intervening between to-be-tested study images.

Experiment 4.2

Probe trials with three images inserted between to-be-discriminated images, and probe trials with yoked elongated inter-stimulus intervals were pseudo-randomly intermixed with normal trials in 120-trial sessions. Half of the probe tests were *image* trials in which three extra images appeared between images 3 and 4. The other half of the probe tests were *time* trials in which a yoked extended ISI occurred between images 3 and 4. The yoked ISI exactly matched the interval elapsed in the previous image trial between the offset of image 3 and the onset of image 4. All other procedures remained the same.

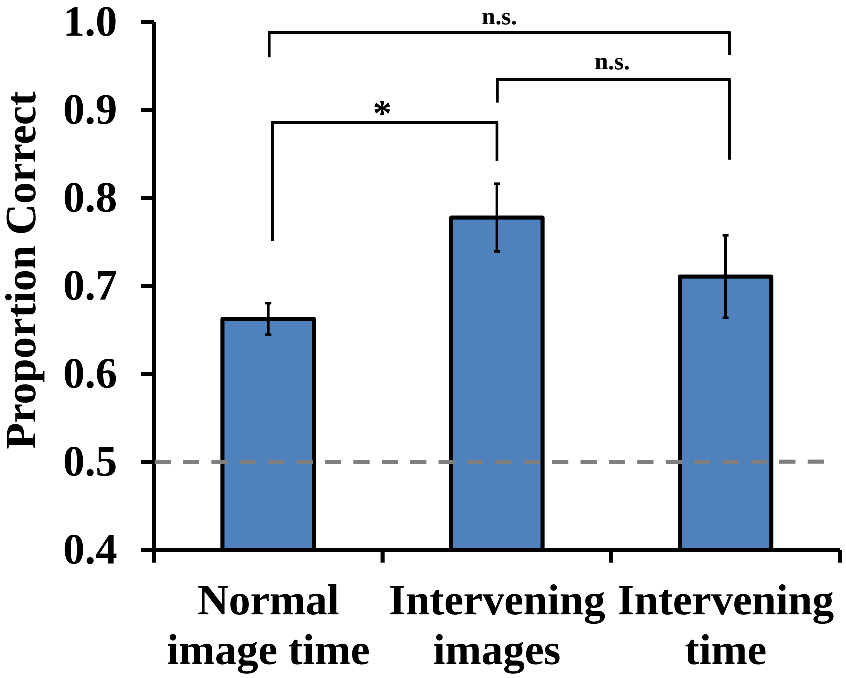

Figure 7. Performance on 3,4 tests in Experiment 4.2. In *intervening image* probe tests, three additional images were inserted between the to-be-discriminated images 3 and 4. In *intervening time* probe tests, the interval between images 3 and 4 in the study list was extended to exactly match that which occurred in the previous *item* probe test. Error bars indicate standard errors of the means. The “*” indicates that the two conditions differ significantly from each other (p<.05; paired t-test). Chance is indicated by the dashed line.

If it is the passage of time per se that accounts for the discriminability of images, monkeys should be equally accurate whether or not the interval between images 3 and 4 was blank or filled with images. If however, the number of intervening images is more important for making the order of images discriminable; accuracy on *image* trials should be significantly higher than on normal 3 vs. 4 tests.

Results and discussion

The discriminability of the order of images was affected more by intervening images than by the passage of time. Subjects performed significantly better on *image* probe trials than they did on normal trials, and performance on extended ISI trials was not significantly better than that on normal trials (Figure 7; paired-sample t-tests: *image* probe trials vs. normal: t_5=-4.06, p=.010; *time* trials vs. normal trials: t_5=-1.42, p=.214). However, image and time probe trials did not differ significantly from one another (*image* probe trials vs. extended ISI *time* trials: t_5=1.81, p=.130). These results show that additional intervening images clearly enhance the discriminability of the order in which images occurred. Simply inserting an unfilled interval of the same duration as that required for inserting additional images did not have as strong an effect on discriminability. However, the absence of a significant difference between image and time trials, combined with the numerically better performance on time trials than on normal trials, suggests that the insertion of additional time did have some effect on discriminability. It is probable that even though no experimenter-generated images were presented during the unfilled interval in time probe trials, events that were not experimenter controlled still did occur in the interval, such as sights the monkeys saw, and calls or noises they heard. The occurrence of these events may have acted less strongly than the occurrence of additional images to enhance the discriminability of the order in which images occurred. Whether or not this is the case, it should be recognized that it is not possible to generate a pure manipulation of the passage of time per se, absent the occurrence of events of one kind or another. What is clear in these results is that the occurrence of salient events between to-be-discriminated images enhanced performance.

5.8. Discussion

Representing the order of unique events is one of the defining functions of episodic memory and one that distinguishes it from semantic memory (Tulving, 1983). Here we studied the cognitive mechanism underlying memory for the order of unique events by establishing which features of events are critical for accurate performance. This work complements study of the neurobiology of memory for the order of events, and allows us to better understand the relations between cognitive and neural mechanisms.

In Experiment 1 six monkeys learned to select, from among two choices, the image that had appeared earlier in sequences of five briefly studied images. Monkeys learned this discrimination with non-adjacent images, and generalized these judgments to more difficult tests with images that had been adjacent in the studied list. We observed symbolic distance and recency effects suggesting that monkeys may form linear representations of the temporal order of the sequences. Charles et al (2004) similarly found recency effects in a test where monkeys were trained to select the most recent item from a study list. To better evaluate the extent to which representations of temporal order controlled choice, we conducted a series of experiments that ruled out alternative mechanisms and better defined the nature of the representations controlling choice. We found that the occurrence of intervening images exerted the strongest effect on the discriminability of the order in which images appeared.

To test whether relative memory strengths controlled responses at test, we directly manipulated memory strengths of test images in Experiment 2. When images from studied lists were paired with novel images, monkeys chose the image from the list. Had memory judgments been made on the basis of memory strength, subjects would have selected the novel image, which had the lower memory strength.

In Experiment 3, monkeys chose between test images from separate but adjacent study lists. Monkeys tended to select the images that had occurred in the earlier list, not the images that had occurred earliest in their respective list. This contrasts with the results from similar tests with mice, which found that animals had no preference for choosing the item from the earlier or later list (DeVito & Eichenbaum, 2011). Because subjects treated items that appeared between lists as unrelated, DeVito and Eichenbaum concluded that animals regarded each list as an independent temporally organized experience. Our monkeys seem to have done just the opposite. Two features of the DeVito & Eichenbaum study may account for this difference. Mice were exposed to the same sequences repeated 15 times over five days, which would favor treating specific lists as independent units; lists in the present study were trial unique. Between-list tests in the mouse study occurred three days after training and presentation of the successive lists was separated by a three hour delay; lists in the current study followed one another after just 500 milliseconds making them much more like a continuous list.

Selection of items from the earlier list, as reported here, is consistent with choice by temporal order rather than choice by list position. Evidence from simultaneous chaining tests, in which subjects learn to respond to a fixed set of stimuli in a fixed order, indicates that monkeys choose on the basis of list position (e.g., Terrace 2005). Unlike the training with repeating sequences used in simultaneous chaining, which causes monkeys to represent the list position appropriate for each image (S. F. Chen, K. B. Swartz, & H. S. Terrace, 1997; H. S. Terrace, 2005; H.S. Terrace et al., 2003), the lists used in our study were trial-unique. Learning list positions may occur only after repeated presentations, which were not available to the monkeys in this study.

Experiments 2 and 3 identified temporal order as the most likely determinant of choice, so we attempted to better define what constituted temporal order in Experiment 4. We found that the order of events was better discriminated when intervening images occurred, compared to unfilled intervals of equivalent duration. So it is unlikely that classic timing mechanisms that use an internal clock or oscillator to measure elapsed time (Meck, 1983; Ortega, Lopez, & Church, 2009; S. Roberts, 1981) are responsible for discrimination of temporal order in this task. It may seem counterintuitive that performance would increase when there is more that happened, and thus more to remember, as when additional images intervene between target images. The occurrence of intervening events may serve to mark the passage of time, thereby increasing the subjective separation of two events.

Electrophysiological evidence suggests that the hippocampus represents changes in context. Recordings from rat hippocampal neurons show gradual changes in firing patterns over time that may be the basis of memory for order (Manns et al., 2007). These results are consistent with the idea that hippocampus is critical for keeping memories of similar events that occurred at different times distinct from one another (Hasselmo & Eichenbaum, 2005; Ross, Brown, & Stern, 2009). Recently identified “time cells” in the hippocampus that encode successive moments (MacDonald, Lepage, Eden, & Eichenbaum, 2011) reinforce this position (Eichenbaum & Cohen, 2001).

Human neuroimaging studies (Gelbard-Sagiv et al., 2008; Lehn et al., 2009; Mayes & Montaldi, 2001) also demonstrate that the hippocampus supports memory for the order of events. This role of the hippocampus is also supported by the finding that monkeys with lesions of the fornix, a major output pathway of the hippocampus, are impaired in recency judgments (Charles et al., 2004). These results, combined with the findings that rats demonstrated impaired memory for order performance but intact performance on recognition tests following hippocampal lesions

(Fortin et al., 2002; R.P. Kesner et al., 2002), suggest that monkeys with hippocampal lesions would likely be impaired in our order task, but not on recognition tests. The prefrontal cortex (PFC) may interact with the hippocampus to store explicit memories (Ramus, Davis, Donahue, Discenza, & Waite, 2007), including memory for order (DeVito & Eichenbaum, 2011). While the PFC has been implicated in memory for order (DeVito & Eichenbaum, 2011; Petrides, 1991b, 1995), the studies that tested memory for order in monkeys with PFC lesions were self-ordered working memory tasks (Petrides, 1995). Self-ordered tasks likely engage strategic use of working memory, potentially including planning. These capacities are probably not critical for memory for unique sequences of events that are experienced rather than generated. It would be particularly interesting to compare the performance of monkeys with PFC lesions to that of monkeys with hippocampal lesions on the current task to evaluate this hypothesis.

Researchers using rodent models have made significant progress identifying the neural basis of memory the order of events (Ramus et al., 2007) as distinct from the neural bases of recognition (Agster, Fortin, & Eichenbaum, 2002; DeVito & Eichenbaum, 2010, 2011; Fortin et al., 2002; R.P. Kesner et al., 2002). Here, we have adapted techniques developed in rodents to study memory for trial unique sequences of images in monkeys, and we have characterized the content of the cognitive representations responsible for accurate performance. Given that the performance of rats in odor order tasks showed similar symbolic distance effects, it is likely that rats represented sequences in the same way our monkeys did – as a temporal order dependent on the occurrence of events. Our monkeys appear to have represented the order of images with greater fidelity that rats were reported to represent the order of odors. Monkeys accurately discriminated images that were adjacent in the study list, whereas rats tested so far were unable to do this. Future neurobiological work that tests whether memory for order in monkeys is also dependent on the hippocampus, and behavioral work in rats that evaluates the cognitive bases of their performance will determine the extent to which the mechanisms responsible for memory for the order of events is conserved across species.

6. Introduction to Paper 3

This paper arose from the goal of gaining a more comprehensive understanding of memory for ordered stimuli. Memory for serial order had been tested in monkeys by Terrace's group (e.g. H. S. Terrace, 2005) and it was suggested that subjects did not rely on image-image associations to remember order despite the fact that routinized ability to select images in a fixed order appears to be much like habit memory. We first examined if these findings provided by other groups that suggest that monkeys have knowledge of ordinal position of images (S. Chen et al., 1997; H.S. Terrace et al., 2003) could be replicated with a larger group of monkeys. We then evaluated candidate cognitive mechanisms used in SC to probe the contents of memory during list execution. We aimed to answer questions about ordinal processing to determine: 1) if monkeys use prospective or retrospective coding to determine where in list execution they are, and 2) if responses made are used to track progression in the list. Another goal was to characterize memory for ordinal position further, much like we did with temporal order in Paper 2, by determining if static or more dynamic positional coding supported memory for ordinal position for routinized series of responses. Characterization of the content of this ordinal representation was important for the comparison of the TO and SC tasks, as these tasks are similar in some ways, but is also critically different.

7. Paper 3

Memory for ordinal position in monkeys

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7.1. Abstract

The ability to learn arbitrary sequences is critical for intelligent action, and may have important implications for diverse cognitive feats, including planning and counting. We studied the memory representations controlling execution of five-image action sequences by training rhesus monkeys *(Macaca mulatta)* to touch five images in a pre-determined order. In Experiment 1 monkeys represented the ordinal position of images using the same code for multiple lists of images, such that when presented with pairs of images, they reliably selected the image with the earlier ordinal position whether the images were from the same or different lists (e.g., H. S. Terrace, 2005; H.S. Terrace et al., 2003). In Experiment 2, distracters inserted between choices during list execution caused forward errors to images that should have been selected later, indicating prospective, rather than a retrospective, coding of position within a sequence. In Experiment 3, errors did not correspond to the number of responses made to the distracters, indicating that position in a sequence was not based simply on the number of responses made, but rather on anticipation of upcoming responses. In Experiment 4 subjects were trained to select the last image of list 1 before the first image of list 2. In contrast to findings in transitive inference tasks (Gazes, Chee, & Hampton, 2012; F. R. Treichler & Raghanti, 2010a), the two lists were not linked into one large list but instead responses continued to be controlled by absolute position within the originally trained lists. Thus, monkeys plan execution of routinized sequences of responses at least two responses ahead based on absolute ordinal position. These results help document the mixture of relatively dynamic and relatively static components contributing to the representation of arbitrary sequences in monkeys.

7.2. Introduction

The ability to learn arbitrary sequences allows us to plan and execute a series of actions. Foraging, communication, and language rely on correct execution of serially organized sequences of behaviors (Biegler, 2006; Scarf & Colombo, 2008). S*imultaneous chaining* (SC; H. S. Terrace, 1984) is a method for testing the ability to remember defined order of actions (H.S. Terrace et al., 2003). In a typical SC test, subjects are required to select five simultaneously presented images in a pre-determined order (e.g. A→B→C→D→E; Terrace, 2005). The spatial arrangement of the images is varied randomly from trial to trial, eliminating the possibility of a spatially-guided motor program, and monkeys are required to learn by trial and error. Many species successfully learn lists consisting of at least three images, indicating that the ability to learn and execute new orders of responses is widespread (humans: Inoue & Matsuzawa, 2009; D. Merritt, MacLean, Jaffe, & Brannon, 2007; D. J. Merritt & Terrace, 2011; apes: Inoue & Matsuzawa, 2009; monkeys: D'Amato & Colombo, 1989; Orlov, Yakovlev, Hochstein, & Zohary, 2000a; Scarf, Danly, Morgan, Colombo, & Terrace, 2011; and birds: Pfuhl & Biegler, 2012; H. S. Terrace & McGonigle, 1994).

It might seem possible that fixed sequences such as those in SC can be learned associatively (Osgood, 1953). Memorization of fixed sequences was originally thought to be habitual, relatively inflexible, and dependent on chains of image-image associations or stimulus-response units where selection A cues response B, for example (Osgood, 1953; Pierce & Cheney, 2008). However, a variety of results from human and nonhuman primate experiments in SC cannot be explained by associative chaining. Instead, the order in which primates select images in SC tests appears to be controlled by a mental representation of ordinal position. For example, image C in the list A→B→C→D→E is encoded as belonging in the 3rd list position, while image D is encoded as belonging in the 4th list position. Representation of ordinal position has been evidenced by the finding that monkeys and humans spontaneously respond to pairs of nonadjacent images according to ordinal position, for example selecting image B first and D second, when these two images are presented together in non-differentially reinforced probe tests (D'Amato & Columbo, 1988; Scarf & Colombo, 2008). Even stronger evidence for ordinal coding is the fact that ordinal position determines the sequence in which images are selected even when the images come from different lists. Thus, image A from list 1 (A_1) is selected before image D from list 2 (D_2), even though these images have never appeared together in training (H. S. Terrace, 2005). In accord with the symbolic distance effect (SDE), test pairs with larger distances between images were ordered more reliably than those with shorter distances. For example A_1 was selected before D_1 more often than B_1 was selected before C_1 (e.g. B_1C_1, Scarf & Colombo, 2008; Swartz, Chen, & Terrace, 1991). The SDE is found in humans and monkeys, and provides additional evidence for an ordinal code rather than a chain of image-image associations.

The ability to learn five-image lists likely matches the learning rules that also support conditioned responses and chains of associations, even if the underlying cognitive mechanism supporting knowledge is not maintained by image-image associations (Pfuhl & Biegler, 2012). What remains underdetermined is what the underlying cognitive mechanism is that might work in tandem with basic habit memory used to learn chains of correct responses during list acquisition. Evidence suggests that ordinal position information contributes to the representation of order and though this might help explain the overall basic structure of the cognitive representation, the process by which this information is used to construct an internal representation of serial order is not yet a well-developed model. To address the issue that knowledge of ordinal position does not provide a full characterization of the mnemonic representation that controls responding in SC, we aimed to identify the underlying cognitive mechanisms that maintain ordinal representations of routinized lists by examining the contents of memory during list execution.

We conducted Experiment 1 to test the robustness of the basic phenomena described by Terrace (e.g. 2005) by first training six monkeys with four lists and then testing them on two-image probe tests. Because it is surprising that image-image associations do not appear to maintain the ordinal representation of such a rote learned task, we aimed to determine under what conditions, and why, does processing of ordinal position become necessary. Here we characterize the underlying representational process used to remember ordered sequences in monkeys by directly evaluating several possible mechanisms for serial learning including, but not limited to, associative chaining and ordinal position that are investigated in Experiment 1. In Experiment 2 we determined the extent to which ongoing choices were guided by retrospective memory for selected images or prospective memory for to-be-selected images. The content of memory during list execution was further evaluated in Experiment 3 by testing whether the number of responses made, independent of the memory for the images to which those responses were made, represented the current position in an ongoing list. In Experiment 4, we assessed the extent to which the ordinal position associated with each image could be flexibly updated with training designed to promote “linking” of one list with another.

7.3. Materials and Method

Subjects and apparatus

Subjects in Experiments 1-3 were six 6-7 year old male rhesus monkeys *(Macaca mulatta*). Subjects in Experiment 4 were twelve different 9-10 year old male rhesus monkeys. All monkeys had at least three years of computerized testing experience. Monkeys were pair-housed whenever possible and kept on a 12:12 light:dark cycle with light onset at 7:00 am. Subjects were fed a full ration of food each day and water was available *ad libitum*.

Monkeys were tested on computerized touch-screen systems in their home cages. Each system consisted of a 15-inch LCD color monitor (3M, St. Paul, MN and Elo, Milpitas, CA) running at a resolution of 1024 X 768 pixels, generic stereo speakers, two automated food dispensers (Med Associates Inc., St. Albans, VT), and two food cups located below the screen.

General Procedure

Pair housed monkeys had access to a cage-mate at all times except during testing and during feeding at the end of the day. Before testing, pair housed monkeys were separated by insertion of opaque plastic dividers with slits that allowed limited visual and physical contact, but prevented access to the cage-mate’s testing equipment. Testing systems were locked to the front of each monkey’s cage and cage doors were raised, giving subjects full access to the screen during testing. Food rewards were nutritionally balanced banana or mixed-fruit flavored pellets (Bio-Serv, Frenchtown, NJ). Testing was conducted daily between 10 am and 5 pm, six days per week. Monkeys worked at their own pace during these hours, completing as few as 120 and as many as 840 trials. Occasionally monkeys completed other cognitive tasks on the same day as testing on experiments presented here.

Colored digital images (200 pixels X 200 pixels) were randomly-selected photographs.

Data analysis

Proportions were arcsine transformed before statistical analysis to better approximate the normality assumption underlying parametric statistics (Keppel & Wickens, 2004, p. 155). The Geisser-Greenhouse correction was used, and appropriately adjusted degrees of freedom reported, whenever the sphericity assumption was violated (Keppel & Wickens, 2004, p.378). All t-tests were two-tailed. All latencies reported were medians for correct responses only. An alpha level of $p<.05$ was applied to all analyses.

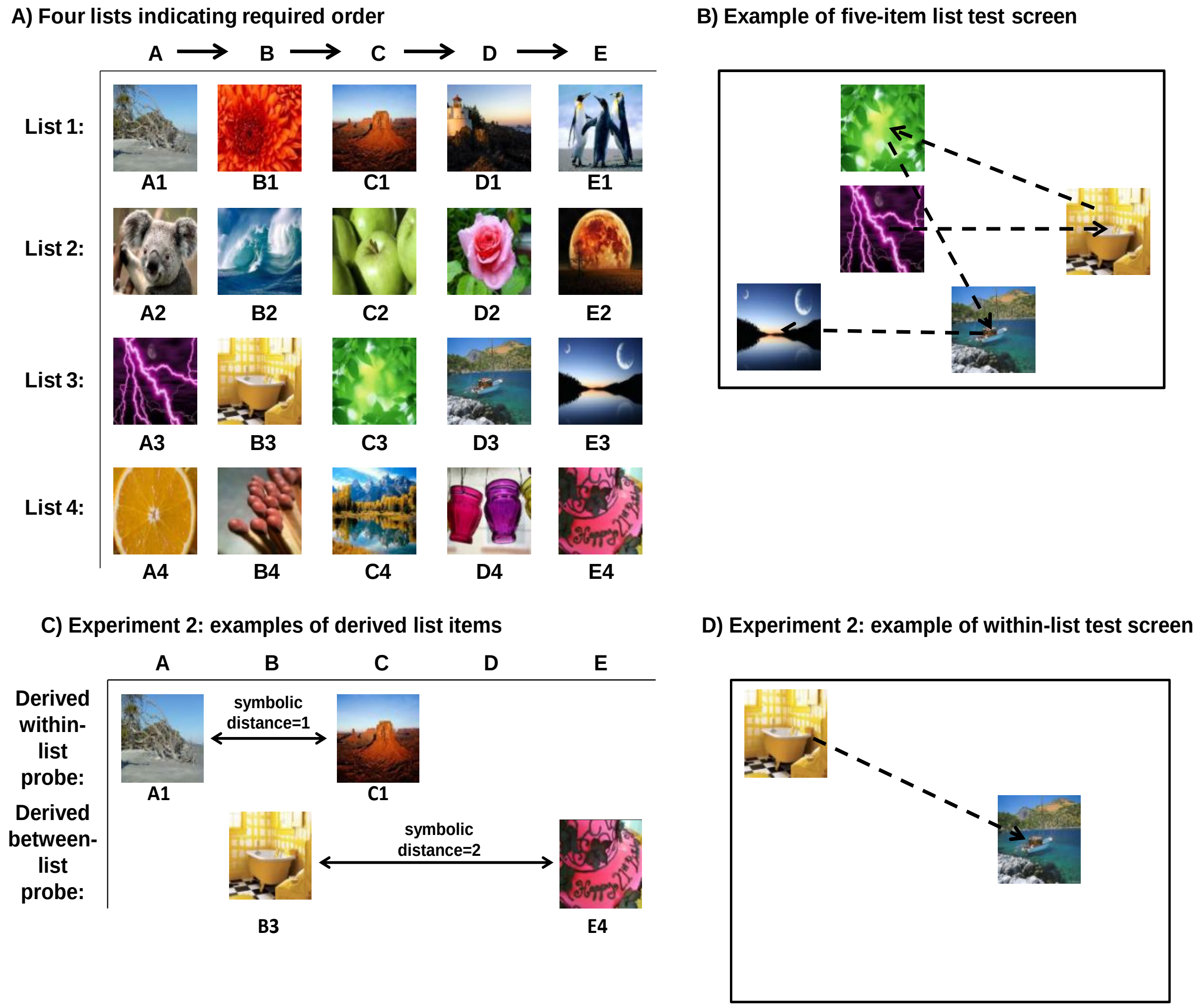


Figure 1. Task design. A) Required lists trained in Experiment 1 and used in Experiments 2-3. B) Possible test screen from list 3 in which list images appear in any of 12 possible locations. Image configuration changed from trial to trial. Dotted lines represent correct order as indicated in A; touches to each image this order resulted in a reward. C) Examples of within and between-list probe test images in Experiment 2, which were randomly intermixed with normal trials from all four lists (as shown in B). Symbolic distance is indicated by the number of missing images in between the two tested images. In the within-list probe test A_1-C_1, one image, B, is “missing”, so symbolic distance is 1. Between-list probe tests tested one image from list 1 and one from list 2 or one from list 3 and one from list 4, as shown in the bottom example, B_3-E_4. D) Example of a within-list B_3-D_3 test screen in which the correct order is indicated by the dotted line; touches both in this correct order or the opposite order would have been rewarded.

7.4. Experiment 1- Image-to-image associations vs. ordinal position

We trained monkeys to select lists of five images in a pre-determined order (Harris, Beran, & Washburn, 2007; D. Merritt et al., 2007; Scarf & Colombo, 2008; H. S. Terrace, 2005). After learning, subjects were given probe tests consisting of any two images from the learned lists in order to determine the extent to which choice was controlled by ordinal position or chains of image-image associations. The ordinal coding hypothesis predicts the following on two-image tests: 1) the symbolic distance effect (SDE), evidenced by increased accuracy on test images that are more distant, and 2) the first-item effect, evidenced by a linear relationship between the latency to respond to the first image and the position of that image in the sequence (D. Merritt et al., 2007; Scarf & Colombo, 2008; H. S. Terrace, 2005). The SDE, as explained above, indicates a well-organized linear representation of order rather than an externally guided habit memory, which would be predicted if image-image associations were used (Colombo & Frost, 2001). The first-item effect also indicates a mentally ordered representation (Scarf & Colombo, 2008). Quicker responses to earlier images in the list is consistent with the hypothesis that determination of where the image is located in the list is guided by a covert execution of the list, beginning at the first image and terminating when the currently activated image in memory matches the target image on the screen. Mentally accessing and advancing through the linear representation until the image is located would explain why latencies to respond to images at the end of the list are longer.

Method

Training on five-image lists. After a green ready start square was touched twice (FR 2), the trial began and two touches (FR 2) were required to select each image. Training on the first list began with the first and second images to be selected, A and B, presented simultaneously on a white background. The order in which monkeys were to select the images was predetermined randomly then held constant. All monkeys learned the same order through trial and error (Figure 1). On each trial every image in the list was randomly assigned to one of twelve locations. This ensured that order of the images, independent of location, was the to-be-remembered information. Touches to each correct image in the sequence were followed by a tone and a 200 millisecond flash of the screen. At the end of a successful trial subjects were rewarded with a different positive auditory stimulus and food reward on 100% of trials. If any image at any point in the sequence was selected in the incorrect order the trial was immediately terminated and a negative auditory signal and a 10-second timeout, during which the screen was black. Once a criterion of 70% correct was reached over a 50-trial session, a third image (C) was added to the list, and was to be selected after A and B for a reward. This procedure, with the same accuracy criterion preceding the addition of each additional image, was applied until a five-image list was learned: $A_1 \rightarrow B_1 \rightarrow C_1 \rightarrow D_1 \rightarrow E_1$ at which point a new five-image list was then introduced using the same procedure, starting with A_2 and B_2.

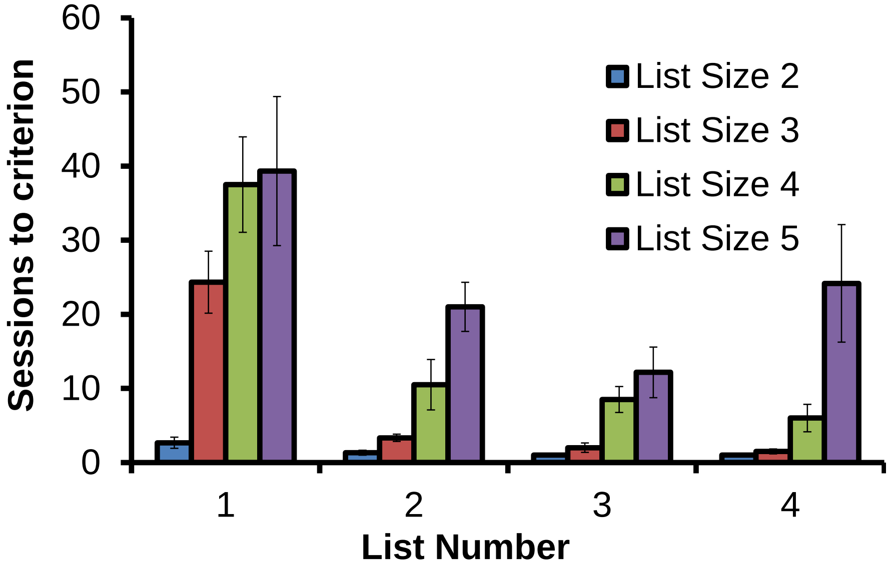


Figure 2. Number of sessions required to reach criterion for each list and list size. List number represents the sequential order in which monkeys learned lists. Error bars represent standard errors of the mean.

Repeat responses in which the list order was not violated were not counted as errors (e.g. A→B→B→B→C→D→E). Thus, the probability of selecting the first image correctly by chance is 1 in 5, whereas the probability of guessing correctly on each of choices 2 through 5 is 1 in 4. The probability of completing all five choices correctly by chance is the product of these probabilities (1/5 x 1/4 x 1/4 x 1/4 x 1/4), or .078%. After four five-image lists were learned, subjects were presented with two-image probe tests.

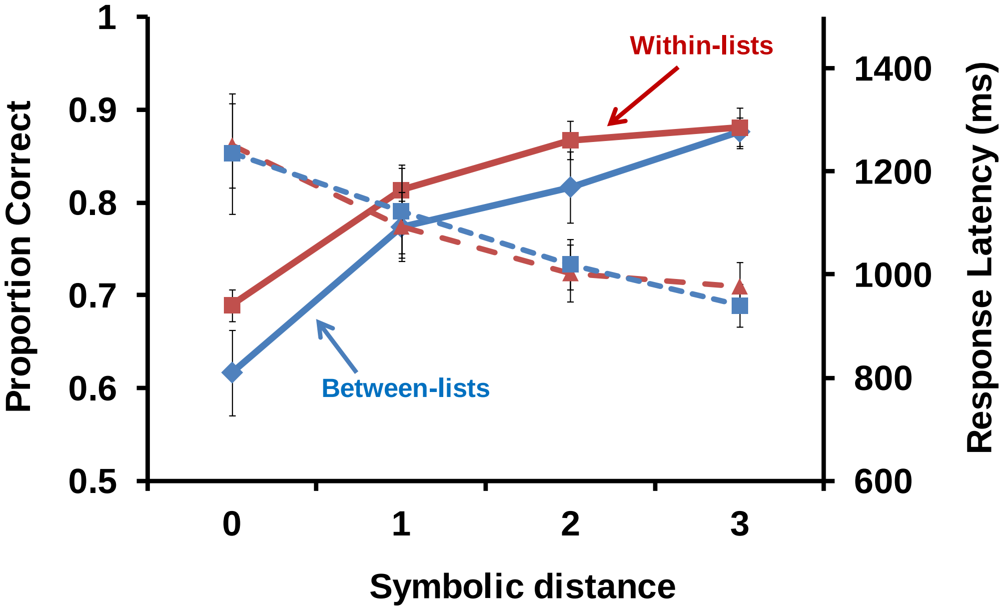


Figure 3. Accuracies and response latencies on within and between-list probe tests in Experiment 1 according to symbolic distance. Performance Accuracy on within-list tests is displayed as the red solid line, and performance on between-list tests is shown in by the blue solid line, both corresponding to the left-hand y-axis. Dotted lines in red and blue indicate response latencies to touch the first image for within and between list tests, respectively, both corresponding to the right-hand y-axis. Error bars represent standard errors of the mean.

Two-image probe tests. To determine if we would find evidence for the ordinal coding hypothesis evidenced by the SD and first-image effects, subjects were presented with two-image probe trials randomly intermixed with normal five-image lists (D'Amato & Columbo, 1988; H. S. Terrace, 2005; H. S. Terrace & McGonigle, 1994; H.S. Terrace et al., 2003). On probe trials, the two images, either from within the same list (within-list tests; e.g., A_1, B_1) or from two separate lists (between lists; e.g. D_3, E_4; Figure 1 C and D), were presented on the white screen in 2 of the 12 random locations. Sessions consisted of 120 trials: 40 trials were normal five-image lists and 80 trials were two-image probe tests. Of the probe trials, 40 trials were between-list tests, in which images were either from list 1 and 2 or from list 3 and 4, creating 40 unique trial types, and 40 trials were within-list tests consisting of 10 distinct trial-types for each list.

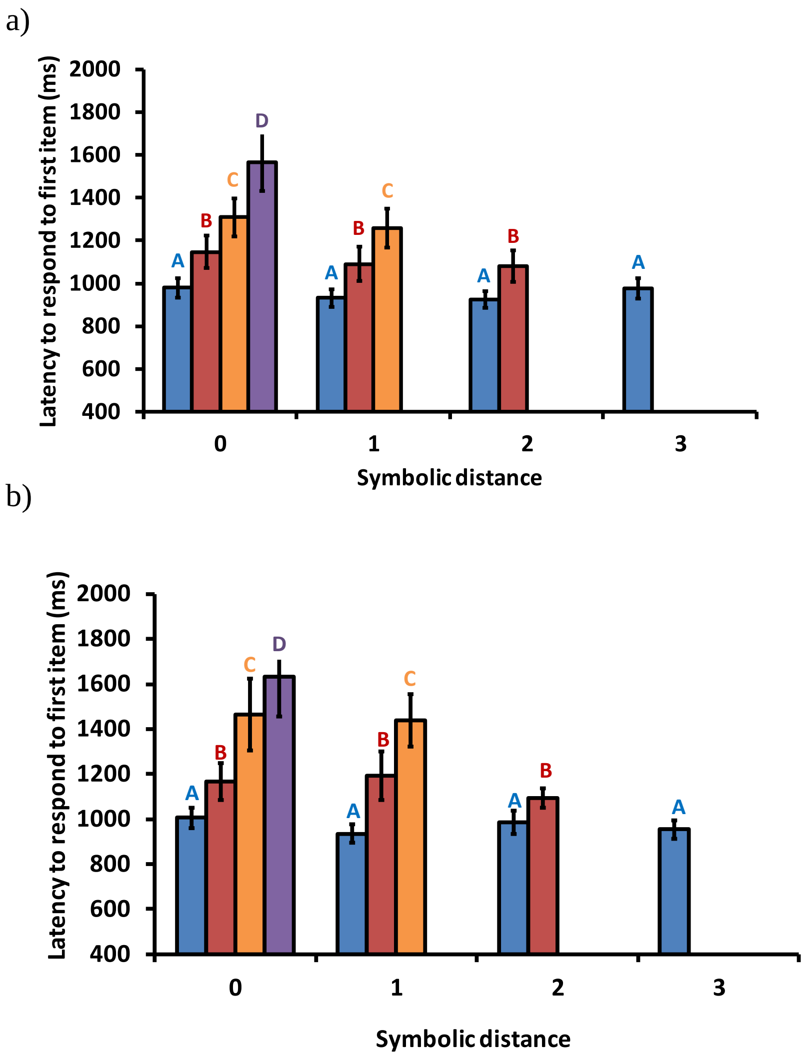


Figure 4. Response latencies on a) within-list probe tests and b) between-lists probe tests in Experiment 1. Median latencies to touch the first image are labeled above the corresponding bars. For example, at symbolic distance 0, A (far left blue bar) indicates the average latency to touch A when A and B were presented together. For symbolic distance 1, B (red bar) indicates the average latency to touch B when B and D were presented together. Errors bars are standard errors of the means.

Probe trials did not end until subjects selected both images; reward followed every trial regardless of the order in which images were selected to prevent new learning on probe trials. As in normal trials, repeated selection of the same image was not counted as an error. Subjects received 30 probe sessions.

Results and Discussion

Monkeys learned lists faster as they gained experience executing lists, and as list size increased and chance rate decreased, errors increased (Figure 2; RMANOVA; list size: $F_{1.62, 8.1}$=18.07, P=.023; list number: $F_{3, 15}$=29.29, P=.000, list size x list number: $F_{2, 45}$=3.28, P=.004; Figure 2). Subjects demonstrated evidence of "learning to learn" by solving new instances of serial lists faster and efficiently (Harlow, 1949; D. Merritt et al., 2007; H.S. Terrace et al., 2003).

On non-adjacent probe test trials, including both within and between-list tests, the image belonging earlier in the list in which it was trained was selected first (one sample t-tests; within-list SD1: t_5=11.63, P=.000; within-list SD2: t_5=14.17, P=.000; within-list SD3: t_5=13.44, P=.000; between-list SD1: t_5=8.70, P=.000; between-list SD2: t_5=7.21, P=.001; between-list SD3: t_5=17.56, P=.000; Figure 3). As would be expected given that subjects had already met criterion with adjacent images in trained lists, adjacent within-list images were selected according to ordinal position more often than expected by chance (one sample t-test, t_5=10.29, P=.000). On between-list tests, however, performance only approached significance (one-sample t-test: t_5=2.47, P=.057). This difference between within and between-list adjacent image tests may be attributable to the fact that within-list test selection is partially controlled by associations acquired during training. According to this account, behavior on adjacent within-list tests results from both ordinal position coding and image-image associations. Scarf and Colombo (2008) maintain that these two properties, a well-organized internal representation and an associative chain, combine to maintain high-performance on the two-image tests. In the case of between-list tests, behavior is controlled only by ordinal position because no image-image associations exist. Nevertheless, the absence of a significant effect on adjacent between-list tests does not actually indicate a difference with performance on within-list tests. To test whether there was in fact a difference between within and between-list tests we performed an RMANOVA. There was no main effect of trial type ($F_{1,5}$=2.537, P=0.172), indicating that was no difference in test difficulty on within and between-list tests.

Subjects were more likely to select images according to ordinal position with larger distances between images (RMANOVA, main effect of symbolic distance: $F_{3, 15}$=34.95, P=0.000; Figure 3). The same trend in the opposite direction was found with response latencies: a main effect of symbolic distance, but not trial type was found (2x2 factorial RMANOVAs; symbolic distance: $F_{3,15}$=12.74, P=.000; trial type: $F_{1,5}$=.002, P=.965). If the memory representation controlling choice was limited to image-image associations, choice in all non-adjacent probe tests would not have been predicted by correct ordinal position and there would have been a significant main effect of trial type with performance on between-list tests being significantly lower than performance on within-list trials. Instead, subjects performed most inconsistently according to ordinal position on adjacent images with symbolic distance of zero and performed better and more rapidly on images that were psychologically further apart (Figure 3).

Monkeys responded more quickly to images with earlier ordinal positions (e.g. A) than they did to images with later ordinal positions (e.g. D; RMANOVAs and paired sample t-tests; within-list tests Figure 4A: symbolic distance 0: $F_{3, 15}$ =8.393, P=0.002; symbolic distance 1: $F_{2, 10}$=16.34, P=.001; symbolic distance 2: t_5= -7.208, P=.001; between-list tests Figure 4B: symbolic distance 0: $F_{3, 15}$ =26.13, P=.000; symbolic distance 1: $F_{2, 10}$=17.74, P=.001; symbolic distance 2: t_5= -3.555, P=.016). The monotonic relationship between latency to respond to the first image and the position of that image is consistent with the possibility that monkeys mentally execute the list from memory. During covert list execution when the current position actively represented matches the image on the screen, relatively short response latencies would occur at the beginning of the list and relatively long response latencies would correspond with target images at the end of the list. While it is likely that choice may have been guided by such a mechanism that relies on a mentally ordered representation, the presence of the first-item effect is only one piece of suggestive evidence that monkeys covertly execute lists. To more directly evaluate the representation subjects used to mentally update position in the list when executing a sequence we evaluated possible mnemonic coding mechanisms in Experiment 2.

7.5. Experiment 2- Prospective vs. retrospective coding

Planning requires holding future action(s) in memory in anticipation of future use. In the context of list execution, planning might manifest as a prospective, rather than retrospective code of one's location in progression through the list. Therefore, here we use "planning" to denote maintenance of an active representation of images to which the subject is to respond. Recent evidence suggests that monkeys (Beran, Evans, Klein, & Einstein, 2012; Beran & Parrish, 2012; Scarf, Danly, Morgan, Colombo, & Terrace, 2011) and jackdaws (Pfuhl & Biegler, 2012) may plan one response ahead when executing ordinal lists. Use of a prospective code would mean subjects actually remember two responses: the current one and the next image in the list, such images are in mind before every choice. Use of such a code would support rapid and fluid list execution and may support memory load needed to complete multiple actions to achieve the goal of successfully executing serial lists. Cook, Brown & Riley (1985) proposed three types of coding to support working memory load: prospective coding of anticipated stimuli, retrospective coding of previously encountered stimuli, or a combination of prospective and retrospective coding. In a 12-arm radial arm maze a rat must remember which arms have been visited or which ones remain to be visited. In order to minimize the memory load by appropriately updating current position in the series, rats switched from a retrospective code in the early in the trial, when there are less previous responses to remember, to prospective code in the middle of the list, when there are less to-be remembered responses to remember (Cook et al., 1985). Similar to Cook's method of interjecting a delay between responses to increase errors, we interposed a delay and distracter, a dot, that monkeys must touch to advance the trial, at different points of interpolation (POIs) during list execution in order to determine what mnemonic code controls choice. If the first, correct move is forgotten, it is possible that the next planned move is remembered. This would be indicated by execution of the second forward move as a delay would lead to these prospective, forward errors. However, if subjects code retrospectively and the content of memory during the retention interval is the already experienced moves, a delay would lead to backwards errors because that is what is actively represented in memory. Secondly, we tested if the number of forwards versus backwards errors varied as a function of position in the list to accommodate memory load. This would indicate flexible memory processing, mirroring rats' dual-code strategy (Cook et al., 1985).

Method

List 1 was used in this experiment (Figure 1A). Each 120 trial session consisted of 72 normal five-image list tests, run as in previous experiments, and 48 five-image probe tests, in which a delay and distracter task interrupted the exaction of the sequence at one of four possible POIs: between images A-B, B-C, C-D, or D-E. A 200 milliseconds blank white screen preceded presentation of the distracter stimulus, a blue dot (100 pixels x 100 pixels), which appeared on a plain white screen. The purpose of the required touch of the dot was to prevent monkeys from touching the correct image location during the delay. For example, on a POI A-B probe, subjects saw all list images in random locations on the screen, as they normally do, and if A was touched first, the screen would go white and a blue dot would appear. After the dot was touched (FR2), all five images reappeared in the same spatial locations as before the delay. If images were not correctly selected before the POI, the trial ended, as in normal trials such that the distracter was never presented. The dot could appear in any of the seven available screen locations not occupied by list images. Touches made after the distracter to the image previously touched right before the distracter (-1 error) were counted and reinforced as errors. For example, selection of A, then B, then the distracter dot, and then B again, resulted in negative auditory feedback and a time-out.

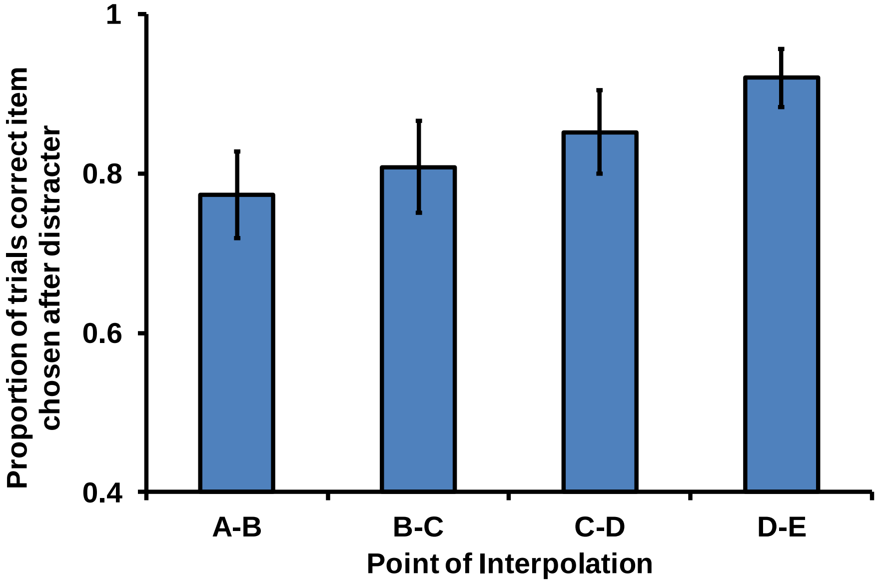


Figure 5. Performance on probe tests as measured by proportion of tests in which the correct image was chosen after the distracter dot. From left to right, proportion is the amount of time B, C, D, and E, were chosen for each respective POI. Error bars represent standard errors of the mean.

Results and Discussion

Accuracy in selecting the entire five-image list was significantly worse with a distracter dot than without one (normal trials = 85%; probe trials = 68%; paired sample t-test: t_5=2.76, P=.040), indicating that the distracter dot significantly increased total errors in execution of the five-image list. Accuracy on probe trials, 68% correct, was significantly above chance (one-sample t-test: t_5=8.45, P=.000). Of all possible responses only at the time of choice after the distracter image was touched 84% of responses made were to the next, correct, image in the list. This indicates that subjects anticipated future responses and engaged in those responses when those responses became available. Fewer errors were made when the distracter dot occurred later in the list (RMANOVA: $F_{3,15}$=18.27, P=.000; Figure 5). Pair-wise comparisons of all POIs were significant ($P<.05$), except for probe type A-B vs. B-C (P=0.224). This could be because when attention is disrupted at the beginning of list execution, it is more difficult to reset where in the list one is because more attention is required when list execution is not yet in progress.

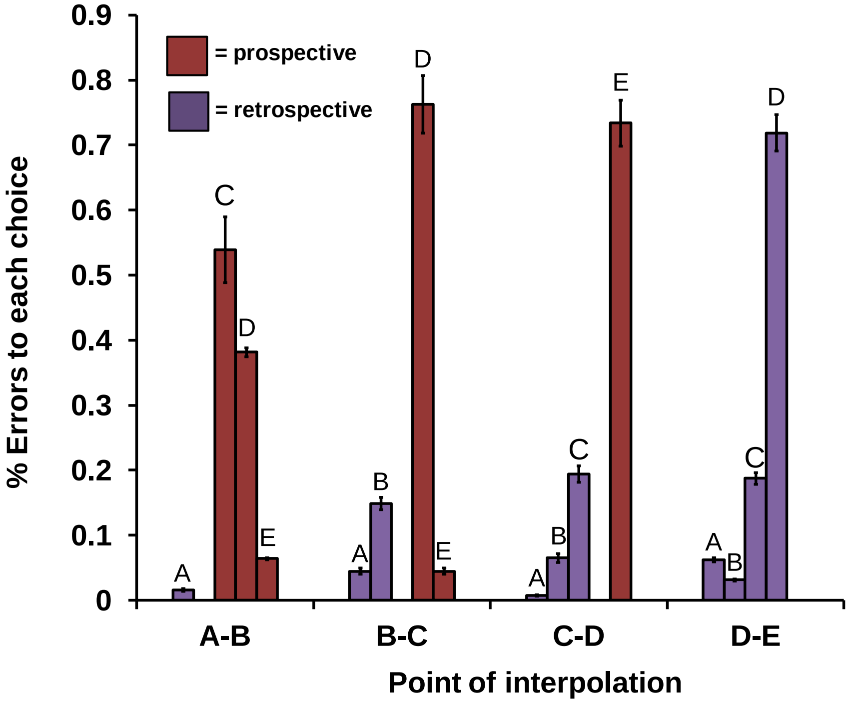


Figure 6. Errors at each point of interpolation to each incorrect image in the list. Note that unlike in Experiment 1, repeat errors (-1 errors), were counted as errors and terminated the trial. Point of interpolation (POI) indicates in between which two images the short delay and distracter occurred. For example, B-C indicates that the delay occurred after A and B was touched. In this case, selection a -1 error is selection of A→B→delay→B. Maroon bars indicate forwards errors; purple bars indicate backwards errors.

Furthermore, use of a prospective code is consistent with this result because there are more anticipated moves to code at the beginning of the list and relatively few towards the end of the list, causing errors at A-B and B-C to be the most likely and errors at the end of the list (i.e. D-E) least likely. To directly evaluate the hypothesis that subjects planned future responses, forwards and backwards errors were analyzed next.

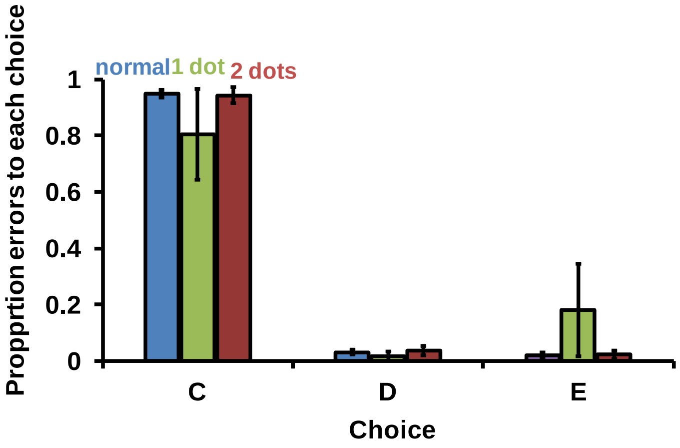
To determine if backwards or forward errors were more likely all backward and forward errors were summed, except for those at POI D-E where no forward errors were possible. Summing all forwards and backwards errors was feasible because an equal number of forward and backward errors were possible when opportunities were summed across all POIs. Forward errors were more common than backwards errors (one-sample t-test: t_5=-20.767, P=.000). The most common error was to the next image in the list: a +1 error, such as choice of C when B is correct; +1 errors occurred at every POI except D-E, where no forward error was possible. These results indicate that monkeys use only a prospective code, rather than a retrospective code, further supporting the conclusion that monkeys do plan, at least in the short term**.**

At POI D-E, however, subjects were most likely to choose D, a -1 retrospective “error” to the next closest image in the list, rather than starting the list over and selecting A, for example. Certainly, subjects did not show evidence of a dual-coding strategy like rats did in the radial arm maze in which retrospective coding was most efficient at the beginning rather than the end of the list (Cook et al, 1985). While -1 errors at POI D-E may indicate some evidence for retrospective coding, if subjects were actually remembering previously experienced responses, we would expect errors to increase towards the end of the list when there are more responses to remember, but this is the opposite of what was found. Between D and E, even with a distracter dot at that POI, there is only one image to remember. It is possible that monkeys were more attentive on trials on which a POI at D-E was possible as they had already gotten far in list progression without error (A→B→C→D), compared to ones in which they erred early and the trial terminated. This would lead to a disproportionate number of POI D-E trials (Figure 6; *far right*) on which subjects were performing with increased attention. Similarly, it is also possible that increased attention may have occurred as subjects neared the end of the list, because they get closer to reward. Monkeys might have attended better in anticipation of reward, or that their choices might have been more strongly controlled because of proximity to reinforcement. Finally, it is possible that fewer errors occurred later in the list because less forward errors, the errors that are most likely, are possible at the end of list execution where at the beginning of list execution there are several possible forward errors. Therefore, while there is suggestive evidence of retrospective coding at POI D-E because a -1 error is the most likely error, we cannot firmly conclude that monkeys also coded retrospectively because of task parameters. The fact that subjects made fewer errors later in the list is consistent with the hypothesis that monkeys prospectively code their location in lists during list execution. The main result of more prospective than retrospective errors, specifically +1 errors on all POIs on which prospective errors were possible, indicates that monkeys mentally update which ordinal position or image was just selected and what image needs to be selected. It is, however, also possible that the tendency to skip one response ahead occurred because subjects treated the dot as a list image. To evaluate this alternate hypothesis that monkeys were counting responses made, rather than updating true ordinal position in the sequence, we directly tested the counting hypothesis in Experiment 3.

7.6. Experiment 3-Evaluating the possibility of tracking responses made

The most likely error made in Experiment 2 was a prospective, +1, forward error to the next image in the list. It is possible that subjects made selection errors to the next image in the list because the distracter dot was treated as an item in the list. If progression in the list was tracked by estimating the number of responses made this would mean knowledge of ordinal position would not be required to guide choice selection. If the dot was in fact treated as an image and this information was used as a mechanism to track progression in list execution, then the number of dots touched should predict how far the forward errors go, such that touching more dots should increase the degree to which errors are forward of the correct response: 1 dot should result mostly in +1 errors, as was seen in Experiment 2, whereas touching 2 dots should result in mostly +2 errors.

a)



b)

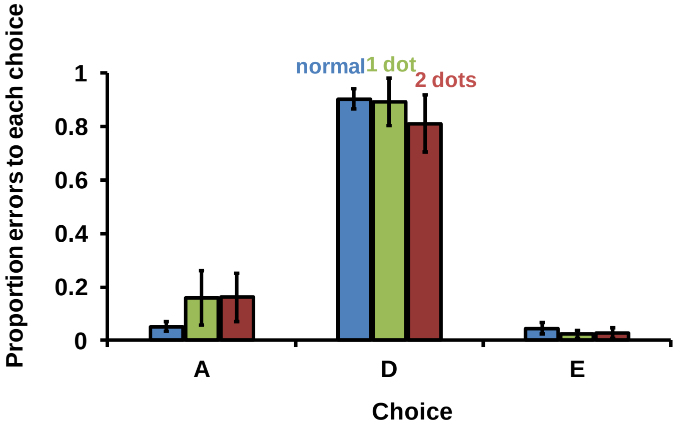


Figure 7. Proportion of errors made on normal tests (blue; far left bars) versus probes with 1 distracter dot (green bars) or 2 distracter dots (red bars) after image A (7A) and after B (7B). In A, C is a +1 error and D is a +2 error. In B, D is a +1 error, E is a +2 error, and A is a -2 error. The counting hypothesis predicts a shift from +1 errors to +2 errors when 2 dots occur, as compared to 1 dot. Error bars represent standard errors of the means.

If however, responses made did not represent current position in the list, and monkeys instead attended to true ordinal position of images, touching 2 dots would not result in +2 errors.

Methods

We tested the counting hypothesis by having either one or two distracter dots appear either both after A was touched or after B was touched. All task parameters were the same as in Experiment 3. On trials with two distracter dots, the second blue dot appeared in one of the twelve random locations excluding the ones where the first dot and the images appeared. As usual, monkeys were required to touch each distracter dot twice (FR 2) after a 200 millisecond delay to make it disappear and to illuminate the same set of images in the original locations, or a second dot, allowing completion of the trial.

Results & Discussion

There was no difference in errors as a function of whether one or two dots were touched (Figure 8; paired sample t-tests; distracter dot(s) after A: t_5=-1.38, P=.225; dot(s) after B t_5=-050, P=.962). As found in Experiment 2, monkeys were less accurate on probe tests compared to normal tests with no distracter dot (Probe test mean=.76; Normal test mean= .87; paired sample t-test: t_5=-9.78, P=.000), but monkeys were only moderately disturbed by the delay and distracter test, performing significantly above chance on all probe tests combined (one-sample test: t_5=21.5, P=.000). Because subjects were never reinforced for remembering the dot, it is possible that subjects may have gradually learned to perform well on these probe tests with the distracter dot. To examine possibility that subjects gradually learned to ignore the distracter dot, we directly analyzed performance when 1 distracter dot appeared after image A was selected in Experiment 2 as compared to in Experiment 3, and found that monkeys did not become significantly better on probe tests in Experiment 3 (paired sample t-test: t_5=1.24, P=.271). This, and the fact that that performance on probe tests was significantly impaired as compared to chance in both Experiment 2 and Experiment 3, shows that monkeys were likely not able to simply ignore the distracter dot.

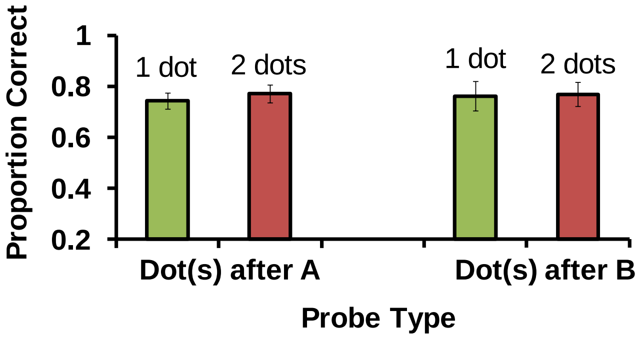


Figure 8. Performance on single and double distracter tests. Distracter dots either occurred after image A (left bars) or after image B (right bars). Error bars represent standard errors of the mean.

If subjects were using numbers of responses made to represent current position in the list then they would have made most errors to C (+1 error) when 1 dot occurred after A, and most errors to D (+2 error) when 2 dots occurred. While errors were reliably to C after one dot, most errors after 2 dots were also to C, indicating that on these probe tests monkeys were not skipping responses ahead based on number of responses made to distracter dots (Figure 7A). On the second set of probe tests, when the distracter dot occurred after selection of A and B, subjects chose D most often both after 1 distracter dot and after 2 distracter dots (Figure 7B). If subjects were using responses made as indication of location in the list, then the majority of errors would be to D (+ 1 error) when 1 dot occurred, and to E (+ 2 error) when 2 dots occurred. This was not the case: regardless of whether 1 or 2 dots occurred, +1 errors were the most likely error, revealing that the distracter dot was not treated like a responded image.

As indicated by high performance levels on probe tests with distracters (Figure 8) subjects were frequently able to remember the correct image. When the correct image was forgotten, however, subjects remembered the next forward move in the list, as indicated by robust +1 errors (Figure 7). Together, these reliable responses to the correct image and to the next forward image in the list indicate subjects remember where they are going two steps ahead. These results further suggest planning in that performance reflected a propensity to keep the next two responses in mind.

7.7. Experiment 4- Evaluating the possibility of list-linking

The results of Experiment 1 demonstrated that choice was not controlled by image-image associations, and suggest control by ordinal position. Experiments 2 and 3 further highlighted that monkeys maintain a linearly organized representation because they plan one to two responses ahead. Because Experiment 3 indicated that current ordinal position was not determined by estimating number of responses, we aimed to determine how position in a list was represented and what type of positional information is maintained. Specifically, we tested if the representation of ordinal position is based on a static coding of position within natively learned lists or based on more dynamic positional information unconstrained to native lists.

In transitive inference (TI), which shares some features with SC, positional information appears to be more dynamic than static in nature. In TI subjects learn two lists (A>B>C>D>E>F>G and H>I>J>K>L>M>N) by training on premise pairs (e.g. A>B) and are able to make ordinal judgments both within (B >F) and between (B>K) lists based on ordinal position within the five-image lists, much like they do on two-image probe tests in SC. However, when lists are then “linked” with training on the between lists premise pair, G>H, subjects changed from reliance on position constrained within a list to relative position across the newly constructed 14-image list, now selecting D_1 instead of B_2. (Gazes et al., 2012; F. R. Treichler & Raghanti, 2010a, 2010b). Because two lists can be linked in TI, as evidenced by ordinal judgments across lists, this indicates that a change from static positional coding within native lists to more dynamic ordinal coding beyond natively-learned lists is possible in the TI context. Much like in TI, in SC, we know that knowledge of ordinal position is robust because subjects order two-image between-list probe tests according to ordinal position. However, it is not yet determined whether that positional information is dynamic enough to result in ordinal judgments unconstrained to natively learned lists, which would result from successfully list-linking, or if ordinal judgments would continue to be made on the basis of static ordinal position of natively learned lists even after linking training. In Experiment 4 we asked the extent to which the representation of ordinal position is based on static or dynamic coding of position by employing list-linking training. We determined if monkeys would link lists by positively rewarding selection of the first image in list 2 when selected after the last image in list 1, and then testing whether this linking training would cause selection of images according to ordinal position from a newly constructed 10-image list or ordinal position within native five-image lists on two-image probe tests.

Method

Twelve 9-10 year old male rhesus monkey subjects were used in Experiment 4. These subjects did not participate in any of the previous experiments, although they had tested on the basic SC task by learning four lists and tested on two-image tests as described in Experiment 1. Throughout all three phases food reinforcement was adjusted to keep maximal potential reinforcement between 75 and 80%.

Phase 1: Pre-list-linking

Monkeys were first trained on two new five-image lists as in Experiment 1. After reaching 70% criterion on each list separately, monkeys received intermixed sessions with both lists on which they had to reach a criterion level of 50% on each list simultaneously within a 120-trial session.

Monkeys who did not perform above 50% on the two intermixed lists after five sessions received remedial training, in which the poorly performed list was retrained starting with three images and incrementing back up to the five-image list using the same training method as used for novel lists. After subjects reached 70% on this five-image list, they were reintroduced to the sessions with two intermixed lists.

Once subjects performed above 50% on both lists on intermixed sessions, they received five 120-trial test sessions identical to those presented in Experiment 1, except it contained images from only two new lists rather than from four. Performance on between-list tests during these sessions indicates if monkeys' choices continued to be guided by absolute (ordinal) position before linking training occurred.

Phase 2: List-linking

Subjects received 25-trial sessions of two-image trials containing image E_1 (last image from list 1) and image A_2 (first image from list 2) until 80% criterion was reached. Images were displayed as they were in two-image probe tests, except that subjects were only reinforced for correctly choosing image E_1 and then A_2, and trials would terminate for incorrect initial choice of image A_2. Correct responses were reinforced with 100% positive auditory feedback accompanied by a food reinforcer on 80% of trials. Incorrect responses resulted in negative auditory feedback and a 10-second timeout. Which list was first (list 1 or 2) in the new linked order was counterbalanced across subjects; six monkeys were trained that list 1 was linked before list 2 and six monkeys were trained that list 2 was linked before list 1. Though the images in each list were different for subjects, here list 1 will consistently refer to the first list, which was trained to be linked to the beginning of list 2.

After subjects reached criterion on the linking pair, they were given 84-trial sessions that consisted of 28 two-image linking pair trials, 28 five-image list 1 trials, and 28 five-image list 2 trials. To ensure that subjects remembered each list and the linking pair, a criterion of 80% on the linking pair and 50% on each list (chance= .078%) was required to move onto phase 3 of testing. Reinforcement for the five-image lists was 100% food and auditory, as in training, and the linking pair was 90% food and 100% auditory. Food reinforcement for the linking pair was increased slightly from training when it was 80% to 90% to accommodate the more difficult five-image lists so that overall potential food reinforcement would be about 75-80%.

Phase 3: Static or dynamic coding of position

In phase 3, subjects received five 128-trial sessions that consisted of 40 normal list presentations (20 from list 1; 20 from list 2), 10 linking pair tests, 40 within-list probe tests (20 from list 1; 20 from list 2), and 38 between-list probe tests, which included all possible combinations except the linking pair. Reinforcement for the linking pair and normal tests remained the same as in training. Probe trials were non-differently reinforced; regardless of selected order a positive auditory reinforcer was presented on 100% of trials, accompanied by a food reward on 60% of trials. Food reinforcement was relatively low on the probe trials in order to maintain an average intermittent reinforcement rate of approximately 75-80% given average performance levels as food reinforcement was 90% on linking pair and 100% on the more difficult five-image SC trials.

Test trials were classified as either *consistent* if ordinal coding constrained to static five-image lists and ordinal coding across a constructed dynamic 10-image list would yield the same response and *inconsistent* when these two codes would generate different responses. For example, test B_1, C_2 is a consistent trial because both codes indicate selection of B_1 before C_2. Test B_2, C_1, on the other hand, is an inconsistent trial because dynamic coding indicates selection of C_1 (list 1) before B_2, but static coding indicates selection of B_2 before C_1. The number of consistent and inconsistent trials was randomized and counterbalanced within sessions for each trial type. Selection of the image from list 1 before selection of the image from list 2 on inconsistent trials would indicate that monkeys linked the two lists after training on only one pair of images from Lists 1 and 2.

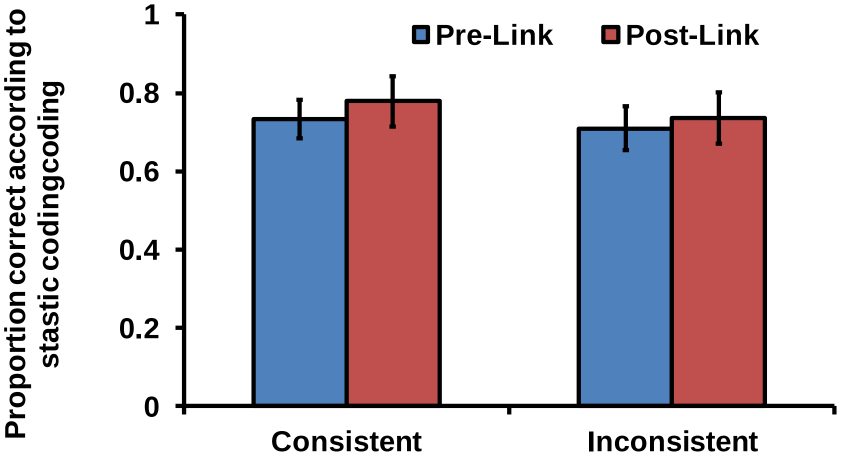


Figure 9. Proportion of correct trials according to static coding within five-image lists. Choice based on dynamic coding of a linked 10-image list would have resulted in the blue bar post-link training for inconsistent pairs (far right) significantly below chance. Error bars represent standard errors of the mean.

In other studies in which subjects received linking training of two lists critical internal test pairs were examined instead of examining all possible test pairs including end-anchor items

(Gazes et al., 2012; F. R. Treichler & Raghanti, 2010a). Because test pairs with end-anchors might be contaminated by linking training or have enhanced salience from proximity to the reward, we also excluded examining test pairs that included end-anchors. For example, on an E_1, B_2 test, E_1 may have been so reliably trained to be selected first from linking training ($E_1 \rightarrow A_2$) that performance on tests containing E_1 would not accurately reflect unbiased choice tendencies. We therefore averaged performance on the only inconsistent tests that did not contain any images from the linking pair resulting in the following critical internal test-pairs: C_1, B_2; D_1, B_2; and C_1, D_2.

Results & Discussion

On two-image tests before linking training subjects chose images according to position coding of static five-image lists significantly more than chance for both consistent and inconsistent between-list trials (Figure 9; *blue bars*; one-sample t-tests: consistent: t_{11}=5.64, P=.000; inconsistent: t_{11}=3.72, P=.003), as they did in Experiment 1. After linking training subjects continued to select images according to ordinal position within five-image lists significantly above chance for both consistent and inconsistent between-list trials (Figure 9; *red bars*; one-sample t-tests: consistent: t_{11}=5.20, P=.000; inconsistent: t_{11}=3.99, P=.002). Subjects performed similarly pre and post linking training on consistent and inconsistent pairs (paired sample t-tests: consistent: t_{11}=.191, P=.852; inconsistent: t_{11}=-372, P=.717), revealing that linking training did not affect choice behavior. This indicates that the ordinal representation for the new 10-image list was either non-existent or not strong enough to cause subjects to reliably choose according to dynamic coding. If linking had been successful and a 10-item list was mentally constructed, tendency to choose based on ordinal position within native five-image lists on inconsistent trials would have decreased significantly after linking training.

Monkeys did not show evidence that they linked two separately learned lists. Choice behavior continued to be guided by the ordinal positions learned in initial training on five-image lists, which provides further evidence that monkeys have a robust internal representation of serial order and that use ordinal information is based on static, rather than more relative dynamic position. This result is in direct contrast to what is found in TI tasks in which lists are successfully linked (Gazes et al., 2012; F. R. Treichler & Raghanti, 2010a), as discussed in the general discussion.

7.8. Discussion

In the present experiments we aimed to provide information about the mechanisms of memory for serial lists in the SC paradigm. In this demonstration of nonverbal serial organized behavior rhesus monkeys demonstrated the “learning to learn” effect by gradually becoming faster at learning lists as more lists were experienced (Harlow, 1949). This effect is consistent with abstraction of general learning sets applied to new instances of a problem, suggesting serial expertise (H. S. Terrace, 2005). Extraction of ordinal knowledge was more directly assessed in Experiment 1 by giving subjects non-differently reinforced two-image probe tests containing any combination of images from lists, including images from both within and between-lists.

Monkeys spontaneously and reliably selected images according to ordinal position, even when the images had never before been seen together, or ever differentially reinforced in that order, in between-list tests. Selection of B_1 before selecting D_2, for example, is incompatible with image-image associations. Use of image-image associations to guide choice behavior would have resulted in selection of images according to ordinal position only on adjacent images from within a list, such as $A_1 \rightarrow B_{1.}$ On all other two-image tests images carry no direct image-image associations, such that use of an image-image association mechanism would result in unreliable selection of images according to ordinal position on non-adjacent tests pairs within a list and on all between-list images. Actual results yielded the exact opposite of the image-image association prediction: ordinal selection on two-image tests was most consistent on non-adjacent images occupying the greatest distance between images. The SDE was reflected on both within-list and between-list probe tests, and selection according to ordinal position was not any less consistent on between-list tests, indicating choice behavior was not guided by image-image associations. These results, which corroborate similar findings in rhesus monkeys (S. F. Chen et al., 1997; H.S. Terrace et al., 2003) and other non-human primates (chimpanzees: Inoue & Matsuzawa, 2009; marmosets: Koba, Takemoto, Miwa, & Nakamura, 2012; cotton-top tamarins: Locurto, Dillon, Collins, Conway, & Cunningham, 2013; lemurs: D. Merritt et al., 2007), indicate that subjects likely accessed an internal representation of ordinal position and applied this knowledge to choice behavior on two-image tests.

Use of an ordinal code was further supported by the presence of the first item-effect. The latency to respond to the first image in the two-image tests was faster when the image was earlier in the list and that latency successively increased as the end of the list approached. This effect is consistent with the theory that subjects mentally progressed through the five-image list until that image was found when accessing ordinal information about the relative order of those images (e.g. Scarf & Colombo, 2008).

Does choice selection according to ordinal position necessitate "mental flexibility"?

It is surprising that monkeys appear to use knowledge of ordinal position that can only be based on internal cues to guide choice selection in such a rote-learned task. Ability to spontaneously select images according to ordinal position suggests a capacity to apply general knowledge of ordinal position information across lists. Most researchers who have investigated SC learning and find that subjects respond to two-image tests according to ordinal position posit this ability denotes flexible use of information, and is therefore explicit in nature (D. Merritt et al., 2007; H. S. Terrace, 2005). We, however, do not argue that responses on two-image tests requires “mental flexibility”, nor do we think that this task necessarily captures explicit memory. Though memory on this task might very be explicit, and some evidence that directly tests cognitive access to these memories (Kornell, Son, & Terrace, 2007) might hint in that direction, robust evidence remains to be provided.

Ability to select two images according to ordinal position may not be such a remarkable feat. Knowledge of ordinal position does tell us what the animal has knowledge about, and that they are able to use this information in a relational manner, but the fact that they code this information does not mean monkeys made the “correct” or most sensible ordinal decisions when presented with non-differentially reinforced probe trials. In the laboratory, selection of B before D is not necessarily a “smarter” decision than selection of D before B: both selection orders would result in the same positive feedback. It is rather the context in which the subject is in that informs whether such an ordinal decision is useful or not. For example, when combining a few recipes to invent a new recipe for the first time, it is useful to know that onions should be cut before frying the onions. You know this stepwise information because of the relation these two actions have to each other; you do not blindly put the onion in the pan before cutting it even though frying the onion is step 2 in one recipe and cutting the onion is step 3 in another recipe. If one had outstanding knowledge of ordinal position information but no ability to use this information relatively, this would not make for a very good cook. Selection of B before D may very well be sensible, but could just as likely be nonsensical. Unless it could be determined what is useful for a rhesus monkey in the case of SC, it is premature to conclude that knowledge of ordinal position is necessarily flexible, adaptive, or explicit.

Comparisons with other species

Lists that contain at least five images are critical because they allow testing critical internal test pairs on two-image tests that do not only contain end-items or adjacent items; two-image tests drawn from three and four-image lists unavoidably contain either an end-item and/or adjacent items. Humans, old and new world monkeys, and lemurs, have been shown to select two-image tests from lists of at least five-images according to ordinal position (S. F. Chen et al., 1997; Colombo & Frost, 2001; D'Amato & Colombo, 1989; D. Merritt et al., 2007). Pigeons, however, performed at chance on internal test pairs (e.g. BD) that did not contain end images A or E, indicating weaker versatility in use of ordinal position information (D'Amato & Columbo, 1988; Scarf & Colombo, 2008, 2011; H. S. Terrace, 1991, 1993). Jackdaws have recently been found to maintain knowledge of ordinal position in another similar ordinal task, but such abilities have only been seen with three-image lists (Pfuhl & Biegler, 2012). This list-size constraint in jackdaws and pigeons might mirror the low BD test performance when five-image lists are used in pigeons (H. S. Terrace, Chen, & Newman, 1995) in that only end images and one middle image exist in three-image lists.

There is evidence that ordinal pairs that contain an end image are processed differently than those not containing an endpoint (Leth-Steensen & Marley, 2000). In human transitive inference (TI) tasks in which relationships between images must be inferred (e.g. A>D) to relationally construct an overall order (A>B>C>D>E), greater hippocampal activation occurred when TI pairs did not contain an end-image (Martin Zalesak & Stephan Heckers, 2009), indicating tests with end-items might not rely on the same process as that used with more difficult internal tests pairs. This dissociation in processing mechanisms, depending on images tested, has been found in human fMRI studies (Heckers, Zalesak, Weiss, Ditman, & Titone, 2004; Leth-Steensen & Marley, 2000; Martin Zalesak & Stephan Heckers, 2009) and might also extend to other animals. Indeed, in SC humans perform similar to monkeys, showing patterns that are characteristic of ordinal processing such as the SDE and first-item effect(Colombo & Frost, 2001). While the order is inferred in TI tasks, but explicitly taught in SC, recent evidence suggests these two tasks share an underlying ordinal code (Jensen, Altschul, Danly, & Terrace, 2013; Gazes, Templer, & Hampton, in prep). It is therefore likely that within both TI and SC tasks, there are different processes that could be differentially activated depending on which images are in the pair, such as if it includes adjacent vs. non-adjacent images or end-images vs. internal test pairs, like BD. It is also likely the case that some animals, which may include bird species, are not capable of the more integrative use of ordinal information required for high performance on internal non-adjacent test pairs that appears to be dependent, at least in part, on the hippocampus.

Content of memory during list execution

While the negation of a purely image-image association mechanism may be evident from the SD and first-item effects found on two-image between-list tests in Experiment 1 that are characteristic of internal linear representations of order, the specific content of the ordinal representation had yet to be defined. In Experiments 2-4 we aimed to characterize the contents of memory during list execution that allow for strong knowledge of the ordinal position of each image in the list.

When images are presented in a fixed order, subjects can use long-term memory to store ordinal positions instead of relying only on working memory (Orlov, Yakovlev, Hochstein, & Zohary, 2000b). However, even if long-term memory is used, working memory is also required to continually update progress in the completion of a given list. Radial arm mazes require more working memory than SC tasks as SC also depends on long-term memory, but both provide a means to understand coding mechanisms used to appropriately order responses made. Rats

(Cook et al., 1985), pigeons (Steirn, Zentall, & Sherburne, 1992; T. R. Zentall, Steirn, & Jacksonsmith, 1990 although see also DiGian & Zentall, 2007) and humans (R. P. Kesner & Despain, 1988) appear to use a dual-coding strategy in radial-arm maze by switching from a retrospective to a prospective memory code to decrease working memory load. Monkeys have shown evidence for retrospective coding in computerized radial-arm maze (Klein, Evans, & Beran, 2011) but have also shown evidence for prospective coding in SC tasks when errors were increased by switching locations of remaining images to be touched and masking images on the screen (Scarf et al., 2011). Other evidence that examines eye movements, suggests monkeys do not plan responses ahead during list execution in SC (Scarf & Colombo, 2009). Because the evidence for the coding mechanism used in SC was equivocal, we investigated which mechanism controlled choice during executing a list by examining retrospective and prospective coding in Experiment 2.

Interposing a delay and a distracter dot between images in Experiment 2 significantly increased errors, but monkeys still performed relatively well on these probe tests. Most responses after touching the distracter dot were to the next correct image in the sequence, indicating strong knowledge of ordinal position. The distracter dot, did however, impair performance, creating different types of errors that could be analyzed to probe the contents of memory during the retention interval. When monkeys did not choose the correct image after a distracter dot, they showed a reliable tendency to touch one forward response ahead, suggesting short-term planning and prospective coding. Monkeys, unlike rats in a radial arm maze that shifted strategies to accommodate working memory load depending on position in the list (Cook et al., 1985), performed better further into the list and showed consistent prospective responding across all POIs on which prospective errors were possible. It is perhaps not surprising, however, that monkeys did not show the same effect as rats since SC and the radial-arm-maze have very different demands on memory. In the radial arm maze there is no fixed ordered remembered from experience with previous trials on which to rely. Rather, the “correct order” is defined solely by not returning to previously visited arms. In SC there is a defined order subjects remember over trials, and specific future responses must be made rather than simply responding to ones that haven’t been selected yet. This difference in task demands might explain why subjects in SC use a prospective, rather than a retrospective or dual-code strategy.

Evidence for a prospective rather than a retrospective code found here supports existing evidence in rhesus monkeys (Scarf et al., 2011) and other non-human primates, including chimpanzees (Beran, Pate, Washburn, & Rumbaugh, 2004; Biro & Matsuzawa, 1999; Kawai & Matsuzawa, 2000), marmosets (Koba et al., 2012), and capuchin monkeys (Beran & Parrish, 2012) plan selection of responses in fixed sequences. Future studies that vary task parameters to increase working memory load, like increasing delay and list-length, may be useful in determining conditions under which a dual-code strategy may become necessary. In Experiment 2 errors made after the distracter dot were reliably and consistently made to the next image in the sequence, indicating anticipation of future actions. It was a possibility that responses made served as a means for knowing what image to touch next, effectively counting touches to distracter dots as a list image, but this alternative mechanism was ruled out in Experiment 3. We manipulated the number of distracter dots to determine if choice was in fact controlled by tracking responses made, which would have resulted in appropriately adjusted positions in list execution based on number of distracter dots. Errors to list images did not correspond to number of distracter dots; when two dots occurred after selection of A, selection of to D (+2 forward errors) did not significantly increase. Instead, +1 errors to the next image in the list continued to be most likely error, eliminating the possibility of tracking responses made to update position in the list, and further supporting the robustness of the prospective coding finding.

Reliable image selection according to ordinal position on between-list probe tests and prospective errors found in Experiments 2-3 indicate that knowledge of positional information is processed. To investigate if the ordinal position information was integrative enough to link two five-image lists that each have the same five positions into one large 10-image list, monkeys received linking training in Experiment 4. Subjects' choices on between-list two-image tests was not based on the dynamic linking position, but instead was based on static position within native five-image lists. Knowledge of position that helps guide list execution appears to rely more heavily on static ordinal positional information rather than more dynamic positional information that would have resulted in list-linking.

Comparisons with other ordinal tasks

Representation of ordinal positions may emerge because repeated and routinized execution of a list images maintain consistent positions, and these static positions also occupy the same, or analogous "mental slots" in other five-item lists. In contrast, when lists do not repeat and the five-image response series is not routinized, such as in trial-unique orders, knowledge of ordinal position does not emerge. In a trial-unique ordinal task, when monkeys were required to select the earlier image from amongst two images from a list of five images, subjects did not show evidence for knowledge of ordinal position, but rather showed evidence for temporal order (Templer & Hampton, 2012a). This might be because when lists are composed of unique stimuli, ordinal position does not provide salient information to guide memory for order.

Here monkeys did not show evidence for list-linking and instead ordered stimuli based on static position constrained to natively learned lists. Monkeys were, however, able to link lists in a TI task that used fixed lists that were inferred based on premise pair training by selecting images according to dynamic linking order rather than static position (list 1:A>B, B>C, C>D, D>E, E>F, F>G; list 2: H>I, I>J, J>K, K>L, L>M, M>O; linking training pair: G>H; Gazes et al., 2012; F. R. Treichler & Raghanti, 2010b; F. Robert Treichler, Raghanti, & Van Tilburg, 2007). Though SC and TI both use fixed stimulus sequences, serial reorganization may not be as dynamic when entire lists are explicitly taught like in SC, as it has been shown to be in inferred order tasks like TI. Relative positional information is necessary to construct primary lists in TI and training itself is based on relations between items. In contrast, in SC the order is explicitly trained with simultaneous presentation of images. Thus dynamic positional knowledge might be more cognitively available in TI, leading to successful linking of primary lists in TI but not in SC. Similarly, as explained above, repeated simultaneous chaining of lists in SC might cause knowledge of ordinal position information to be much more salient, and therefore static, rather than dynamic as in TI where list images are never presented simultaneously or required to be selected in sequence.

Another critical difference in SC and TI is that here the two lists were intermixed during list training before linking training occurred and were never intermixed in TI (Gazes et al., 2012). It is possible that intermixing lists may have encouraged monkeys to continue to use an absolute ordinal code rather than a more relative one. Additionally, because continued list execution on fixed and contained five-image lists appears to cause knowledge of image-position information to be the salient feature remembered, perhaps linking would be successful in SC if future studies attempt to link lists in SC by creating six-image lists (A→B→C→ D→ E→ **F**; **E**→F→G→H→ I→ J) instead of training on an individual end-item test pair (E→F). Future studies should explore such seemingly slight but possibly critical differences in ordinal task parameters. Equalizing as many ordinal task characteristics as possible might help illuminate critical differences in cognitive representations between tasks. It will be especially informative to the understanding of memory systems in monkeys to understand the similarities and differences in the ordinal codes that underlie different types of ordinal tasks, including TI tasks and trial-unique order tasks (DeVito & Eichenbaum, 2011; Templer & Hampton, 2012a).

Conclusions

Control of choice in SC appears to be mediated by knowledge of ordinal position. Pfuhl and Biegler (2012) raise a noteworthy discussion about the dissociation between an image-image associative mechanism and an ordinal position representation. While interest in ordinality has stemmed from the idea that knowledge of ordinal position reflects complex cognition rather than simple image-image associations, this "ranking" may not be useful, especially when the underlying computations used to represent ordinal position are not fully understood (Pfuhl & Biegler, 2012). Our goal here was to better characterize these underlying computations, and while our results inform the mechanisms responsible for ordinal coding, the distinction between ordinal position and an associative mechanism warrants further investigation. Image-image associations might support behaviors and provide information than ordinality cannot (Pfuhl & Biegler, 2012), and it has not yet been concluded that that these mechanisms are always mutually exclusive. Indeed, it is possible that strings of associations, rather than only adjacent image-image associations, could help maintain linear representation of order. This possibility should be explored in future studies. However, in the present task choice based on ordinal position has emerged as the dominant salient feature monkeys rely on rather than image-image associations.

Amongst several paradigms used to test for the ability to plan in nonhuman animals (Beran & Parrish, 2012; Mulcahy & Call, 2006; Paxton & Hampton, 2009) strong evidence for prospective coding provided here indicate the feasibility of testing planning in the SC paradigm. Monkeys here showed evidence of expertise, the ability to solve novel instances of a problem quickly and efficiently in a serial task (H.S. Terrace et al., 2003). Subjects performed well on within and between-list tests indicating choice by ordinal position rather than associations between stimuli. Additional experiments tested for alternative cognitive mechanisms in order to better characterize the ordinal position mechanism used, indicating that monkeys planned one response ahead and did not track list progression by consecutive responses made to stimuli. Better capturing the cognitive mechanism that supports this type of memory will have important implications for cognitive abilities the SC task is used to test, including planning, the conceptual ability of retrieving ordinal categories from long-term memory (Orlov, Yakovlev, Hochstein, & Zohary, 2000a), and the interaction of working memory and long-term memory. Importantly, results here shed light on the broad concept of ordinarily by determining that static rather than dynamic positional information is the more salient ordinal feature underlying mnemonic representation for serial lists.

8. Introduction to Paper 4

This paper was motivated by an invitation to Victoria L. Templer and Robert R. Hampton to write a review paper for the journal, Current Directions in Psychological Science, based on results from Paper 2, Paper 3, and a few other experiments related to order memory after Victoria presented this work at an invited to presentation at Georgia Institute of Technology in the fall of 2013 where the editor was present.

This short paper reviews the main results found in Paper 2 (herein labeled Templer & Hampton, 2012a) and Paper 3 (herein labeled Templer, Gazes, and Hampton, in prep) as well as two other papers: one authored by Regina Paxton Gazes, Nicholas Chee, and Robert R. Hampton about another ordinal task, Transitive Inference (TI), and one by Regina Paxton Gazes and Victoria L. Templer, and Robert R. Hampton. The latter paper, herein labeled Gazes, Templer, & Hampton, in prep, examines the question of whether a common ordinal code is used in SC and a TI task, in which monkeys learned fixed lists through inference rather than explicitly taught lists as orders are trained in SC.

The goal of this review paper was to examine the cognitive mechanisms in each of the three ordinal tasks, TO, SC, and TI, and evaluate whether memory in each task relies on similar representational structures of order. It is our hope that this paper will be published after Paper 3 and the Gazes, Templer & Hampton paper are submitted or published.

9. Paper 4

Mental representation of order in non-human primates

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9.1. Abstract

There are a variety ways humans and other animals order stimuli. Fixed orders are remembered when actions are taken in routinized sequence, such as the series of actions taken to execute a cooking recipe. In the laboratory we can study a similar ability to remember order by requiring responses to images in a particular order: select A, then B, then, C etc. in a simultaneous chaining (SC) task. Fixed orders can also be learned when relations between stimuli are inferred based on relations between other stimuli: for example Joel is taller than Eric, and Eric is taller than Debbie, so by transitive inference, Joel must be taller than Debbie. Learning of orders by transitive inference (TI) can be studied in the laboratory by training subjects with premise pairs of images (e.g. A+B- and B+C-; where "+" indicates the reinforced item and "-" indicates the non-reinforced item) and testing for inference with untrained pairs (e.g. A vs. C; where A is the correct selection). Memories for the temporal order in which unique events occurred, as in episodic memory, are also based on a representation of ordered stimuli. For example, you may remember the order of activities from a day of your vacation: you first went scuba diving, ate lunch, and then went boating. Knowledge of relative order of events can be tested in the laboratory by requiring subjects to select the earliest of a pair of images from a list of consecutively presented images in the temporal order (TO) paradigm. Here, we highlight common properties and identify salient differences in the mental representations resulting from SC, TI, and TO in nonhuman primates. Understanding the types of memory systems monkeys possess will be enhanced by improved characterizations of the specific features of the cognitive representations underlying different kinds of memory for ordered stimuli. Conducting this work with nonhuman primates informs our understanding of the evolution of memory systems and provides an assessment of how these memory systems operate in the absence of language.

Order is critical in the production and comprehension of language, in generating organized goal-directed behavior, and in understanding causality. Karl Lashley argued that the “problem of serial order in behavior” was one of the most important problems in psychology (Lashley, 1951). Here we discuss three major tests used to study memory for order in nonhuman primates, simultaneous chaining (SC), transitive inference (TI), and temporal order (TO). We identify similarities and differences in the mnemonic representations active in these tests and suggest how these tests may be relevant to taxonomies of memory systems.

9.2. Three types of ordinal memories: common features and critical differences

Order of responses: Cooking recipes necessitate a fixed order of actions. The first time you make a dish, you probably check the recipe frequently, but with practice the fixed order of responses may become routinized so you can execute it from memory. Learning of this type of fixed order can be assessed in nonhumans using **Simultaneous Chaining** (**SC**; Table 1; *top*). Subjects learned to select five images in a defined order (A→B→C→D→E) through successive approximations, starting with the first two images (A→B), followed by additional images one at a time until the full sequence is learned (S. Chen et al., 1997; H. S. Terrace, 2005). After such training, monkeys select non-adjacent images presented in novel pairings according to ordinal position, for example selecting B first and D second, demonstrating that image-image associations are not responsible for accurate performance (e.g. Terrace et al., 2005; Templer, Gazes, Hampton, in prep; Table 1, top). The fact that monkeys encode the ordinal position of each image is even more clearly demonstrated by the observation that they also selected images from two independently learned lists according to ordinal position, for example selection B_2 before D_1 (where the subscripts indicate that images B and D were learned in separate lists and presented together only in probe trials; H. S. Terrace, 2005; Templer, Gazes, & Hampton, in prep; Figure 1 left). Rather than relying on image-image associations, subjects must have accessed internal representations of lists including ordinal position information that is not publicly available on probe tests (Scarf & Colombo, 2008; H. S. Terrace, 2005).

Inferred Order. In **transitive inference (TI;** Table 1, middle) order is not explicitly trained. It is inferred from premise cases. For example, if we learn that Joel is taller than Eric (A>B), and Eric is taller than Debbie (B>C), we can infer that Joel is taller than Debbie (A>C). Monkeys readily learn pairs of overlapping visual discriminations (A+,B-; B+C-, C+D-, D+E-, where + indicates the reinforced image in each pair). After learning these premise pairs, monkeys select the image higher in the inferred hierarchy on never before seen non-adjacent pairs of images (e.g. B>D; Gazes et al., 2012; F.R. Treichler & Van Tilburg, 1996), consistent with inference of the order (A>B>C>D>E).

Order of Events. Humans often encode the order in which unique event occurred, such as events on a holiday: snorkeling came first, followed by a volcano visit and then a boat trip. Memory for **temporal order** (**TO**; Table 1; bottom) has been studied in nonhumans by presenting subjects with a series of events and then testing for memory of which came first (Allen & Fortin, 2013; Eichenbaum, 2013; Fortin et al., 2002; Howard & Eichenbaum, 2013; R.P. Kesner et al., 2002). Monkeys saw five images, presented one after another. At test, two of these images reappeared and monkeys were rewarded for selecting the image that occurred earlier in the sequence (Table 1, bottom; Templer & Hampton, 2012a). Monkeys learn to select the earlier image after seeing and touching five trial-unique images, suggesting order of the list items is remembered (Templer & Hampton, 2012).

The SC, TI, and TO tests just described are clearly different in training procedures and in whether it is actions, magnitude, or time of occurrence that is ordered. But as we describe below, there are also commonalities in the patterns of performance observed in these tests, and

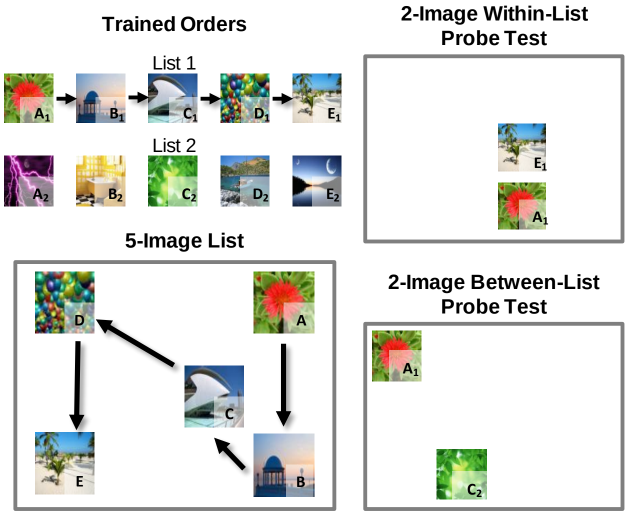
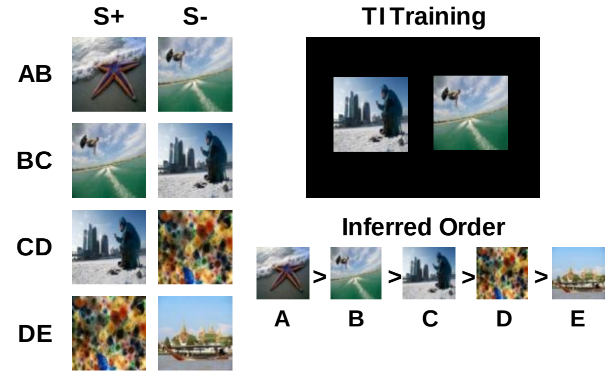
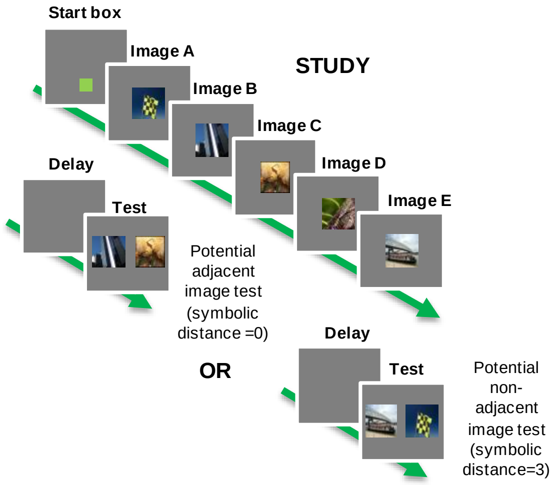
Task	Order is	Task examines	Schematic
Simultaneous Chaining (SC)	Fixed; explicitly taught	**Order of responses** Serial learning; ability to correctly order five simultaneously presented images presented in random screen locations across trials	
Transitive Inference (TI)	Fixed; inferred	**Inferred order** Ability to infer order of nonadjacent /explicitly trained items	
Temporal Order (TO)	Trial-unique (images drawn without replacement from set of 6,000)	**Order of events** Ability to select the earlier image that occurred after seeing five consecutive stimuli appear (here image B should be selected instead of image E)	

Table 1. Features and schematic of the three order tasks reviewed. *Top.* Examples of a 5-image simultaneous chaining (SC) trial, within-list probe test, between-list probe test, and the orders in which monkeys were trained to respond to the images (Templer, Gazes, & Hampton, in prep; Terrace et al 2005). *Middle.* Example of premise pair training images in transitive inference (TI), the presentation of images during training, and the inferred order of these images according to TI (Gazes, Chee, & Hampton, 2012; Triechler & Ranghanti, 2010). *Bottom.* Schematic of a trial

from a test of temporal order (TO) with two potential tests with different symbolic distances (Templer & Hampton, 2012a).

suggestions that performance in these different tests may depend on a common representational code. Below we discuss alternative mechanisms that might control ordinal judgments in each task as well as overlapping performance patterns.

9.3. Evidence for common ordinal coding

Within SC, TI, and TO it is argued that adaptable use of ordinal information relies on an integrated internal representation of ordered stimuli (Hinton, Dymond, von Hecker, & Evans, 2010; Howard & Eichenbaum, 2013; Leth-Steensen & Marley, 2000; Scarf & Colombo, 2008). Examination of performance patterns that are common across these tasks allows determination of the extent to which these orders share a common code.

The Symbolic Distance Effect. A ubiquitous phenomenon in ordinal tasks that suggests linear representations of order is the symbolic distance effect as evidenced by performance on two-image tests. This manifests itself by the finding that widely separated pairs of images are easier to order, and thus result in higher accuracies and shorter response latencies than pairs with smaller symbolic distances. Performance by monkeys on SC, TI, and TO tasks all produce the symbolic distance effect (e.g. Figure 1 from left to right; SC: Templer, Gazes, Hampton, in prep; TI: Gazes et al 2012, TO: Templer & Hampton, 2012), suggesting that despite major differences in training and testing, the representation underlying performance across might share a common code.

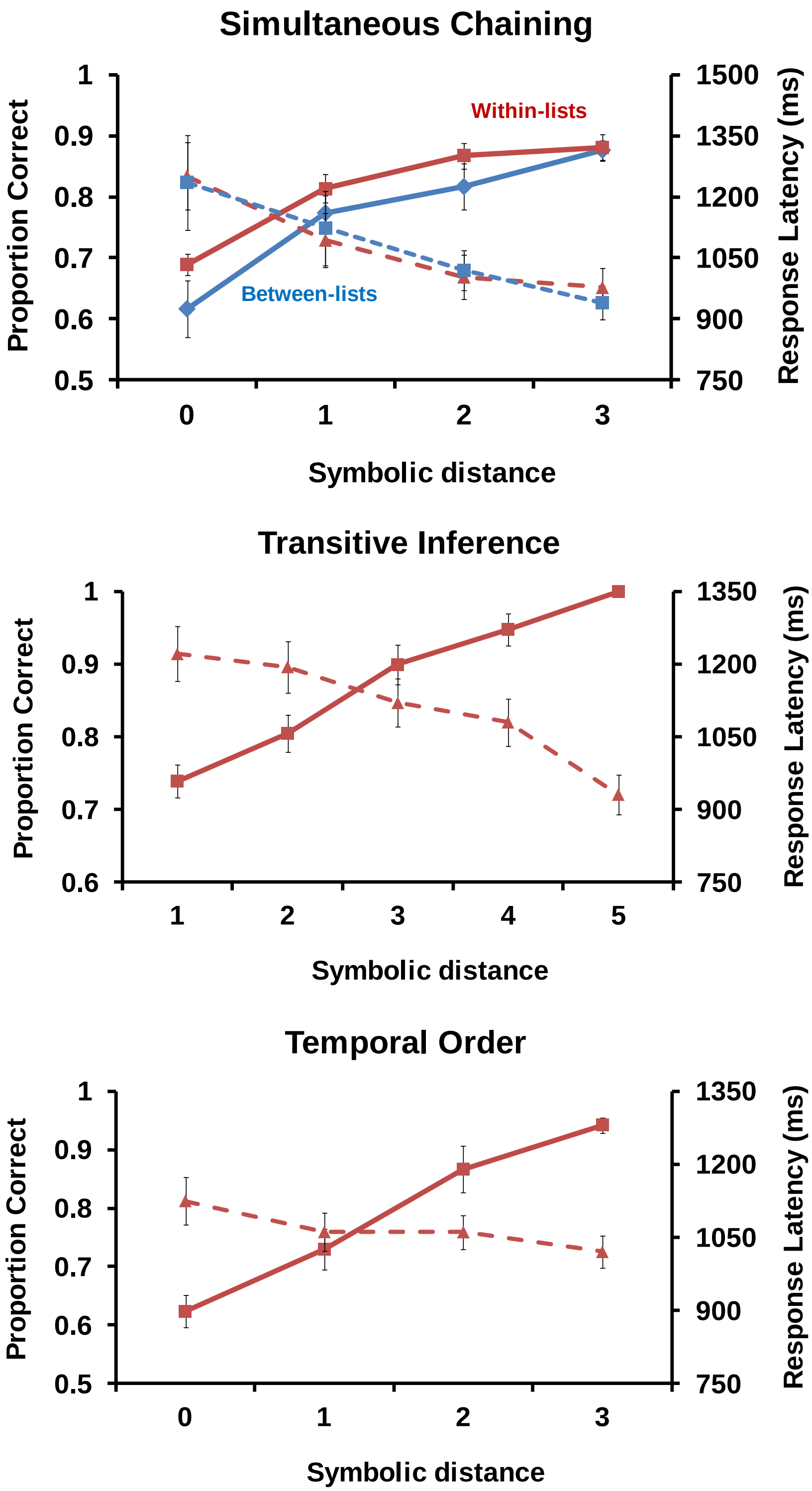


Figure 1. Significant symbolic distance effects found in Simultaneous Chaining (SC; Templer, Gazes, & Hampton, in prep), Transitive Inference (TI; Gazes, Chee & Hampton, 2012), and Temporal order (Templer & Hampton, 2012) tasks as evidenced by performance (solid lines; corresponding to primary y-axis) and response latencies (dotted lines; corresponding to the secondary y-axes). In SC, within-list tests (e.g. A_1, C_1) are shown in red and between-list tests (e.g. A_1, C_2) are shown in blue; no significant differences between within-list and between-list tests were found (Templer, Gazes, & Hampton, in prep).

List linking. Order of images can either be with respect to the images constrained to discrete lists, or more continuously with respect to linking of lists. When probe tests in TO are presented with images from two different sequences by presenting one image (D) from the previous list (list A, B, C, D, E) as one of the two choice images at test along with an image (G) from the current list (list F, G, H, I, J), monkeys spontaneously chose the image from the earlier list, D, rather than selection based on within-list ordinal position (Templer & Hampton, 2012a). Choice behavior indicates spontaneous linking of lists that likely result from the fact that images are experienced as a continuous stream of events. In TO, continuous passage of time is a salient feature rather than the lists themselves as discrete sets. The opposite is true for SC and TI. Unlike in TO, choice based on ordinal position does guide ordinal judgments in SC and TI. When presented with probe trials containing two images from two independently learned lists, monkeys select the image with the earlier ordinal position in its native list in both SC and TI tasks (Gazes et al., 2012; F. R. Treichler, Raghanti, & Van Tilburg, 2003; Templer, Gazes, & Hampton, in prep), indicating coding of specific static positions of images can be compared across separately learned orders based on stable representations of ordinal positions.

As time is not a relevant feature in SC and TI as in TO, the possibility of list-linking was evaluated with additional training to determine if positional information would be updated through successful linking, and is therefore dynamic, rather than static, with respect to natively-learned lists. With two independently learned lists in TI (A>B>C>D>E>F>**G**; **T**>U>V>W>X>Y>Z) monkeys successfully linked lists when trained on object discriminations of the lowest image of one of the lists (G+) and the highest image in the other list (T-) by selecting any image from the higher list over any image from the lower list (Gazes et al., 2012; F. R. Treichler & Raghanti, 2010a; F. Robert Treichler et al., 2007). Choice was therefore guided by dynamic construction of a 14-image list by inference. Using a similar manipulation in SC, in which monkeys were trained to select E before F on two-image tests pairs from two separate lists

(A→B→C→ D→ **E**; **F**→G→H→ I→ J), monkeys did not link the lists into one unified representation, but instead continued to select images according to static ordinal position within the individual natively-learned lists (i.e. G→D; Templer, Gazes, & Hampton, in prep).

TI and TO share the commonality that linking was possible, but lists were linked for different reasons. In TO, spontaneous list-linking likely occurred because continuous passage of time and images marked the order of events. In TI, additional training was required to cause a switch from static judgments of ordinal position within natively-learned lists to more dynamic judgments of position across a newly constructed list. It is possible that linking did not occur in SC because continued execution of fixed lists caused such a strong, and therefore static, representation for ordinal position to emerge.

Interactions across tasks. Despite the difference in dynamic versus static positional coding in SC and TI, recent evidence suggests that these tasks might share a common ordinal code (Jensen et al., 2013; Gazes, Templer, Hampton, in prep). Monkeys learn SC lists made up of TI-trained images faster than they learn lists of unfamiliar images (Jensen et al., 2013), suggesting that the ordinal representation of TI stimuli facilitated performance on the SC task. Further supporting the hypothesis that SC and TI activate the same mental coding system, monkeys spontaneously order five images that were trained in the TI format when they are presented as novel probe tests in the SC format. Additionally, monkeys perform similarly on two image between-list tests containing one TI and one SC image as they do on trials containing two images from different SC lists, and show symbolic distance effects across these list types (Gazes, Templer, & Hampton, in prep). Together these findings suggest that the representations created through SC and TI training might share a common ordinal code.

Neural overlap. Determining if similar brain processes underlie performance in each task may help determine the extent to which a common code underlies performance on SC, TI, and TO. For example, in monkeys, neurons in the ventrolateral and dorsolateral PFC were selectively tuned to the visual properties of stimuli and the ordinal position of those stimuli, respectively, in an ordinal task similar to SC (Ninokura, Mushiake, & Tanji, 2003; Ninokura et al., 2004), suggesting neural underpinnings for ordinal categorization. In a TO task in which rats sampled odors, subjects with hippocampal and medial PFC lesions lost their ability to select the earlier image in the sequence, but still performed above chance on recognition tests of the images from those lists (DeVito & Eichenbaum, 2011; Fortin et al., 2002; R.P. Kesner et al., 2002). This indicates that representation of order is something distinct from recognition of items and relies on the hippocampus and PFC, which is known to be involved in spatial and ordinal processing.

The hippocampus and adjacent entorhinal cortex have been implicated in TI performance in humans and monkeys (Buckmaster, Eichenbaum, Amaral, Suzuki, & Rapp, 2004; M. Zalesak & S. Heckers, 2009). After human subjects learned TI lists with similar premise pair training, increased activation in the inferior frontal cortex, dorsolateral prefrontal cortex, and bilateral parietal cortex accompanied tests items with greater symbolic distances when accuracy was higher, indicating the behavioral evidence for the symbolic distance effect might represent underlying neurological processes (Hinton et al., 2010). Since performance in SC, TI, and TO all produce the symbolic distance effect, it is possible that the same regions would be activated across tasks and future studies should examine this question.

9.4. Differences in the contents of memory during ordinal judgments

Though SC, TI, and TO tasks all rely on linear representations of order, the mnemonic requirements in each task are quite different. It is therefore essential the contents of memory during ordinal judgments are characterized so that the resulting representational structures underlying each of these ordinal tasks can be better understood.

SC and Order of Responses. Selection of the earlier image in the list on non-adjacent two-image tests (Table 1; top, far right) indicates reliance on an ordered representation through knowledge of ordinal position rather than image-image associations. However, probing the contents of memory informs how knowledge of ordinal position is used during list execution. By requiring subjects to respond to extra stimuli, a distracter dot, during a short delay with the list stimuli not present for a moment in order to increase errors, it was determined that forward errors did not correspond to the number of extra stimuli touched, indicating that monkeys were not tracking responses made as indication for position in the list (Templer, Gazes, & Hampton, in prep). Instead, when monkeys erred, they made forward errors rather than backwards errors indicating use of a prospective rather than retrospective code (Templer, Gazes, & Hampton, in prep; Scarf et al., 2011). Anticipation of upcoming responses is likely unique to execution of SC lists as several consecutive ordinal judgments are required where as only a one ordinal judgment is made per trial in TI and TO.

TI and Inferred Order. Like SC, TI also leaves long-term traces of lists that allow knowledge of ordinal position to emerge. However in TI, the content of memory is not based on a plan, or prospective code like in SC. The contents of memory were probed by determining what the specific cue is that guides “higher” choice selections on inference pairs. TI images are reinforced and non-reinforced at different rates based on an individual animals' performance during training. Each image therefore has a unique history of reinforcement. If these values follow the same order as the inferred order, above chance performance on test trials could simply be produced through selection of the image with the higher value, without reference to order (Von Fersen, Wynne, Delius, & Staddon, 1991). Recent research suggests that associative values alone cannot account for TI performance in monkeys (Gazes, Lazareva, Hampton, in prep, Gazes et al 2012), and that TI may instead rely on inferred ordinal representation (F. R. Treichler et al., 2003; Gazes, Lazareva, Bergene, & Hampton, submitted). Additionally, monkeys pre-trained on a physical order of images performed better on TI tasks when the physical order was the same as the inferred order than when it differed (Gazes, Lazareva, Bergene, & Hampton, submitted).

TO and Order of Events. Unlike SC and TI, long-term traces of lists likely do not occur in TO as many different trial-unique sequences are seen one after the other. TO tasks are temporal in nature; subjects select the image that occurred earlier in the list, and therefore more distantly in time. However performance on these tasks does not appear to be driven simply by a temporal judgment based on relative recency, but instead relies on the relative order of images. On probe tests, monkeys selected the image from the list rather than a novel image that has an effective memory strength of zero that would have been selected if images were chosen based on relative strengths of images, indicating representation of list order (Templer & Hampton, 2012a). To further characterize the mechanism labeled “temporal order” and disentangle experiencing more images in time from the passage of time alone we created probe trials in which the amount of time it took a subject to select three inserted images (A, B, C, X1, X2, X3, D, E) in a list was yoked and set to the amount of time that passed between C and D on other probe tests so that passage of time could be equated. Accuracy on order judgments was significantly better on “inserted image” tests than on “inserted time” tests (A, B, C _____D, E), indicating that more images, rather than mere passage of time, contributes most strongly to representations of unique orders (Templer & Hampton, 2012a). These results suggest that a well-organized representation of the relative order of unique sequences of images is encoded on these tests, and that judgments are not based simply on memory strength or mere passage of time.

9.5. Implications for characterization of memory types

While we cannot yet determine with certainty what memory systems are engaged by each ordinal task, the studies reviewed characterize the structure of mnemonic representations of order that are similar in some ways but also different from each other. Routinely executing sequences in the same order when images are simultaneously presented in SC gives rise to robust long term memory for the ordinal position of images (Kornell et al., 2007; H. S. Terrace, 2005). SC and TI appear to be governed by a common ordinal code as evidenced by SC-TI hybrid probe tests (Gazes, Templer, & Hampton, submitted), but TI is more dynamic than SC, as evidenced by the ability to link lists in TI but not in SC. SC and TI have semantic memory properties as knowledge of the fact that list one is A→B→C→D→E, for example, could function as a fact about the world. In comparison, ordinal positional information is not an emergent property in TO, which likely results from the use of trial-unique stimuli, and leads to the fact that TO does not have the same semantic properties as TI and TO. Instead, memory for order of events may model the temporal aspect of episodic memory and recent evidence suggests that memories for images on this task are accessible to memory monitoring (Templer, Brown, & Hampton, 2013), a critical feature of episodic memories. While it might be tempting to assign SC to semantic memory, TI to semantic memory and logical processing, and TO to episodic memory, without converging evidence these labels are not productive. Such categorizations are especially counterproductive if they lead to: 1) fixed conceptualizations of cognitive abilities required for these tasks, or 2) decreased motivation to probe the contents of memory during ordinal judgments, which is our principle aim in these pursuits. Nevertheless, ordinal tasks explored in this review likely include several types of memory systems, mirroring natural mnemonic processing in humans (Mizumori, Yeshenko, Gill, & Davis, 2004).

9.6. Conclusions

We engage constantly in a world full of order. Rhesus monkeys, with whom we share a common ancestor with that existed about 25 million years ago (Gibbs et al., 2007), also appear equipped to perceive and respond to ordered stimuli in useful ways. We have argued that determining the cognitive mechanisms of memory for order in monkeys provides a means to objectively understand non-linguistic memory processes and the structure of how memories are mentally organized with respect to dimensions of time and space. Whether stimuli are behaviorally executed in sequence, ordered based on inference, or experienced consecutively, it appears that all three of these ordinal tasks result in an organized mnemonic representation of order rather than reliance on an exclusively associative mechanism.

10. Conclusions and future directions

The papers presented here add to the existing empirical literature on the study of memory for order in monkeys, as demonstrated in Papers 2 and 3, and review research on episodic memory in nonhuman animals in Paper 1 and in the study of order memory in monkeys in Paper 4.

Paper 2 was motivated by modeling the temporal aspect of episodic memory, a type of long-term memory (LTM). One important consideration is the extent to which LTM was tested rather of WM as the experiments presented here were conducted using relatively short delays. In TO, as outlined in Paper 2, the retention interval was half a second, but the delay between the time since the first image during study was touched and the test was about 6-9 seconds. The distinction between short-term or WM and LTM is a significant issue, but there is little consensus on what retention intervals should be used for the study of LTM rather than WM, especially with nonhuman animals. In future studies, it is my goal to develop methods to distinguish between long-term and working memory (WM), as we are beginning to do now.

LTM refers to what information can be recalled that is not actively maintained, either because attention was diverted or because immediate memory capacity was exceeded (Jeneson, Wixted, Hopkins, & Squire, 2012). WM is a memory system that actively maintains representations for events on a specific trial (Shettleworth, 2010), and a limited amount of information can be held in immediate memory and actively maintained in WM (Baddeley, 1992). WM and has been shown to rely on regions including the prefrontal cortex (PFC), anterior cingulate, parietal cortices, and parts of the basal ganglia (Ashby, Ell, Valentin, & Casale, 2005; Fuster, 1973, 2001). One argument that the WM system would be exclusively engaged in tasks with short delays is the notion that WM holds information for up to approximately 20-30 seconds (Andrade, 2001). Though some researchers hold that WM lasts longer, up to 15 minutes (Milner, 1970) and sometimes even up to a day (W. A. Roberts, Medin, D.L., Davis, R.T, 1976), it is not clear how any arbitrary cutoff contributes to an understanding of memory systems (Marshuetz, 2005). Furthermore, LTM has been shown to support performance in memory tasks with relatively short delays (Buffalo, Reber, & Squire, 1998; Holdstock, Shaw, & Aggleton, 1995), and when the delays are short and the to-be-remembered information exceeds WM capacity (Hannula, Tranel, & Cohen, 2006; Jeneson, Mauldin, Hopkins, & Squire, 2011; Jeneson et al., 2012). It therefore can be inappropriate to equate a certain delay with a specific memory process.

The relationship between memory process and delay length becomes even more problematic when we take into account that animals often remember stimuli for much shorter delays than humans, especially when lists are used. When monkeys, humans, and pigeons were tested for memory of lists, similar performance levels were obtained with 100 second retention intervals for humans, 30 seconds for monkeys, and 10 seconds for pigeons (Wright, Santiago, Sands, Kendrick, & Cook, 1985). Therefore, while it may be inappropriate to equate a memory delay with a memory system in humans, it is perhaps even more misleading to use a candidate delay for LTM in humans with animals. Furthermore, the hypothesis that LTM comes online when WM is exceeded with high cognitive loads, as described above, is a relatively new idea (e.g. Jeneson et al., 2012), and has not been directly applied in animal studies. Some studies in which it is thought LTM is tested, the test difficulty is relatively easy or delay length is short, WM might be involved more than expected. Similarly, it is possible that some animal studies in which it is thought WM is tested, but the test difficulty is relatively high or delay is long, LTM might be involved. It is therefore possible that the TO task in monkeys may have taxed LTM rather than WM because of task demands, regardless of delay length.

It is possible, but unlikely, that the abridged time-course in the TO task, explored in Paper 2, engages a completely different memory system than one that might be engaged if a longer delay was used. Even if WM was engaged instead of LTM, for example, such exclusive characterizations may not appropriately apply to performance in this tasks, especially if we accept the interpretations that LTM and WM share many of the same properties (Brown, Neath, & Chater, 2007; Nairne, Neath, Serra, & Byun, 1997) and that this distinction may be theoretical rather than functional (Neath & Crowder, 1990). Moreover, according to some theories of memory and time, like the SIMPLE theory (scale-independent memory, perception, and learning), memory strength depends on the temporal ratio at the time of retrieval rather than absolute temporal duration (Brown et al., 2007). If memory follows the logarithmically transformed dimension of "time elapsed since memory formation" then memory should be time-scale invariant. This argument that the same operating properties mediate memory over all time scales is supported by the fact that many memory effects such as serial position effects are qualitatively analogous over many time-scales (Brown & Chater, 2001).

Nevertheless, the role of WM and LTM in the tasks presented here should be investigated through careful manipulations. For example, in the lab we have recently altered the delays in the TO paradigm, described in Paper 2, and have introduced a classification interference task during the retention interval that was designed to disrupt WM. We are currently evaluating how this interference task might differentially effect memory for order and recognition of the items with yes-no recognition tests. We have also prepared a test within TO in which the inter-stimulus intervals, retention intervals, and required study times for each image are longer and tests are unexpected for monkeys with hippocampal lesions in order to more closely resemble passage of distinct events that comprise an episode. Use of relatively short delays may be less problematic in the SC task. SC likely involves WM within a given trial, but also involves LTM for the fixed lists that are remembered over days, weeks, and even months. Study of the interaction of these memory systems within these two tasks, and also between semantic and episodic memory, may lead to fruitful lines of research.

It is important to remember that memory systems such as WM, implicit memory, and semantic and episodic memory, are theoretical constructs based on human memory. Use of such distinctions have lead to an abundance of informative findings about human memory, and have provided us with useful motivations for experimental designs in nonhumans. However, over-attachment these dissociations, especially in nonhuman animal research, can sometimes be detrimental to scientific progress. Even if the initial motivation is perhaps overly anthropocentric in nature, we hope that the actual conclusions presented are careful, based on specific findings we uncover from particular experimental manipulations, and are not weighed down by theoretical baggage that can come with use of these terms for memory systems. The goal is to strike the right balance between not letting the semantics of these terms drawn from the human literature cloud what we conclude about what is found and still relate our findings in applicable, useful way to that of memory in humans. As stated in the episodic memory review in Paper 1, we should be focused on what is found about specific cognitive mechanisms using our experimental methods within each task rather than focusing on unproductive questions like “do monkeys have episodic memory?”

The goal of determining if memory used in task X is episodic memory, for example, is far-reaching and perhaps an immature question. It may never be possible to conclude that we have modeled episodic or semantic memory in its entirety in monkeys. Rather than all-encompassing conclusions, comparative cognition research should focus on one or a few of the properties of a memory system, like the temporal organization that characterizes episodic memory (Templer & Hampton, 2013). Because memory systems are defined by a constellation of properties, comparative cognition research can in fact help determine the essential features of memory types in humans and lessen characterizations that appeal to immeasurable, subjective phenomena (Hampton & Schwartz, 2004). Furthermore, strong cognitive models of memory types in nonhuman animals allow for more informed neurobiological investigations that are critical for biomedical advancements.

Here, we present evidence that the study of order memory across several paradigms, but along analogous cognitive behavioral manipulations, is a promising avenue to answer more appropriate questions about how monkeys remember ordered stimuli. Future studies will build on the results presented here by distinguishing between LTM and WM by altering memory load, using interference tasks, and manipulating delays. Future studies should also combine cognitive behavioral methods, like the ones presented here, with neurobiological techniques such as electrophysiology, brain scanning, and lesions of brain structures like the hippocampus.

11.

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